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PRIMARY RESEARCH PAPER

Shifts in small-bodied fish assemblages resulting from drought-induced water level recession in terminating lakes of the Murray-Darling Basin, Australia

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Abstract Over-abstraction of water places unsustainable pressures on river ecosystems, with the impacts amplified under drought conditions. Freshwater fishes are particularly vulnerable due to associated changes in water quality, and habitat availability, condition and connectivity. Accordingly, fish assemblages are ideal indicators of the impacts of drought and over-abstraction. The Murray-Darling Basin (MDB), south-eastern Australia, terminates at the Ramsar listed Coorong and Lower Lakes, which comprise Lake Alexandrina and Lake Albert. Over-abstraction and extreme drought during the last decade has placed these lakes under severe environmental stress. The purpose of this study was to investigate shifts in fish assemblages caused by substantial water level recession and salinization in the Lower Lakes. Small-bodied fish assemblages were sampled at the beginning and several years into the drought. Off-lake habitats held diverse fish assemblages in 2003, but most sites were dry by 2009. Remaining habitats were disconnected, salinities increased substantially, and aquatic vegetation shifted from freshwater to salt-tolerant species. There was a substantial decline in the proportion of specialist species, especially diadromous and threatened species, and an emerging dominance of generalist freshwater and estuarine species. The findings warn of the inevitable ecological impact of over-allocating water for human use in drought-prone regions, and highlight the need for adequate environmental water allocations. This study also emphasises that understanding the ecological attributes of a fish species, and the subsequent assignment to a functional group, will help predict vulnerability to decline and extirpation.

Keywords Fish · Threatened species · Drought · *Craterocephalus* · *Nannoperca* · Salinization

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Introduction

Flow regime is the major driver of river ecosystem structure and processes (Ward et al., 1999), and therefore its disruption alters a river's ecological character. The over-abstraction of water for human use often accompanies river regulation, exacerbating the impacts on aquatic ecosystems (Collares-Pereira & Cowx, 2004). The impacts of abstraction are amplified during dry periods and especially under drought (Magalhães et al., 2007) due to competing water demands (e.g. irrigation versus environment: Bond et al., 2008).

Worldwide, freshwater fish are impacted by numerous river modifications and perhaps most pervasively by flow regulation (Lévêque et al., 2008). Species that rely on specific habitats, have specialised diets or exhibit obligate life-history strategies (e.g. diadromy) are especially vulnerable to the effects of reduced freshwater flows due to associated changes in water quality, physical habitat and connectivity (Lucas & Baras, 2001). Therefore, fish can provide a reliable measure of the effects of altered flow regimes and other human-induced impacts (e.g. Lasne et al., 2007). For example, research on Mediterranean stream fish assemblages predicts that severe drought, exasperated by growing demands for water, could result in population declines or extinctions of short-lived (<5 years) species because of recruitment failure in very dry years (Magalhães et al., 2007).

Rivers of the intensively regulated Murray-Darling Basin (MDB), south-eastern Australia, feed two Ramsar-listed freshwater lakes, Lake Alexandrina and Lake Albert ('Lower Lakes'). The Lower Lakes are separated from the River Murray estuary ('Coorong') by five tidal barrages that were constructed in ca. 1940 in response to river regulation and water abstraction that was causing periodic marine incursion in an otherwise predominately freshwater environment (Fluin et al., 2007). Increased abstraction for irrigated agriculture followed, so that now only a third of the natural mean annual discharge of the MDB reaches the sea (Walker, 2006).

The Lower Lakes harbour the highest diversity of fishes in the MDB (Wedderburn & Hammer, 2003). This is largely because of the presence of estuarine and diadromous fish species, but also because the region holds a relatively high number of freshwater taxa, including three threatened small-bodied (<10 cm) species that are ecological specialists (see Angermeier, 1995 for definition). Within the MDB, a genetically distinct population of Yarra pygmy perch [*Nannoperca obscura* (Klunzinger, 1872)] is restricted to the Lower Lakes (Hammer et al., 2010). The species is 'Vulnerable' under the federal Environment Protection and Biodiversity Conservation Act 1999 (EPBC Act) due to population decline and regional extinctions. Southern pygmy perch (*N. australis* Günther, 1861) has a patchy distribution in the upper River Murray and small population fragments in the lower reaches, and is 'Protected' under the South Australian Fisheries Management Act 2007. Murray hardyhead (*Craterocephalus fluviatilis* McCulloch, 1912) is endemic to the MDB, occurring in sparsely scattered isolates from the Lower Lakes to approximately 2,000 km upstream (Wedderburn et al., 2007; Adams et al., 2011). It is 'Vulnerable' under the EPBC Act due to localised extinctions resulting from broad habitat change.

Drought and over-abstraction of water in the MDB led to a dramatic reduction in water levels and quality in the Coorong and Lower Lakes from 2003 to 2009 (Aldridge et al., 2009). Diminished lake water levels led to substantial increases in salinity, reductions in aquatic vegetation cover and the disconnection of the Coorong from the Lower Lakes (Kingsford et al., 2011). Correspondingly, there were reductions in fish species diversity and abundance in the Coorong, including dramatic declines in diadromous species, and an increasing predominance of marine fish (Zampatti et al., 2010). Concurrent shifts in fish assemblages in the Lower Lakes have not been previously documented.

The purpose of this study was to investigate shifts in fish assemblages at the Lower Lakes caused by substantial water level recession resulting from over-abstraction and drought. Accordingly, small-bodied fish assemblages were compared between the beginning and several years into a prolonged drought. We hypothesised that the receding lake levels, and the associated disconnection of habitats and reduction in water quality, would lead to a decline in diversity and proportional abundance of obligate freshwater fish species, including the decline of ecological specialists.

Materials and methods

Study area

The MDB is the largest catchment in Australia, covering 1,063,000 km^2 (Fig. 1). At the end of the system, the River Murray discharges into Lake Alexandrina and Lake Albert before flowing over five tidal barrages into the Coorong estuary. The Lower Lakes have a maximum depth of 4.1 m and cover over 750 km^2 (Eastburn, 1990). The eastern shores are mostly wind-swept, sandy beaches and the western

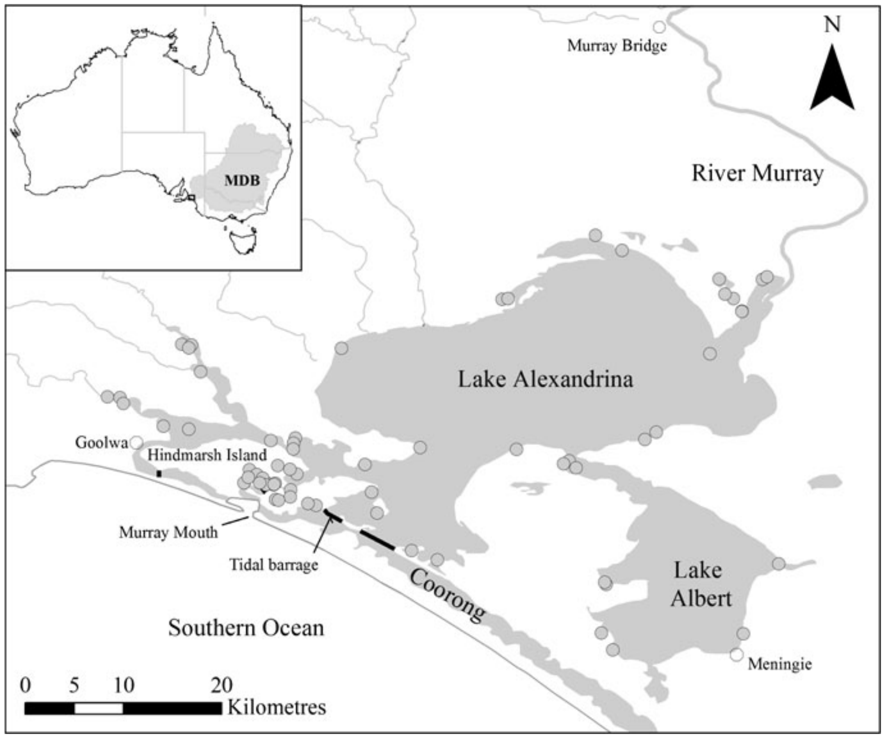

Fig. 1 The study region and sites (*solid dots*)

shores have numerous channels, small islands and well-vegetated wetlands.

Before the current drought, barrages were operated to hold lake water levels at approximately 0.75 m Australian Height Datum (AHD). During the drought, lake water levels lowered to <0.6 m AHD (Fig. 2). Consequently, from 2007 to 2009, the littoral, off-channel waterbodies fringing the Lower Lakes dried or salinised following disconnection. Further, there were no flows over the barrages from the Lower Lakes to the Coorong, and the two areas remained disconnected.

Fish sampling

Sampling at 43 sites was conducted from January to April 2003 throughout the Lower Lakes and their associated habitats. The sites were re-sampled in November 2008 if they held water over the drought period (eight sites), and additional sites were selected to establish an adequate data-set representative of the remaining habitat. Consequently, 18 sites were sampled in November 2008 and re-sampled in March 2009 if water remained (16 sites).

In 2003, small-bodied fish were sampled during the day in a 30 × 10 m site with three seine net

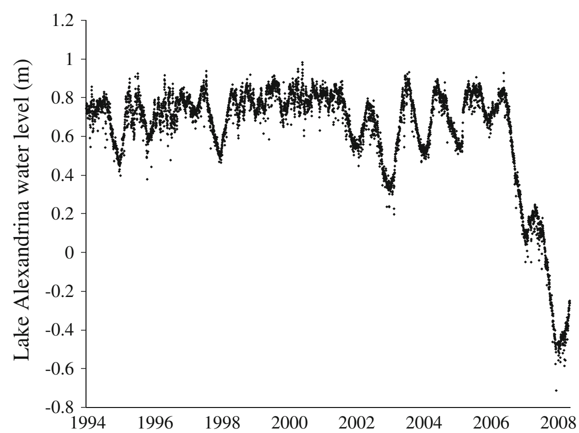

Fig. 2 Daily water levels (AHD) at Lake Alexandrina from April 1994 to August 2008 (Department for Water, unpublished data)

(7 m long × 1.5 m deep, 5-mm half mesh) hauls for 10 m, within 10 m of the shoreline. In 2008–2009, however, seine netting was inhibited by extensive mud because of water level recession. Smith et al. (2009) demonstrated that seine nets and fyke nets equally capture all small-bodied fish species in the lower River Murray, and thus comparisons of sampling

proportions of fish species (proportional abundance) between sampling methods are warranted. Therefore, in 2008–2009, fish were sampled in a 30 × 10 m area, using three fyke nets (6 m single-leader, 5-mm half mesh) set overnight 10 m apart perpendicular to the bank or angled when in narrow channels. Grids (50-mm mesh) at the entrances of nets excluded turtles, and were not expected to influence the effectiveness in catching small-bodied fishes (see Fratto et al., 2008). All fish were identified to species (Lintermans, 2007) and counted. An exception was the carp gudgeon complex (*Hypseleotris* spp.), as it is yet to be formerly classified and was therefore only identified to genus.

Habitat data

Four broad habitat types were distinguished a priori based on their predominance in the Lower Lakes: (1) *natural channels* are off-lake water-bodies that supply flows from the Lower Lakes to the Coorong and are generally >10 m wide; (2) *artificial channels* are off-lake water-bodies that resemble natural channels but were established for stock and irrigation supply and are <10 m wide; (3) *lake edges* are the littoral zones of the lakes; (4) *wetlands* are expansive, shallow, well-vegetated, off-lake waterbodies. Notably, all wetlands were dry by 2008.

At each site on each sampling occasion, salinity, pH and water temperature were measured 30 cm below the surface with a TPS WP-81 meter (TPS, Springwood, Queensland, Australia). Secchi depth was measured. Average water depth was determined from five measurements 1 m apart, beginning 1 m from the water's edge. Bank gradient was estimated from 0 to 90°. The percentage cover by aquatic plants of each 30 × 10 m site was estimated visually as a measure of habitat complexity. Sediment was categorised as sand, clay, mud/silt or sand/silt.

Data analyses

To determine relationships between fish assemblages and their habitats, data were analysed by Non-metric Multi-dimensional Scaling ordination using the Relative Sørensen distance metric, in PC-ORD (ver. 4.36, McCune & Mefford, 2002). The seine data from January to April 2003 and the March 2009 catch per unit effort data (number of fish captured/fyke net hour) were relativised in PC-ORD (i.e. data rescaled to dampen the effect of extreme values: McCune & Grace, 2002). Multi-response Permutation Procedures (MRPP), using the Relative Sørensen distance measure, determined if fish assemblages differed between the broad habitat types in early 2003 and early 2009 (McCune & Grace, 2002). Indicator Species Analysis (Dufrêne & Legendre, 1997) was used to characterise the fish assemblages associated with the four habitat types in 2003 and the three remaining habitat types in 2009. The November 2008 data were omitted from the analyses because of seasonal differences in fish assemblages.

Results

Catch summary

Seventeen native fish species were recorded in 2003, and all but Yarra pygmy perch were captured in 2008–2009 (Table 1). Of the 15 native species recorded in November 2008, the freshwater unspecked hardyhead and the diadromous congolli were not captured in March 2009. The most numerous fish species were flathead gudgeon, common galaxias and western blue-spot goby in 2003, Australian smelt, small-mouth hardyhead and carp gudgeon in 2008, and Gambusia, flathead gudgeon and Australian smelt in 2009.

The proportions of alien fish in the total samples were 20, 4 and 23% in 2003, 2008 and 2009, respectively (Fig. 3). The proportions of diadromous fishes were 11, 2 and 1% in 2003, 2008 and 2009, respectively. Estuarine fishes comprised 24, 37 and 29% in 2003, 2008 and 2009, respectively; the increase is predominantly due to high numbers of smallmouth hardyhead and Tamar River goby. Freshwater ecological generalists constituted 32, 52 and 42% of the catches, respectively; the increase is due to high numbers of Australian smelt and flathead gudgeon in the 2008 and 2009 samples. The three threatened fish species (three of the four freshwater ecological specialists) comprised 13% of the total catch in 2003, of which more than half was Yarra pygmy perch. Southern pygmy perch was a minor proportion (<0.4%) of the total catch in 2008 and 2009. The proportion of Murray hardyhead increased slightly in the total catches throughout the study, comprising 3, 4 and 5% in 2003, 2008 and 2009, respectively.

Table 1 Total number of each fish species captured in January–April 2003, November 2008 and March 2009, and their broad life history habitat requirement and functional group (see Angermeier, 1995 for description)

Common name	Taxon	Life history	Functional group	2003	2008	2009
Common galaxias	*Galaxias maculatus* (Jenyns, 1842)	Diadromous	Ecological specialist	574	363	67
Australian smelt	*Retropinna semoni* (Weber, 1895)	Freshwater	Ecological generalist	468	4,953	854
Bony herring	*Nematalosa erebi* (Günther, 1868)	Freshwater	Ecological generalist	61	50	23
Smallmouth hardyhead	*Atherinosoma microstoma* (Günther, 1861)	Estuarine	Ecological generalist	415	3,888	757
Unspecked hardyhead	*Craterocephalus stercusmuscarum fulvus* Ivantsoff, Crowley & Allen, 1987	Freshwater	Ecological generalist	157	25	0
Murray hardyhead[a]	*Craterocephalus fluviatilis* McCulloch, 1912	Freshwater	Ecological specialist	162	662	296
Southern pygmy perch[a]	*Nannoperca australis* Günther, 1861	Freshwater	Ecological specialist	147	16	22
Yarra pygmy perch[a]	*Nannoperca obscura* (Klunzinger, 1872)	Freshwater	Ecological specialist	373	0	0
Carp gudgeon	*Hypseleotris* spp (species complex)	Freshwater	Ecological generalist	79	1,859	527
Flathead gudgeon	*Philypnodon grandiceps* (Krefft, 1864)	Freshwater	Ecological generalist	685	909	1,048
Dwarf flathead gudgeon	*Philypnodon macrostomus* Hoese & Reader 2006	Freshwater	Ecological specialist	195	24	3
Lagoon Goby	*Tasmanogobius lasti* Hoese, 1991	Estuarine	Ecological generalist	260	639	172
Tamar River goby	*Afurcagobius tamarensis* Johnston, 1883	Estuarine	Ecological generalist	2	444	370
Western blue spot goby	*Pseudogobius olorum* (Sauvage, 1880)	Estuarine	Ecological generalist	544	602	342
Bridled goby	*Arenigobius bifrenatus* (Kner, 1865)	Estuarine	Ecological generalist	0	69	25
Congolli	*Pseudaphritis urvillii* (Valenciennes, 1832)	Diadromous	Ecological specialist	11	5	0
Golden perch	*Macquaria ambigua ambigua* (Richardson, 1845)	Freshwater	Ecological generalist	3	0	1
Sandy sprat	*Hyperlophus vittatus* (Castelnau, 1875)	Marine	Ecological generalist	3	0	1
Alien species						
Carp	*Cyprinus carpio* Linnaeus, 1758	Freshwater	Ecological generalist	90	81	7
Goldfish	*Carassius auratus* (Linnaeus, 1758)	Freshwater	Ecological generalist	30	0	0
Gambusia	*Gambusia holbrooki* Girard, 1859	Freshwater	Ecological generalist	854	445	1,109
Redfin	*Perca fluviatilis* Linnaeus, 1758	Freshwater	Ecological generalist	52	59	210

[a] Threatened species

Habitat summary

In 2003, salinity averaged 1.06 g/l and ranged from 0.34 g/l in sites near the River Murray confluence to 5.40 g/l in a lagoon. In November 2008, salinity averaged 4.91 g/l and ranged from 0.83 g/l near the Murray confluence to 19.96 g/l in an artificial channel. In March 2009, salinity averaged 9.62 g/l and ranged from 1.10 g/l at the Murray confluence to 34.75 g/l in an isolated artificial channel at Lake Albert. Average salinity was <1.5 g/l in the four habitat types in 2003, but in 2009 it had risen to 20.34, 11.64 and 6.20 g/l in artificial channel, natural channel and lake edge habitats, respectively (Fig. 4).

Aquatic plant cover was the highest in artificial channels in 2003 (Fig. 5), and was predominantly water milfoil (*Myriophyllum* spp.) and hornwort (*Ceratophyllum demersum* L.). By March 2009, many sites had either dried, or emergent aquatic plants had been left exposed by receding water levels. Cover, mostly salt-tolerant stonewort (*Chara* sp), was generally greater in sites isolated from Lake Alexandrina, predominantly in artificial channels on Hindmarsh Island and Mundoo Island.

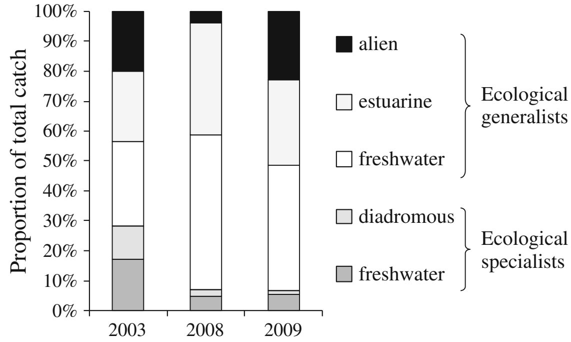

Fig. 3 Fish sampling proportions of ecological specialists and ecological generalists in January to April 2003, November 2008 and March 2009

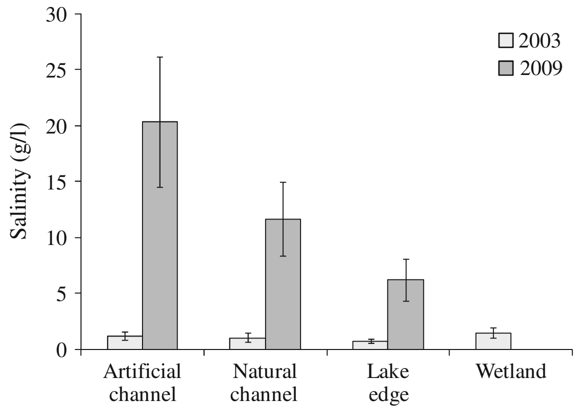

Fig. 4 Comparisons of average salinity (standard error bars) in the four habitat types, and between January to April 2003 and March 2009

Ordination

The 2003 data yielded a three-dimensional ordination that exhibits partial separation of broad habitat types, with lake edge to the left and channel habitats to the right of Axis 2 (Fig. 6). MRPP indentifies a significant difference between fish assemblages at the four broad habitat types ($P = 0.018$). Cover is the variable most strongly associated with the structure of fish assemblages along Axis 2 (correlation between cover and axis score: $r = 0.61$). This is largely associated with artificial and natural channels, and some wetland habitats. There is an association between depth and sites along Axis 3 ($r = 0.43$). There are also correlations for several fish species on Axis 2, which have a positive association with cover: dwarf flathead

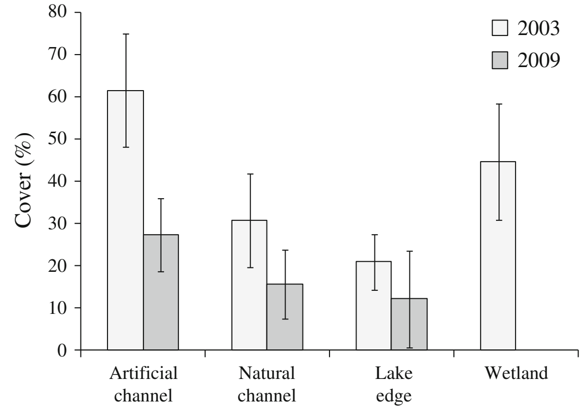

Fig. 5 Comparisons of average percentage aquatic vegetation cover (standard error bars) in the four habitat types, and between January to April 2003 and March 2009

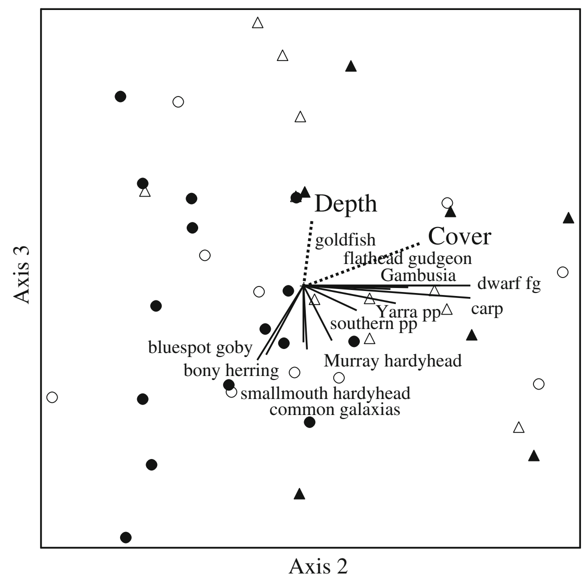

Fig. 6 Three-dimensional NMS ordination of sites based on the composition and abundances of fishes sampled in January–March 2003 (stress = 18.3). *Symbols* represent artificial channel (*solid triangle*), natural channel (*open triangle*), lake edge (*solid circle*) and wetland (*open circle*)

gudgeon ($r = 0.57$), carp ($r = 0.57$), Gambusia ($r = 0.51$), flathead gudgeon ($r = 0.45$), Yarra pygmy perch ($r = 0.42$) and southern pygmy perch ($r = 0.32$).

Murray hardyhead, unspecked hardyhead, southern pygmy perch, sandy sprat and goldfish were removed from ordination of the 2009 data, because they were

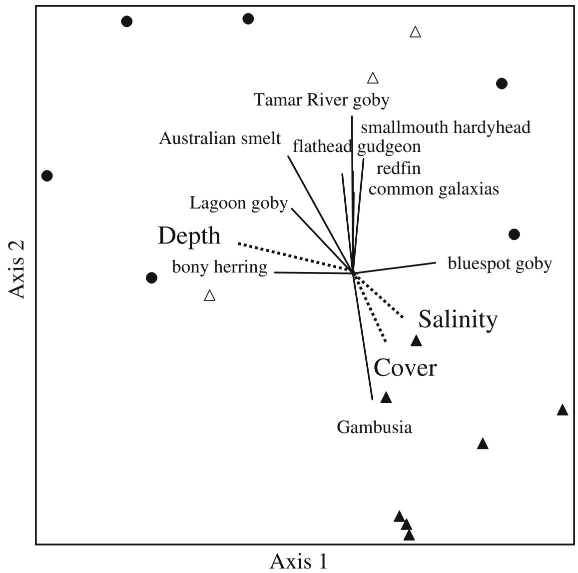

Fig. 7 Two-dimensional NMS ordination of sites based on the composition and abundances of fishes sampled in March 2009 (stress = 15.3). *Symbols* represent artificial channel (*solid triangle*), natural channel (*open triangle*) and lake edge (*solid circle*). All wetlands were dry during this sampling period

captured at fewer than three sites (McCune & Grace, 2002). The 2009 data yielded a two-dimensional ordination with a separation of fish assemblages into broad habitat categories (Fig. 7). MRPP supports this by indicating a significant difference between fish assemblages from different habitat categories ($P < 0.001$). First, there is a cluster of artificial channel sites on the bottom right of the plot that corresponds to the vector for cover, which is the variable most strongly associated with fish assemblage structure along Axis 2 ($r = -0.38$). Second, all lake edge and natural channel sites are located at or above the centre of the plot. Salinity has the second strongest association with fish assemblage structure ($r = 0.32$; Axis 1), which is also positively associated with the artificial channel sites. The correlation for Gambusia ($r = -0.74$) on Axis 2 suggest a positive relationship with cover and salinity in artificial channels. Conversely, correlations on Axis 2 for flathead gudgeon ($r = 0.63$), Australian smelt ($r = 0.78$), lagoon goby ($r = 0.71$), common galaxias ($r = 0.84$), Tamar River goby ($r = 0.62$), smallmouth hardyhead ($r = 0.67$) and redfin ($r = 0.51$) suggest a negative relationship with cover and salinity in lake edge and natural channel habitats.

Indicator species analysis

Indicator species values were calculated for the broad habitat types sampled in 2003 and 2009. Distinct fish assemblages were identified for each habitat and differed considerably between 2003 and 2009 (Table 2). In 2003, there were no significant indicator species in natural channels. In 2009, smallmouth hardyhead ($P = 0.021$) and flathead gudgeon ($P = 0.033$) were significant indicator species in natural channels. In artificial channels, significant indicators species shifted from dwarf flathead gudgeon ($P = 0.002$), Gambusia ($P = 0.006$) and Yarra pygmy perch ($P = 0.029$) in 2003 to solely Gambusia ($P = 0.003$) in 2009. Lagoon goby ($P = 0.043$) was the only significant indicator of lake edge habitat in 2003, whereas there were no significant indicator species in 2009. Wetlands were dry by 2009, but in 2003 unspecked hardyhead, flathead gudgeon and common galaxias were notable indicator species in wetland fish assemblages.

Discussion

Substantially reduced freshwater inflows to the Lower Lakes of the River Murray, resulting from a combination of over-abstraction of water and several years of drought (Bond et al., 2008), caused considerable water level recession and salinization between 2003 and 2009 (Aldridge et al., 2009; Kingsford et al., 2011). This study provides evidence of concurrent declines of obligate freshwater fish species that are ecological specialists, including three threatened species, across most broad habitat types sampled. Furthermore, by 2009 fish assemblages were increasingly characterised by estuarine species, whilst diadromous fishes became scarce. Contrary to our hypothesis, there were higher proportions of freshwater fish in 2009 compared to 2003, attributed to alien and native ecological generalists.

Ecological specialists

Absence of Yarra pygmy perch in 2008–2009 indicates the likely extirpation of the sole population in the MDB (Hammer et al., 2010). Further, a trend of decline is also evident for the congeneric southern pygmy perch. The two species formerly inhabited

Table 2 Indicator species (percentage 'perfect indication') based on habitat type

Natural channel	Artificial channel	Lake edge	Wetland
2003			
Carp gudgeon (24)	Dwarf flathead gudgeon (68)[a]	Bony herring (42)	Common galaxias (32)
Carp (23)	Gambusia (53)[a]	Lagoon goby (37)[a]	Unspecked hardyhead (33)
	Yarra pygmy perch (35)[a]	Blue-spot goby (36)	Flathead gudgeon (21)
	Flathead gudgeon (32)	Australian smelt (32)	
	Southern pygmy perch (25)	Redfin (21)	
		Common galaxias (22)	
2009			
Smallmouth hardyhead (98)[a]	Gambusia (86)[a]	Lagoon goby (52)	
Common galaxias (87)		Australian smelt (51)	
Flathead gudgeon (81)[a]		Carp (23)	
Bony herring (81)			
Bridled goby (63)			
Tamar River goby (53)			
Redfin (53)			
Blue-spot goby (28)			
Carp gudgeon (25)			

[a] Significant indicator based on a Monte Carlo test of observed maximum indicator values (species <20% removed for clarity)

well-vegetated, off-channel sites with low salinity (<1.57 g/l: Wedderburn & Hammer, 2003), which were absent by 2009 because of salinization and the subsequent establishment of halophytic plants and algae. The re-establishment of Yarra pygmy perch relies on its re-introduction from a captive breeding program, whilst southern pygmy perch might re-colonise from a local Eastern Mount Lofty Ranges tributary, although populations there are similarly small and fragmented. Further, populations at the Lower Lakes are genetically differentiated from neighbouring catchments, implying geographic barriers to dispersal and gene flow (Hammer, 2008). Hence, recovery after the drought might be prolonged given the low mobility of pygmy perch (cf. Albanese et al., 2009). Ultimately, population recovery relies on regular inundation of habitat, which promotes zooplankton emergence and enhances recruitment of pygmy perch (Tonkin et al., 2008). Importantly, given that the frequency and intensity of drought and salinization are forecast to increase in the MDB (Lake & Bond, 2007), research is required to predict the population responses of pygmy perch to inform conservation strategies (e.g. use of environmental water allocations).

Murray hardyhead exhibited an apparent increase in proportional abundance in artificial channels that were disconnected from the lakes, but these habitats were sparse by 2009. Salinity has a positive association with the abundance of Murray hardyhead and is linked to its fragmented distribution (Wedderburn et al., 2007). Its apparent minor increase in the proportion of total fish sampled relates to its aggregation in saline artificial channels as lake water levels receded, which allowed for easier capture. Although salinity rose sharply because of evaporation over summer 2008–2009, the species was unlikely to be impacted given its high tolerance (upper $LD_{50} > 85$ g/l: Wedderburn et al., 2008). This gives it an advantage over formerly co-occurring species with a lower salinity tolerance (Wedderburn et al., 2007). This corresponds to patterns observed in other parts of the world, where extended drought reduces fish species diversity because only the most tolerant taxa persist (Matthews, 1998). Crucially, the physicochemical tolerances of most fishes in the MDB are untested, making it difficult to predict the population impacts of salinization caused by drought and over-abstraction.

Diadromous fish populations declined at the Lower Lakes during the drought. Congolli was relatively widespread and numerous in 2003, but was infrequently captured in natural channels in 2008–2009. Only adult congolli were captured, reflecting the disconnection of the Lower Lakes from the estuary in 2007 and obstruction of its catadromous migrations (Zampatti et al., 2010). Adult female congolli undertake synchronised downstream migrations during the austral winter, presumably for the purpose of spawning (Crook et al., 2010a). Its gradual decline throughout the drought appears a reflection of limited access to adult spawning habitats and, hence, failed recruitment (Zampatti et al., 2010). Indeed, Zampatti et al., (2010) report declines in the abundance of juvenile upstream migrants of >99% from 2006–2007 to 2007–2008 at the tidal barrages.

The anadromous pouched lamprey (*Geotris australis* Gray, 1851) and short-headed lamprey [*Mordacia mordax* (Richardson, 1846)], and the catadromous short-finned eel (*Anguilla australis* Richardson, 1841) and estuary perch [*Macquaria colonorum* (Günther, 1863)] were not detected in this study but their declines were apparent before the drought (Sim et al., 2000). Conversely, the catadromous common galaxias remained abundant in 2008, but its reduction in relative numbers by March 2009 was related to poor recruitment due to diminished freshwater inflows to the estuary (Zampatti et al., 2010). Indeed, the disruption to migration caused by the tidal barrages, and the diminished freshwater inflows due to drought and over-abstraction, were obviously key factors restricting the life-cycles of all diadromous species.

Ecological generalists

The predominance of flathead gudgeon at the Lower Lakes in 2008–2009 corresponds with fish assemblages in the Surrey estuary, south-eastern Australia, where it was the most abundant species (Becker & Laurenson, 2008). The species was widespread in 2003 but was mostly associated with natural channels and lake edges in 2008–2009, suggesting flexibility in habitat use as an ecological generalist. This successful habitat shift might relate to a combination of its relatively wide salinity tolerance, benthic nature or broad diet (see Becker & Laurenson, 2007). Conversely, the congeneric dwarf flathead gudgeon declined over the study duration, suggesting a less flexible nature of habitat use with a preference for low salinity. Therefore, this ecological specialist appears more prone to drought-induced extirpation than its generalist congener.

The freshwater unspecked hardyhead was not captured in 2009. The species has a high salinity tolerance in the laboratory ($LD_{50} > 40$ g/l) but only inhabits waterbodies with <7 g/l in the wild (Wedderburn et al., 2007; Wedderburn et al., 2008), which was consistent with this study. Thus, the current findings support the proposition that salinity and inter-specific variation in osmoregulatory ability are key factors causing habitat separation of the congeneric unspecked hardyhead and Murray hardyhead (Wedderburn et al., 2007; Wedderburn et al., 2008). Although considered an ecological generalist, the apparent extirpation of unspecked hardyhead from the Lower Lakes is possibly linked to its migration to the river channel when off-channel sites are salinised during drought (Conallin et al., 2011).

The high numbers of Australian smelt were comparable to several other species in 2003, but it was the most abundant small-bodied fish species in the Lower Lakes in 2008. The species has a high salinity tolerance (upper LD_{50} 58.7 g/l: Williams & Williams, 1991) and prefers open water habitats (Conallin et al., 2011). Thus, it appears well adapted to drought in the Lower Lakes. Similarly, Australian smelt dominated fish assemblages in the lower River Murray during the drought (70% of catch), where it was positively associated with salinity (Conallin et al., 2011).

Gambusia predominated fish assemblages in artificial channels during both sampling periods and was positively associated with aquatic plant cover, which corresponds to findings in other Australian catchments (Chapman & Warburton, 2006). Its persistence might be explained by its wide salinity tolerance, and its ability to consume relatively large items (e.g. terrestrial insects: Rehage et al., 2005) when microfauna are diminishing during salinization (Shiel et al., 1982). Its predominance in refuge sites might be reduced when lake levels rise and habitats reconnect. For example, in the Lake Eyre Basin, central Australia, flooding apparently gave native fish a recruitment advantage over Gambusia (Puckridge et al., 2000).

Redfin was widespread in 2003, but it increased in proportional abundance and was a notable indicator of fish assemblages in natural channels over summer 2008–2009. Slightly elevated salinity (1.2 g/l) can increase larval survivorship in redfin, which is not significantly impacted until between 4.8 and 9.6 g/l (Bein & Ribi, 1994). Its ability to breed in elevated salinities is a possible explanation for its persistence at the Lower Lakes during drought, where salinity averaged 2.7 g/l at lake edge habitats in November 2008.

Several estuarine species apparently have benefited from water recession in the formerly freshwater lakes, predominating fish assemblages in natural channels during 2008–2009. There was an increase in the diversity and proportional abundance of estuarine species in natural channels between 2003 and 2008–2009, which was largely attributable to the incursion of bridled goby and Tamar River goby, and the increased proportional abundance of smallmouth hardyhead. Given its preference for estuarine conditions (salinity 5–30 g/l: Gill & Potter, 1993), the establishment of bridled goby likely relates to salinization in the Lower Lakes during drought. Western blue-spot goby was relatively abundant at lake edges in 2003, but mainly inhabited natural channels in 2008–2009. Correspondingly, the species often dominates fish assemblages in natural channels at other Australian estuaries (e.g. Becker & Laurenson, 2008) and inhabits sheltered areas with silty substrates (Gill & Potter, 1993).

Smallmouth hardyhead is numerically dominant in fish assemblages in many estuaries in southern Australia (Becker & Laurenson, 2008; Bloomfield & Gillanders, 2005), which is generally attributed to its broad salinity tolerance (lower–upper LD_{50} 3.3–108 g/l: Lui, 1969) and ability to recruit even when habitats are disconnected from the sea (Potter et al., 1986). At the Lower Lakes, smallmouth hardyhead was numerous in all habitat types in 2003, but was abundant only at natural channels in 2008–2009. Its high abundance in 2008 is likely related to its 1-year life cycle in which population size peaks during the August–November breeding season (Potter et al., 1986). Further, the species showed no preference for aquatic plant cover during either sampling occasion, which corresponds with other research (Bloomfield & Gillanders, 2005; Connolly, 1994). Given these findings, and that salinity up to 70 g/l has no marked effect on reproductive potential or population parameters of smallmouth hardyhead (sex ratio, final size, general health: Molsher et al., 1994), it is obviously well adapted to drought.

Conclusions

This study emphasises that understanding the ecological attributes of a fish species, and the subsequent assignment to a functional group, will help predict vulnerability to decline and extirpation during prolonged drought in regulated catchments. This is supported by Magalhães et al., (2007) who demonstrated that prolonged dry spells (>6 years) can lead to failed recruitment and extirpation of short-lived ecological specialists in Mediterranean stream fish assemblages. Importantly, the impacts of drought can be exacerbated by anthropogenic factors (e.g. abstraction of water, barriers to migration) that hinder population recovery, and must be addressed to ensure long-term viability of ecological specialists (Crook et al., 2010b). Our findings especially highlight the ecological implications of over-allocating water for human use in drought-prone regions. Therefore, because competing water demands are strained under drought, environmental water allocations should be prearranged to prevent drying (and salinization) of refugia and maintain migratory pathways. This is pertinent, given that increased frequency of drought and its impacts on rivers will increase worldwide under long-term forecasts (Ormerod, 2009). Clearly, in all heavily regulated catchments, research and monitoring programs are necessary so that conservation strategies are adequately prepared.

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References

Adams, M., S. D. Wedderburn, P. J. Unmack, M. P. Hammer & J. B. Johnson, 2011. Use of congeneric assessment to reveal the linked genetic histories of two threatened fishes in the Murray-Darling Basin, Australia. Conservation Biology 25: 767–776.

Albanese, B., P. L. Angermeier & J. T. Peterson, 2009. Does mobility explain variation in colonisation and population recovery among stream fishes? Freshwater Biology 54: 1444–1460.

Aldridge, K. T., B. M. Deegan, S. Lamontagne, A. Bissett & J. D. Brookes, 2009. Spatial and Temporal Changes in Water Quality in Lake Alexandrina and Lake Albert During a Period of Rapid Water Level Drawdown. CSIRO Water for a Healthy Country National Research Flagship, Canberra.

Angermeier, P. L., 1995. Ecological attributes of extinction-prone species: loss of freshwater fishes of Virginia. Conservation Biology 9: 143–158.

Becker, A. & L. J. B. Laurenson, 2007. Seasonal and diel comparisons of the diets of four dominant fish species within the main channel and flood-zone of a small intermittently open estuary in south-eastern Australia. Marine and Freshwater Research 58: 1086–1095.

Becker, A. & L. J. B. Laurenson, 2008. Presence of fish on the shallow flooded margins of a small intermittently open estuary in south eastern Australia under variable flooding regimes. Estuaries and Coasts 31: 43–52.

Bein, R. & G. Ribi, 1994. Effects of larval density and salinity on the development of perch larvae (*Perca fluviatilis* L.). Aquatic Sciences 56: 97–105.

Bloomfield, A. L. & B. M. Gillanders, 2005. Fish and invertebrate assemblages in seagrass, mangrove, saltmarsh, and nonvegetated habitats. Estuaries 28: 63–77.

Bond, N. R., P. S. Lake & A. H. Arthington, 2008. The impacts of drought on freshwater ecosystems: an Australian perspective. Hydrobiologia 600: 3–16.

Chapman, P. & K. Warburton, 2006. Postflood movements and population connectivity in gambusia (*Gambusia holbrooki*). Ecology of Freshwater Fish 15: 357–365.

Collares-Pereira, M. J. & I. G. Cowx, 2004. The role of catchment scale environmental management in freshwater fish conservation. Fisheries Management and Ecology 11: 303–312.

Conallin, A. J., K. A. Hillyard, K. F. Walker, B. M. Gillanders & B. B. Smith, 2011. Offstream movements of fish during drought in a regulated lowland river. River Research and Applications 27: 1237–1252.

Connolly, R. M., 1994. A comparison of fish assemblages from seagrass and unvegetated areas of a southern Australian estuary. Australian Journal of Marine and Freshwater Research 45: 1033–1044.

Crook, D. A., W. M. Koster, J. I. Macdonald, S. J. Nicol, C. A. Belcher, D. R. Dawson, D. J. O'Mahony, D. Lovett, A. Walker & L. Bannam, 2010a. Catadromous migrations by female tupong (*Pseudaphritis urvillii*) in coastal streams in Victoria, Australia. Marine and Freshwater Research 61: 474–483.

Crook, D. A., P. Reich, N. R. Bond, D. McMaster, J. D. Koehn & P. S. Lake, 2010b. Using biological information to support proactive strategies for managing freshwater fish during drought. Marine and Freshwater Research 61: 379–387.

Dufrêne, M. & P. Legendre, 1997. Species assemblages and indicator species: the need for a flexible asymmetrical approach. Ecological Monographs 67: 345–366.

Eastburn, D., 1990. The river. In Mackay, N. & D. Eastburn (eds), The Murray. Murray-Darling Basin Commission, Canberra: 3–15.

Fluin, J., P. Gell, D. Haynes, J. Tibby & G. Hancock, 2007. Palaeolimnological evidence for the independent evolution of neighbouring terminal lakes, the Murray Darling Basin, Australia. Hydrobiologia 591: 117–134.

Fratto, Z. W., V. A. Barko & J. S. Scheibe, 2008. Development and efficacy of a bycatch reduction device for Wisconsin-type fyke nets deployed in freshwater systems. Chelonian Conservation and Biology 7: 205–212.

Gill, H. S. & I. C. Potter, 1993. Spatial segregation amongst goby species within an Australian estuary, with a comparison of the diets and salinity tolerance of the two most abundant species. Marine Biology 117: 515–526.

Hammer, M. P., P. J. Unmack, M. Adams, J. B. Johnson & K. F. Walker, 2010. Phylogeographic structure in the threatened Yarra pygmy perch *Nannoperca obscura* (Teleostei: Percichthyidae) has major implications for declining populations. Conservation Genetics 11: 213–223.

Kingsford, R., K. Walker, R. Lester, P. Fairweather, J. Sammut & M. Geddes, 2011. A Ramsar wetland in crisis—the Coorong, Lower Lakes and Murray Mouth, Australia. Marine and Freshwater Research 62: 255–265.

Lake, P. S. & N. R. Bond, 2007. Australian futures: freshwater ecosystems and human water usage. Futures 39: 288–305.

Lasne, E., B. Bergerot, S. Lek & P. Laffaille, 2007. Fish zonation and indicator species for the evaluation of the ecological status of rivers: example of the Loire Basin (France). River Research and Applications 23: 877–890.

Lévêque, C., T. Oberdorff, D. Paugy, M. L. J. Stiassny & P. A. Tedesco, 2008. Global diversity of fish (Pisces) in freshwater. Hydrobiologia 595: 545–567.

Lintermans, M., 2007. Fishes of the Murray-Darling Basin: An Introductory Guide. Murray-Darling Basin Commission, Canberra.

Lucas, M. C. & E. Baras, 2001. Migration of Freshwater Fishes. Blackwell Science, Oxford.

Lui, L. C., 1969. Salinity tolerance and osmoregulation of *Taeniomembras microstomus* (Gunther, 1861) (Pisces: Mugiliformes: Atherinidae) from Australian salt lakes. Australian Journal of Marine and Freshwater Research 20: 157–162.

Magalhães, M. F., P. Beja, I. J. Schlosser & M. J. Collares-Pereira, 2007. Effects of multi-year droughts on fish assemblages of seasonally drying Mediterranean streams. Freshwater Biology 52: 1494–1510.

Matthews, W. J., 1998. Patterns in Freshwater Fish Ecology. Chapman and Hall, New York.

McCune, B. & M. J. Mefford, 2002. PC-ORD. Multivariate Analysis of Ecological Data, Version 4.36. MjM Software Design, Oregon

McCune, B. & J. B. Grace, 2002. Analysis of Ecological Communities. MjM Software, Oregon.

Molsher, R. L., M. C. Geddes & D. C. Paton, 1994. Population and reproductive ecology of the small-mouthed hardyhead *Atherinosoma microstoma* (Günther) (Pisces: Atherinidae) along a salinity gradient in the Coorong, South Australia. Transactions of the Royal Society of South Australia 118: 207–216.

Ormerod, S. J., 2009. Climate change, river conservation and the adaptation challenge. Aquatic Conservation: Marine and Freshwater Ecosystems 19: 609–613.

Potter, I. C., W. Ivantsoff, R. Cameron & J. Minnard, 1986. Life cycles and distribution of atherinids in the marine and estuarine waters of southern Australia. Hydrobiologia 139: 23–40.

Puckridge, J. T., K. F. Walker & J. F. Costello, 2000. Hydrological persistence and the ecology of dryland rivers. Regulated Rivers: Research and Management 16: 385–402.

Rehage, J. S., B. K. Barnett & A. Sih, 2005. Foraging behaviour and invasiveness: do invasive *Gambusia* exhibit higher feeding rates and broader diets than their noninvasive relatives? Ecology of Freshwater Fish 14: 352–360.

Shiel, R. J., K. F. Walker & W. D. Williams, 1982. Plankton of the Lower River Murray, South Australia. Australian Journal of Marine and Freshwater Research 33: 301–327.

Sim, T., L. Potts, M. Hammer & J. Doube, 2000. Fishes. In Strathalbyn Naturalists Club (ed.), Natural History of Strathalbyn and Goolwa Districts. Douglas Press, Woodville North, SA: 97–108

Smith, B. B., A. Conallin & L. Vilizzi, 2009. Regional patterns in the distribution, diversity and relative abundance of wetland fishes of the River Murray, South Australia. Transactions of the Royal Society of South Australia 133: 339–360.

Tonkin, Z., A. J. King & J. Mahoney, 2008. Effects of flooding on recruitment and dispersal of the Southern Pygmy Perch (*Nannoperca australis*) at a Murray River floodplain wetland. Ecological Management and Restoration 9: 196–201.

Walker, K. F., 2006. Serial weirs, cumulative effects: the Lower River Murray, Australia. In Kingsford, R. (ed.), The Ecology of Desert Rivers. Cambridge University Press, Cambridge: 248–279.

Ward, J. V., K. Tockner & F. Schiemer, 1999. Biodiversity of floodplain river ecosystems: ecotones and connectivity. Regulated Rivers: Research and Management 15: 125–139.

Wedderburn, S. & M. Hammer, 2003. The Lower Lakes Fish Inventory: Distribution and Conservation of Freshwater Fishes of the Ramsar Convention Wetland at the Terminus of the Murray Darling Basin, South Australia. Native Fish Australia (SA), Adelaide

Wedderburn, S. D., K. F. Walker & B. P. Zampatti, 2007. Habitat separation of *Craterocephalus* (Atherinidae) species and populations in off-channel areas of the lower River Murray, Australia. Ecology of Freshwater Fish 16: 442–449.

Wedderburn, S. D., K. F. Walker & B. P. Zampatti, 2008. Salinity may cause fragmentation of hardyhead (Atherinidae) populations in the River Murray, Australia. Marine and Freshwater Research 59: 254–258.

Williams, M. D. & W. D. Williams, 1991. Salinity tolerance of four species of fish from the Murray-Darling Basin River System. Hydrobiologia 210: 145–160.

Zampatti, B., C. Bice & P. Jennings, 2010. Temporal variability in fish assemblage structure and recruitment in a freshwater deprived estuary: The Coorong, Australia. Marine and Freshwater Research 61: 1298–1312.