# Spatial and temporal variability in fish community structure in Mediterranean climate temporary streams

**Nick S. Whiterod[1], Michael P. Hammer[1, 2]** and **Lorenzo Vilizzi[3]**

With 4 figures and 4 tables

**Abstract:** Temporary streams naturally experience flow intermittence and hydrologic discontinuity that act to shape fish community structure. Yet, alteration of the flow regime of temporary rivers may lessen the resilience of fish communities to tolerate hydrologic change imposed by droughts. This long-term study (2001–2013) predicted spatial structuring (across catchments and amongst reaches) in fish community composition and abundance across a hydrologically-altered Mediterranean-type region dominated by temporary streams. Shifts from freshwater specialist and diadromous species to more generalist and tolerant species (i.e. freshwater generalist, aliens and estuarine species) were anticipated as the region experienced low flows (2001–2006) and critical water shortage (2007–2010) associated with a most severe drought. It was anticipated that changes in composition and abundance would be revealed during flood (2011) and post-flood (2012–2013) periods after the drought. Contrary to these predictions, fish community structure was broadly consistent across catchments, despite varying climatic and hydrologic (mainly, flow intermittence) regimes. As expected, significant spatial variability was revealed at the reach scale, with significant differences between upper reaches and terminal wetlands, and with a clear transition in fish community structure between these reach types. Significant temporal variability was also revealed with the reduced abundance of diadromous species (although *Pseudaphritis urvillii* did increase) and increases in the abundance of aliens and surprisingly freshwater specialists over the period of critical water shortage relative to antecedent low flows. This was followed by mixed reach-dependent responses of fish during the flood and post-flood periods. The differential responses of fish communities across reaches and temporal periods must be considered as part of the management of threatened species in hydrologically-altered regions dominated by temporary streams.

**Key words:** functional fish groups; threatened species; flow alteration; millennium drought; Murray-Darling Basin.

## Introduction

Freshwater fish communities are highly dynamic, with their distribution, composition, abundance, recruitment and resilience changing markedly across space and time (Matthews 1998). This spatial and temporal variability is regulated by a myriad of interrelated factors operating at multiple scales (Schlosser 1987; Poff et al. 1997; Bunn & Arthington 2002), but with flow regime considered the overarching influence (Poff et al. 1997). For this reason, alteration of flow regimes (e.g. through river regulation and water abstraction) can detrimentally impact aquatic ecosystems through changes to resource and habitat availability, hydrologic connectivity and its influence on the dispersal of organisms, exchange of energy and materials and magnitude of disturbance (Petts 1984; Poff et al. 1997; Bunn & Arthington 2002; Sponseller et al. 2013). This

**Authors' addresses:**

[1] Aquasave – Nature Glenelg Trust, 7 Kemp St, Goolwa Beach, 5214 SA, Australia

[2] Museum and Art Gallery of the Northern Territory, Darwin, Northern Territory, Australia

[3] Faculty of Fisheries, Muğla Sıtkı Koçman University, Kötekli, Muğla, Turkey

* Corresponding author; nick.whiterod@aquasave.com.au

in turn affects fish communities by disrupting species' life histories, movements and distribution (Bunn & Arthington 2002). Unsurprisingly, the impacts of flow alteration are not constant in time and space, but rather vary complexly.

Temporary streams, which represent the most common and hydrologically dynamic of all freshwater systems, are particularly susceptible to the impacts of flow alteration (Tooth 2000; Larned et al. 2010). These streams are characterised by recurrent flow cessation leading to hydrologic discontinuity, fragmentation and persistence of refuge pools before reconnection as flows recommence (Tooth 2000; Acuña et al. 2014). Flow regime governs these processes by defining the degree of intermittency and, therefore, the extent and quality of habitat available (Poff et al. 1997; Stanley et al. 1997; Larned et al. 2010). The influence of flow alteration is a function of the mode of alteration, and in temporary systems impacted by water abstraction the extent and severity of flow intermittency typically increases as connectivity is reduced (see McMahon and Finlayson 2003; Bunn et al. 2006; Larned et al. 2010). These impacts are being increasingly realised in regions of the world affected by regulation, climate change and droughts (Hughes 2005; Larned et al. 2010).

Droughts represent major hydrologic disturbances that exert significant influence on aquatic ecosystems (Lake 2003) including changes in fish species richness and composition, spawning and recruitment and, ultimately, population structure (Magalhães et al. 2007; Martinho et al. 2007; Bond et al. 2008; Wedderburn et al. 2012). During periods of drought the responses of fish communities are governed by both 'resistance' and 'resilience' mechanisms (Hershkovitz & Gasith 2013). These involve species-specific responses to drying events and refuge pool conditions (resistance) and the ability of species to disperse upon habitat reconnection and expand their distribution (resilience) (Magoulick & Kobza 2003; Bunn et al. 2006; Davey & Kelly 2007; Datry et al. 2014). The responses of fish communities are equally complex, with some studies highlighting limited resilience (Bêche et al. 2009) but with others suggesting that impacts may not necessarily be lasting (Matthews & Marsh-Matthews 2003) as fish species often recover quickly when favourable conditions return (Magoulick & Kobza 2003). Consistently, the impacts of droughts on temporary streams are anticipated to be diminished compared to faunas of perennial streams (Poff et al. 1997; Magoulick & Kobza 2003). For example, fish communities in Mediterranean temporary streams of southwest Portu-

gal have been shown to recover following multi-year (prolonged) drought, but with significant differences in the rate of recovery between reaches (Magalhães et al. 2007). Yet, the impact of drought will be exacerbated by human-induced flow alteration, which may lessen the resilience of fish communities to hydrologic change (Matono et al. 2014; Bunn & Arthington 2002). Thus, fish communities are anticipated to respond in complex ways to the potential interactive effects of drought and flow alteration (and, likely, other stressors) in Mediterranean-type temporary streams (Boix et al. 2010; Matono et al. 2012, 2014; Godinho et al. 2014).

The Eastern Mount Lofty Ranges (EMLR) is a heavily-altered Mediterranean-climate region dominated by temporary streams at the terminal end of the expansive Murray-Darling Basin (MDB) in southeastern Australia (Hammer 2004). The region maintains a diversity of stream and wetland habitats along with connectivity to the Coorong estuary through the lower River Murray and the Lower Lakes (namely, lakes Alexandrina and Albert). Despite the region being small (accounting for only 0.5 % of area of the MDB), considerable climatic and hydrologic (i.e. flow regime and degree of intermittence) variation is experienced and extensive water abstraction (> 8000 farm dams) also has differentially reduced water availability and made many of the streams of the EMLR more temporary in nature (CSIRO 2007). Furthermore, between 1997 and 2010 the MDB was impacted by one of the most severe droughts in recorded history (the millennium drought: van Dijk et al. 2013), with critical water shortage experienced regionally as the drought intensified from 2007 to 2010 (Mosley et al. 2012). Fish communities in nearby regions (e.g. the Coorong and Lower Lakes) were impacted over this period, with reductions in species richness, shifts from specialist (diadromous and threatened species) to generalist salt-tolerant species as well as species expiration (Zampatti et al. 2010; Wedderburn et al. 2012). Only mixed recovery has been observed regionally as freshwater flows have improved significantly over recent years (Bice et al. 2012; Wedderburn et al. 2014).

The present study investigated variability in fish community structure in the EMLR across several spatial scales and temporally over periods of low flow and critical water shortage associated with the drought and subsequent flood and post-flood periods. It was hypothesised that fish communities would vary significantly between catchments and also reaches of the region, guided by distance from the Murray estuary (fewer species, namely diadromous species with dis-

tance from estuary) and longitudinally from headwaters to the terminal wetlands (greater species richness with distance downstream). Temporally, it was anticipated that decreases in streamflow and connectivity associated with drought (low flow and critical water shortage periods) would result in shifts toward salt-tolerant species, whereas limited recovery would be experienced similar to those of comparable nearby regions. The findings of the study are discussed in the context of the management of heavily-altered temporary streams.

## Study area

The EMLR is a small (4693 km²) region containing 17 catchments, eleven of which maintain permanent surface water (Hammer 2004) (Table 1, Fig. 1). In the present study, these eleven catchments were investigated, as was the nearby Inman River catchment (Western Mount Lofty Ranges) given similarity in threatened fish communities and climatic conditions (Hammer 2006). The EMLR is influenced by a local Mediterranean-type climate with moderate Austral winter–spring dominated rainfall and stream flows (VanLaarhoven & van der Wielen 2009), but with clear spatial and inter-annual flow variability (CSIRO 2007) (Fig. 2). For each of the permanent surface water catch-
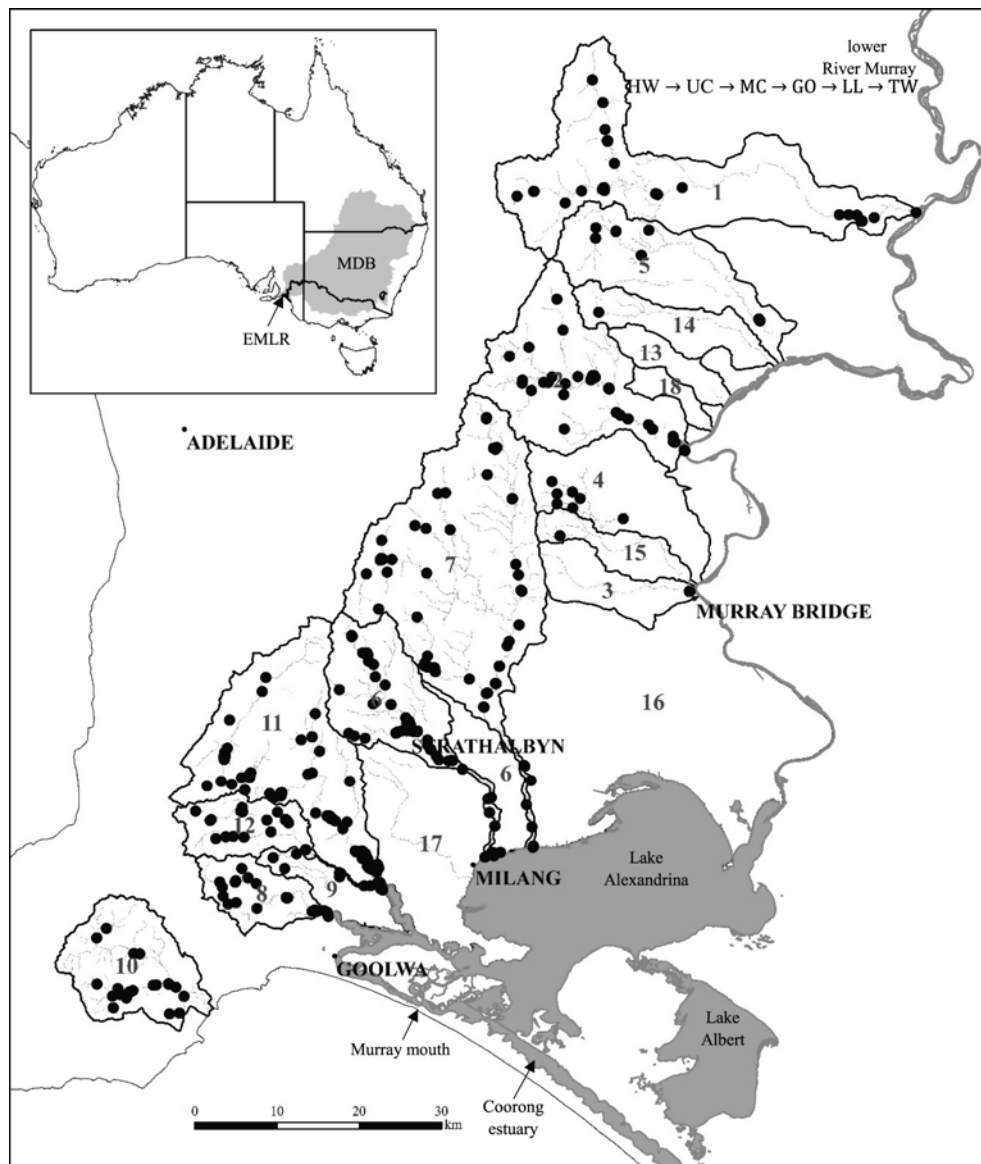


**Fig. 1.** Location of sites (black dots) sampled for fish within the temporary streams (grey lines) of 12 catchments of the Eastern Mount Lofty Ranges (EMLR, black lines) at the terminal end of the Murray-Darling Basin (south-eastern Australia). Numbers relate to catchments shown in Table 1. The direction of the longitudinal transition between reach-types is provided, as headwaters (HW), upper pool-riffle channel (UC), mid pool-riffle channel (MC), gorge (GO), lowland (LL), and terminal wetland (TW).

**Table 1.** Spatial and temporal sampling for fish across the Eastern Mount Lofty Ranges (EMLR). The spatial component consists of catchments (grouped into zones) and of reach types, with sites within reaches and reaches within reach types (in parentheses, $n{:}p,q,\dots$ indicates $n$ reaches and $p$, $q\dots$ sites within each reach); the temporal component consists of the years of sampling grouped according to flow history periods. Reach types: HW = Headwaters; UC = Upper riffle-pool channel; US = Upper riffle-pool channel (spring influence); MC = Mid riffle-pool channel; MS = Mid riffle-pool channel (spring influence); GO = Gorge; LL = Lowland; LS = Lowland (spring influence); TW = Terminal wetland. Catchment numbers in Fig. 1.

| No | Catchment (Code) | Reach type (no. reaches: no, sites in reaches) | Low | | | | | | | Critical | | | Flood | Post-flood | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | 2001 | 2002 | 2003 | 2004 | 2005 | 2006 | 2007 | 2008 | 2009 | 2010 | 2011 | 2012 | 2013 |
| **Dry¹** | | | | | | | | | | | | | | | |
| 1 | Marne River (MR) | HW (3:2,4,1); UC (1:4); MC (1:2); GO (1:2); LS (1:4); TW (1:1) | | ✓ | ✓ | ✓ | ✓ | ✓ | ✓ | ✓ | ✓ | ✓ | ✓ | ✓ | ✓ |
| 2 | Reedy Creek (RC) | UC (1:10); MC (2:5,2); MS (1:3); GO (2:1,1); TW (1:1) | ✓ | | | ✓ | | | | ✓ | ✓ | ✓ | ✓ | ✓ | ✓ |
| 3 | Rocky Gully Creek (RG) | TW (1:1) | | | | | | | ✓ | ✓ | ✓ | ✓ | ✓ | ✓ | ✓ |
| 4 | Salt Creek (SC) | UC (1:3); LS (1:2) | | | | ✓ | | | | | | | | | |
| 5 | Saunders Creek (SA) | HW (1:1); UC (1:2); GO (1:1); LS (1:2) | ✓ | | | ✓ | | | ✓ | | ✓ | | ✓ | ✓ | ✓ |
| **Moderate²** | | | | | | | | | | | | | | | |
| 6 | Angas River (AR) | HW (1:1); UC (2:10,5); MC (1:7); LL (1:3); LS (1:6); TW (1:4) | ✓ | ✓ | ✓ | ✓ | ✓ | ✓ | ✓ | ✓ | ✓ | ✓ | ✓ | ✓ | ✓ |
| 7 | Bremer River (BR) | HW (1:4); UC (2:4,8); US (2:7); LL (2:3,5); LS (1:6); TW (1:1) | ✓ | ✓ | | ✓ | ✓ | ✓ | ✓ | ✓ | ✓ | ✓ | ✓ | ✓ | ✓ |
| 8 | Currency Creek (CC) | HW (1:2); UC (2:2,4)l MC (1:1); GO (1:2); LL (1:2); TW (1:1); | ✓ | | ✓ | ✓ | ✓ | | ✓ | ✓ | ✓ | ✓ | ✓ | ✓ | ✓ |
| 9 | Deep Creek (DC) | MS (1:2) | | | | ✓ | | | | | | | | | |
| 10 | Inman River (IR) | HW (1:1); UC (1:3); MC (3:6,5,2); US (1:2) | ✓ | ✓ | ✓ | ✓ | ✓ | ✓ | ✓ | ✓ | ✓ | ✓ | ✓ | ✓ | ✓ |
| **Wet** | | | | | | | | | | | | | | | |
| 11 | Finniss River (FR) | HW (1:2); UC (2:3,4); MS (2:7,1); US (1:3); LS (2:1,11); TW (1:3) | ✓ | ✓ | ✓ | ✓ | ✓ | ✓ | ✓ | ✓ | ✓ | ✓ | ✓ | ✓ | ✓ |
| 12 | Tookayerta Creek (TC) | UC (1:2); MS (3:1,1,4); US (1:3); LL (1:3); TW (1:4) | ✓ | ✓ | | ✓ | | ✓ | ✓ | ✓ | ✓ | ✓ | ✓ | ✓ | ✓ |

1 Includes Long Gully Creek (no 13), Milendella Creek (14), and Preamimma Creek (15) catchments where no fish were caught and the Bees Knees (18) catchment that was not sampled (given no permanent surface water).
2 Includes Ferries-McDonald (16) and Sandergrove Plains (17) catchments that were not sampled (given no permanent surface water).

ments, distinct river reaches (representing key features such as major tributaries, changes in landform, distinct geomorphology and points of regulation) have been delineated (Hammer 2007; VanLaarhoven & van der Wielen 2009).

Across each of the study catchments, the headwater reach typically contains several small tributaries that subsequently flow into the main stream of that catchment. In turn, catchments progress through upper and mid riffle-pool reaches before entering a confined gorge reach. Below the gorge reach, streams are low-gradient large channels (lowland reach) and finally enter terminal wetlands, which are often under the influence of the River Murray channel and Lower Lakes (VanLaarhoven & van der Wielen 2009). As such, the following reach types were defined across the catchments investigated in this study: headwater (HW), upper pool-riffle channel (UC), mid pool-riffle channel (MC), gorge (GO), lowland (LL), and terminal wetland

(TW). Additionally, reaches influenced by springs were distinguished into upper (US), mid (MS) and lowland (LS) to reflect significant areas with groundwater expression to the surface, which are considered to be important hydrologic features of the EMLR (Hammer 2009) (Table 1).

According to the changes in water availability and streamflow experienced across the EMLR over the study period (Fig. 2), the millennium drought was defined as a *low-flow* period (2001−2006, mean annual streamflow over period at representative gauge, 2352 ML year$^{-1}$) occurring before the period of *critical* period of water shortage (2007−2010, 836 ML year$^{-1}$), which resulted in reduced daily flows and a corresponding drop in regulated Lower Lakes levels ($\approx 0.75$ m Australian Height Datum: AHD) to 0.6 m below sea level. This was followed by significant regional inflows in late 2010, resulting in increased daily stream flows and lake levels over the *flood*
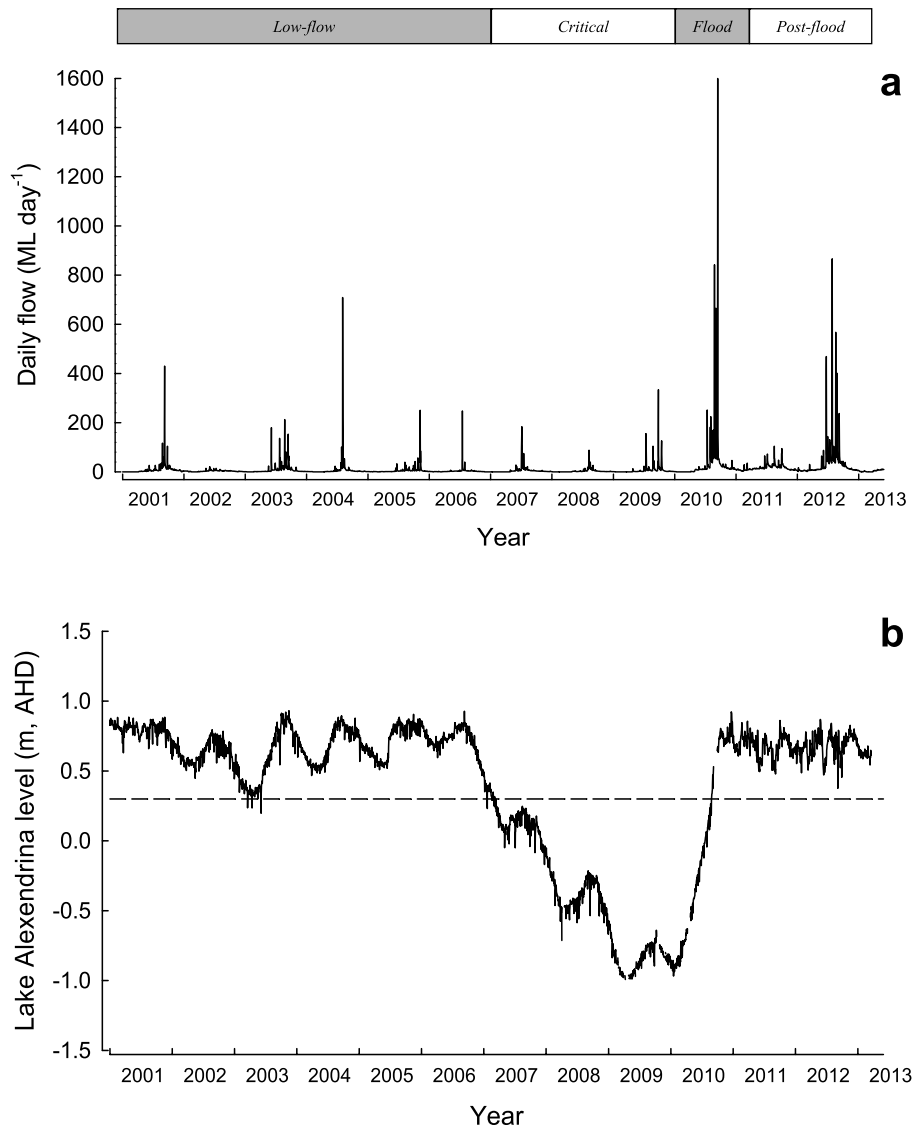


**Fig. 2.** **(a)** Representative mean daily flow (ML day$^{-1}$) for streams of the EMLR, and **(b)** main daily water level (m, Australian height datum: AHD) in Lake Alexandrina throughout the study period (2001−2013). Flow data from Angas River at Weir (station A4260503) gauge; water level data from Lake Alexandrina at Milang Jetty (station A4260524) (DEWNR, unpublished data). Water level where major habitat loss occurred (0.3 m AHD) represented by dashed horizontal line.

**Table 2.** Fish sampling methods and effort employed for fish monitoring across the EMLR from 2001 to 2013. Reach type codes as in Table 1.

| Method | Sampling effort | | Reach types | | | | | | Composite gear |
|---|---|---|---|---|---|---|---|---|---|
| | Replicates | Time (h) | HW | UC/US | MC/MS | GO | LL/LS | TW | |
| Large fyke nets (N) | 1–4 | 17.70 (0.50–23.58) | | ✓ | ✓ | | ✓ | ✓ | B, D, E, A, S, DB, SB, SD, DBA, DA |
| Small fyke nets (N) | 1–4 | 17.88 (0.50–23.58) | | ✓ | ✓ | | ✓ | ✓ | B, D, E, A, S, DB, SB, SD, DBA, DA |
| Seine nets (S) | 1–3 | 1.75 (0.25–22.75) | | ✓ | ✓ | ✓ | ✓ | ✓ | B, D, DB, DN, N, NB |
| Dip nets (D) | 1–4 | 2.39 (0.25–1.00) | ✓ | ✓ | ✓ | ✓ | ✓ | ✓ | B, E, A, N, NB, NA, NBA, S, SB, SN |
| Bait traps (B) | 8–10 | 2.26 (0.67–4.00) | | ✓ | ✓ | ✓ | ✓ | ✓ | E, A, D, N, S, DN, SD, SN, DNA |
| Backpack electrofishing (E) | 2–15 | 0.33 (0.07–0.88) | | ✓ | ✓ | ✓ | ✓ | | B, D, N, NA |
| Angling (A) | 10–15 | 4.00 (1.00–6.00) | | | ✓ | | ✓ | | B, D, N, DN, NE, DNB |

period (2011, 12080 ML year$^{-1}$), with lake levels maintained over the *post-flood* period (2012−2013, 7887 ML year$^{-1}$). Notably, across the EMLR twelve emergency recovery actions (including alien species control, environmental watering and species re-introductions) were undertaken predominantly over the *critical* period (Hammer et al. 2013), but were not considered to influence significantly the broad outcomes of the present study.

# Material and methods

## Fish sampling and identification

Data from long-term and ongoing fish monitoring across the EMLR (including Hammer 2004; Hammer 2007; Hammer 2009; Whiterod & Hammer 2014) were collated for this study. To account for the complexity of habitats from which fish were sampled (including varying depths and salinities) and for the sensitivity of threatened species present in the study region, a range of gear types (both active and passive: cf. Smith et al. 2009; Wedderburn et al. 2012) and sampling effort was selected to estimate the relative abundance of all species in all prevailing habitats. The range of gear consisted of: (i) fyke nets (large: 6 m long wing, 4 mm mesh, 0.6 m opening; small: 3 m long wing, 4 mm mesh, 0.6 m opening; both with 50 mm rigid mesh grids on entrance to exclude turtles), which were set overnight in deep areas (> 1 m) with high dissolved oxygen concentrations; (ii) seine nets (7 m long, 1.5 m deep, 5 mm half mesh), which were hauled along 10 m of bank in shallow (< 1 m) or drying habitats; (iii) dip nets (0.3 m diameter square head, 4 mm mesh); (iv) bait traps (0.4 m length × 0.24 m width × 0.24 m height, 30 mm opening), which were deployed in complex habitat with high conductivities; (v) backpack electrofishing (LR-24, Smith-Root Inc., Pulsed DC, 90−125 W, 150−250 V, 60−80 Hz), which was employed in wadeable areas with dense habitat cover, lower conductivities and high clarity; and (vi) occasional angling (Table 2).

All sampled fish were identified to species (McDowall 1996; Lintermans 2007), except for the carp gudgeon complex *Hypseleotris* spp. owing to taxonomic uncertainty (Bertozzi et al. 2000; Vilizzi & Kováč 2014). All native species were returned alive to the water at the point of capture, whereas alien species were killed as per requirements of research permits. Each sampled species was then ascribed to one of seven different functional groups (after Hammer 2007, Hammer 2009): freshwater stream specialists, wetland specialists, freshwater generalists, diadromous, estuarine, brackish, and alien species. For analytical requirements (see below), distinction was also made between large- and small-bodied species (after Lintermans 2007).

## Data treatment

Although sampling occurred predominantly in autumn (70 % of the samples), the spring (16 %), summer (12 %) and winter (3 %) samples were still retained in the dataset. This was because, despite the Mediterranean climate of the region (*Csa* type under the updated Köppen-Geiger climate scheme of Peel et al. 2007), the anomalous climatic conditions experienced in the study area (i.e. *low-flow* and *critical* periods followed by the *flood*) represented an overriding disturbance to historical, seasonally-related precipitation patterns. Also, from a statistical

**Table 3.** Fish species sampled across the EMLR from 2001 to 2013, with indication of abundance (absolute and relative), occurrence across catchments and years of sampling, and relative abundance over flow periods (see Table 1). Functional groups: BR = Brackish (marine); DI = Diadromous; ES = Estuarine; FG = Freshwater generalists; FS = Freshwater stream specialists; FW = Freshwater wetland specialists; AL = Alien.

| Species | | | Guild | Abundance | | Occurrence (%) | | Relative abundance (%) | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Scientific name | Common name | Code | | n | % | Catchments | Years | Low-flow | Critical | Flood | Post-flood |
| *Native* | | | | | | | | | | | |
| **Large-bodied** | | | | | | | | | | | |
| *Gadopsis marmoratus* | River blackfish | Gad.mar | FS | 721 | 0.55 | 33.3 | 92.3 | 0.34 | 0.42 | 1.82 | 0.42 |
| *Geotria australis* | Pouched lamprey | Geo.aus | DI | 1 | <0.01 | 8.3 | 7.7 | <0.01 | 0.00 | 0.00 | 0.00 |
| *Macquaria ambigua* | Golden perch | Mac.amb | FG | 20 | 0.02 | 50.0 | 30.8 | 0.00 | <0.01 | 0.01 | 0.10 |
| *Nematalosa erebi* | Bony herring | Nem.ere | FG | 947 | 0.73 | 50.0 | 53.8 | 0.17 | 1.31 | 0.45 | 0.28 |
| *Pseudaphritis urvillii* | Congolli | Pse.urv | DI | 361 | 0.28 | 66.7 | 100.0 | 0.04 | 0.08 | 0.35 | 1.40 |
| *Tandanus tandanus* | Freshwater catfish | Tan.tan | FW | 44 | 0.03 | 16.7 | 23.1 | 0.00 | 0.01 | 0.26 | 0.00 |
| **Small-bodied** | | | | | | | | | | | |
| *Afurcagobius tamarensis* | Tamar goby | Afu.tam | ES | 23 | 0.02 | 41.7 | 23.1 | 0.00 | 0.04 | 0.00 | 0.00 |
| *Arenigobius bifrenatus* | Bridled goby | Are.bif | ES | 9 | 0.01 | 16.7 | 15.4 | 0.00 | 0.01 | 0.04 | 0.00 |
| *Atherinosoma microstoma* | Small-mouthed hardyhead | Ath.mic | ES | 12258 | 9.40 | 50.0 | 46.2 | 0.09 | 20.91 | 0.49 | 0.00 |
| *Craterocephalus fluviatilis* | Murray hardyhead | Cra.flu | FW | 508 | 0.39 | 33.3 | 38.5 | 0.00 | 0.85 | 0.10 | 0.01 |
| *C. stercusmuscarum fulvus* | Un-specked hardyhead | Cra.ste | FG | 505 | 0.39 | 58.3 | 76.9 | 0.29 | 0.08 | 1.28 | 0.88 |
| *Galaxias brevipinnis* | Climbing galaxias | Gal.bre | DI | 15 | 0.01 | 16.7 | 30.8 | 0.03 | 0.00 | 0.01 | 0.01 |
| *Galaxias maculatus* | Common galaxias | Gal.mac | DI | 2382 | 1.83 | 66.7 | 92.3 | 0.58 | 3.36 | 0.46 | 0.73 |
| *Galaxias olidus** | Mountain galaxias | Gal.oli | FS | 8547 | 6.56 | 58.3 | 100.0 | 8.65 | 5.97 | 5.61 | 4.50 |
| *Hyperlophus vittatus* | Sandy sprat | Hyp.vit | BR | 1 | <0.01 | 8.3 | 7.7 | <0.01 | 0.00 | 0.00 | 0.00 |
| *Hypseleotris* spp. | Carp gudgeon | Hyp.spp | FG | 15980 | 12.26 | 75.0 | 100.0 | 22.32 | 8.68 | 3.60 | 8.27 |
| *Melanotaenia fluviatilis* | Murray-Darling rainbowfish | Mel.flu | FG | 71 | 0.05 | 8.3 | 23.1 | 0.00 | 0.03 | 0.12 | 0.19 |
| *Mogurnda adspersa* | Southern purple-spotted gudgeon | Mog.ads | FW | 6 | <0.01 | 8.3 | 15.4 | 0.00 | 0.00 | 0.00 | 0.03 |
| *Nannoperca australis* | Southern pygmy perch | Nan.aus | FS | 6035 | 4.63 | 33.3 | 100.0 | 7.91 | 3.53 | 2.11 | 2.86 |
| *Nannoperca obscura* | Yarra pygmy perch | Nan.obs | FW | 60 | 0.05 | 16.7 | 23.1 | 0.15 | 0.01 | 0.00 | 0.00 |
| *Philypnodon grandiceps* | Flathead gudgeon | Phi.gra | FG | 20779 | 15.94 | 58.3 | 100.0 | 10.84 | 18.45 | 15.15 | 19.90 |
| *Philypnodon* (hybrid) | Philypnodon hybrid | Phy.hyb | FG | 2 | <0.01 | 16.7 | 15.4 | 0.00 | <0.01 | 0.00 | 0.00 |
| *Philypnodon macrostomus* | Dwarf flathead gudgeon | Phi.mac | FG | 3751 | 2.88 | 66.7 | 100.0 | 3.15 | 3.49 | 0.77 | 1.99 |
| *Pseudogobius olorum* | Western blue-spot goby | Pse.olo | ES | 371 | 0.28 | 50.0 | 76.9 | 0.42 | 0.34 | 0.04 | 0.00 |
| *Retropinna semoni* | Australian smelt | Ret.sem | FG | 1400 | 1.07 | 66.7 | 92.3 | 1.26 | 0.99 | 2.19 | 0.03 |
| *Tasmanogobius lasti* | Lagoon goby | Tas.las | ES | 51 | 0.04 | 33.3 | 46.2 | 0.02 | 0.07 | 0.01 | 0.00 |
| *Alien* | | | | | | | | | | | |
| **Large-bodied** | | | | | | | | | | | |
| *Carassius auratus* | Goldfish | Car.aur | AL | 290 | 0.22 | 58.3 | 92.3 | 0.19 | 0.18 | 0.64 | 0.10 |
| *Cyprinus carpio* | Common carp | Cyp.car | AL | 2746 | 2.11 | 66.7 | 92.3 | 0.23 | 3.46 | 1.57 | 2.37 |
| *Oncorhynchus mykiss* | Rainbow trout | Onc.myk | AL | 31 | 0.02 | 33.3 | 30.8 | 0.08 | 0.00 | 0.00 | 0.00 |
| *Perca fluviatilis* | European perch (redfin) | Per.flu | AL | 2809 | 2.16 | 66.7 | 100.0 | 1.12 | 0.80 | 11.87 | 1.01 |
| *Salmo trutta* | Brown trout | Sal.tru | AL | 138 | 0.11 | 33.3 | 69.2 | 0.30 | 0.03 | 0.01 | 0.00 |
| *Tinca tinca* | Tench | Tin.tin | AL | 104 | 0.08 | 16.7 | 61.5 | 0.02 | 0.15 | 0.00 | 0.02 |
| **Small-bodied** | | | | | | | | | | | |
| *Gambusia holbrooki* | Eastern mosquitofish (gambusia) | Gam.hol | AL | 49382 | 37.88 | 100.0 | 100.0 | 41.76 | 26.76 | 51.03 | 54.92 |

*Two species, *Galaxias olidus* and *Galaxias oliros*, are now recognised to occur extralimitally in the EMLR as part of a larger species complex (see Raadik 2014); these species will be referred to as *Galaxias olidus* in the present study, as no differentiation of biological information presently exists.

**Table 4.** PERMANOVA results for spatial patterns in functional group and species CPUE abundance (fish m$^{-2}$ day$^{-1}$) across the EMLR from 2001 to 2013 (see Table 1). Significant ($\alpha = 0.05$, in bold) effects for the spatial component are followed by *a posteriori* pair-wise comparisons (only significant ones displayed). For the temporal component, *a priori* contrasts are provided. $F^{\#}$ = pseudo-$F$ statistic; $t^{\#}$ = permutational $t$-value; $p^{\#}$ = permutational $p$-value. Reach type (upstream to downstream): UC = Upper riffle-pool channel; US = Upper riffle-pool channel (spring influence); LL = Lowland; TW = Terminal wetland.

| Source of variation | df | Functional groups MS | $F^{\#}$ | $t^{\#}$ | $p^{\#}$ | Species MS | $F^{\#}$ | $t^{\#}$ | $p^{\#}$ |
|---|---|---|---|---|---|---|---|---|---|
| Catchment zone | 2 | 5932.2 | 2.19 | | 0.065 | 5819.5 | 1.78 | | 0.103 |
| Reach type | 8 | 6977.4 | 1.97 | | **0.036** | 8968.1 | 2.12 | | **0.012** |
| UC *vs* LL | 1 | | | – | – | | | 1.75 | **0.047** |
| UC *vs* TW | 1 | | | 2.85 | **0.001** | | | 2.55 | **0.001** |
| US *vs* TW | 1 | | | 2.03 | **0.009** | | | 1.92 | **0.007** |
| LL *vs* TW | 1 | | | 1.85 | **0.041** | | | – | – |
| Catchment zone × Reach type | 12 | 3075.6 | 0.81 | | 0.694 | 4438.5 | 0.98 | | 0.490 |
| Reach(Catchment zone × Reach type) | 28 | 4737.3 | 3.59 | | **<0.001** | 5605.5 | 3.36 | | **<0.001** |
| Residual | 372 | 1320.8 | | | | 1669.2 | | | |

perspective retention of the entire number of samples into the dataset maximised 'information content' (see below).

To account for the active (i.e. seine and dip nets, electro-fishing, angling) and passive (i.e. fyke nets, bait traps) gear types used throughout the study period and often in different combinations at the same sampling site (Table 2), fish catch-per-unit-effort (CPUE) abundance (hereafter, 'abundance') was computed as the sum over the gear types used at any site and expressed as number of fish per square metre sampled per day (fish m$^{-2}$ day$^{-1}$). This approach, which has been used successfully in other studies (Vilizzi 2012), provides for an 'aggregated' CPUE measure, which is critical to maximise the amount of information retrievable from a dataset.

## Statistical analysis

### Spatial variability

Hypotheses relating to spatial variability in fish community abundance and composition were investigated by a nested-factorial survey design. This consisted of the fixed factors Catchment zone and Reach type and of the random factor Reach (nested within Catchment zone × Reach type). Catchments (excluding those in which no fish were caught: Table 1) were grouped into zones, after preliminary analysis revealed that the total number ($n = 12$) of retained catchments in the dataset would result in too large and problematic a number of *a posteriori* pair-wise comparisons. In addition, the grouping of catchments into zones was designed to reflect the broad patterns of climatic and hydrologic conditions encountered across the EMLR. This consists of drier northern catchments (Marne, Reedy, Rocky Gully and Salt), which are located further from the Coorong estuary, and of moderately-wet (Angas, Bremer, Currency, Deep and Inman) and wet (Finniss, and Tookayerta) catchments with greater connectivity to the estuary (see Hammer 2009).

Analysis was by permutational multivariate analysis of variance (PERMANOVA). The resulting $423 \times 7$ (samples × functional groups) and $423 \times 33$ (samples × species) data matrices were √-transformed (due to abundance values spanning two orders of magnitude) and a zero-adjusted Bray-Curtis dissimilarity measure (zero-adjusted because of blank samples: Clarke et al. 2006) was applied. In all cases, the samples were represented by the combinations of reaches within Catchment zone × Reach type, and with data from reaches pooled at the site level (the experimental unit in the design). Analyses were carried out in PERMANOVA+v1.0.1 for PRIMER v6.1.11 (Anderson et al. 2008), with probability values obtained with 9999 permutations of the residuals under a reduced model (Anderson & Robinson 2001) and with the significance level set at $\alpha = 0.05$.

### Temporal variability

The hypotheses relating to temporal variability in fish community abundance and composition were tested by min-max autocorrelation factor analysis (MAFA: Solow 1994). In MAFA, axes are produced that have maximum autocorrelation with time lag *k*. The first MAF axis represents the main trend or underlying pattern in the data associated with the highest autocorrelation at lag 1, the second MAF axis has the second highest autocorrelation at lag 2, and so forth. Cross-correlations (or canonical correlations) between variables and trends are then computed and tested for significance.
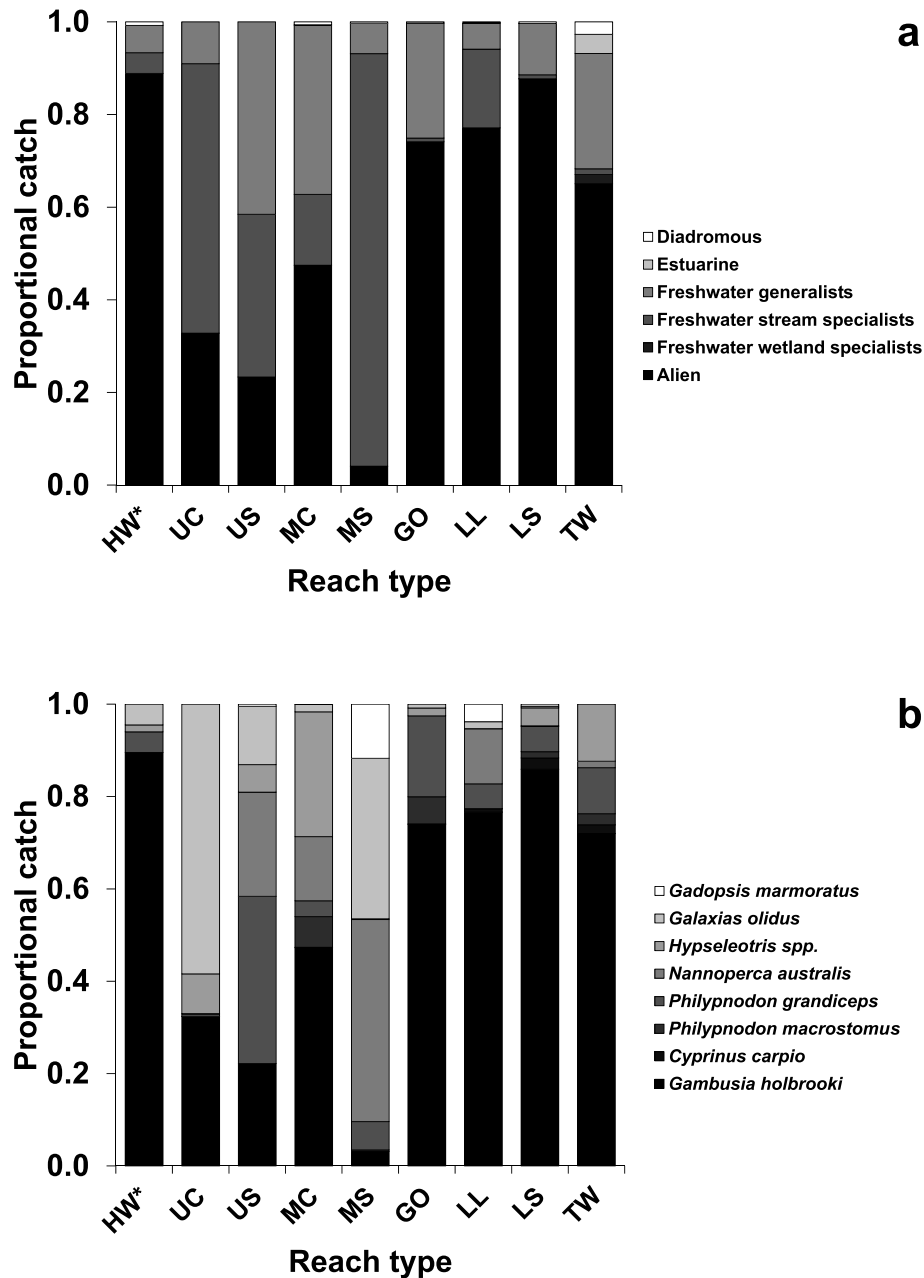
**Fig. 3.** Proportion of total catch of **(a)** the functional groups and **(b)** most abundant species over reach types in the EMLR. For simplicity, the only brackish fish *Hyperlophus vittatus* sampled over the study period was removed. Reach type codes as in Table 1 (HW marked by an asterisk to warn that sampling for this reach type mostly occurred in 2004).

Because in MAFA the number of time points (i.e. the 13 years of sampling in this study) is constrained to be larger than the number of variables, the 33 fish species that were recorded in total were first divided into large-bodied and small-bodied (Table 3). The first 10 (out of the 12 in total) large-bodied species and the first 11 (out of the 21 in total) small-bodied species in abundance were then retained as the maximum number of species suitable for analysis, whereas all functional groups ($n = 7$) were included. Following √-transformation and cen-

tering of the abundance data, the first three MAF axes were estimated (corresponding to lags 1, 2 and 3: i.e. differences between two consecutive years, two years apart, and three years apart, respectively), and canonical correlations between individual variables (i.e. for the functional groups, large-bodied and small-bodied species) and the three MAF axes were tested for significance ($\alpha = 0.05$). Analyses were carried out in R (R Development Core Team 2014) using code provided in Woillez et al. (2009).
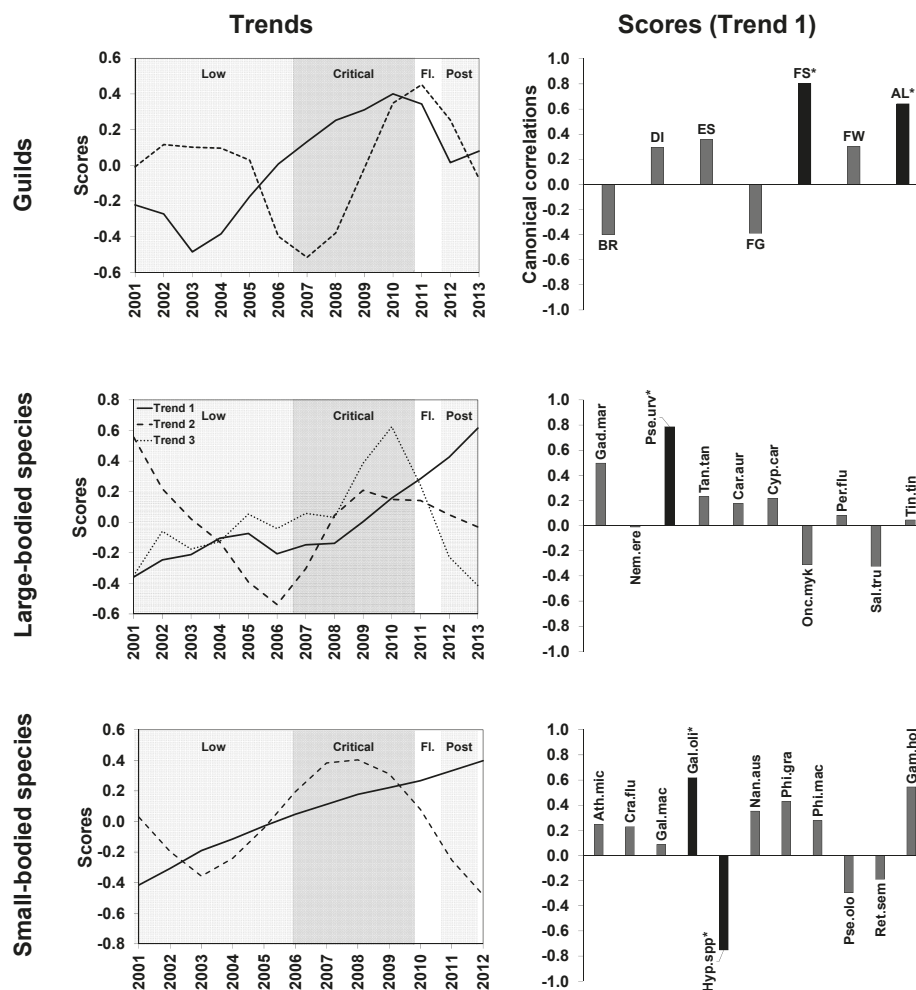
**Fig. 4.** Min-max autocorrelation factor (MAF) trends and corresponding canonical correlations for the abundance (CPUE: fish m$^{-2}$ day$^{-1}$) of functional groups, large-bodied species and small-bodied species of fish (codes in Table 3) sampled across the Eastern Mount Lofty Ranges (EMLR) from 2001 to 2013. For the trends, indication of the flow periods (see Table 1) is provided. Trends associated with significant ($\alpha = 0.05$) canonical correlations in black, otherwise in grey. Functional groups and species with significant canonical correlations marked by an asterisk and with corresponding bar highlighted in black.

## Results

In total, 130,348 fish were sampled consisting of seven functional groups and 33 species, of which 27 were native (six large-bodied and 21 small-bodied) and seven alien (six large-bodied and one small-bodied) (Table 3). Of these fish, the majority were small-bodied natives (72,754 fish, 55.8%) and aliens (49,382, 37.9%) whereas the large-bodied species comprised a smaller proportion (natives: 2094, 1.6%; aliens: 6118, 4.7%). Based on raw abundance, the alien *Gambusia holbrooki* was by far the most abundant species, followed by natives *Philypnodon grandiceps*, *Hypseleotris* spp. and *Atherinosoma microstoma*; whereas *Galaxias olidus*, *Nannoperca australis*, *Philypnodon macrostomus* and the

remaining 26 species accounted for < 10% of the total catch. Amongst the rare species were *Arenigobius bifrenatus*, *Mogurnda adspersa*, *Geotria australis* and *Hyperlophus vittatus* (the latter two each sampled as only one individual).

Spatially, *Gambusia holbrooki* was the only species that occurred across all catchments, although *Pseudaphritis urvillii*, *Galaxias maculatus*, *Hypseleotris* spp., *Philypnodon macrostomus*, *Retropinna semoni* (amongst the native species) and alien *Cyprinus carpio* and *Perca fluviatilis* were found in more than seven of the 12 catchments investigated. Conversely, *Geotria australis* and *Mogurnda adspersa* occurred only in the Finniss, *Hyperlophus vittatus* in the Bremer, and *Melanotaenia fluviatilis* in the Rocky Gully catchment (Table 3). Temporally,
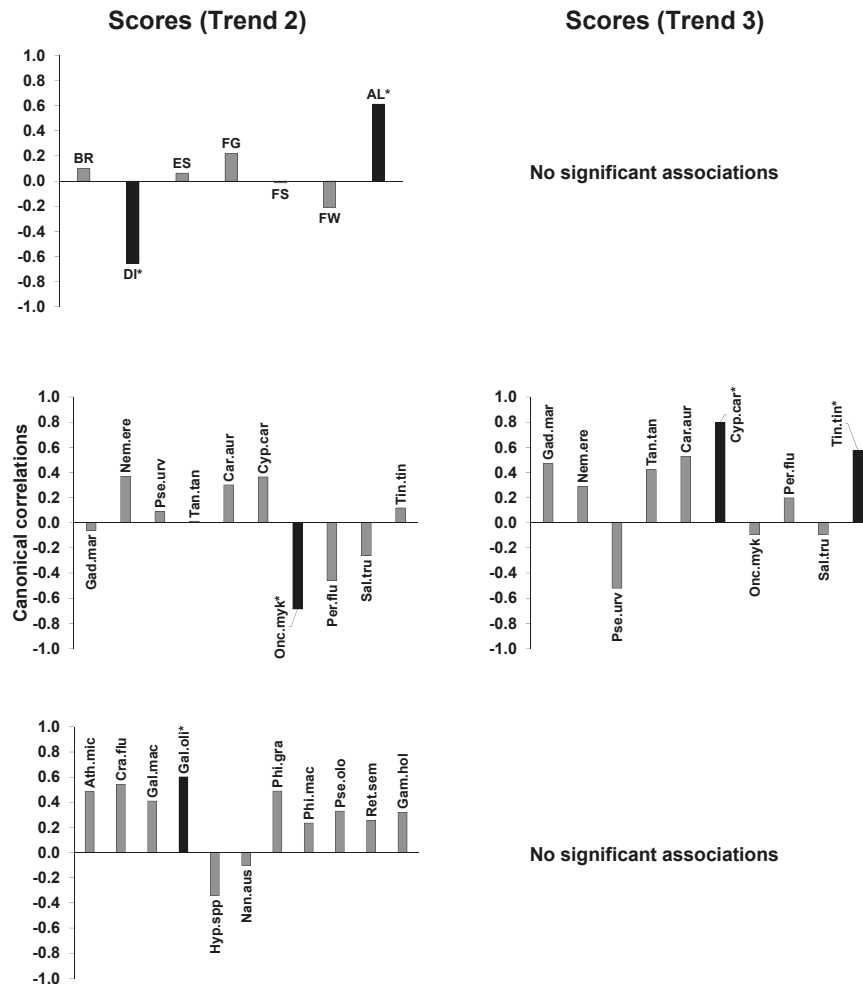
**Fig. 4.** Continued.

*Pseudaphritis urvillii, Galaxias olidus, Hypseleotris* spp., *Nannoperca australis, Philypnodon grandiceps* and *Philypnodon macrostomus* amongst the native species and *Perca fluviatilis* and *Gambusia holbrooki* amongst the aliens were recorded in all years of sampling (Table 3).

### Spatial variability

For both functional groups and species, there were statistically significant differences in abundance and composition amongst reach types, but not amongst catchment zones. Also, there was significant (random) variation at the reach level (Table 4). The LS and TW (codes in Table 1) were the only reach types where all functional groups were found, and this was due

to the occurrence of freshwater wetland specialists (but also of the brackish-water *Hyperlophus vittatus* in the Bremer River terminal wetland), which were absent elsewhere. Diadromous and estuarine species made up the largest proportion of the fish community in TW; freshwater generalists in US and MC (and, to some extent, also in GO and TW); freshwater stream specialists in MS and UC; whereas alien species dominated the fish community across the majority of reach types, but with higher abundances in HW, GO and LL (Fig. 3a). Statistically, there were significant differences between TW relative to UC/US and LL reach types (Table 4).

In total, eight species were identified to be mainly responsible for the observed patterns. Thus, *Gadopsis marmoratus* was more abundant in MS; *Galaxias*

*olidus* in UC and MS; *Hypseleotris* spp. in MC and, to some extent, TW; *Nannoperca australis* in MS; *Philypnodon grandiceps* in US and GO; *Philypnodon macrostomus* in MC and GO; *Cyprinus carpio* in LL and TW; whereas *Gambusia holbrooki* was abundant across all reach types except for MS (Fig. 3b). Statistically, TW and LL differed significantly from UC (Table 4).

### Temporal variability

There were significant associations between functional group abundance and the first two MAF axes of variation (hence, trends) (Fig. 4). Trend 1 highlighted a significant increase from 2003 through to 2010 in the abundance of freshwater wetland specialists and alien species, followed by a decrease thereafter; Trend 2 also was associated with an overall increase in the abundance of alien species, and especially so during the *critical* period (after a decline towards the end of the *low-flow* period). Conversely, diadromous species followed an opposite trend of decreasing abundance.

Significant associations were observed between large-bodied species abundance and all three MAF axes of variation (Fig. 4). Accordingly, throughout the study period there was a significant increase in the abundance of *Pseudaphritis urvillii* (and especially so from 2008 onwards), but also of *Gadopsis marmoratus* (although this was not statistically significant) (Trend 1). An increase in abundance during the *critical* period was observed for *Nematalosa erebi* and for the aliens *Cyprinus carpio* and *Carassius auratus*, paralleled by a corresponding decrease in the abundance of *Oncorhynchus mykiss* (statistically significant), *Perca fluviatilis* and alien *Salmo trutta* (Trend 2). Finally, Trend 3 highlighted a statistically significant peak in the abundance of *Cyprinus carpio* and the other alien species *Tinca tinca* towards the end of the *critical* period.

Finally, small-bodied species were significantly associated with the first two MAF axes of variation (Fig. 4). Specifically, Trend 1 indicated an increase in the abundance of *Galaxias olidus* (statistically significant) and *Gambusia holbrooki*, and a corresponding decrease in the abundance of *Hypseleotris* spp. Trend 2 was again related to a significant increase in the abundance of *Galaxias olidus* especially during the *critical* period.

### Discussion

The present study distinguished the EMLR as an altered region dominated by temporary streams yet capable of maintaining diverse freshwater fish communities (33 species present, of which 27 were native) compared to nearby freshwater regions (McNeil et al. 2011; Wedderburn et al. 2012; 2014) and to other regions of temporary streams worldwide (Matono et al. 2014). Across the region, significant spatial patterns in the structure of the fish community were revealed. In partial support of our prediction of fewer species with increasing distance from the Murray estuary, northern catchments supported the least number of species (11 species). However, the pattern was not held with mid-catchments supporting more species than the catchments closest to the estuary. Regardless, the differences in fish species composition were not significant, with almost half of all species being present in more than 50 % of the catchments therein. The broad homogeneity observed at this scale is somewhat surprising given the variation in flow intermittency driven by climatic and hydrologic differences, and also influenced by the degree of flow alteration that prevails across the EMLR (CSIRO 2007; VanLaarhoven & van der Wielen 2009). Yet, greater understanding of the patterns of flow intermittency across the region may reveal finer scale responses of fish communities to hydrologic regimes (see Matono et al. 2014).

Spatial differences were best described at the reach-type scale, with the mid and upper reaches supporting significantly different fish communities than those of terminal wetland reaches, but with a gradual transition between these reach types. This transition reflected changes from an assemblage of freshwater stream specialists dominated by *Galaxias olidus* in the upper pool-riffles to mid reaches (mid pool-riffle and gorge) characterised by freshwater generalists, and with alien species most abundant in the lower reaches—a pattern that has been observed in other comparable regions of temporary streams (Matono et al. 2014). The presence of diadromous (i.e. *Pseudaphritis urvillii* and *Galaxias maculatus*) and estuarine species differentiated the terminal wetlands, which supported a more diverse fish community (all functional groups and 25 species sampled over the study period), hence with a composition more aligned to that of the nearby Lower Lakes (Wedderburn et al. 2012; Wedderburn et al. 2014).

### Impact of low flows and critical water shortages

Antecedent conditions help to determine ecological responses to drought (Rolls et al. 2012), and the long history (i.e. 80 years: CSIRO 2007) of water abstraction and altered stream flows ensured that

fish communities in the EMLR were already highly stressed prior to the millennium drought (see Hammer 2004; Hammer et al. 2009). Several native species, for instance, have already disappeared from the EMLR (including Murray cod *Maccullochella peelii* and silver perch *Bidyanus bidyanus*), whilst others have declined in range and abundance and seven alien species have established (Hammer 2004). The millennium drought was severe in its duration and magnitude but decline was initially gradual and fish communities were broadly maintained over the *low-flow* period (as revealed by the MAFA trends of the present study).

As the millennium drought intensified over 2007, significantly diminished regional inflows and critical water shortages resulted in flow cessation, habitat disconnection and drying of (once refuge) habitats across the EMLR (Hammer 2009; Hammer et al. 2013). The transition from *low-flow* to *critical* periods corresponded with sharp declines in the overall abundance of fish species, but with increased relative abundance of species with broader habitat requirements and environmental tolerances, such as alien species (i.e. *Gambusia holbrooki, Cyprinus carpio* and *Tinca tinca*). The diadromous *Pseudaphritis urvillii* also increased over this time, despite regional declining trends (Zampatti et al. 2010; Wedderburn et al. 2012), highlighting the possibly that the lower reaches of the EMLR may have acted as a refuge in the face of critical water shortage and broad-scale habitat loss in nearby lake and estuary environments (see Zampatti et al. 2010; Wedderburn et al. 2012; Bucater et al. 2013). To a lesser extent, the abundance of the estuarine *Atherinosoma microstoma* and the *Craterocephalus fluviatilis,* a freshwater wetland specialist that possesses a high salinity tolerance (Wedderburn et al. 2007) increased initially over this period, which is consistent with shifts to more salt tolerant species observed not only regionally (Zampatti et al. 2010; Wedderburn et al. 2012; Bucater et al. 2013) but also in other Mediterranean-climate regions following an extreme drought (Martinho et al. 2007).

An interesting observation of the present study was the increase in the abundance of freshwater specialists revealed over the period of drought. This pattern largely reflected *Galaxias olidus*, which has been shown to tolerate hypoxic conditions (as low as $< 1.0\,\mathrm{mg\,L^{-1}}$) often through aquatic surface respiration and to possess strong dispersal ability (Closs & Lake 1995; McMaster & Bond 2008; Dexter et al. 2014). This suggests that the species would have been able to move to and persist in refuge pools that were maintained in the upper reaches of the EMLR during the drought. In sharp contrast, another freshwater specialist, *Nannoperca obscura*, was lost from the drying terminal wetlands of the EMLR and the broader region, over the *critical* period (see also Wedderburn et al. 2012). Consistently, limited recruitment and localised extinctions of some populations of freshwater specialists were observed (Hammer 2009), suggesting that the long-term resilience of this functional group was tested during the *critical* period.

## Responses to flooding and post-flood periods

In the EMLR, the response of fish communities following the *critical* period was mixed, with differential patterns between species and functional groups and also amongst reaches (Magalhães et al. 2007). The diadromous *Pseudaphritis urvillii* benefited from improved flows and connectivity with abundant catches in the terminal wetlands and lowland reaches of the EMLR streams as well as in the Lower Lakes (Wedderburn et al. 2014), largely explained by significant recruitment in the Coorong estuary (Bice et al. 2012). Conversely, the relative abundance of *Galaxias maculatus* declined in the study region over the *flood* and *post-flood* periods, but this may have reflected the greater availability of preferred habitat in the nearby Lower Lakes over the time. Reflecting broader recovery, the freshening of the lower reaches corresponded with declines in the relative abundance of estuarine species, most notably *Atherisnosoma microstoma* – an expected outcome given the species' intolerance to low salinities (Wedderburn et al. 2008).

The *flood* period was characterised by continued increase in the abundance of alien species, reflecting large numbers of juveniles of *Perca fluviatilis* in the terminal wetlands as well as in the Lower Lakes (Wedderburn et al. 2014). This response may contribute to heighten predation of threatened native species across the EMLR as this species rapidly transitions to diets dominated by fish (Wedderburn et al. 2015). As the region moved into the *post-flood* period, aliens became less common with the exception of *Gambusia holbrooki*, which increased in prevalence over the study period to the extent that it now dominates habitats across all reaches of all catchments of the EMLR. In the region, widespread impacts of *Gambusia holbrooki* are anticipated (see Pyke 2008) and targeted removals, where populations of key threatened species persist, may be warranted.

The conservation of threatened freshwater specialists was of considerable management interest over the *critical* period (see Hammer et al. 2013), so

the responses of these functional groups as hydrologic conditions improved were pertinent. *Galaxias olidus* was well placed to readily respond as refuge pools expanded during the *flood* period and, given its good dispersal ability (Dexter et al. 2014), gradually re-colonised previously dry habitats across the mid to upper reaches. The present study revealed contrasting patterns for other freshwater specialists: *Nannoperca obscura* were not detected and only low numbers of *Craterocephalus fluviatilis* have been recorded since peaks in the abundance of this salt-tolerant species during the *critical* period. This is in spite of re-introductions of the these two species into the lower reaches of the EMLR and Lower Lakes (Bice et al. 2013; Ellis et al. 2013; Hammer et al. 2013). However, in the Lower Lakes short-term survival and, possibly, recruitment in the wild of these two species have been witnessed (Bice et al. 2014), highlighting a regional presence that may facilitate re-establishment in the EMLR. Overall, the findings of this study emphasise that the differential responses of fish communities across reaches and temporal periods must be considered as part of the management of fish community in hydrologically-altered regions dominated by temporary streams.

## Acknowledgements

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