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Fish movement strategies in an ephemeral river in the Simpson Desert, Australia

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Abstract Arid zone catchments experience extreme hydrological variability and some rivers are entirely ephemeral, replenished only by intermittent flooding. The ecological roles of ephemeral systems are rarely studied. This paper describes movement patterns of fish in the Mulligan River, an ephemeral system in the Lake Eyre Basin, central Australia. Several sites were sampled along a temporal gradient encompassing floods and dry periods. After a single major flood in 2007 up to seven fish species were found at sites up to 300 km from the closest permanent waterhole. Following a series of floods (when waterholes were replenished and remained wet between 2009 and 2011) a further five species were recorded including the first records for the Lake Eyre hardyhead, *Craterocephalus eyresii*, from the rivers of far western Queensland. The presence of all species known from the parent catchment (the Georgina, where permanent waterholes occur) in the ephemeral catchment (the Mulligan) suggests that many fish species present in the river systems of central Australia are capable of dispersing long distances following the opening of movement pathways during flooding. However, two distinct groups of species were identified: extreme dispersing species, that move as far as possible into intermittently wetted habitats, and conservative dispersing species, that do not move as far, tending to inhabit deeper waterholes within mid-reaches of the river that are more likely to hold water for longer. Preservation of the natural flow regime of Australia's arid-zone rivers is important for maintaining these fish communities and facilitating study of their adaptations to ephemerality.

Key words: arid-zone river, central Australia, conservative dispersing species, extreme dispersing species, fish assemblage, Lake Eyre Basin.

INTRODUCTION

Arid zone rivers exhibit extreme hydrological variability (Walker *et al.* 1995; Puckridge *et al.* 1998) and if permanent water exists it is often present as isolated channel waterholes, rockholes or springs emanating from subterranean aquifers (Box *et al.* 2008; Fensham *et al.* 2011). However, some arid zone rivers are entirely ephemeral, and aquatic habitats are only replenished following unpredictable flooding (Silcock 2009). Biota with entirely aquatic life cycles such as fish have limited opportunities to move into, inhabit and recruit in ephemeral rivers. Furthermore, without replenishing flows and renewed connectivity, extirpation of fish populations is likely to occur in such rivers (Fausch & Bramblett 1991). Gaining an understanding of the ecological roles of ephemeral waterways in arid environments has the potential to contribute to our knowledge of the diversity and productivity of arid-zone river systems, and the magnitude of change associated with unpredictable flooding and 'boom and bust' ecological dynamics (Kingsford 2006; Larned *et al.* 2010).

Studies of the community structure of fishes have demonstrated that variation occurs along stream gradients from variable shallow to stable deep habitats (Schlosser 1987), and that species richness typically increases with depth, water persistence, channel size and downstream distance (Schlosser & Angermeier 1995). In systems prone to seasonal drying, permanent pools have been shown to provide habitat for larger, predatory species, whereas smaller more tolerant species inhabit shallower areas (Pusey *et al.* 1993; Magoulick & Kobza 2003). Capone and Kushlan (1991) identified several 'pioneer species' based on their ability to colonize and survive in comparatively harsh conditions, and suggested that such species are likely to be successful in areas where populations of other species are low. Extending these concepts to Australia's arid-zone-rivers suggests that ephemeral areas in rivers prone to drying are likely to provide habitat for a subset of riverine species rather than complete assemblages similar to those

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from areas of greater water permanence, and that pronounced dispersal ability, combined with broad environmental tolerances, will characterize this species subset.

Investigating the establishment and extirpation of fish species in natural or near-natural arid catchments has the potential to yield information on the dispersal potential and biogeography of the species concerned, however few studies have been published. Medeiros and Maltchik (2001) concluded that the fish communities in intermittent semi-arid Brazilian streams were characterized by low species diversity. Turner *et al.* (2010) investigated recruitment of fish in the arid Rio Grande River in New Mexico, and Eby *et al.* (2003) used a long-term dataset from Aravaipa Creek in the Sonoran Desert, Arizona, to demonstrate that conservation of native fish species in such a system is best facilitated by retention of high flow variability.

Within the Lake Eyre Basin of central Australia the fish fauna is comprised of a combination of widespread species (occurring in most catchments) and locally endemic species occurring in fewer catchments (Wager & Unmack 2000; Kerezsy 2010). In this study we investigated fish assemblage patterns in the ephemeral Mulligan River on the eastern edge of the Simpson Desert, central Australia, at the extreme limit of freshwater habitation in an arid-zone environment. Investigating assemblage patterns of the fish fauna following the opening of movement pathways has the potential to identify species that are most likely to disperse opportunistically, and those unable, or less able, to disperse in this fashion. Additionally, establishing the dispersal distances of individual species has been identified as a necessary step in predicting colonization patterns in ephemeral systems (Larned *et al.* 2010). Given that waterholes in ephemeral systems are only likely to hold water for a limited time, the age/size structure of resident populations may provide evidence of the advantages of usage. An age/size structure skewed towards juveniles may infer successful recruitment whereas age/size structure dominated by adults suggests the importance of resource and/or reproductive requirements.

We developed three main objectives as the focus of this research: (i) to investigate whether all fish species present in an arid-zone catchment undertake movement into ephemeral rivers and habitats following flooding; (ii) to estimate the distance species are likely to travel from permanent waterholes; and (iii) to infer whether movement into such areas is advantageous by facilitating recruitment opportunities. We addressed these questions of movement potential, distance moved and recruitment opportunities in ephemeral habitats by repeat sampling of several sites along a temporal connectivity gradient generated by floods and dry periods from 2007 to 2011.

METHODS

Study area, hydrology and sampling sites

The Mulligan River is situated in the Australian arid zone (Fig. 1) and receives average annual rainfall of approximately 120 mm per year. The river rises close to the Queensland/Northern Territory border and then follows a southerly course before joining Eyre Creek at Kalidawarry Waterhole. There are 22 permanent waterholes in the Georgina/Eyre Creek catchment (Silcock 2009), making it the most arid of the three major catchments in the Lake Eyre Basin (the other two being the Diamantina and Cooper). Rainfall within the study area is erratic and unpredictable, and most of the waterholes are dry within seven to eight months of filling (Silcock 2009). Analysis of temperature and rainfall patterns across the Simpson Desert for the last 100 years indicates that there has been significant warming in the area as well as an increase in the frequency of high rainfall events (Greenville *et al.* 2012). There are no flow-gauging stations in the Mulligan catchment, and the closest station is located at Roxborough Downs (in the Georgina catchment), approximately 100 km to the east of the headwaters of the Mulligan River. Consequently, rainfall records from gauges close to the headwaters of the Mulligan River were used to estimate the magnitude of flooding, combined with the observations of local landholders, managers and researchers for the period immediately prior to and during the study (Fig. 2). Mid-catchment waterholes (Pulchera, Wongitta and Cootadoo) were sections of the main channel of the river that became inundated after flooding and were less than 200 km from the confluence of the Mulligan River with Eyre Creek. Upper-catchment waterholes were either further than 200 km from the confluence of the Mulligan and Eyre Creek (S Bend, KK Crossing) or separated from the main river channel (Lake Namabooka and Lake Amaroo; Fig. 1).

The Mulligan River was dry from at least November 2006 until flooding occurred in January and February 2007 (Fig. 2; Scott Morrison, Ethabuka Station, pers. comm., 2007), after which the Mulligan was connected with Eyre Creek at Kalidawarry Waterhole for between 1 and 2 weeks (Jim Smith, Bedourie Hotel, pers. comm., 2007). Waterholes in the Mulligan then dried sequentially in 2007: S Bend Gorge was dry by September, Pulchera by December (Kerezsy, pers. obs., 2007), and all Mulligan waterholes remained dry throughout 2008. In early 2009 rainfall was sufficient to fill Mulligan River waterholes and re-connect the river to Eyre Creek (Fig. 2). Although most waterholes were dry by the following summer, the large waterhole Pulchera persisted until re-filling occurred again in 2010 (Greg Woods, Carlo Station, pers. comm., 2010). In March 2010 heavy rainfall occurred in the Mulligan catchment (Fig. 2) and a larger number of waterholes (such as Wongitta and Cootadoo; Fig. 1) held water. Smaller rain events throughout 2010 ensured that waterholes high in the catchment (such as S Bend Gorge; Fig. 1) and separated from the main channel (such as Lake Namabooka; Fig. 1) retained water throughout the year. Summer rainfall in 2011, though not as heavy as the previous year (Fig. 2), was still sufficient to allow the larger waterholes such as Pulchera, Cootadoo and Wongitta to persist until November (Fig. 1; A. Kerezsy and M. Tischler pers. obs., 2011).

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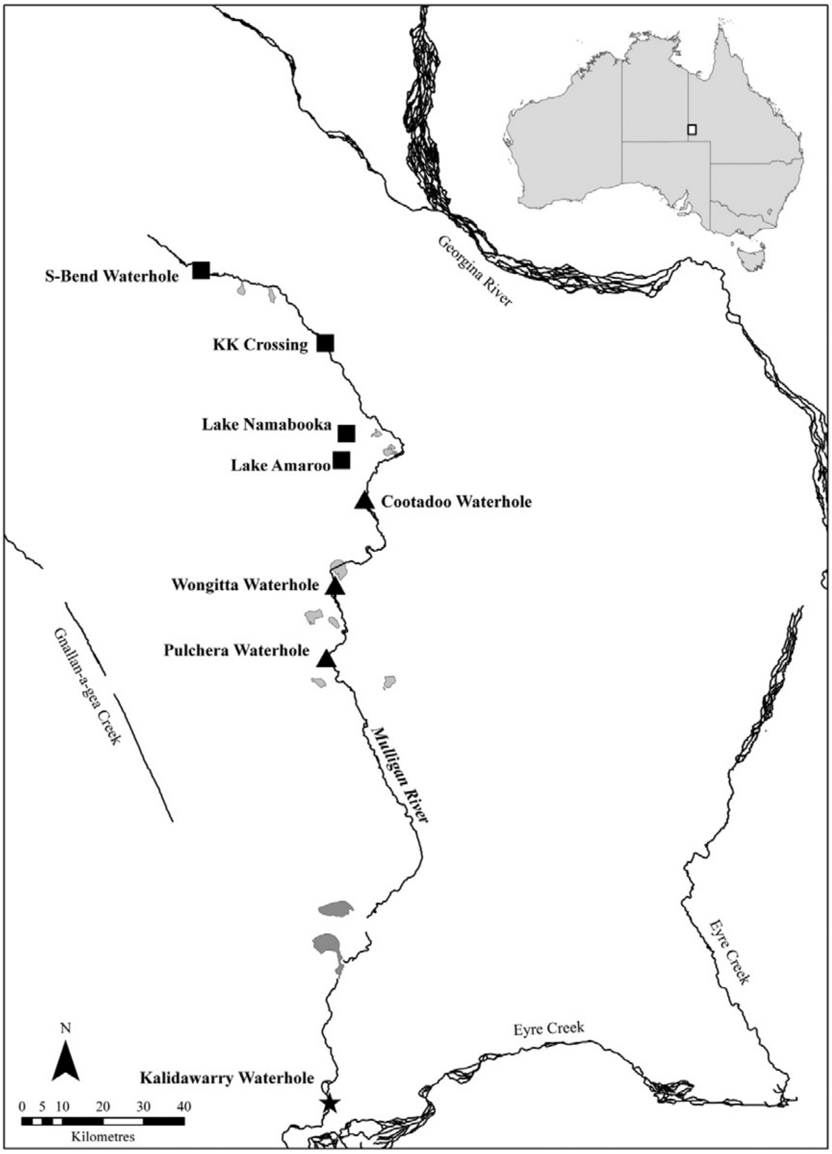

Fig. 1. Map of sites in the Mulligan River catchment sampled between April 2007 and November 2011. Upper catchment sites are marked with squares, mid-catchment sites are marked with triangles.

Sampling was conducted opportunistically between April 2007 and November 2011 at up to seven sites in the Mulligan River catchment (Fig. 1). In August and November 2010 and June 2011 the mid-river sites Pulchera, Wongitta and Cootadoo waterholes were sampled, as well as the off-channel sites Lake Namabooka and Lake Amaroo and the upper-reach site S Bend Gorge (Fig. 1). In April 2010 all sites were sampled except Wongitta, as wet conditions prevented access to this waterhole. In November 2011 all sites were sampled except Lake Namabooka, Lake Amaroo and S Bend Gorge as these sites were dry. Pulchera and S Bend Gorge sites were also sampled in April and August 2007. By November 2007 S Bend had dried and Pulchera was the only site sampled. During the dry year 2008 the Mulligan contained no water and consequently no sampling was undertaken. In August and November 2009 Pulchera was sampled, whereas Wongitta was sampled in November 2009 only.

Fish sampling

Fish populations were sampled in all waterholes and on all sampling occasions using a combination of three methods: large fyke nets, small fyke nets (or a 5-m seine net) and a larval trawl net. These methods successfully capture fish of all body sizes and life stages in Australia's inland rivers (Arthington *et al.* 2005; Balcombe *et al.* 2007; Balcombe & Arthington 2009; Kerezsy *et al.* 2011). Large double-winged fyke nets with 13 mm stretched mesh and 8 m wings (1 m deep) were set parallel to the bank with their openings facing in opposite directions upstream and downstream from a central post. Cod-ends were secured above the water surface in order to allow air-breathing vertebrates to survive if they became trapped. Small double-winged fyke nets with a stretched mesh of 2 mm and a wing width of 3 m (1 m deep) were set in an identical manner. All fyke nets were set in the afternoon (as

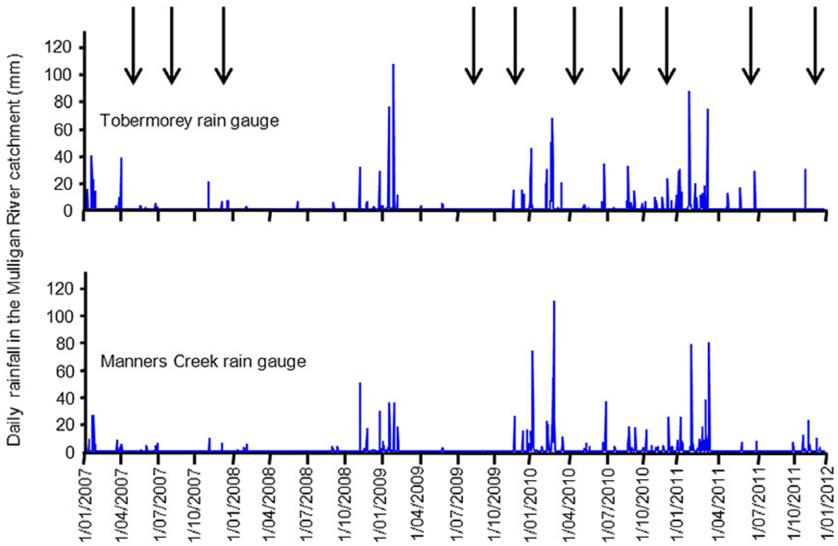

Fig. 2. Daily rainfall at the Tobermorey and Manners Creek gauges located within the Mulligan River catchment. Arrows indicate sampling occasions. (Source: Bureau of Meteorology 2012).

close as possible to 14.00 hours) and retrieved the following morning (as close as possible to 9.00 hours). During sampling from 2010 onwards the small fyke nets were replaced by a 5 m seine net with 2 mm mesh (1 m deep) because this allowed sampling of different habitats within waterholes and lakes using the same mesh size as the small fyke nets. At each site the seine was dragged by two operators for 10 m on three occasions. A larval trawl net (500 μm mesh, 2 m long, 58 cm diameter opening) was also used at each site. The larval trawl net was suspended on a 10 m rope and manually dragged through the water for a period of 5 min at each site. Following the clearing of fyke nets, seine nets and larval trawl nets all fish were held in shaded water-filled buckets prior to processing. Sampling was replicated through time at each site, with one set of sampling gear deployed in each discrete waterbody to avoid pseudo-replication.

Fish species were identified using published literature relating to fishes of Australian arid rivers (Wager & Unmack 2000; Allen *et al.* 2002). All sampled fish were measured from the tip of the snout to the base of the hypural bones to obtain standard length measurements (SL in mm). Following identification and measurement all sampled animals were returned to the water alive. On each sampling occasion catch per unit effort (CPUE), biomass and the median and range of standard length for all species at each waterhole sampled were collated. CPUE was calculated using a sampling duration of 19 h for fyke nets, a drag length of 30 m for the seine net and a drag time of 5 min for the larval trawl net. Biomass was calculated using derived length-weight relationships for species previously collected in the Lake Eyre Basin (S. Balcombe, unpubl. data, 2007). For species where length-weight data were not available we used published relationships for each species or closely related taxa cited in Pusey *et al.* (2004).

Data analysis

Fish species CPUE, biomass and presence/absence data were analysed using SIMPER to identify the main species associated with differences in assemblages between sites on each sampling occasion. Assemblage patterns for each occasion were plotted in ordination space based upon hybrid non-metric multidimensional scaling (MDS). These MDS plots were generated from Bray–Curtis similarity matrices produced from $\log_{10}$(CPUE + 1), $\log_{10}$(biomass + 1) and species presence/absence data. One-way analyses of similarities (ANOSIM – non-parametric equivalent of MANOVA) based upon the same Bray–Curtis similarity matrices were used to identify assemblage differences between upper and mid-catchment waterholes (fixed factors) across all sampling dates (fixed factors) for CPUE, biomass and species presence/absence (response variables). SIMPER was used to describe the main species contributing to differences among each pairwise comparison. All multivariate analyses were undertaken in the PRIMER version 5 software package (Clarke & Gorley 2001).

RESULTS

Fish distribution and abundance in the catchment

All fish species known to be present in the Mulligan's parent catchment – the Georgina – were collected at study sites in the Mulligan between 2007 and 2011 (Kerezsy 2010; Table 1). Bony bream, desert rainbowfish, glassfish, spangled perch, silver tandan, banded grunter and Barcoo grunter were recorded following all channel flows and flooding (Table 1 and Figs 2 and 3). Welch's grunter, Hyrtl's tandan and yellowbelly were only recorded following flooding in 2010 and into 2011 (when the waterholes remained wet), and a single golden goby was collected

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Table 1. Fish species presence/absence at upper and mid-catchment sites, average adult size and evidence of recruitment in the Mulligan River between 2006 and 2011

Species (from smallest to largest)	Common name	Presence/Absence (% of all sites and times) Upper sites	Mid sites	Average size at adulthood (mm) (from Allen *et al.* 2002)	Evidence of recruitment
Ambassis sp.	Glassfish	100	90.5	55	Yes
Melanotaenia splendida tatei	Desert rainbowfish	70	62	80	Yes
Craterocephalus eyresii	Lake Eyre hardyhead	10	47.6	60–70	Yes
Amniataba percoides	Banded grunter	0	38.1	100–120	No
Glossogobius aureus	Golden goby	0	4.8	140	No
Nematolosa erebi	Bony bream	100	100	150–200	Yes
Porochilus argenteus	Silver tandan	80	76.2	200	No
Neosiluris hyrtlii	Hyrtl's tandan	10	38.1	200	No
Bidyanus welchi	Welch's grunter	20	57.1	230	No
Scortum barcoo	Barcoo grunter	20	57.1	250	No
Leiopotherapon unicolor	Spangled perch	90	80.95	300	Yes
Macquaria sp.	Yellowbelly	0	57.1	400–500	No

No fish were recorded from Lake Amaroo on any occasion so this site has been excluded.

in Cootadoo waterhole in June 2011. Lake Eyre hardyhead was recorded in the Mulligan River from 2009 onwards.

Biomass and abundance followed the same pattern for all species, with highest abundances coinciding with highest biomass (Fig. 3 and Appendix S1). In general, maximum abundances of the smaller-bodied species (glassfish, desert rainbowfish, Lake Eyre hardyhead: Table 1) occurred at either end of the wet to dry trajectory of the waterholes. For example, glassfish and desert rainbowfish maxima were recorded in April 2007 directly after a flood, while the maximum for Lake Eyre hardyhead occurred in November 2009 after an extended dry period (Fig. 3 and Appendix S1). The highest abundances of medium-sized species also coincided with recent floods (for example silver tandan in April 2007 and August 2010 at Pulchera, and April 2010 at Cootadoo). Spangled perch similarly exhibited high abundances in April 2010 at Namabooka and in August 2010 at Pulchera, S-Bend and Wongitta. In contrast, high abundances of large-bodied species such as yellowbelly, Welch's grunter and Barcoo grunter were only found in the wettest period of sampling (2010/2011) associated with serial flooding: for yellowbelly particularly June 2011 at Cootadoo and Wongitta and for Welch's grunter in April 2010 (Cootadoo and Pulchera), November 2010 (Pulchera and Wongitta) and June 2011 (also at Pulchera and Wongitta; Fig. 3 and Appendix S1). Similarly, Barcoo grunter was most abundant in August and November 2010 at Pulchera and Wongitta. Maxima of bony bream abundance appeared to be independent of hydrological period, occurring during both low and high water post-flood periods. The highest abundances were recorded in June 2011 after high flows at Namabooka and in November 2011 at Cootadoo when waterholes were drying down (Fig. 3 and Appendix S1).

Total fish abundances were often driven by one or two abundant species at a particular site and time. Examples include November 2009, when bony bream and Lake Eyre hardyhead were abundant at Wongitta; June 2011, when bony bream and desert rainbowfish were abundant at Namabooka; and November 2011 when bony bream and glassfish were abundant at Cootadoo (Appendix S1). Total biomass did not always follow total abundance, especially given the overwhelming influence of the large-bodied species yellowbelly compared with most other species. For example, there were spectacular biomass totals in June 2011 at Cootadoo (147 kg) and Wongitta (197 kg) and these coincided with mid-range total abundances (Appendix S1).

Fish length variation within the catchment through time

For fish of small-to-medium body size, mid-to-high abundance levels were frequently characterized by large numbers of smaller individuals, suggesting the influence of recruitment processes (Table 1, Fig. 4). Where there were high abundances of a given species at a given time (and at a specific site) length distributions demonstrated that numbers were dominated by new recruits (Fig. 4). Examples of a recruitment response include bony bream at Lake Namabooka in June 2011, silver tandan at Pulchera in April 2007, desert rainbowfish at S Bend Gorge in August 2007, glassfish at Pulchera in November 2011, Lake Eyre hardyhead at Wongitta in November 2009 and spangled perch at Namabooka in April 2010 (Fig. 4). No

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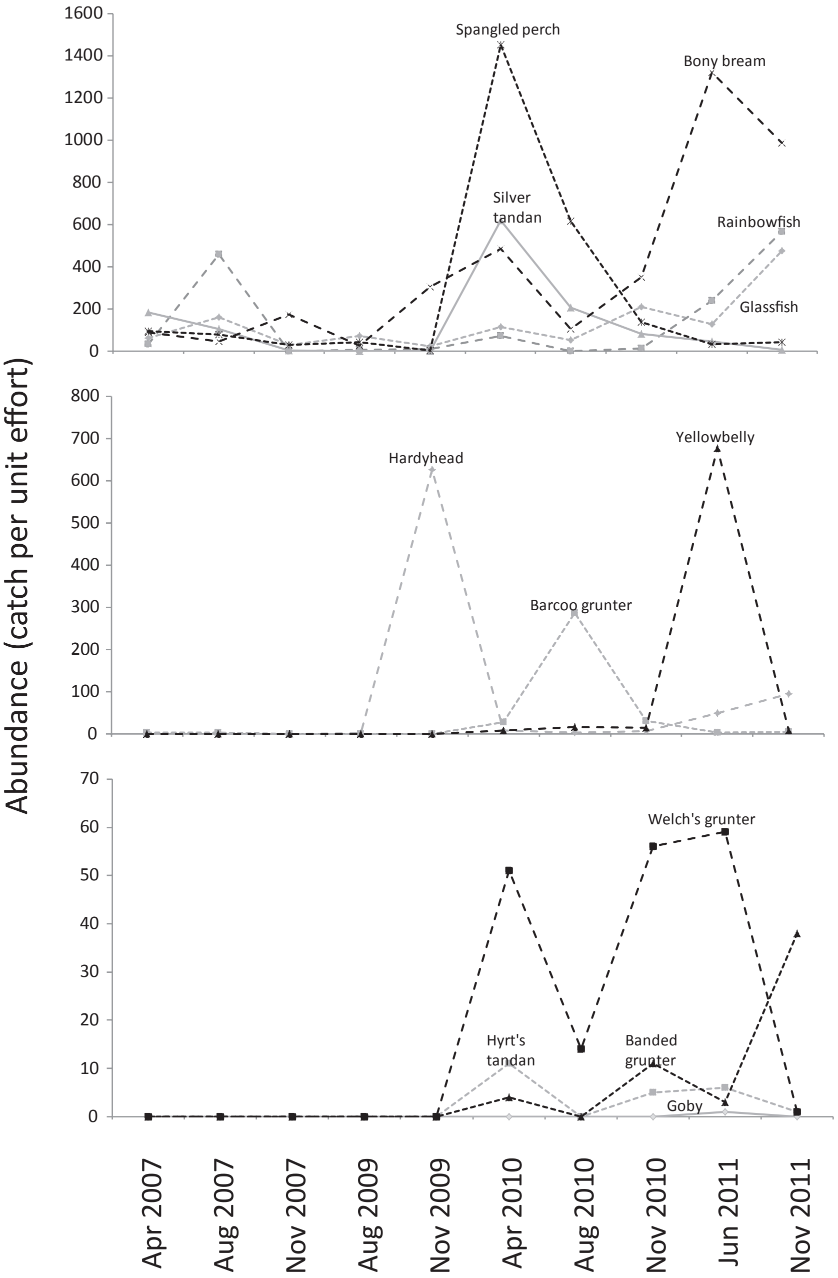

Fig. 3. Total fish abundance (catch per unit effort summed from all sites on each sampling occasion) in the Mulligan River between 2007 and 2011. Extreme dispersing species are presented in the top graph and more conservative dispersing species are presented in the middle and bottom graphs.

recruitment was evident for the large-bodied species, despite occasionally high abundances (for example yellowbelly at Cootadoo in June 2011 and Welch's grunter at Pulchera in November 2010: Fig. 3 and Appendix S1).

Spatial distribution of fish in the catchment

Analysis of fish presence/absence, abundance and biomass shows a separation of upstream and mid-stream sites in the Mulligan River (Fig. 5a–c). In upstream waterholes the fish community was consistently composed of bony bream, spangled perch, rainbowfish and glassfish, with the medium-sized predator spangled perch dominant (Table 2). In contrast, sites in the mid-stream reaches of the Mulligan River were inhabited by a wider variety of Lake Eyre Basin fish species, especially larger species such as yellowbelly, Welch's grunter and Barcoo grunter. Yellowbelly, the largest carnivorous fish in the Lake Eyre Basin, was only found in mid-stream waterholes such as Pulchera, Wongitta and Cootadoo and

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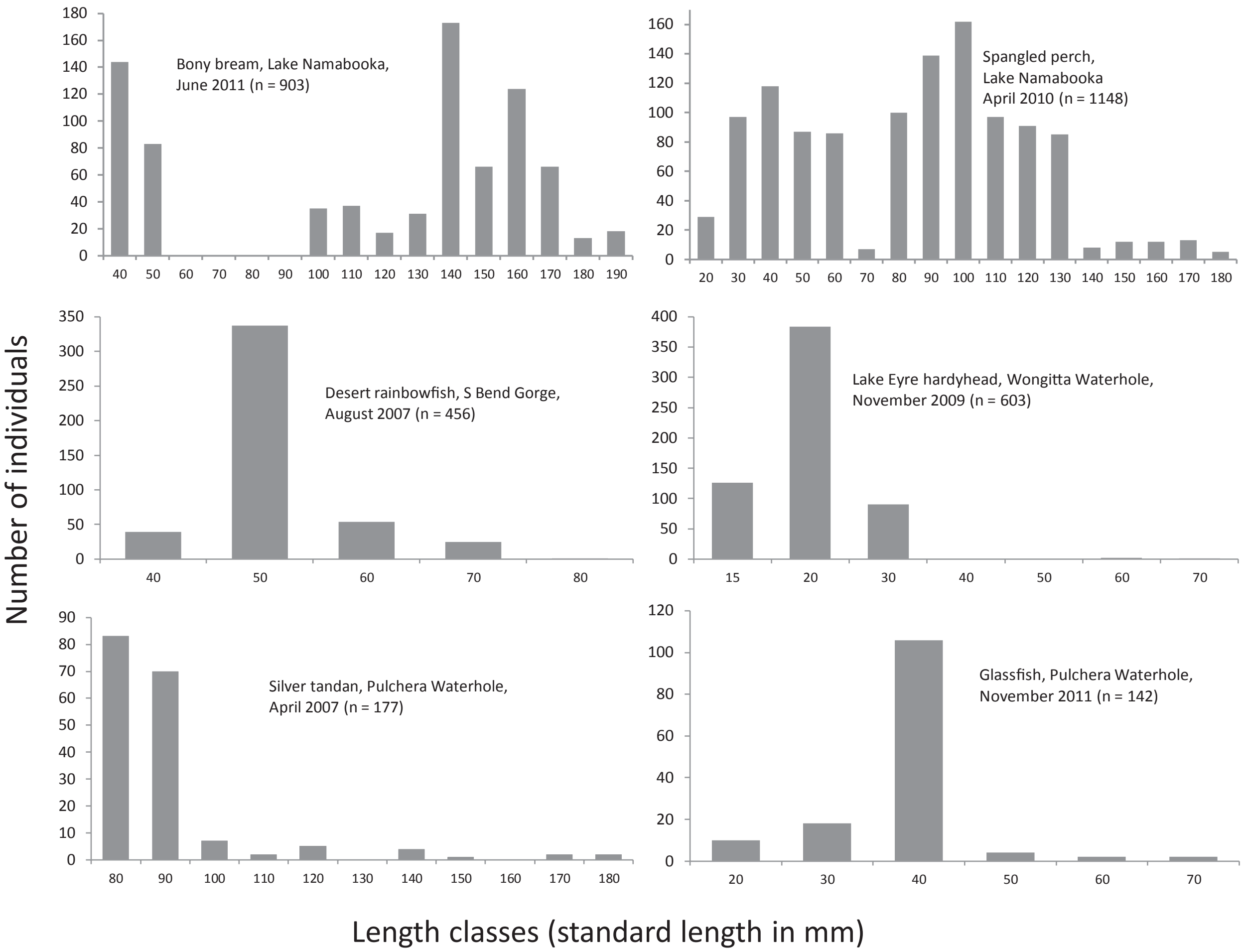

Fig. 4. Length frequency histograms of populations of fish species demonstrating recruitment in waterholes of the Mulligan River between 2007 and 2011.

Table 2. Fish species making a significant contribution to the similarity patterns (at >5% contribution) of fish assemblages in upper and mid-catchment waterholes of the Mulligan River, based on SIMPER analysis

Catchment position	Transformation	Significant species contributing to difference (%) between upper and mid-catchment fish assemblages
Upper	Log_{10} CPUE	AS = 66; Spangled perch (34), Bony bream (31), Glassfish (20), Rainbowfish (9)
Mid	Log_{10} CPUE	AS = 51; Bony bream (39), Glassfish (19), Spangled perch (11), Silver tandan (11), Rainbowfish (5)
Upper	Log_{10} Biomass	AS = 63; Spangled perch (43), Bony bream (42), Glassfish (7)
Mid	Log_{10} Biomass	AS = 49; Bony bream (49), Yellowbelly (11), Spangled perch (11), Welch's grunter (8), Hyrtl's tandan (8), Glassfish (6)
Upper	Presence/absence	AS = 76; Bony bream (28), Spangled perch (22), Glassfish (22), Silver tandan (17), Rainbowfish (10)
Mid	Presence/absence	AS = 68; Bony bream (22), Glassfish (19), Spangled perch (13), Silver tandan (10), Rainbowfish (8), Barcoo grunter (6), Yellowbelly (6), Welch's grunter (6)

AS, average similarity; CPUE, catch per unit effort.

never in off-channel or upstream areas (Tables 1 and 2). Other large-bodied fish such as Welch's grunter and Barcoo grunter were sometimes sampled at the off-channel ephemeral site Lake Namabooka (Fig. 1, Table 1), but not at sites further upstream (such as S-Bend). No fish were sampled at Lake Amaroo, an indication that this waterbody fills from local rainfall only and that migration pathways between it and the main channel of the Mulligan River are unsuitable for facilitating fish dispersal.

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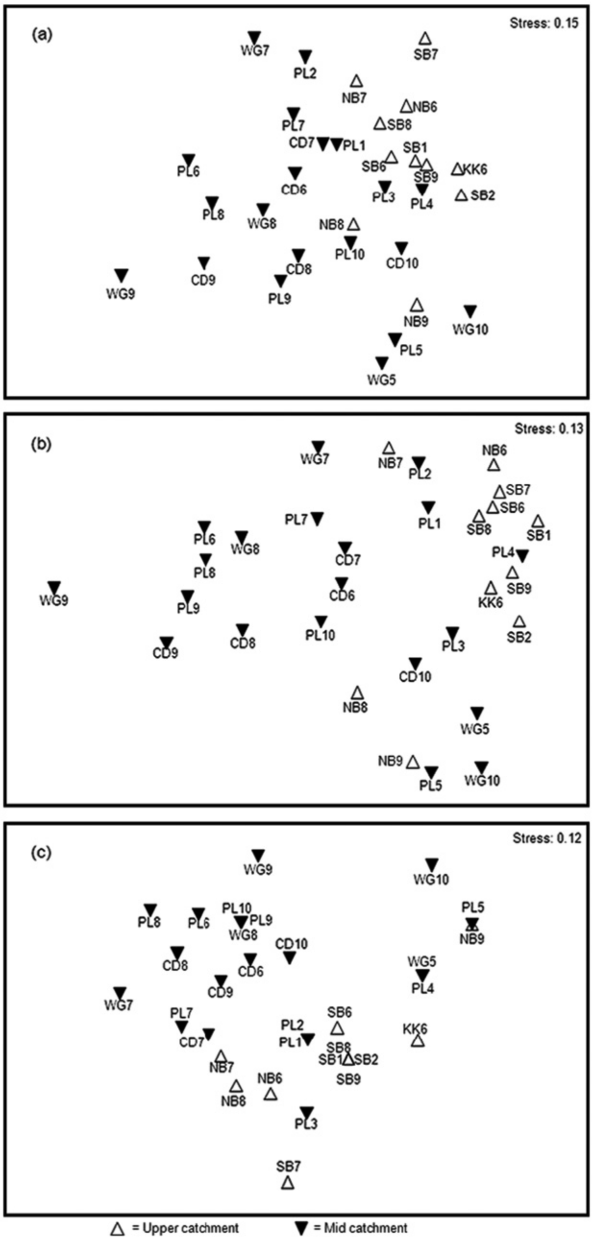

Fig. 5. MDS plot of fish assemblage data in upper and mid-catchment sites on four sampling occasions based upon (a) $\log_{10}$ transformed catch per unit effort, (b) $\log_{10}$ transformed biomass and (c) fish species presence/absence. Site codes: PL = Pulchera, SB = S Bend Gorge, WG = Wongitta, CD = Cootadoo, KK = KK Crossing, NB = Namabooka. Time Codes: 1 = April 2007, 2 = August 2007, 3 = November 2007, 4 = August 2009, 5 = November 2009, 6 = April 2010, 7 = August 2010, 8 = November 2010, 9 = June 2011, 10 = November 2011.

Analysis of the ordination patterns revealed that upstream waterholes differed significantly from mid-stream waterholes for fish abundance (CPUE), biomass and species presence absence (Fig. 5, Table 3). Spangled perch had the largest influence on differences in abundance and biomass between these catchment positions. However, apart from spangled perch, two different but discernible groups of species had the next largest influence on the dissimilarity of assemblages in terms of biomass and abundance. The small-bodied species had a greater influence on the pattern for abundance (desert rainbowfish, glassfish and Lake Eyre hardyhead; 32% dissimilarity), while the large-bodied species contributed a major difference in the biomass patterns (yellowbelly, Welch's grunter and Barcoo grunter; 33% dissimilarity). The main difference in assemblage structure between upper and mid-stream waterholes based on species occurrence was because of the distribution pattern of large-bodied species (39% dissimilarity) followed by small-bodied species (23% dissimilarity).

DISCUSSION

The important role played by periodically inundated or temporary habitats as fish nursery and feeding areas has been demonstrated (Cucherousset *et al.* 2007), as has the role of isolated waterbodies as refugia from disturbance associated with drying (Magoulick & Kobza 2003; Dekar & Magoulick 2007). However, despite the recognized ecological value of temporary habitats, prior studies have not considered entirely ephemeral catchments, nor the behaviour of their resident biota through time. The timeframe of this central Australian study is important as it has included periods (2006 and 2008) when the entire catchment dried, a single flood in 2007 and a sequence of floods from 2009 to 2011. These flooding and drying sequences have provided a unique opportunity to study fish assemblages and species/movement patterns in an isolated arid-zone river that is situated in an unregulated catchment.

It is noteworthy that the Mulligan River was found to contain all fish species known from its parent catchment the Georgina (Kerezsy 2010) despite the fact that permanent waterholes – obvious drought refuges – occur in the Georgina but not the Mulligan (Silcock 2009). It is also notable that species richness increased during the series of wet years (from 2009 to 2011), and that prior to this wet period only a subset of species was detected following the single flood of 2007. These species occurrence patterns suggest that although all fish species in the Georgina catchment are capable of dispersing long distances (at least up to 300 km) during floods, some large-bodied species may be unlikely to undertake such movements until aquatic habitats are replenished by a sequence of floods.

In the Simpson Desert area of central Australia where the Mulligan is situated, sites furthest from the closest permanent water were most likely to dry within a few months of inundation. Therefore, although movement

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Table 3. Summary of ANOSIM results comparing waterhole fish assemblages based on CPUE, biomass and presence/absence among upper and mid-catchment waterholes in the Mulligan River

Transformation	Global R	*P*	Significant species contributing to difference (%) between upper and mid-catchment fish assemblages
Log (CPUE + 1)	0.125	0.04	AD = 49; Spangled perch (20), Rainbowfish (14), Silver tandan (11), Glassfish (11), Bony bream (9), Yellowbelly (8), Hardyhead (7), Welch's grunter (7), Barcoo grunter (6)
Log (BIOMASS + 1)	0.234	0.006	AD = 54; Spangled perch (22), Yellowbelly (14), Silver tandan (11), Welch's grunter (11), Bony bream (11), Rainbowfish (9), Barcoo grunter (8), Glassfish (8)
Presence/absence	0.176	0.01	AD = 35; Yellowbelly (13), Barcoo grunter (13), Welch's grunter (13), Hardyhead (12), Rainbowfish (11), Silver tandan (9), Hyrtl's tandan (9), Golden goby (9), Spangled perch (7)

Species contributing to the differences in fish assemblages between catchment positions are based on SIMPER analysis. AD, average dissimilarity. ANOSIM, analysis of similarity; CPUE, catch per unit effort.

was a possibility for all species present in the catchment (Fagan *et al.* 2005), only spangled perch, bony bream, rainbowfish and glassfish were always found at the upstream sites, with silver tandan also occasionally present. We therefore suggest that these common and widespread species are the most likely to move the furthest during sporadic flooding in central Australia. In the following sections, we distinguish two major groups of fishes based upon this movement behaviour: 'extreme' dispersing species and 'conservative' dispersing species, and discuss their characteristics.

Extreme dispersing species

Given that the S Bend site is approximately 300 river kilometres north of the closest permanent waterhole (Kalidawarry, at the confluence of the Mulligan River with Eyre Creek), and that the entire Mulligan River was dry prior to the 2007 flood, this study demonstrates that some species (bony bream, spangled perch, desert rainbowfish, glassfish, silver tandan) are capable of moving at least 300 km following the opening of dispersal pathways in this ephemeral river. This finding supports observations of mass movement of many fish species in Australia's arid-zone river systems (Puckridge 1999; Wager & Unmack 2000), and provides an approximate movement distance for the species mentioned. After reaching an isolated waterhole high in the catchment, predation risk from other large-bodied fish species would likely be diminished. As both bony bream and spangled perch recruit in these isolated desert waterholes (Kerezsy *et al.* 2011), it is also likely that the vagility of this group of species confers recruitment advantages. This study also indicates that other small-bodied species such as desert rainbowfish and glassfish (and also Lake Eyre hardyhead) probably maintain their populations in isolated waterholes through local recruitment. The fact that these species can move long distances in ephemeral rivers and then persist and breed in drying habitats suggests that within the broad range of 'pioneer species' they may occupy a specialized niche. We therefore characterize this group of species (bony bream, spangled perch, desert rainbowfish, glassfish and silver tandan) as extreme dispersing species – those that (i) migrate the furthest to the most marginal of aquatic habitats; and (ii) are most prone to become locally extirpated because of rapid drying of ephemeral habitats.

The detection of the small schooling species Lake Eyre hardyhead in the Mulligan catchment in Queensland is a considerable range extension for this species, which previously was known only from the Lake Eyre Basin in South Australia (Wager & Unmack 2000). Size of flood and distance of connectivity are the most likely factors influencing the geographic range of this species in central Australia, particularly as the species was found in several wet years (2009, 2010 and 2011) but not in 2007. Given that this hardyhead has a predominantly southern distribution in the Lake Eyre Basin, it is possible that during the 2007 flood the movement pathway between Lake Eyre and the Mulligan River remained un-connected south of the Mulligan/Eyre Creek confluence. Alternatively, it is possible that movement into the Mulligan River may have been unsuccessful for this species in 2007 because of unknown factors. Future monitoring of all catchments in the south-western corner of Queensland following flooding is recommended to establish the geographic range of this species.

Conservative dispersing species

In contrast to the fish assemblages in the most distant and marginal Mulligan River habitats, the fish assemblages at all mid-river sites (which were consistently deeper, and

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likely to hold water for longer) were characterized by the presence of the large-bodied fish species known from the Georgina River system, such as Barcoo grunter, Welch's grunter and yellowbelly. It is likely that the productivity of these mid-stream waterholes (Bunn *et al.* 2006; Arthington & Balcombe 2011) combined with their proximity to permanent waterholes (~150 km) and their water residence time (>1 year in serial wet seasons) contribute to their suitability as habitat for large animals with a comparatively long lifespan. Indeed, in a series of wet years (2009–2011), ephemeral rivers like the Mulligan temporarily behave like Lake Eyre Basin rivers with permanent waterholes, where these large species have been recorded during several studies of fish assemblage patterns (Bailey & Long 2001; Arthington *et al.* 2005; Kerezsy 2010).

Although these large-bodied and long-lived species (Pritchard 2004; Pusey *et al.* 2004) undertake migrations of >150 km into an ephemeral river, even under a best-case scenario, extirpation of local communities will inevitably occur before maturity is attained. A good example of this ephemerality is the drying of the Mulligan system in recent years (2006 and 2008). These observations suggest that the resource advantages afforded by temporary systems such as the Mulligan outweigh or at least ameliorate the disadvantages of ephemerality. Fish production has been shown to be higher in more ephemeral arid-zone rivers (such as Cooper Creek) compared with dryland rivers (such as the Warrego in the Murray-Darling Basin) with stable base-flows and similar physical attributes such as landscape and waterhole features (Balcombe *et al.* 2010). The fact that this second group of fish species (yellowbelly, Welch's grunter, Barcoo grunter, Hyrtl's tandan and golden goby) prefer mid-river habitats that are likely to hold water for up to one year following flooding (and occasionally longer) suggests that they have more conservative movement habits, and that they are not likely to disperse as far, as readily or as frequently as the extreme dispersing group.

Boom periods caused by serial flooding

Arid zone aquatic systems are frequently referred to as 'boom and bust' ecosystems because of the massive seasonal fluctuations in populations of biota (Arthington *et al.* 2005; Kingsford 2006). Evidence from the Mulligan catchment during a period of serial flooding (such as that which occurred from 2009–2011) provides an example of a prolonged boom phase, as there was an increase in both the number of fish species present in the catchment and an increase in fish biomass (particularly in the larger, deeper waterholes). These patterns in species richness and fish production are consistent with previous work in rivers of the Australian arid zone (Puckridge 1999; Costelloe *et al.* 2004; Balcombe & Arthington 2009; Kerezsy 2010) but unique in that they have been documented in an entirely ephemeral system. The fact that the increase in biomass peaked during the sampling event of June (winter) 2011 provides further evidence that water retention in an arid-zone river creates the potential to support large populations of fish (notably large-bodied fish) at any time when replenishing flows occur, and that seasonal factors (such as thermal minima) may be less influential in arid systems than the presence of water per se (Labbe & Fausch 2000).

Overall, these results suggest that periodic flooding in this arid-zone river provided resource opportunities for all species present in the catchment, and that during productivity 'booms', mass movement into such areas should be expected rather than being thought of as a stochastic event. This is an unusual interpretation given that the ephemerality of such areas will also result in the extirpation of dispersing species and/or their progeny, unless fish can move back into more permanent habitats.

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REFERENCES

Allen G. R., Midgley S. H. & Allen M. (2002) *Field Guide to the Freshwater Fishes of Australia*. Western Australian Museum, Perth.

Arthington A. H. & Balcombe S. R. (2011) Extreme flow variability and the 'boom and bust' ecology of fish in arid-zone floodplain rivers: a case history with implications for environmental flows, conservation and management. *Ecohydrology* **4,** 708–20.

Arthington A. H., Balcombe S. R., Wilson G. A., Thoms M. C. & Marshall J. (2005) Spatial and temporal variation in fish assemblage structure in isolated waterholes during the 2001 dry season of an arid-zone river, Cooper Creek, Australia. *Mar. Freshw. Res.* **56,** 25–35.

Bailey V. & Long P. (2001) *Wetland, Fish and Habitat Survey in the Lake Eyre Basin, Queensland: Final Report*. Queensland Department of Natural Resources and Mines, Brisbane.

doi:10.1111/aec.12075

Balcombe S. R. & Arthington A. H. (2009) Temporal changes in fish abundance in response to hydrological variability in a dryland floodplain river. *Mar. Freshw. Res.* **60,** 146–59.

Balcombe S. R., Bunn S. E., Arthington A. H., Fawcett J. H., McKenzie-Smith F. J. & Wright A. (2007) Fish larvae, growth and biomass relationships in an Australian arid zone river: links between floodplains and waterholes. *Freshwater Biol.* **52,** 2385–98.

Balcombe S. R., Huey J. A., Lobegeiger J. S. *et al.* (2010) Comparing fish biomass models based on biophysical factors in two northern Murray-Darling Basin rivers: a cautionary tale. In: *Ecosystem Response Modelling in the Murray Darling Basin* (eds N. Saintilan & I. Overton) pp. 67–83. CSIRO Press Canberra, Canberra.

Box J. B., Duguid A., Read R. E. *et al.* (2008) Central Australian waterbodies: the importance of permanence in a desert landscape. *J. Arid Environ.* **72,** 1395–413.

Bunn S. E., Thoms M. C., Hamilton S. K. & Capon S. J. (2006) Flow variability in dryland rivers: boom, bust and the bits in between. *River Res. Appl.* **22,** 179–86.

Bureau of Meteorology (2012) [Cited July 2012.] Available from URL: http://www.bom.au/climate/data/index.shtml

Capone T. A. & Kushlan J. A. (1991) Fish community structure in dry-season stream pools. *Ecology* **72,** 983–92.

Clarke K. R. & Gorley R. N. (2001) *Primerv5: User Manual Tutorial*. Primer-e, Plymouth Marine Laboratory, Plymouth.

Costelloe J. F., Hudson P. J., Pritchard J. C., Puckridge J. T. & Reid J. R. W. (2004) *ARIDFLO Scientific Report: Environmental Flow Requirements of Arid Zone Rivers with Particular Reference to the Lake Eyre Drainage Basin*. School of Earth and Environmental Sciences, University of Adelaide, Adelaide. Final Report to South Australian Department of Water, Land and Biodiversity Conservation and Commonwealth Department of Environment and Heritage.

Cucherousset J., Carpentier A. & Paillisson J.-M. (2007) How do fish exploit temporary waters throughout a flooding episode? *Fisheries Manag. Ecol.* **14,** 269–76.

Dekar M. P. & Magoulick D. D. (2007) Factors affecting fish assemblage structure during seasonal stream drying. *Ecol. Freshwater Fish* **16,** 335–42.

Eby L. A., Fagan W. F. & Minckley W. L. (2003) Variability and dynamics of a desert stream community. *Ecol. Applic.* **13,** 1566–79.

Fagan W. F., Kennedy C. M. & Unmack P. J. (2005) Quantifying rarity, losses, and risks for native fishes of the lower Colorado River Basin: implications for conservation listing. *Conserv. Biol.* **19,** 1872–82.

Fausch K. D. & Bramblett R. G. (1991) Disturbance and fish communities in intermittent tributaries of a Western Great Plains river. *Copeia* **3,** 659–74.

Fensham R., Silcock J., Kerezsy A. & Ponder W. (2011) Four desert waters: setting arid zone wetland conservation priorities through understanding patterns of endemism. *Biol. Conserv.* **144,** 2459–67.

Greenville A. C., Wardle G. M. & Dickman C. R. (2012) Extreme climatic events drive mammal irruptions: regression analysis of 100-year trends in desert rainfall and temperature. *Ecology and Evolution* **2,** 2645–58.

Kerezsy A. (2010) *The distribution, recruitment and movement of fish in far western Queensland*(PhD Thesis). Griffith University, Brisbane.

Kerezsy A., Balcombe S., Arthington A. & Bunn S. (2011) Continuous recruitment underpins fish persistence in the arid rivers of far western Queensland, Australia. *Mar. Freshw. Res.* **62,** 1178–90.

Kingsford R. T., ed. (2006) *Ecology of Desert Rivers*. Cambridge University Press, Cambridge.

Labbe T. R. & Fausch K. D. (2000) Dynamics of intermittent stream habitat regulate persistence of a threatened fish at multiple scales. *Ecol. Applic.* **10,** 1774–91.

Larned S. T., Datry T., Arscott D. B. & Tockner K. (2010) Emerging concepts in temporary-river ecology. *Freshwater Biol.* **55,** 717–38.

Magoulick D. D. & Kobza R. M. (2003) The role of refugia for fish during drought: a review and synthesis. *Freshwater Biol.* **48,** 1186–98.

Medeiros E. S. F. & Maltchik L. (2001) Diversity and stability of fishes (Teleostei) in a temporary river of the Brazilian semi-arid region. *Iheringia* **90,** 157–66.

Pritchard J. C. (2004) *Linking fish growth and climate across modern space and through evolutionary time. Otolith chronologies of the Australian freshwater fish, golden perch (*Macquaria ambigua, Percichthyidae*)* (PhD Thesis). Australian National University, Canberra.

Puckridge J. T. (1999) *The role of hydrology in the ecology of Cooper Creek, Central Australia: implications for the flood pulse concept* (PhD Thesis). The University of Adelaide, Adelaide.

Puckridge J. T., Sheldon F., Walker K. F. & Boulton A. J. (1998) Flow variability and the ecology of large rivers. *Mar. Freshw. Res.* **49,** 55–72.

Pusey B., Kennard M. & Arthington A. (2004) *Freshwater Fishes of North-Eastern Australia*. CSIRO Publishing, Collingwood.

Pusey B. J., Arthington A. H. & Read M. G. (1993) Spatial and temporal variation in fish assemblage structure in the Mary River, S.E. Queensland: the influence of habitat structure. *Environ. Biol. Fishes* **37,** 355–80.

Schlosser I. J. (1987) A conceptual framework for fish communities in small warmwater streams. In: *Community and Evolutionary Ecology of North American Stream Fishes* (eds W. J. Matthews & D. C. Heins) pp. 17–24. University of Oklahoma Press, Norman.

Schlosser I. J. & Angermeier P. L. (1995) Spatial variation in demographic processes of lotic fishes: conceptual models, empirical evidence, and implications for conservation. *Am. Fish. Soc. Symp.* **17,** 392–401.

Silcock J. (2009) *Identification of Permanent Refuge Waterbodies in the Cooper Creek and Georgina-Diamantina River Catchments for Queensland and South Australia*. South Australian Arid Lands Natural Resources Management Board, Port Augusta.

Turner T. F., Krabbenhoft T. J. & Burdett A. S. (2010) Reproductive phenology and fish community structure in an arid-land river system. *Am. Fish. Soc. Symp.* **73,** 427–46.

Wager R. & Unmack P. J. (2000) *Fishes of the Lake Eyre Catchment in Central Australia*. Queensland Department of Primary Industries, Brisbane.

Walker K. F., Sheldon F. & Puckridge J. T. (1995) A perspective on dryland river ecosystems. *Regulated Rivers: Research and Management* **11,** 85–104.

SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

Appendix S1. Details of fish species captured at each site on each sampling occasion.

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