

## Spatial and temporal variation in fish-assemblage structure in isolated waterholes during the 2001 dry season of an arid-zone floodplain river, Cooper Creek, Australia

Angela H. Arthington<sup>A,E</sup>, Stephen R. Balcombe<sup>A</sup>, Glenn A. Wilson<sup>A,B</sup>, Martin C. Thoms<sup>C</sup> and Jon Marshall<sup>D</sup>

<sup>A</sup>CRC for Freshwater Ecology (CRCFE), Centre for Riverine Landscapes, Griffith University, Nathan, Qld 4111, Australia.

<sup>B</sup>CRCFE, Murray–Darling Freshwater Research Centre, Goondiwindi, Qld 4390, Australia.

<sup>C</sup>CRCFE, University of Canberra, ACT 2016, Australia.

<sup>D</sup>Department of Natural Resources and Mines, Brisbane, Qld 4068, Australia.

<sup>E</sup>Corresponding author. Email: a.arthington@griffith.edu.au

**Abstract.** Spatial and temporal variation in fish-assemblage structure within isolated waterholes on the floodplains of Cooper Creek, Australia, was studied during the 2001 dry season, a period of natural drought in this arid-zone river. Spatial variation in fish-assemblage structure and the abundance of five species in disconnected waterholes early in the dry season (April 2001) were related to the extent of floodplain inundation 14 months previously, and to the interconnectedness of waterholes and waterhole habitat structure. As the dry season progressed, waterhole volumes decreased owing to evaporative water loss and structural habitat elements (anabranches, bars, boulders) became exposed. Marked changes in fish assemblage structure between the early (April) and late (September) dry season were related to habitat loss but not to water chemistry. Interactions between flow and habitat across a nested hierarchy of spatial scales (the floodplain, the waterhole and habitat patches within waterholes) were crucial to the persistence of fish assemblages through the 2001 dry season. We conclude that the magnitude, timing and frequency of floodplain inundation and natural variations in waterhole volume must be maintained if we wish to sustain the distinctive habitats and fish assemblages of this arid-zone floodplain river.

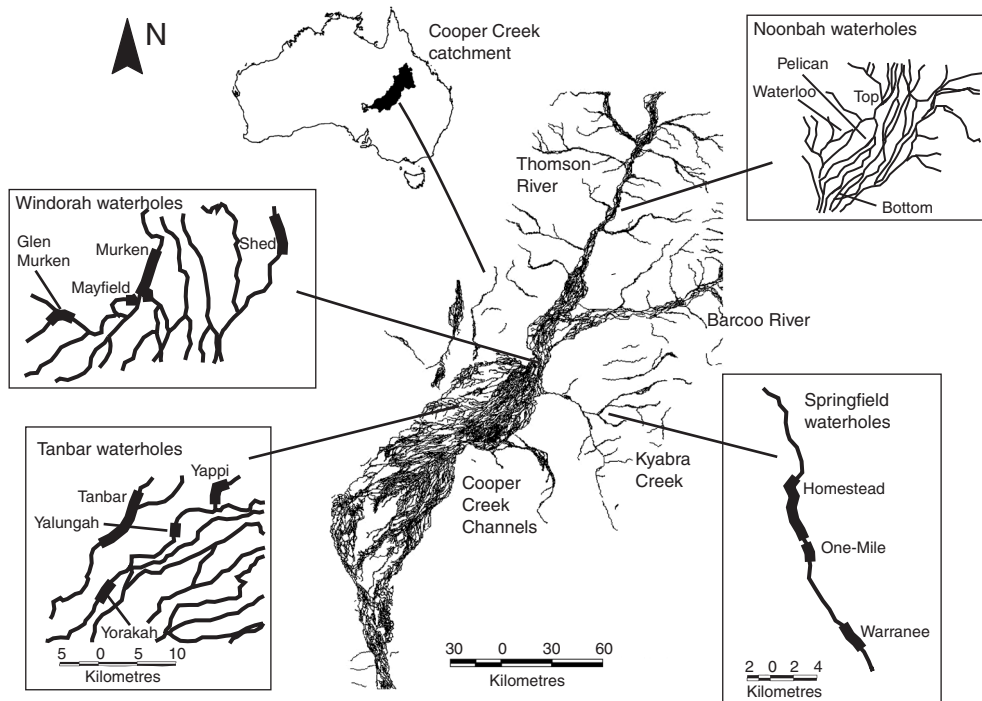
**Extra keywords:** drought, flooding, Lake Eyre Basin, refugia.

### Introduction

In large floodplain rivers, fish-assemblage structure often varies significantly among isolated waterbodies that remain on the floodplain after flood recession. These differences occur even when lakes and lagoons are situated in close proximity (Welcomme 1985; Kennard 1995; Rodriguez and Lewis 1997; Tejerina-Garro *et al.* 1998; Puckridge 1999). Early workers suggested that fish assemblages in isolated floodplain lakes are simply random associations of species (e.g. Lowe-McConnell 1987; Goulding *et al.* 1988), whereas Welcomme (1985, Welcomme 2001) concluded that active selection of habitats is involved, with some fish species remaining near to, or in, the same depressions occupied before flooding. More recent investigations suggest an increasing role for deterministic biotic processes. Thus, random processes may predominate during the early phase of waterbody isolation but changes in habitat conditions and consequences for predation and/or competition success become increasingly important with progression of the dry season (Kennard 1995; Rodriguez and Lewis 1997;

Tejerina-Garro *et al.* 1998; Matthews and Marsh-Matthews 2003).

Many Australian rivers flow for much of their length through semi-arid or arid landscapes (Thoms and Sheldon 2000). These dryland rivers experience some of the most variable and unpredictable flow regimes on earth (Walker *et al.* 1995; Puckridge *et al.* 1998, 2000). Those of the Lake Eyre Basin, such as Cooper Creek, experience infrequent high-magnitude flow events (linked to El Niño/Southern Oscillation) that can inundate extensive areas of floodplain, stimulating bursts of algal, plant, invertebrate and fish production (Puckridge *et al.* 1998; Bunn *et al.* 2003; Kingsford *et al.* 2004). After flood recession, Cooper Creek dries down into a complex system of anastomosing channels (the ‘channel country’) and several hundred relatively deep channel segments, termed ‘waterholes’ (Knighton and Nanson 1994). These waterholes are the equivalent of the isolated floodplain lakes and lagoons of tropical floodplain rivers. They act as refugia for aquatic biota during dry periods (Morton *et al.* 1995; Lancaster and Belyea 1997; Magoulick and Kobza



**Fig. 1.** Cooper Creek catchment and the four study reaches (Noonbah, Windorah, Tanbar and Springfield), with insets showing configuration of waterholes sampled in each reach.

2003), sustaining fish assemblages of ecological and conservation significance and species that are valued socially and economically for recreational fishing (Wager and Unmack 2000; Pusey *et al.* 2004).

In Cooper Creek and other dryland rivers, isolated waterholes are threatened by human activities in their catchments (Kingsford *et al.* 2004). Alterations to hydrological regimes as a consequence of water-resource development (particularly for irrigated agriculture) are a potential threat, illegal fishing is an issue and some waterholes have been invaded by alien fish species (Kingsford *et al.* 1999, 2004; Puckridge 1999; Wager and Unmack 2000). We need to understand the processes sustaining fish assemblages in isolated floodplain waterholes if we wish to protect local, landscape and regional biodiversity and manage water-resource development and other activities impinging on these aquatic ecosystems (Boulton *et al.* 2000; Bunn *et al.* 2003; Kingsford *et al.* 2004).

This paper examines spatial and temporal variation in fish-assemblage structure within isolated waterholes in the Cooper Creek catchment during the 2001 dry season. This dry period can be regarded as a natural drought, i.e. a period of low to no flow that acts as a 'press' disturbance by imposing physical and chemical stresses on biota (Lake 2000, 2003; Humphries and Baldwin 2003; Matthews and Marsh-Matthews 2003; McMahon and Finlayson 2003). Our objectives were to describe spatial patterns of variation in fish-assemblage structure at the scale of the waterhole and

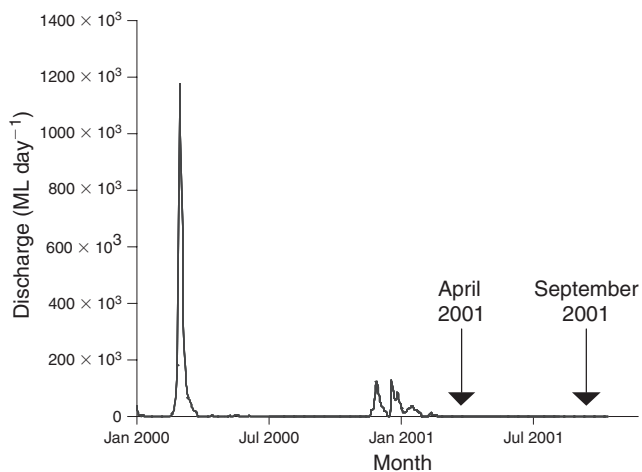
river reach over time, and to determine whether such patterns could be related to characteristics of the surrounding floodplains, the morphology of waterholes or habitat structure within waterholes. Influences of water chemistry on fish-assemblage structure were also examined. This study contributes to the Dryland River Refugia Project, a multidisciplinary investigation of processes sustaining waterhole biodiversity in Cooper Creek and other dryland rivers of western Queensland (e.g. Bunn *et al.* 2003).

## Materials and methods

### Study area

Studies on waterhole fish assemblages were conducted at one reach of the Thomson River near Stonehenge ('Noonbah'), two reaches ('Windorah' and 'Tanbar') on Cooper Creek below the confluence of the Thomson and Barcoo Rivers and one reach on Kyabra Creek ('Springfield') (Fig. 1). Within each reach, three or four waterholes were selected on the basis of coarse flow and physical characteristics such as history of permanence, surface area and location. The objective was to include waterholes of different shape, size and water permanence. A large 'main' waterhole was selected plus several 'satellite' waterholes situated in an adjacent channel or upstream/downstream of it within the same channel, and generally within 5–10 km of the main waterhole (Fig. 1). All of the study reaches were unregulated by water infrastructure.

The Cooper Creek catchment has a semi-arid climate with mean annual rainfall varying from 400 to 500 mm in the headwaters to <100 mm at its entry to Lake Eyre (Puckridge 1999; Bunn *et al.* 2003). Most stream flow is generated by seasonal monsoon rainfall in the headwaters, and periodic local rainfall, resulting in highly variable patterns of floodplain inundation and flow pulses along channels (Knighton



**Fig. 2.** Daily discharge of the Thomson and Barcoo rivers (combined) in 2000 and 2001. The highest total daily discharge calculated by adding flows from the Thomson and Barcoo Rivers was 1 175 326 ML on 29 February 2000. Arrows mark each fish sampling date. Data provided by the Bureau of Meteorology for stream gauges at Stonehenge (Thomson River) and Retreat (Barcoo River).

and Nanson 1994; Puckridge *et al.* 1998). At Currareva, near Windorah (Fig. 1), the mean annual discharge is  $3.05 \text{ km}^3 \text{ yr}^{-1}$  ( $97 \text{ m}^3 \text{ s}^{-1}$ ), with wide inter-annual variation and periods of zero flow lasting up to 21 months (based on 49 years of record). Episodic floods can inundate tens of thousands of square kilometres of floodplain (equivalent to 35% of the catchment) and serve to reconnect channels, distributaries and isolated waterholes.

Mean daily maximum air temperatures at Windorah range from  $38.1^\circ\text{C}$  in January to  $21.4^\circ\text{C}$  in July and mean daily minima range from  $24^\circ\text{C}$  in January to  $7^\circ\text{C}$  in July. Mean annual evaporation exceeds 3 m and this, together with transpiration and groundwater recharge, results in transmission losses below Windorah accounting for more than two-thirds of the discharge by the time it reaches the South Australian border (Anonymous 1998; Bunn *et al.* 2003).

During extended periods of low or no flow, Cooper Creek dries down to mosaics of highly turbid waterholes that provide the only habitat sustaining aquatic biota. Waterholes range in length from a few hundred metres to over 20 km, have well developed levees and typically range from 2 to 5 times wider and 2 to 3 times deeper than associated channels (Knighton and Nanson 1994). Basin morphometry and physical habitat structure vary greatly (Davis *et al.* 2003) and influence the persistence times of water in these refugia (S. Hamilton, personal communication).

Before our study there was a large flood in January–February 2000 (Fig. 2), connecting all waterholes at Noonbah, Windorah and Tanbar but not those along Kyabra Creek (Springfield), where flows remained within the channel (B. Morrish, personal communication). A small in-channel flow in December 2000–January 2001 linked all Springfield sites and also connected all waterholes at Noonbah, Windorah and Tanbar. Thereafter, there was no flow through the study reaches and all waterholes decreased in volume between the early (April) and late (September) 2001 dry season.

#### Field methods – fish

All 15 sites in the study area were sampled for fish twice, during April and September 2001. Fish assemblages within each waterhole were assessed using four sampling methods (fyke nets, beach seine, small purse-shaped drag net, zooplankton net) with most sampling effort related to the use

of replicate fyke nets and beach seining. Fyke nets were almost identical to those used in the lower Cooper Creek system (Puckridge 1999; Puckridge *et al.* 2000). Nets were randomly located parallel to the shoreline in 1–2.0 m depth with their wings up to 14 m apart (10 m on average), spaced at least 100 m apart in an attempt to avoid catch interference between neighbouring nets. Codends were secured out of the water to ensure that any reptiles or mammals captured would not drown. Nets were set in the late afternoon and retrieved the next morning, with an average duration of 19-h capture time. Both the wing width and sampling duration were recorded for the subsequent calculation of catch per unit effort (CPUE). Beach seining ( $15 \text{ m} \times 1.5 \text{ m}$ , 9.5 mm stretched mesh size) was undertaken during daylight hours in the littoral area to sample individuals and species too small to be collected by the fyke nets. The width and length of the littoral area sampled were recorded.

Waterholes were fished with three fyke nets and a single beach-seine haul. As fyke net catches typically took around 1.5 h per net to process, a greater level of fyke net replication was impractical. Similarly, it was often difficult to locate suitable stretches of bank for beach-seine use and a single littoral transect per site was chosen for practical reasons. In waterholes retracted to  $<300 \text{ m}$  owing to natural drying, we only set two fyke nets. Trial sampling with up to 10 nets suggested that two fyke nets and one beach-seine haul were sufficient to determine the total number of species in any waterhole. Fyke-net efficiency appeared not to be affected by the contraction of waterholes and potential concentration of fish in shallow water; very low rather than high numbers of fish were still caught. Conversely, high numbers of fish were caught in most large, deep waterholes where a dilution effect might be expected. Thus, the large differences in catch recorded in small, shallow versus large, deep waterholes could be conservative. A small purse-shaped drag net ( $2.5 \times 1.1 \text{ m}$  wide, 2.2 m deep with 1 mm mesh) used for the collection of small fish and invertebrates for other components of the project occasionally captured additional small fish species (e.g. *Hypseleotris* spp.) that were missed in the fyke nets or beach-seine. Plankton tows also caught small fish on occasion. Additional species collected by these methods were added to the presence/absence data for each waterhole.

Fish were identified to species level using Allen *et al.* (2002) and species lists for the Lake Eyre Basin (Puckridge 1999; Wager and Unmack 2000) and counted. Apart from alien species (goldfish, *Carassius auratus* and mosquitofish, *Gambusia holbrooki*) and small samples retained for genetic and food-web analyses, all fish were returned to the water alive. Three catches from Murken, Mayfield and Yappi waterholes in April 2001 contained extremely high numbers of fish ( $>2000$  individuals in one fyke net). These catches were sub-sampled by counting two 70-L bins full of fish and scaling up to give the total number of individuals per species.

#### Field methods – waterhole physical character and water chemistry

Processes that influence fish assemblages in river systems operate at multiple spatial scales (Frissell *et al.* 1986; Schlosser and Angermeier 1995; Labbe and Fausch 2000; Ward *et al.* 2002). In floodplain systems, it is appropriate to focus on three scales – the floodplain, the entire waterbody and habitat heterogeneity within each waterbody (Junk *et al.* 1989; Kennard 1995; Rodriguez and Lewis 1997; Amoros and Bornette 2002; Fausch *et al.* 2002; Davis *et al.* 2003). Thirty-eight physical variables (Table 1) were measured at these spatial scales from either remotely sensed imagery, aerial photographs or by surveying individual waterholes following methods developed by Parsons *et al.* (2004). Physical data were collected in April 2001 in association with fish sampling, with additional observations made and photographs taken during September 2001 to document changes in waterhole characteristics over time.

Ten physico-chemical water variables were determined for each waterhole on both sampling occasions: pH; conductivity; turbidity; total suspended solids; total hardness; total carbonates; total nitrogen; N:P ratio; sulphates; and silicates. Water samples were collected at

**Table 1. Floodplain and waterhole variables (and abbreviations) measured at three spatial scales in Cooper Creek**  
Highlighted variables were removed by redundancy analysis before BIO-ENV analysis

Floodplain	Waterhole	Within waterhole
Total floodplain width (TFW)	Surface Area (A)	Mid-channel bars (MCB)
Effective floodplain width (EFW)	Perimeter (P)	Backwater (BAW)
Floodplain setting (FS)	Length (L)	Off-take channels (OC)
Bifurcation ratio (BR)	Width (W)	Bench 0–1/3 (B1)
Number of channels (NOC)	Fetch length (FL)	Bench 1/3–2/3 (B2)
Channel distance to nearest waterhole (CD)	Circularity index	Bench 2/3–3/3 (B3)
Straight line distance to nearest waterhole (SLD)	Elongation ratio (ER)	Sidebars (SB)
	Length to width ratio (LW)	Miscellaneous bars (BAR)
	Bankfull cross-sectional area (CSA)	Anabranches (AN)
	Width to depth ratio (WD)	Bed and bank complexity (BBC)
	Hydraulic radius (HR)	Eroding banks (EB)
	Wetted perimeter (WP)	Snags (SN)
	Shape index (SI)	Scour holes (SH)
	Depth of cross section (DCS)	Boulders (BOU)
	Volume (V)	Fringing vegetation (FV)
		Overhanging vegetation (OV)

EFW = Distance from obstructions such as sand hills to the edge of the floodplain; FS = ratio of the distance from a waterhole to the right and left floodplain edge; BR = degree of floodplain dissection (number of channels present on a floodplain divided by floodplain width). Circularity index =  $4\pi A/P^2$ , where A is the surface area and P is the perimeter of the waterhole. Bankfull cross-sectional area, width : depth ratio, hydraulic radius, wetted perimeter, shape index, bankfull depth and volume were calculated from cross sections (5–20) surveyed at 500-m intervals along each waterhole. Waterhole variables were recorded as presence/absence at 100-m intervals along each waterhole and standardised for waterhole size by dividing the number of positive readings by the number of observation intervals.

the surface and analysed in the laboratory following standard methods (APHA 1975).

#### Statistical analysis

Patterns of variation in fish-assemblage structure across waterholes were analysed using standardised CPUE data (sum of three fyke net catches with a wing width of 10 m and sampling duration of 19 h). Catch-per-unit-effort data were also used as a measure of total fish abundance and the abundance of individual species per waterhole. The total number of species per waterhole on each sampling occasion was calculated from the pooled results of all sampling methods (fyke nets, beach seine, purse seine, zooplankton net).

Ordination analyses, based on Bray–Curtis similarity matrices obtained from  $\log_{10}(\text{CPUE} + 1)$ , and species presence/absence data, were performed using hybrid non-metric multi-dimensional scaling (PRIMER-E version 5, available at <http://www.primer-e.com/>, verified January 2005) to identify any patterns in fish presence/absence and assemblage structure among waterholes. One-way analysis of similarities (ANOSIM – non-parametric equivalent of MANOVA) based on the same Bray–Curtis matrices was used to identify significant differences in fish-assemblage structure among the four river reaches in April and September 2001. Two-way crossed ANOSIMs based on the April and September 2001 sampling data were used to identify differences in fish-assemblage structure between sampling occasions and study reaches.

BIO-ENV (Clarke and Warwick 2001) was used to investigate relationships between floodplain features, waterhole characteristics, water chemistry and fish-assemblage structure. Before BIO-ENV, auto-correlated variables describing waterholes and water chemistry were removed after redundancy analysis identified variables that were highly correlated (Spearman rank correlations,  $r_s > 0.8$ ) (see Table 1). Similarity matrices used in BIO-ENV analyses were also used to generate ordination plots. Environmental similarity matrices were based on normalised Euclidean distance rather than Bray–Curtis measures. Relationships between fish spatial patterns, environmental patterns at the floodplain, waterhole and within waterhole scales, and water chemistry,

were examined for the April and September sampling trips using CPUE and presence/absence data.

Relationships between the abundance of fish species, floodplain and waterhole characteristics and water chemistry were investigated using Spearman rank correlations (SPSS 11.5; SPSS Inc., Chicago, IL). The likelihood of Type I errors was reduced by setting the  $\alpha$  level at  $<0.001$  (Keppel 1991). To avoid committing Type II errors, we also noted correlations at  $\alpha < 0.05$  if there was a consistent pattern of response to any environmental variable (i.e. two or more fish species or assemblage metrics correlated with any one variable within a dataset).

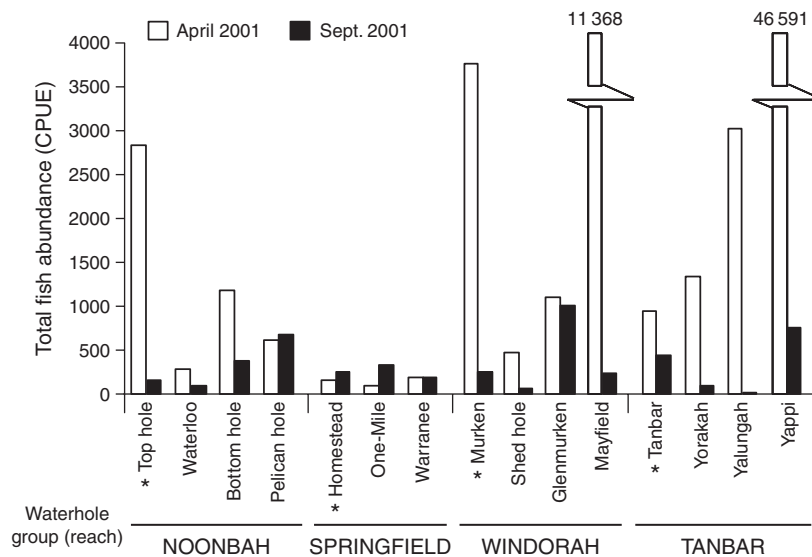
#### Results

Fish were collected from all 15 waterholes on both sampling occasions (Table 2) and spatial variation in total abundance was pronounced. Total CPUE (fish per waterhole) in April 2001 varied from 84 at One-Mile (Springfield) to 46 591 at Yappi waterhole on the Tanbar reach (Fig. 3). The largest catch was collected from the ‘main’ waterhole only at Noonbah (Top waterhole). Spatial variability in total abundance was also apparent in September 2001, but much less pronounced than in April, with a maximum CPUE of 1028 at Glenmurken waterhole on the Windorah reach and a minimum CPUE of 30 at Yalungah on the Tanbar reach of Cooper Creek.

The fauna was comprised of 12 indigenous fish species in eight families and two alien species, the goldfish and mosquitofish (Table 2). Five widespread indigenous species contributed 96% of total CPUE (based on fyke net samples) – the silver tandan, *Porochilus argenteus* (45.5%); *Ambassis* sp. (19.9%); spangled perch, *Leiopotherapon unicolor* (12.5%); bony bream, *Nematolosa erebi* (9.7%); and Hyrtyl’s tandan, *Neosilurus hyrtlii* (8.4%). We caught the endemic Cooper

**Table 2. Fish species found in waterholes of the Thomson River, Cooper Creek and Kyabra Creek, contributions to total CPUE and number of waterholes occupied in April and September 2001**

Family/species	Common name	% of total CPUE	No. of waterholes (max. 15) with species present	
			April 2001	Sept. 2001
<b>Indigenous species</b>				
Chandidae				
<i>Ambassis</i> sp.	Northwest ambassis	19.9	14	10
Clupeidae				
<i>Nematalosa erebi</i> (Günther, 1868)	Bony bream	9.7	15	13
Gobiidae				
<i>Hypseleotris</i> spp.	Carp gudgeons	0.3	2	9
Melanotaeniidae				
<i>Melanotaenia splendida tatei</i> (Zietz, 1896)	Desert rainbowfish	0.3	12	3
Percichthyidae				
<i>Macquaria</i> sp. B (after Musyl & Keenan, 1992)	Lake Eyre golden perch	0.5	14	8
Plotosidae				
<i>Neosiluroides cooperensis</i> (Allen & Feinberg, 1998)	Cooper Creek tandan	<0.1	4	2
<i>Neosilurus hyrtlii</i> Steindachner, 1867	Hyrtl's tandan	8.4	15	13
<i>Porochilus argenteus</i> (Zeitz, 1896)	Silver tandan	45.5	15	14
Retropinnidae				
<i>Retropinna semoni</i> (Weber, 1895)	Australian smelt	<0.1	2	2
Terapontidae				
<i>Bidyanus welchi</i> (McCulloch & Waite, 1917)	Welch's grunter	<0.1	4	0
<i>Leiopotherapon unicolor</i> (Günther, 1859)	Spangled perch	12.5	15	13
<i>Scortum barcoo</i> (McCulloch & Waite, 1917)	Barcoo grunter	2.6	15	4
<b>Alien species</b>				
Cyprinidae				
<i>Carassius auratus</i> Linnaeus, 1758	Goldfish	0.1	10	6
Poeciliidae				
<i>Gambusia holbrooki</i> (Girard, 1859)	Mosquitofish	<0.1	3	1



**Fig. 3.** Total fish abundance per waterhole in April and September 2001, based on untransformed catch per unit effort data. \* Denotes the 'main' waterhole in each reach.

Creek tandan, *Neosiluroides cooperensis*, in six of the 15 waterholes, but not in Springfield waterholes on Kyabra Creek, nor from Tanbar waterholes along the southern reach of the study area.

Indigenous species richness per waterhole based on all sampling methods varied from 7 to 11 species in April to 4 to 8 species in September 2001. The most diverse assemblages were recorded at Windorah (7–11 species) followed by



Noonbah (8–10 species), Tanbar (8–9 species) and Springfield (7–8 species). In April, the main waterholes in most reaches did not support more species than satellite waterholes. The exception was the Windorah reach, where both Murken (main) and Mayfield (satellite) waterholes supported 11 species, with 10 species in common. In September 2001, more species were found in the main waterholes at Springfield and Tanbar than in their satellites.

Spatial variation in species composition of waterhole fish assemblages was accompanied by considerable variation in patterns of relative abundance. In April 2001, mean faunal similarity based on the Bray–Curtis metric for CPUE data ranged from  $69.3 \pm 2.7$  at Tanbar to  $77.5 \pm 3.3$  at Springfield, whereas by September 2001, fish assemblages were considerably more differentiated, especially at Tanbar (Table 3). Ordination plots based on CPUE and presence/absence data highlight the increasing spatial variation of fish assemblages with the passage of the dry season (Fig. 4). Significant

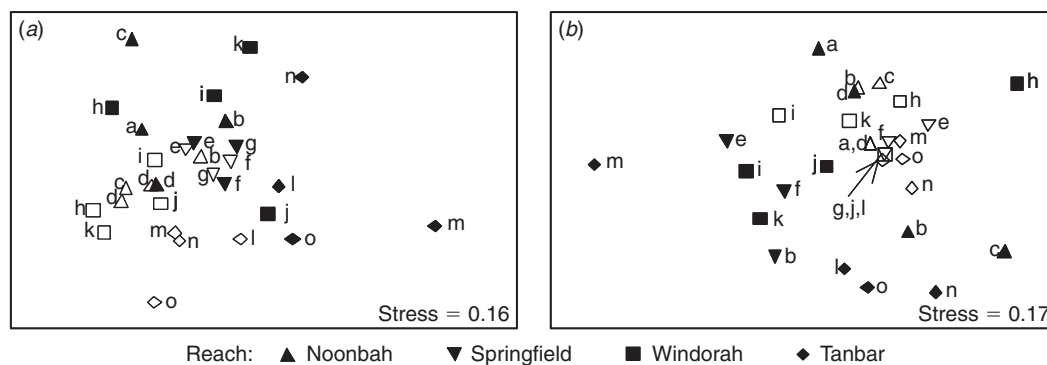
**Table 3.** Summary of mean ( $\pm$  s.e.) measures of fish species richness and Bray–Curtis similarity of assemblages among waterholes of each reach in April 2001 (time 1) and September 2001 (time 2)

Reach	Time	Mean no. species	Similarity (CPUE)	Similarity (presence/absence)
Noonbah	1	8.5 (0.5)	77.3 (4.2)	90.3 (2.0)
Noonbah	2	6.3 (0.9)	60.6 (3.3)	71.3 (5.7)
Springfield	1	9.7 (0.3)	77.5 (3.3)	89.7 (3.0)
Springfield	2	6.7 (0.3)	82.3 (0.9)	79.9 (2.9)
Windorah	1	10.8 (1.0)	72.3 (2.7)	80.4 (2.4)
Windorah	2	7.5 (0.7)	52.9 (2.9)	72.4 (6.1)
Tanbar	1	9.3 (0.5)	69.3 (2.7)	91.9 (1.2)
Tanbar	2	6.0 (0.9)	45.4 (7.4)	55.6 (9.9)
All sites	1	9.5 (0.4)	66.9 (1.0)	85.3 (0.7)
All sites	2	6.6 (0.4)	55.6 (1.5)	65.2 (1.4)

differences in fish-assemblage structure were also evident at the reach scale, as shown by ANOSIM results (Table 4), especially between the Noonbah and Tanbar reaches – the northern and southern parts of the study area (see Fig. 1).

Temporal variation in fish-assemblage structure was pronounced. At most waterholes, far more fish were caught in April than September (Fig. 3) and the overall decline in fish abundance (CPUE) across all waterholes during the 2001 dry season was 93%, with widespread species declining in abundance as follows: *Ambassis* sp. (97%); *P. argenteus* (95%); *N. hyrtlilii* (95%); *N. erebi* (85%); and *L. unicolor* (83%). Species richness was, with two exceptions (Pelican waterhole at Noonbah, Tanbar waterhole at Tanbar), lower in September than in April. Highly significant temporal differences in CPUE and presence/absence patterns were detected using two-way crossed ANOSIM (Table 4). Ordination plots based on CPUE and presence/absence data highlight these temporal changes in fish-assemblage structure (Fig. 4), the CPUE data showing marked repositioning of reach groups in ordination space from bottom left (April 2001) towards the top left (September 2001) of ordination space. Presence/absence patterns were also more variable by September (Fig. 4).

Some of the drivers of these spatial and temporal variations in fish-assemblage structure among waterholes and river reaches are suggested by results of BIO-ENV analyses. In April 2001, four variables (straight-line distance to nearest waterhole, scour holes, hydraulic radius and miscellaneous bars) explained 36% of variation in fish-assemblage structure based on CPUE data (Table 5). Similar characteristics accounted for 36% of the variation in species presence/absence patterns (Table 5). In September 2001, fish-assemblage structure based on CPUE was related to bifurcation ratio, waterhole morphology (cross-sectional area, width to depth ratio) and within-waterhole characteristics (off-take



**Fig. 4.** Spatial and temporal variations in fish-assemblage structure in 15 waterholes sampled in April 2001 (open symbols) and September 2001 (closed symbols), with symbol for each reach. Non-metric multi-dimensional scaling plots for: (a) fish-assemblage structure based on  $\log_{10}(\text{CPUE} + 1)$ , and (b) fish-assemblage structure based on species presence/absence (data from all sampling methods). Waterhole legends for each study reach: Noonbah reach on Thomson River (upward triangle), a = Top, b = Waterloo, c = Bottom, d = Pelican; Springfield reach on Kyabra Creek (downward triangle), e = Homestead, f = One-Mile, g = Warranee; Windorah reach on Cooper Creek (square), h = Murken, i = Shed, j = Glenmurken, k = Mayfield; Tanbar reach on Cooper Creek (diamond), l = Tanbar, m = Yorakah, n = Yalungah, o = Yappi.

channels and boulders). These variables explained about 33% of observed spatial patterns in fish-assemblage structure in September.

*Melanotaenia splendida tatei*, *P. argenteus*, *L. unicolor*, *Macquaria* sp. B and *S. barcoo* were all more abundant in waterholes with large total and/or effective floodplain width (Table 6), total fish abundance being maximal at Yappi waterhole (Tanbar), where the floodplain is about 7 km wide. The shape index of waterholes, and/or the frequency of occurrence of sidebars, was correlated with the abundance of *Macquaria* sp. B, *N. hyrtlii*, *S. barcoo*, *M. s. tatei*, *Ambassis* sp. and *N. erebi* in April. There is also evidence that the occurrence of anabranches influenced some species as well as total fish abundance both early and late in the dry season; this relationship varied from negative to positive over time (Table 6).

Spatial variation in fish-assemblage structure was not generally influenced by the chemical characteristics of the water remaining in isolated waterholes apart from an apparent association between conductivity and fish numbers early in the isolation phase. At this time, total fish abundance and the abundance of four fish species were correlated with conductivity levels, but there was no effect of conductivity on the structure of fish assemblages or particular species in September 2001 (Tables 5 and 6).

## Discussion

The fauna of the study area included four species confined to central Australia – the Cooper Creek endemic *N. cooperensis*, *Macquaria* sp. B, *M. s. tatei*, and *B. welchi*. Five species

**Table 4. Summary of ANOSIM results comparing Cooper Creek fish assemblage structure (based on  $\log_{10}(\text{CPUE} + 1)$  and presence/absence data) among study reaches and sampling dates (1 = April 2001, 2 = September 2001)**

Sampling date	Transformation	Factor	Global R	P	Significant pairwise tests
1	$\log_{10}(\text{CPUE} + 1)$	Reach	0.459	0.001	N–T (0.03), W–T (0.03)
1	Presence/absence	Reach	0.262	0.011	N–SF (0.03), N–T (0.03)
2	$\log_{10}(\text{CPUE} + 1)$	Reach	0.067	n.s.	
2	Presence/absence	Reach	0.226	0.040	N–W (0.03)
1 & 2	$\log_{10}(\text{CPUE} + 1)$	Reach	0.263	0.001	N–SF (0.02), N–T (0.001) SF–T (0.03), W–T (0.02)
1 & 2	$\log_{10}(\text{CPUE} + 1)$	Time	0.396	0.001	
1 & 2	Presence/absence	Reach	0.244	0.001	N–SF (0.003), N–W (0.005) N–T (0.006)
1 & 2	Presence/absence	Time	0.407	0.001	

N = Noonbah reach on Thomson River, W = Windorah reach on Cooper Creek, T = Tanbar reach on Cooper Creek, SF = Springfield reach on Kyabra Creek, n.s. = not significant.

**Table 5. Summary of BIO-ENV results based on Spearman rank correlations ( $r_s$ ) between fish-assemblage structure, waterhole variables and water-chemistry variables**  
Results presented for best possible solution only

Sampling time	Transformation	Best variable combination
Floodplain and waterhole variables		
1	$\log_{10}(\text{CPUE} + 1)$	SLD, SH, HR, BAR (0.603)
1	Presence/absence	EFW, BBC, BAR, OC (0.60)
2	$\log_{10}(\text{CPUE} + 1)$	BR, CSA, WD, OC, BOU (0.572)
2	Presence/absence	BR, WD, B, BOU, OV (0.477)
Water-chemistry variables		
1	$\log_{10}(\text{CPUE} + 1)$	Conductivity, N : P (0.488)
1	Presence/absence	Turbidity (–0.247)
2	$\log_{10}(\text{CPUE} + 1)$	pH, turbidity, total N (0.161)
2	Presence/absence	Silicates (0.178)
1 & 2	$\log_{10}(\text{CPUE} + 1)$	Silicates, total carbonates, N : P (0.499)
1 & 2	Presence/absence	Silicates, sulphates (0.381)

SLD = Straight-line distance to nearest waterhole, SH = scour holes, HR = hydraulic radius, BAR = bars, EFW = effective floodplain width, BBC = bed and bank complexity, OC = off-take channels, BR = bifurcation ratio, CSA = cross-sectional area, WD = width to depth ratio, BOU = boulders, B = bench, OV = overhanging vegetation.

**Table 6. Significant Spearman rank correlations ( $r_s$ ) between fish species abundance, waterhole variables and water-chemistry variables**

Sampling time	Factor	Fish species, $r_s$ (p)
Floodplain and waterhole variables		
1	TFW	<i>M. s. ta.</i> : 0.658 (0.008), <i>P. arg.</i> : 0.675 (0.006), <i>Lei. uni.</i> : 0.689 (0.005). Total: 0.675 (0.006)
1	EFW	<i>Macqu.</i> : 0.666 (0.007), <i>P. arg.</i> : 0.579 (0.024), <i>Sc. bar.</i> : 0.517 (0.048)
1	SI	<i>Macqu.</i> : 0.635 (0.011), <i>N. hyrtl.</i> : 0.530 (0.042), <i>Sc. bar.</i> : 0.577 (0.024)
1	AN	<i>M. s. ta.</i> : -0.581 (0.023). Total: -0.539 (0.038)
1	SB	<i>Amb.</i> : 0.696 (0.004), <i>Nem. er.</i> : 0.821 (0.0002)
2	AN	<i>Amb.</i> : 0.541 (0.04), <i>Nem. er.</i> : 0.629 (0.0002). Total: 0.709 (0.003)
Water-chemistry variables		
1	Conductivity	<i>Amb.</i> : 0.654 (0.008), <i>Nem. er.</i> : 0.691 (0.004), <i>P. arg.</i> : 0.577 (0.025) <i>Lei. uni.</i> : 0.560 (0.005). Total: 0.671 (0.006)
2	No factors	

TFW = Total floodplain width, EFW = effective floodplain width, SI = shape index, AN = anabranches, SB = sidebars. Total = total fish abundance pre waterhole based on CPUE data from fyke net samples. *M. s. ta.* = *Melanotaenia splendida tatei*, *P. arg.* = *Porochilus argenteus*, *Sc. bar.* = *Scortum barcoo*, *Lei. uni.* = *Leiopotherapon unicolor*, *Macqu.* = *Macquaria* sp. B, *N. hyrtl.* = *Neosilurus hyrtlilii*, *Amb.* = *Ambassis* sp., *Nem. er.* = *Nematalosa erebi*.

collected have a tropical and central Australian distribution – *P. argenteus*, *N. hyrtlilii*, *L. unicolor*, northwest *Ambassis* and *S. barcoo*, whereas *R. semoni* has a subtropical and temperate distribution and *N. erebi* is widespread in central, eastern and northern Australia (Allen *et al.* 2002; Pusey *et al.* 2004). Only one species known from the Cooper Creek system, the Lake Eyre hardyhead, *Craterocephalus eyrsii*, was not collected in our study area. This was expected, given that it occurs only occasionally in the lower reaches of Cooper Creek near Lake Eyre (Puckridge 1999; Wager and Unmack 2000).

Spatial and temporal variation in fish-assemblage structure in Cooper Creek waterholes over the 2001 dry season was influenced by processes operating in a nested hierarchy of spatial scales – the floodplain around each waterhole, the entire waterhole and patches of habitat within waterholes (cf. Frissell *et al.* 1986; Rodriguez and Lewis 1997; Labbe and Fausch 2000). The influence of floodplain processes on fish-assemblage structure was most apparent early in the 2001 dry season (April), when fish-assemblage structure, total fish abundance and the abundances of five species were related to total and/or effective width of surrounding floodplains. We suggest that these measures of floodplain width served as surrogates for the actual area of floodplain inundated during the summer flood of 1999–2000 (14 months prior to April 2001 sampling). This large flood (see Fig. 2) inundated the full width of the floodplain around all waterholes except those along Kyabra Creek.

Many studies in large floodplain rivers have found similar relationships between fish catches in dry season habitats in one year and the area of floodplain inundated in the same or in preceding years (Christensen 1993; Welcomme 2001). These relationships arise because inundated floodplains provide important nursery areas for larval and juvenile fishes and also allow older fish to disperse, feed and accumulate sufficient fat

reserves to survive the dry season and complete reproduction (Humphries *et al.* 1999; Welcomme 2001; King *et al.* 2003). When floodwaters recede, large numbers of fish are available to colonise dry-season lakes and waterholes (Welcomme 2001). These uses of inundated floodplains are central to the ‘Flood Pulse Concept’ (Junk *et al.* 1989). In Cooper Creek, all indigenous fish species, except possibly *N. cooperensis*, make use of inundated floodplains as juveniles and maturing individuals and/or as spent adults (S. Bunn and S. Balcombe, unpublished data). Their use of floodplain habitats has also been reported in other Australian floodplain rivers (Bishop and Forbes 1991; King *et al.* 2003; Mallen-Cooper and Stewart 2003; Pusey *et al.* 2004). Our evidence of the influence of antecedent flooding on dry-season fish assemblages is also consistent with the work of Puckridge (1999) and Puckridge *et al.* (2000) on fish assemblages of the Coongie Lakes along the lower Cooper Creek system. The most distinctive variations in fish-assemblage structure recorded in the intermittently inundated Coongie Lakes were associated with the largest antecedent flow pulse and its effects on fish populations compounded over successive years.

Two other floodplain factors influenced spatial variations in fish-assemblage structure in dry-season waterholes – connectivity (SLD = straight-line distance of each waterhole to the nearest waterhole) and bifurcation ratio (number of channels present within a floodplain divided by floodplain width). Waterholes that were closer together on a floodplain (low SLD) (e.g. Murken and Mayfield waterholes at Windorah) were more likely to have similar fish faunas than those far apart (high SLD). However, channel distance to nearest waterhole (CD), another route for fish movement between waterholes, was not associated with spatial variations in fish-assemblage structure. It is possible that these simple measures of ‘connectivity’ (SLD and CD) do not adequately represent



the spatial configurations and degree of interconnectedness of isolated waterholes in the study area (cf. Olden *et al.* 2001; Amoros and Bornette 2002; Sheldon *et al.* 2002). Surprisingly, the relative density of channels on the floodplain (bifurcation ratio) influenced variations in fish-assemblage structure only in September 2001, seven months after floodplain inundation. We might expect the influence of floodplain channels to be important shortly after flooding and flood recession, when auxiliary channels dissecting the floodplain provide depth, velocity and directional cues that 'funnel' fish into waterholes or floodplain lakes (Welcomme 1985; Bishop *et al.* 1995). Alternatively, the bifurcation ratio may be a surrogate for other floodplain or channel features correlated with fish-assemblage structure in September 2001, such as off-take channels and anabranches that enter waterholes at various elevations along the basin profile. The exposure of these features as water levels fell over the dry season could equate to loss of habitat availability/heterogeneity, with effects on fish likely to be more evident later in the dry season.

Planform dimensions, such as surface area, perimeter and shoreline complexity, often influence fish-assemblage structure in lakes and floodplain lagoons (e.g. Eadie and Keast 1983; Jackson *et al.* 2001), with larger waterbodies typically receiving more fish during floodplain recession than small ones (Kennard 1995; Welcomme 2001). This was not the case in Cooper Creek. Instead we found relationships between fish-assemblage structure, waterhole cross-sectional area and width-to-depth ratio in September 2001. These factors influence variation in water loss owing to evaporation, the major process governing water loss from Cooper Creek waterholes between episodic floods and flow pulses (S. Hamilton, personal communication). Evaporation rates are highly variable among waterholes, in part owing to their different sizes, their effective width for wind action, the degree of channel incision below levees and the height and width of riparian vegetation (S. Hamilton, personal communication). These features affect wind-induced turbulence at the water surface, exposure of the surface to solar heating and convective air circulation above the water surface (Brutsaert 1982). Thus some Cooper Creek waterholes experienced much greater water loss than others over the 2001 dry season (S. Hamilton, personal communication) and this influenced their habitat structure and fish assemblages.

The effect of variation in the structure, heterogeneity and availability of wetted habitat was clearly apparent in both April and September 2001. With decline in waterhole depth and volume, waterhole features, such as benches, bars, off-take channels and anabranches, can be exposed and desiccated, depending on their elevation along the basin profile, presence of sills and bars and other basin irregularities (A. Arthington, personal observations). As water levels recede, fish may become trapped and stranded, much as they do on the floodplain during flood recession (Ruello 1976; Welcomme 1985; Puckridge 1999). At low water levels,

exposure of boulders, root masses and large woody debris, and decreasing depth of scour holes, can reduce the range of sheltered places where fish can rest and forage, or conceal themselves from predators, lurk in ambush and launch attacks on prey (Crook and Robertson 1999). The influence of habitat structure (especially structurally complex habitat such as submerged branches, leaf litter and aquatic vegetation) on fish-assemblage structure has been demonstrated in other dry-season floodplain habitats (Kennard 1995; Welcomme 2001). Loss of habitat is also important in intermittent streams subject to periods of natural drought (Stanley *et al.* 1997; Labbe and Fausch 2000; Magoulick and Kobza 2003; Matthews and Marsh-Matthews 2003).

A notable feature of this study was the low total abundance of fish (Fig. 3) and significantly different fish assemblages in Springfield waterholes along Kyabra Creek (Table 3). These differences may reflect the fact that the floodplains at Springfield have not experienced major flooding since 1989 (12 years prior to this study). Small summer flow pulses have occasionally over-topped the banks at Springfield, but these have resulted in localised flooding with inundation being restricted to very small areas around waterholes for a few days (B. Morrish, personal communication). The floodplains around Springfield waterholes are highly constrained, with effective floodplain widths (1640–6060 m) that are the lowest recorded in the study area. Infrequent floodplain inundation, relatively small areas flooded and short periods of inundation appear likely to diminish opportunities for production of fish species that typically use floodplain habitats for feeding, growth and maturation. An additional factor with potential to depress fish populations could be the high turbidity and low primary production levels recorded in Springfield waterholes (S. Bunn and C. Fellows, unpublished data).

Spatial and temporal patterns of fish-assemblage structure in Cooper Creek waterholes reinforce many investigations of fish assemblages in floodplain rivers during their dry-season isolation phase (e.g. Kennard 1995; Rodriguez and Lewis 1994, 1997; Tejerina-Garro *et al.* 1998; Puckridge *et al.* 2000; Saint-Paul *et al.* 2000; Welcomme 2001). Findings from this study are also consistent with the impacts of natural, seasonal droughts on fish assemblages and species-abundance patterns in intermittent streams (Closs and Lake 1996; Humphries and Baldwin 2003; Magoulick and Kobza 2003; Matthews and Marsh-Matthews 2003). Importantly, this study shows that factors affecting fish-assemblage structure and abundance in isolated floodplain waterbodies cannot be fully revealed by investigations conducted only at the local (waterhole) scale. Our hierarchical, multi-scale approach was needed to reveal the influence of antecedent flooding, interconnectedness of waterholes and waterhole habitat structure on fish-assemblage structure in dry-season waterholes (cf. Junk *et al.* 1989; Schlosser and Angermeier 1995; Labbe and Fausch 2000; Amoros and Bornette 2002; Sheldon *et al.* 2002; Magoulick and Kobza 2003; Scheurer *et al.* 2003). Across this

nested hierarchy of spatial scales, interactions between flow and physical habitat were crucial to the persistence of fish assemblages in Cooper Creek during the 2001 dry season, a period of natural drought (Lake 2000, 2003) in this arid-zone river. We conclude that the magnitude, timing, frequency and duration of floodplain inundation and natural variations in waterhole volume (i.e. the natural hydrologic regime, Poff *et al.* 1997) must be maintained if we wish to sustain the distinctive habitats and fish assemblages of this arid-zone floodplain river.

### Acknowledgments

This study contributes to the Dryland River Refugia Project funded by the Cooperative Research Centre for Freshwater Ecology, Canberra. We thank colleagues from the Centre for Riverine Landscapes at Griffith University, the Queensland Department of Natural Resources and Mines, the University of Canberra, the Murray–Darling Basin Freshwater Research Centre (Northern Basin Laboratory) and the New South Wales Department of Infrastructure, Planning and Natural Resources for field assistance, data on river flows, preparation of figures and valuable discussions. We are also indebted to landowners Bob Morrish (Springfield), Angus Emmott (Noonbah), Sandy Kidd (Mayfield), David Smith (Hammond Downs) and George Scott (Tanbar) for allowing access to waterholes on their properties and for their hospitality and encouragement. Three anonymous referees and the Managing Editor are thanked for helpful comments on the manuscript. Our research was conducted under Queensland Fisheries Permit PRM00157K.

### References

- Allen, G. R., Midgley, S. H., and Allen, M. (2002). 'Field Guide to the Freshwater Fishes of Australia.' (Western Australian Museum: Perth.)
- Amoros, C., and Bornette, G. (2002). Connectivity and biocomplexity in waterbodies of riverine floodplains. *Freshwater Biology* **47**, 761–776. doi:10.1046/J.1365-2427.2002.00905.X
- Anonymous (1998). Draft Water Management Plan for Cooper Creek – information paper. Department of Natural Resources, Brisbane.
- APHA (1975). 'Standard Methods for the Examination of Water and Wastewater.' 14th edn. (American Public Health Association: Washington, DC.)
- Bishop, K. A., and Forbes, M. A. (1991). The freshwater fishes of northern Australia. In 'Monsoonal Australia: Landscape, Ecology and Man in the Northern Lowlands'. (Eds C. S. Haynes, M. G. Ridpath and M. A. Williams.) pp. 70–108. (AA Balkema: Rotterdam.)
- Bishop, K. A., Pidgeon, R. W., and Walden, D. J. (1995). Studies on fish movement dynamics in a tropical floodplain river: prerequisites for a procedure to monitor the impacts of mining. *Australian Journal of Ecology* **20**, 81–107.
- Boulton, A. J., Sheldon, F., Thoms, M. C., and Stanley, E. H. (2000). Problems and constraints in managing rivers with variable flow regimes. In 'Global Perspectives on River Conservation: Science, Policy and Practice'. (Eds P. J. Boon, B. R. Davies and G. E. Petts.) pp. 441–426. (John Wiley and Sons: London.)
- Brutsaert, W. (1982). 'Evaporation into the Atmosphere: Theory, History, and Applications.' (Reidel: Boston, MA.)
- Bunn, S. E., Davies, P. M., and Winning, M. (2003). Sources of organic carbon supporting the food web of an arid zone floodplain river. *Freshwater Biology* **48**, 619–635. doi:10.1046/J.1365-2427.2003.01031.X
- Christensen, M. S. (1993). The artisanal fishery of the Mahakam River floodplain in East Kalimantan, Indonesia. III. Actual and estimated yields, their relationship to water levels and management options. *Journal of Applied Ichthyology* **9**, 202–209.
- Clarke, K. R., and Warwick, R. M. (2001). 'Change in Marine Communities: An Approach to Statistical Analysis and Interpretation.' 2nd edn. (PRIMER-E Ltd: Plymouth.)
- Closs, G. P., and Lake, P. S. (1996). Drought, differential mortality and the coexistence of a native and an introduced fish species in a south east Australian intermittent stream. *Environmental Biology of Fishes* **47**, 17–26.
- Crook, D. A., and Robertson, A. I. (1999). Relationships between riverine fish and woody debris: implications for lowland rivers. *Marine and Freshwater Research* **50**, 941–953.
- Davis, L., Thoms, M., Fellows, C., and Bunn, S. (2003). Physical and ecological associations in dryland refugia: waterholes of the Cooper Creek, Australia. In 'The Structure, Function and Management Implications of Fluvial Sedimentary Systems. Proceedings of an International Symposium, Alice Springs, Australia'. IAHS Publication 276. (Eds F. J. Dyer, M. C. Thoms and J. M. Olley.) pp. 77–84. (International Association of Hydrological Sciences: Wallingford.)
- Eadie, J. M., and Keast, A. (1983). Resource heterogeneity and fish species diversity in lakes. *Canadian Journal of Zoology* **62**, 1689–1695.
- Fausch, K. D., Torgersen, C. E., Baxter, C. V., and Li, H. W. (2002). Landscapes to riverscales: bridging the gap between research and conservation of stream fishes. *Bioscience* **52**, 483–498.
- Frissell, C. A., Liss, W. J., Warren, C. E., and Hurley, M. D. (1986). A hierarchical framework for stream habitat classification: viewing streams in a watershed context. *Environmental Management* **10**, 199–214.
- Goulding, M., Carvalho, M. L., and Ferreira, E. G. (1988). 'Rio Negro, Rich Life in Poor Water.' (SPB Academic Publishing: The Hague.)
- Humphries, P., and Baldwin, D. S. (2003). Drought and aquatic ecosystems: an introduction. *Freshwater Biology* **48**, 1141–1146. doi:10.1046/J.1365-2427.2003.01092.X
- Humphries, P., King, A. J., and Koehn, J. D. (1999). Fish, flows and floodplains: links between freshwater fishes and their environment in the Murray–Darling River system, Australia. *Environmental Biology of Fishes* **56**, 129–151. doi:10.1023/A:1007536009916
- Jackson, D. A., Peres-Neto, P. R., and Olden, J. D. (2001). What controls who is where in freshwater fish communities – the roles of biotic, abiotic and spatial factors. *Canadian Journal of Fisheries and Aquatic Sciences* **58**, 157–170. doi:10.1139/CJFAS-58-1-157
- Junk, W. J., Bayley, P. B., and Sparks, R. E. (1989). The flood pulse concept in river–floodplain systems. In 'Proceedings of the International Large Rivers Symposium (LARS)'. (Ed. D. P. Dodge.) pp. 110–127. *Canadian Journal of Fisheries and Aquatic Sciences Special Publication* 106.
- Kennard, M. J. (1995). Factors influencing freshwater fish assemblages in floodplain lagoons of the Normanby River, Cape York Peninsula: A large tropical Australian river. M.Sc. Thesis, Griffith University, Brisbane.
- Keppel, G. (1991). 'Design and Analysis: a Researcher's Handbook.' (Prentice-Hall: Englewood Cliffs, NJ.)
- King, A. J., Humphries, P., and Lake, P. S. (2003). Fish recruitment on floodplains: the roles of patterns of flooding and life history characteristics. *Canadian Journal of Fisheries and Aquatic Sciences* **60**, 773–786. doi:10.1139/F03-057
- Kingsford, R. T., Curtin, A. L., and Porter, J. L. (1999). Water flows on Cooper Creek determine 'boom' and 'bust' periods for waterbirds

- of the Paroo and Warrego Rivers. *Biological Conservation* **88**, 231–248. doi:10.1016/S0006-3207(98)00098-6
- Kingsford, R. T., Jenkins, K. M., and Porter, J. L. (2004). Imposed hydrological stability on lakes in arid Australia and effects on waterbirds. *Ecology* **85**, 2478–2492.
- Knighton, A. D., and Nanson, G. C. (1994). Waterholes and their significance in the anastomosing channel system of Cooper Creek, Australia. *Geomorphology* **9**, 311–324. doi:10.1016/0169-555X(94)90052-3
- Labbe, T. R., and Fausch, K. D. (2000). Dynamics of intermittent stream habitat regulate persistence of a threatened fish at multiple scales. *Ecological Applications* **10**, 1774–1791.
- Lake, P. S. (2000). Disturbance, patchiness, and diversity in streams. *Journal of the North American Benthological Society* **19**, 573–592.
- Lake, P. S. (2003). Ecological effects of perturbation by drought in flowing waters. *Freshwater Biology* **48**, 1161–1172. doi:10.1046/J.1365-2427.2003.01086.X
- Lancaster, J., and Belyea, L. R. (1997). Nested hierarchies and scale-dependence of mechanisms of flow refugium use. *Journal of the North American Benthological Society* **16**, 221–238.
- Lowe-McConnell, R. H. (1987). 'Ecological Studies in Tropical Fish Communities.' (Cambridge University Press: Cambridge.)
- Magoulick, D. D., and Kobza, R. M. (2003). The role of refugia for fishes during drought: a review and synthesis. *Freshwater Biology* **48**, 1186–1198. doi:10.1046/J.1365-2427.2003.01089.X
- Mallen-Cooper, M., and Stewart, I. (2003). Age, growth and non-flood recruitment of two potamodromous fishes in a large semi-arid temperate river system. *River Research and Applications* **19**, 697–719. doi:10.1002/RRA.714
- Matthews, W. J., and Marsh-Matthews, E. (2003). Effects of drought on fish across axes of space, time and ecological complexity. *Freshwater Biology* **48**, 1232–1253. doi:10.1046/J.1365-2427.2003.01087.X
- McMahon, T. A., and Finlayson, B. L. (2003). Droughts and anti-droughts: the low flow hydrology of Australian rivers. *Freshwater Biology* **48**, 1147–1160. doi:10.1046/J.1365-2427.2003.01098.X
- Morton, S. J., Short, J., and Baker, R. D. (1995). Refugia for biological diversity in arid and semi-arid Australia. Biodiversity Series, Paper No. 4. Department of Environment, Sport and Territories, Canberra.
- Musyl, M. K., and Keenan, C. P. (1992). Population genetics and zoogeography of Australian freshwater Golden Perch, *Macquaria ambigua* (Richardson 1845) (Teleostei: Percichthyidae), and electrophoretic identification of a new species from the Lake Eyre Basin. *Australian Journal of Marine and Freshwater Research* **43**, 1585–1601.
- Olden, J. D., Jackson, D. A., and Peres-Neto, P. R. (2001). Spatial isolation and fish communities in drainage lakes. *Oecologia* **127**, 572–585. doi:10.1007/S004420000620
- Parsons, M. E., Thoms, M. C., and Norris, R. N. (2004). Development of a standardised approach to river habitat assessment in Australia. *Environmental Monitoring and Assessment* **98**, 109–130. doi:10.1023/B:EMAS.0000038182.03176.97
- Poff, N. L., Allan, J. D., Bain, M. B., Karr, J. R., Prestegard, K. L., Richter, B. D., Sparks, R. E., and Stromberg, J. C. (1997). The natural flow regime – a paradigm for river conservation and restoration. *Bioscience* **47**, 769–784.
- Puckridge, J. T. (1999). The role of hydrology in the ecology of Cooper Creek, Central Australia: implications for the flood pulse concept. Ph.D. Thesis, The University of Adelaide.
- Puckridge, J. T., Sheldon, F., Walker, K. F., and Boulton, A. J. (1998). Flow variability and the ecology of large rivers. *Marine and Freshwater Research* **49**, 55–72. doi:10.1071/MF94161
- Puckridge, J. T., Walker, K. F., and Costelloe, J. F. (2000). Hydrological persistence and the ecology of dryland rivers. *Regulated Rivers. Research Management* **16**, 385–402.
- Pusey, B. J., Kennard, M. J., and Arthington, A. H. (2004). 'Freshwater Fishes of North-eastern Australia.' (CSIRO Publishing: Melbourne.)
- Rodriguez, M. A., and Lewis, W. M., Jr (1994). Regulation and stability in fish assemblages of neotropical floodplain lakes. *Oecologia* **99**, 166–180. doi:10.1007/BF00317098
- Rodriguez, M. A., and Lewis, W. M., Jr (1997). Structure of fish assemblages along environmental gradients in floodplain lakes of the Orinoco River. *Ecological Monographs* **67**, 109–128.
- Ruello, N. V. (1976). Observations on some fish kills in Lake Eyre. *Australian Journal of Marine and Freshwater Research* **27**, 667–672.
- Saint-Paul, U., Zuanon, J., Villacorta Correa, M. A., Garcia, M., Fabre, N. N., Berger, U., and Junk, W. J. (2000). Fish communities in central Amazonian white- and blackwater floodplains. *Environmental Biology of Fishes* **57**, 235–250. doi:10.1023/A:1007699130333
- Scheurer, J. A., Fausch, K. D., and Bestgen, K. R. (2003). Multiscale processes regulate brassy minnow persistence in a Great Plains River. *Transactions of the American Fisheries Society* **132**, 840–855. doi:10.1577/T02-037
- Schlösser, I. J., and Angermeier, P. L. (1995). Spatial variation in demographic processes in lotic fishes: conceptual models, empirical evidence, and implications for conservation. In 'Evolution and the Aquatic Ecosystem: Defining Unique Units in Population Conservation. American Fisheries Society Monograph Series 17'. (Ed. J. L. Nielsen.) pp. 392–401.
- Sheldon, F., Boulton, A. J., and Puckridge, J. T. (2002). Conservation value of variable connectivity: aquatic invertebrate assemblages of channel and floodplain habitats of a central Australian arid-zone river, Cooper Creek. *Biological Conservation* **103**, 13–31. doi:10.1016/S0006-3207(01)00111-2
- Stanley, E. H., Fisher, S. G., and Grimm, N. B. (1997). Ecosystem expansion and contraction in streams. *Bioscience* **47**, 427–435.
- Tejerina-Garro, F. L., Fortin, R., and Rodriguez, M. A. (1998). Fish community structure in relation to environmental variation in floodplain lakes of the Araguaia River, Amazon Basin. *Environmental Biology of Fishes* **51**, 399–410. doi:10.1023/A:1007401714671
- Thoms, M. C., and Sheldon, F. (2000). Lowland rivers: an Australian perspective. *Regulated Rivers. Research Management* **16**, 375–383.
- Wager, R., and Unmack, P. J. (2000). Fishes of the Lake Eyre catchment of Central Australia. Department of Primary Industries Queensland Fisheries Service, Brisbane.
- Walker, K. F., Sheldon, F., and Puckridge, J. T. (1995). An ecological perspective on dryland river ecosystems. *Regulated Rivers. Research Management* **11**, 85–104.
- Ward, J. V., Tockner, K., Arscott, D. B., and Claret, C. (2002). Riverine landscape diversity. *Freshwater Biology* **47**, 517–539. doi:10.1046/J.1365-2427.2002.00893.X
- Welcomme, R. L. (1985). River Fisheries. FAO Fisheries Technical Paper No. 262. FAO, Rome.
- Welcomme, R. L. (2001). 'Inland Fisheries Ecology and Management.' (Fishing News Books, Blackwell Science Ltd: Oxford.)

Manuscript received 1 June 2004; revised 27 October 2004; and accepted 25 November 2004.