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Persistence of aquatic refugia between flow pulses in a dryland river system (Cooper Creek, Australia)

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Abstract

In many dryland rivers with intermittent flow, relatively deep segments of the river channel serve as refugia for aquatic life during protracted intervals between flows. Semipermanent channel segments are known as waterholes in the semiarid Cooper Creek system of western Queensland. Fractional water loss by evaporation was estimated in 15 Cooper waterholes from the increase in conservative ion (Na⁺ and Cl⁻) concentrations and independently from evaporative fractionation of oxygen and hydrogen isotopes in water. The major solute chemistry and isotope results indicated that evaporative water loss controlled the water levels between flows and that the surface waters were effectively isolated from underlying groundwater that had a distinctive chemical and isotopic composition. Fractional water loss rates combined with stage–volume relationships for each basin showed a mean evaporative loss rate of 2.1 m yr⁻¹; during that time (April–October 2002), pan evaporation averaged 2.5 m yr⁻¹. Site-specific extrapolation of those estimated evaporative loss rates indicated that the waterholes would dry to 10% of their bankfull volumes in 6–23 months, although those estimates were based on sampling in 2002, when pan evaporation rates were 18% higher than the long-term mean. These persistence times show the importance of occasional, irregular flow pulses in sustaining these aquatic refugia; the desiccation of waterholes could become more common if future water withdrawals reduce the frequency and intensity of river flows to the point where they occur less often than annually.

More than half of the Earth's land surface is drained by dryland river systems, yet these systems have received rel-

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atively little attention by limnologists compared to rivers and streams of more humid regions (Davies et al. 1994). Dryland rivers tend to have extremely variable flow regimes (Puckridge et al. 1998, 2000), and they typically experience irregular flow pulses for a few months or less each year. In the protracted intervals between flows, the aquatic biota reside in isolated waterbodies that function as aquatic refugia (Walker et al. 1995; Sheldon et al. 2002). Often, these refugia are within the channels of the river systems.

Occasional large discharge events, particularly when they

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inundate floodplains, stimulate biological productivity in dryland river systems and their environs (Kingsford et al. 1999; Bunn et al. in press). Yet the more frequent but smaller flow pulses that remain within the river channels are also important because they refill aquatic refugia that would otherwise dry, permit dispersal of aquatic animals throughout the river system, and stimulate the breeding of prawns, fishes, frogs, and waterbirds (Cook et al. 2002; Roshier et al. 2002). In addition to seasonal river through-flow, floodplain waterbodies in more humid regions are often sustained by local groundwater inputs, which can represent flow from adjacent uplands or the delayed return of floodwaters that had infiltrated floodplain sediments (Lesack and Melack 1995; Mertes 1997). However, dryland rivers may flow through landscapes that are too arid to provide significant local inputs of water during protracted intervals without precipitation, and standing waters are subject to high evaporative losses.

This study elucidated the hydrology of aquatic refugia located within the channel system of an intermittent dryland river in interior Australia. Our goal was to better understand how long these waterbodies would persist between flow events, which has important implications for the conservation of aquatic biota (Bunn et al. 2003; Hughes and Hillyer 2003). We examined the changes in stable isotopes of water (δ^{18} O and δ D) and major solute concentrations during the isolation phase and compared the observed changes with a null model of evaporative concentration without new groundwater inputs. We also compared the isotopic and major solute composition of waterholes with pumped groundwaters from the vicinity. The results indicated that evaporative water loss was the predominant term in the water budgets of these waterholes between episodic flows, and there was no evidence for inputs of groundwater from the deeper aquifer except, perhaps, in one case. Furthermore, the rates of evaporation inferred from isotope and ionic tracers were variable among waterholes. Given these findings, we were able to use site-specific evaporation rates and the basin morphometry to estimate the persistence times of the waterholes in the absence of new flow pulses, and the results demonstrate the importance of annual flows in maintaining these aquatic refugia.

Cooper Creek and its waterholes

Cooper Creek is one of the larger dryland rivers in Australia, draining 296,000 km² of mostly semiarid-to-arid terrain as it flows for ~1,000 km south and west into the endorheic Lake Eyre Basin (Fig. 1). Most of its runoff originates in the northern part of the watershed and is usually generated by occasional monsoonal incursions during the austral summer. *Acacia* shrubland and grasslands dominate in the watershed, and land use is predominantly extensive livestock grazing. At Windorah, near the middle of the river system, rainfall is highly variable but averages 292 mm yr⁻¹, and evaporation from U.S. class A pans is 2.9 m yr⁻¹. Mean daily maximum air temperatures range from 38.1°C in January to 21.4°C in July (long-term means were obtained from the Australian Bureau of Meteorology).

The hydrology of this remote region has probably been

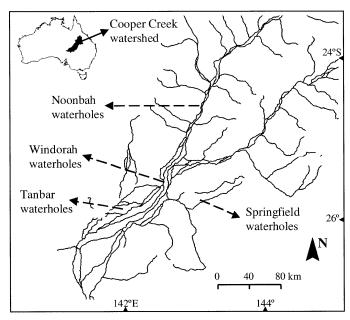


Fig. 1. Map of the study region, showing the major river channels and locations of the four clusters of waterholes that were sampled. The Cooper Creek system is divided into the Thomson River (west branch) and Barcoo River (east branch) above the Windorah waterholes.

little affected by human activities so far, although a recent proposal to extract water from Cooper Creek for irrigated agriculture has engendered interest in understanding the ecological roles of the waterholes and the hydrological processes that maintain them (Kingsford et al. 1998). Discharge through the Cooper Creek system is extremely episodic and variable, but some flow occurs in most years (Puckridge et al. 1998; Kingsford et al. 1999). At Currareva (near Windorah), the mean annual discharge is 8,380 megaliters d⁻¹ (97 m³ s⁻¹), although periods of zero flow are common and have been observed to last for as long as 21 months, based on 49 yr of records. Larger floods can inundate >20,000 km² of floodplain. Losses of water during transmission through the fluvial system exceed 75% during floods; much of this takes place in the extensive floodplains below Windorah, and presumably, this is mostly due to evaporation after waters spread onto the floodplains (Knighton and Nanson 1994b). The lowermost reach of the river system receives water every 4.5 yr on average, but those flows seldom reach Lake Eyre (Kingsford et al. 1999).

Aquatic refugia in Cooper Creek, as in similar river systems throughout Australia, occur as isolated, relatively deep segments of channel, locally known as waterholes (Knighton and Nanson 1994a). The river system is highly anastomosed, especially where flows are unconstrained on the floodplains, and its several hundred waterholes tend to exist at points of flow convergence (Knighton and Nanson 1994a). Waterholes are most abundant across the 500-km reach between Windorah and Nappa Merrie, where the extensive floodplain is composed of 2–9 m of dense clay underlaid by medium-to-coarse sand (Rust and Nanson 1986). Morphometric features of these waterholes measured from aerial photographs

Site	Group	South latitude	East longitude	QNRM No.	Area (km²)	Volume (10 ³ m ³)	Mean depth (m)
Murken Hole	Windorah	25°25′46.6″	142°43′57.9″	0031004	0.254	1,305	5.14
Mayfield	Windorah	25°26′11.5″	142°43′37.3″	0031005	0.023	76	3.36
Glen Murken	Windorah	25°26′52.1″	142°40′43.1″	0031006	0.089	202	2.27
Shed	Windorah	25°23′41.6″	142°49′39.0″	0031007	0.187	546	2.93
Homestead	Springfield	25°48′27.8″	143°02′36.2″	0031009	0.437	1,203	2.75
One Mile	Springfield	25°50′42.0″	143°03′07.2"	0031008	0.060	116	1.95
Warrannee	Springfield	25°54′30.7″	143°05′23.6″	0031010	0.096	310	3.23
Tanbar	Tanbar	25°50′13.3″	141°55′00.3″	0031011	0.910	1,773	1.95
Yorakah	Tanbar	25°57′31.3″	141°52′41.9″	0031012	0.288	507	1.76
Yappi	Tanbar	25°48′58.3″	142°01′41.5″	0031013	0.203	234	1.15
Yalungah	Tanbar	25°51′13.6″	141°58′25.2″	0031014	0.088	379	4.31
Тор	Noonbah	24°11′02.6″	143°21′05.6″	0032024	0.154	547	3.56
Waterloo	Noonbah	24°13′38.2″	143°17′23.3″	0032022	0.160	638	4.00
Bottom	Noonbah	24°16′31.5″	143°18′08.2″	0032023	0.035	84	2.39
Pelican	Noonbah	24°13′35.0″	143°20′06.1″	0032025	0.021	59	2.80

Table 1. Waterhole names, groups, Queensland Department of Natural Resources and Mines (QNRM) codes, and morphometric characteristics at bankfull. Water levels dropped ca. 1 m from bankfull at most sites by the first sampling in Apr 2002.

showed their mean length and width to be 3.7 km and 55 m, respectively (Knighton and Nanson 1994*a*). The longer waterholes are often sinuous, and all tend to be lined with trees (*Eucalyptus camaldulensis* and *Eucalyptus coolibah*).

Available evidence presents contrasting impressions regarding the importance of groundwater inputs to waterholes in dryland regions like Cooper Creek during their isolation phases. The Cooper Creek system is indicated as a "groundwater-dependent ecosystem" in nationwide maps published by Hatton and Evans (1998). This would seem to concur with the observation by local residents that water levels in the waterholes often do not fall as fast as the annual evaporation rate observed in open pans. On the other hand, the floodplain sedimentology reviewed by Gibling et al. (1998) suggests that groundwater exchange is not significant; the waterholes lie on several meters of very fine clay that would tend to seal their basins against groundwater exchange, and an excavation to study the floodplain sedimentology in the southern Cooper Creek region showed that sand deposits beneath the clay bottom of a waterhole were dry. However, the southern Cooper Creek region is outside the area indicated as groundwater dependent.

Sand splays at the downstream ends of some waterholes indicate that they can erode into underlying sand layers, and yet the persistence of these waterholes between flows suggests that infiltration into the underlying sands is limited. The water is extremely turbid, even during prolonged intervals between flows (Bailey 2001; Bunn et al. 2003); the turbid water might quickly form a clay barrier and seal off the bottom (Knighton and Nanson 1994a). Contact with underlying sand layers could open a path for groundwater inflow, but it is unknown whether the hydraulic potential for such inflow exists.

In a set of waterholes along other rivers of the Lake Eyre Basin, Costelloe et al. (2003) analyzed continuous water level records and found that, in most cases, the rate of decrease during isolation fell within a range that could largely be explained by evaporation, although rates were variable

among the waterholes. To our knowledge, such data have not been collected in the Cooper Creek region.

Methods

Sampling and field measurements—We sampled 13 of these waterbodies during their isolation phase in early April and mid October 2002 for major solutes and stable isotopes of water (Fig. 1; Table 1). Two additional waterholes were sampled only in October (Warrannee and Mayfield), and one of the waterholes sampled in April had dried by October (Yalungah). The waterhole sites are clustered in groups; the Noonbah group is on the Thomson River, the Windorah and Tanbar groups are on Cooper Creek below the confluence of the Thomson and Barcoo Rivers, and the Springfield group is on Kyabra Creek, a tributary entering to the south of Windorah.

In April 2002, we also sampled rivers, floodplain pools, groundwater, and rain tanks to show the range in chemical and isotopic composition of potential source waters for the waterholes. River channels that still had slow flow were sampled, including the Thomson River near Jundah and the Barcoo River near Retreat. Freshly pumped groundwater was sampled from windmills to the southeast and west of Windorah (the former pumps from a depth of ~30 m according to the Barcoo Shire). Rain collection tanks that divert runoff from metal roofs and appeared well protected from evaporative loss were sampled at the Windorah Post Office and two cattle ranches (Tanbar Station and Noonbah Station). We also sampled natural floodplain pools of varying sizes containing remnant floodwaters, as well as surface storages of runoff or windmill-pumped groundwater maintained for use by pastoralists, to examine the influence of evaporative water loss on stable isotopic composition of the residual water.

A comparison of vertical profiles of temperature, dissolved oxygen, and conductance at several sites between dusk and dawn showed that the waterholes were not persistently stratified (i.e., the water column became well mixed

at night), as expected given their shallow depths (<3 m), so samples collected from near the surface represented the entire water volume. Water samples collected in April for major solute chemistry were filtered through glass-fiber filters ($\sim1-\mu$ m pore size) in the field and kept refrigerated in polyethylene bottles until analysis. Water samples collected in October for major solute chemistry were not filtered in the field and were stored at ambient temperature. Water samples for stable isotopic analysis were kept in 50-ml polypropylene centrifuge tubes with the caps sealed tightly with polyvinyl chloride tape. Field measurements included turbidity, pH, specific conductance, temperature, and dissolved oxygen.

An evaporation pan was set up beside the Australian Bureau of Meteorology station in Windorah to measure the evaporative fractionation of stable isotopes, from which the isotopic composition of the atmospheric moisture could be estimated for use in isotope mass balance modeling (Gibson et al. 1999). The pan was a plastic basin measuring about 30×50 cm and 40 cm deep. On 9 April 2002, the pan was filled to 30 cm with water from the rain tank at the Windorah Post Office. The pan was sampled and water levels recorded every 4 d at dawn for 32 d, by which time it had dried to a 9.0-cm depth. Air temperature, relative humidity, and openpan evaporation were measured concurrently by the station. There were small (<3 mm) rainfalls on 13 and 15 April during which the pan was kept covered.

Basin morphometry was determined by surveying each waterhole. Initially, the surface area of each waterhole, at the bankfull level, was determined from high-resolution aerial photographs; bankfull levels were determined by the presence of riparian vegetation and changes in slope and confirmed by field reconnaissance. A series of bankfull cross sections were surveyed along each waterhole at approximately 150-m intervals. In addition, the thalweg profile was surveyed along each waterhole. These data were then combined within a geographic information system (ARCView) to produce a digital elevation model of each waterhole. One waterhole lacked morphometric data (Homestead). For this study, bankfull volume is defined as the volume when the waterhole basin is filled up to its sill, or the lowest point along its banks (generally located at a point of channelized outflow). Stage is expressed as meters above the deepest point in the waterhole. This study was not able to measure changes in water levels over time in any of these waterholes.

Laboratory analyses—Analyses of major solutes were performed at the laboratory of S.K.H. at Michigan State University (April samplings) or at Scientific Services (Queensland Health) in Brisbane (October samplings). Ca²⁺, Mg²⁺, Na⁺, and K⁺ were measured by flame atomic absorption; Cl⁻, SO₄²⁻, and NO₃⁻ were measured by ion chromatography; total alkalinity was measured by Gran titration; and silicate was measured by the molybdate colorimetric method (Wetzel and Likens 2000).

Analyses of stable isotopes in water samples were performed at the Adelaide Laboratory of the Commonwealth Scientific and Industrial Research Organization (CSIRO) Land and Water. Isotope ratios were measured following equilibration with CO₂ (for ¹⁸O: ¹⁶O) or H₂ plus a Pt catalyst (for ²H: ¹H) on an automated system attached to a GEO 20-

20 dual-inlet stable isotope ratio mass spectrometer (Europa). Stable isotope measurements are expressed as δ^{18} O or δD (units of ‰) according to the following equation:

$$\delta X = [(R_{\text{sample}}/R_{\text{standard}}) - 1] \times 1,000 \tag{1}$$

where X is 18 O or D, R is the 18 O: 16 O or 2 H: 1 H ratio, and the isotope standard is SMOW (standard mean ocean water).

Data analysis—Rainfall data for determination of the local meteoric waterline (LMWL) were obtained from the Global Network for Isotopes in Precipitation (GNIP), an online database maintained by the International Atomic Energy Agency (http://isohis.iaea.org/). The two closest stations with available data were Brisbane and Alice Springs. The Alice Springs station was chosen as most representative of Cooper Creek because of its similar continental location and precipitation regime. The LMWL for Alice Springs was observed to deviate from the global MWL under the influence of small, isotopically enriched rain events. Since only larger rain events produce river flows, the Alice Springs LMWL was determined using only rain events >100 mm; linear regression yielded the following equation: $\delta D = 7.485 \times \delta^{18}O + 8.666$ ($r^2 = 0.95$; n = 101).

Hydrochemical modeling with the major solute concentrations was performed to investigate the potential for mineral precipitation reactions, using PHREEQC with Aqua-Chem software (version 3.7.42, Waterloo Hydrogeologic). The saturation indices indicated which major solutes were less likely to behave conservatively in solution and thus should not be selected to serve as hydrological tracers.

To model the evaporation of waterholes, we assumed that the preceding flows flushed the waterholes and left them filled to bankfull with river water and that there were no significant new inputs of rain or groundwater thereafter. In that case, the water balance for a waterhole during the isolation phase can be expressed as follows:

$$dV/dt = -E \tag{2}$$

where V is volume, t is time, and E is evaporation rate. This simple water budget was treated as a null model, which we evaluated using three independently measured tracers: the two most conservative solutes (Na⁺ and Cl⁻) as well as δ^{18} O of water. Below, we show how all three were consistent with this null model and provided comparable estimates of evaporative water losses from April to October 2002. We then employed δ^{18} O to estimate the fractional water loss by evaporation from each waterhole from January to October.

The local evaporation line (LEL) is the trajectory of isotopic enrichment that occurs upon evaporation of a standing waterbody, and its slope is largely a function of the relative humidity above the water surface. Extrapolation of the LEL to its intersection with the LMWL indicates the isotopic composition of the rainfall from which the river waters arose (Gonfiantini 1986). The advantage of using δ^{18} O is that the initial starting point at the LMWL can thus be estimated, in contrast to using Na⁺ and Cl⁻. The fractional water loss over time, in combination with the morphological information, yielded an estimate of the rate of drawdown in water levels from bankfull stage for each basin. Extrapolation of this drawdown forward in time yielded an estimate of how long

Site	Date	Na^+	Na^+V_f/V_i	Cl-	$\mathrm{Cl}^- V_f/V_i$	$\delta^{_{18}}{ m O}$	δ^{18} O V_f/V_i
Murken Hole	Apr	0.74		0.28		1.52	
	Oct	1.13	0.64	0.44	0.64	9.44	0.62
Mayfield	Apr	NA		NA		NA	
	Oct	1.44	NA	0.56	NA	12.87	NA
Glen Murken	Apr	0.74		0.29		2.91	
	Oct	2.13	0.35	0.82	0.35	18.56	0.34
Shed	Apr	0.44		0.10		0.41	
	Oct	0.74	0.62	0.20	0.50	8.85	0.61
Homestead	Apr	1.26		0.41		7.22	
	Oct	2.13	0.59	0.68	0.61	14.28	0.61
One Mile	Apr	1.31		0.35		7.65	
	Oct	3.52	0.37	1.14	0.31	21.34	0.34
Warrannee	Apr	NA		NA		NA	
	Oct	2.87	NA	0.89	NA	18.96	NA
Tanbar	Apr	0.65		0.14		1.08	
	Oct	1.04	0.62	0.27	0.52	8.74	0.64
Yorakah	Apr	0.74		0.24		2.70	
	Oct	1.57	0.47	0.54	0.45	14.45	0.47
Yappi	Apr	1.26		0.34		8.23	
	Oct	5.22	0.24	1.47	0.23	26.65	0.20
Top	Apr	0.39		0.17		-6.76	
-	Oct	0.96	0.43	0.38	0.43	6.14	0.51
Waterloo	Apr	0.61		0.15		0.96	
	Oct	1.13	0.54	0.28	0.52	11.5	0.53
Bottom	Apr	0.44		0.17		-5.81	
	Oct	2.13	0.21	1.11	0.16	23.11	0.15
Pelican	Apr	0.83		0.24		4.76	
	Oct	2.04	0.40	0.69	0.34	19.22	0.35

Table 2. Concentrations of Na⁺ and Cl⁻ (meq L⁻¹) and δ^{18} O values (‰) for waterholes in Apr and Oct 2002 and the ratio of final to initial volume (V_r/V_i) calculated from each tracer. Yalungah Waterhole was dry by the Oct sampling. NA, not available.

each waterhole would persist as an aquatic refuge in the absence of new flow inputs, which is critical information for their conservation and management.

Assuming evaporative concentration as the controlling process, the ratio of initial to final Na⁺ or Cl⁻ concentrations equals the ratio of final to initial volume of the waterhole (V_f/V_i) for the April–October period. Table 2 shows good agreement in the V_f/V_i estimates derived from these two ions, which were measured using independent analytical methods.

The stable isotope information was also used to estimate the V_j/V_i for the April–October period. The water balance equation given above was modified to include isotope mass balance (Gonfiantini 1986):

$$d(V\delta_{L})/dt = -E\delta_{E}$$
 (3)

where δ_L is the δ^{18} O of the waterhole, and δ_E is the δ^{18} O of the evaporating moisture. A rearrangement of Eq. 3 yields the following equation:

$$d\delta_{L}/d(\ln f) = \delta_{E} - \delta_{L}$$
 (4)

where $f = V_f/V_i$. The isotopic trajectory of an evaporating waterbody is described by the following equation:

$$\delta_{L} = \delta^* - (\delta^* - \delta_0) f^m \tag{5}$$

where $m = (h - \varepsilon)/(1 - h + \varepsilon_K)$, h is the relative humidity, δ_0 is the initial δ^{18} O, and δ^* is the limiting isotopic composition under the atmospheric conditions of the site (Gat 1995), defined as $(h\delta_A + \varepsilon)/(h - \varepsilon)$. The total (equilibrium

+ kinetic) and kinetic isotope enrichment factors ε and $\varepsilon_{\rm K}$ were estimated from air temperature and relative humidity to be 18.82‰ and 9.80‰, respectively. The $\delta_{\rm A}$ estimated from the evaporation pan experiment (*see* "Sampling and Field Measurements"), together with the temperature and relative humidity, allowed the calculation of both m (mean = 0.43) and δ^* (mean = 48.70‰), following Gibson et al. (1999).

For each waterhole and sampling interval, the estimation of V_f/V_i by Eq. 4 required knowledge of the initial and final δ^{18} O values in the waterhole as well as the δ_E , which was estimated using the linear resistance approximation of Craig and Gordon (Gonfiantini 1986):

$$\delta_{\rm E} = (\delta_{\rm L} - h\delta_{\rm A} - \varepsilon)/(1 - h + \varepsilon_{\rm K}) \tag{6}$$

where $\delta_{\rm A}$ is the $\delta^{\rm 18}{\rm O}$ of atmospheric moisture (estimated at -17.71% from the pan experiment), and h, ε , and $\varepsilon_{\rm K}$ were determined as described. The V_f/V_i ratios estimated from $\delta^{\rm 18}{\rm O}$ agreed well with those derived from Na⁺ or Cl⁻ (Table 2), thereby validating the isotope mass balance model in this situation.

The isotope mass balance approach was extended to include the interval between the river flow through the waterholes in December–January and the first sampling in April 2002. The initial δ^{18} O of the waterholes at bankfull volume, hereafter denoted as V_0 (as opposed to V_p , the initial volume for the interval between sampling), was assumed to be the intersection of the LEL with the LMWL.

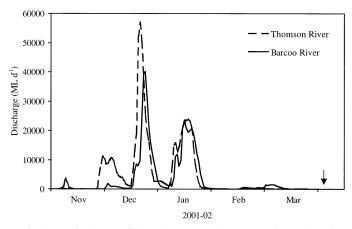


Fig. 2. Discharge of the Thomson and Barcoo Rivers showing the flow pulses preceding the April and October 2002 samplings. The arrow marks the April sampling; no flow occurred in the ensuing interval between April and October. Data were obtained from the Queensland Department of Natural Resources and Mines.

The $V_{\it f}/V_{\it 0}$ estimates for April and October were then graphically compared to the unique stage–volume relation for each waterhole, as determined by morphometric surveys, to determine the corresponding decrease in stage during the January–October period. The resultant stage decreases, together with the elapsed time, yield estimates of mean evaporation rates from each waterhole during the 9-month period. The time periods assume that most of the waterholes began at $V_{\it 0}$ on 24 January 2002 and received no significant new river or rain inputs thereafter. Top and Bottom Waterholes were assumed to begin at $V_{\it 0}$ on 10 March 2002, since the isotopic evidence discussed below indicates that they received water that was distinct from the water received at the other location, presumably from the last significant flow event preceding the April sampling (Fig. 2).

Assuming that this rate of decrease represents the mean rate of evaporative water loss during the intervals between flows, that loss rate was extrapolated forward in time to estimate persistence times for each waterhole in the absence of new flow inputs (Table 3). Ten percent of the bankfull volume was chosen as the point at which a waterhole has been reduced in volume and area so severely that its role as an aquatic refuge is diminished, and therefore, persistence times represent the time to reach $V_{\ell}/V_0 = 0.10$.

Results

River flows and rainfall—Prior to the April 2002 sampling, the waterholes had been flushed by modest river flows in December (mainly from the Thomson River) and January (mainly from the Barcoo River and Kyabra Creek), as shown in Fig. 2. Rainfall during that period was sparse in the vicinity of Windorah and nonexistent at Tanbar. The Windorah flood warning gauge at Currareva Waterhole exceeded the 3-m flood stage from 22 December 2001 to 31 December 2001 and from 12 January 2002 to 24 January 2002, peaking at 5.06 m on 26 December and at 4.03 m on 21 January (data were obtained from the Australian Bureau of Meteorology; the gauge is read only when it exceeds 3 m). Local residents recalled that all of the waterholes sampled in this study were flushed during those flows, although most of the floodplain did not become inundated. The last major flood prior to our sampling that did inundate large expanses of floodplain (~14,000 km²) occurred in February–March 2000, when the Windorah gauge reached 7.45 m (data were obtained from the Australian Bureau of Meteorology).

No significant rainfall or river flow occurred in the Cooper Creek region during the interval between April and October 2002, which is not uncommon during that season. Temperatures were generally above normal, particularly after April

Table 3. Ratio of final to initial volume (V_p/V_0) calculated from δ^{18} O for the Jan–Oct period, corresponding evaporation rate based on stage-volume relations for each waterhole, and estimated persistence time (defined as the time to evaporate to 10% of bankfull volume).

Site	Group	$\begin{array}{c} \text{Jan-Oct} \\ V_{f}/V_{0} \end{array}$	Evaporation rate (m yr ⁻¹)	Persistence time (months)	
Murken Hole	Windorah	0.45	1.15	17.5	
Mayfield	Windorah	0.40*	2.38	13.6	
Glen Murken	Windorah	0.23	2.87	10.6	
Shed	Windorah	0.47	1.05	19.3	
Homestead	Springfield	0.32	†	†	
One Mile	Springfield	0.17	1.71	8.6	
Warrannee	Springfield	0.27*	0.94	12.8	
Tanbar	Tanbar	0.47	1.16	19.1	
Yorakah	Tanbar	0.32	2.27	12.8	
Yappi	Tanbar	0.10	1.12	7.5	
Yalungah	Tanbar	0.50‡	3.80‡	6.0‡	
Тор	Noonbah	0.36	1.15§	22.8§	
Waterloo	Noonbah	0.39	1.49	16.5	
Bottom	Noonbah	0.10	4.98§	8.6§	
Pelican	Noonbah	0.21	3.12	14.8	

^{*} Based only on Oct 2002 sampling; not sampled in Apr.

[†] No morphometric data available for this waterhole.

[‡] Based on the Jan–Apr V_f/V_0 for Yalungah Waterhole because it had dried by the time of the Oct sampling.

[§] Used estimate for Apr-Oct only because of unrealistically high apparent evaporation rate for Mar-Apr (see text).

as El Niño conditions developed. The calendar year 2002 ended with below-normal rainfall and the fifth warmest mean temperatures since 1910 for the Australian continent, although the drought and anomalous warmth were strongest late in the year. The mean daily air temperature at Windorah for February–October 2002 was 22.3°C, compared to a long-term mean daily air temperature of 20.9°C (68 yr). Similar comparisons show lower relative humidity (33.5% in 2002 vs. 46.2% for a 52-yr record). The effect of higher temperature and lower humidity is reflected by pan evaporation rates that were 18% higher than average (8.13 vs. 6.87 mm d⁻¹ for a 32-yr record; all data were obtained from the Australian Bureau of Meteorology).

Major solute hydrochemistry—The Thomson and Barcoo Rivers that join to form the Cooper Creek system were still flowing slowly in April; their ionic compositions were more dilute than the waterholes (Fig. 3), although, based on the isotope data reported later, they may have shown some evaporative concentration compared to the rainfall from which their flow originated. None of the waterholes we sampled was receiving surface flow from these rivers at that time. In April 2002, all of the waterholes contained ionically dilute, slightly basic waters, ranging in specific conductance from 104 to 343 μ S cm⁻¹ (25°C) and in pH from 7.28 to 8.78. By October 2002, their ionic concentrations had increased in each case, and conductance ranged from 220 to 780 µS cm⁻¹ and pH from 7.72 to 9.37. The ionic composition of a waterhole near Windorah (Murken Hole) is shown in Fig. 3 to exemplify the changes between April and October. All of the waterholes we sampled were too shallow to stratify persistently, containing dissolved oxygen throughout the water column, and they were turbid, with high concentrations of very fine suspended clay (turbidity ranged from 334 to 1,010 NTU [nephelometric turbidity units] in April). No saline surface waters were found on the floodplain.

Groundwaters pumped from two windmills near Windorah were considerably richer in ions, with specific conductances of 2,026 and 2,006 μ S cm⁻¹ and ionic compositions that were dominated by Na⁺, Cl⁻, and HCO₃⁻ (Fig. 3). Two rain tanks contained relatively dilute waters, as expected, with specific conductances of 37 and 55 μ S cm⁻¹ and relatively low concentrations of Na⁺ (0.01 meq L⁻¹) and Cl⁻ (0.02 meq L⁻¹).

The initial major solute composition and the degree of increase in concentrations during the isolation phase suggest that calcite and magnesium silicates are likely to be the first minerals to precipitate from these waters as they are concentrated by evaporation (Eugster and Hardie 1978), and this is supported by the results of hydrochemical modeling when PHREEQC is used. The mineral saturation indices for calcite indicated that only two of the most downstream waterholes (Tanbar and Yappi) were supersaturated in April, although by October, most of the waterholes had reached calcite supersaturation; calcite saturation indices did not exceed 1.13 (expressed as the log of the ratio of the ion activity product to the solubility product). Magnesium silicates also showed supersaturation in 5 waterholes in April and in 11 waterholes in October. Thus, the solutes that may be removed from solution by mineral precipitation reactions are Ca²⁺, Mg²⁺, silicate, and HCO_3^- . Other processes that might significantly influence major solute composition in these waters include ion exchange with the suspended sediments, which would most likely influence the divalent cations and K^+ and, perhaps, the diatom uptake of silicate.

Concentrations of Na⁺ and Cl⁻ increased in each waterhole during the April–October period (Fig. 4A). The wind-mill-pumped groundwater had a markedly different ratio of Na⁺:Cl⁻ (Fig. 4B). Only one site (Bottom Waterhole) showed a temporal change in the direction of the windmill water. The remaining waterholes displayed congruent increases in concentrations over time, consistent with evaporative concentration.

Isotope hydrology—The stable isotopic composition of the waterholes indicates enrichment along an LEL (Fig. 5), consistent with the conclusions from conservative solutes. Regression of δD on $\delta^{18}O$ yields similar LEL slopes for the April and October waterhole samples (4.71 and 4.59, respectively), suggesting similar isotopic fractionation upon evaporation between January and April and between April and October, which, in turn, is likely due to similar atmospheric conditions above the water surface across waterholes and over time.

The intersection of the regression line for the combined April and October data with the LMWL, including all waterholes and floodplain pools except for the Noonbah waterhole group (see following), yields an estimate of -4.8% for δ^{18} O and -27.5% for δ D. The isotopic composition of water sampled from rain tanks showed some enrichment, but this could have been caused by slow evaporative losses to the relatively humid air inside the tanks, which would cause a much steeper slope in the evaporation trajectory. For this reason, the rain tanks should not be used as indicators of the isotopic composition of rainfall.

The slowly flowing waters of the Thomson and Barcoo Rivers, sampled in early April at the end of the falling limb of the flow event, were isotopically distinct from one another, and both showed some displacement from the LMWL (Fig. 5). This suggests that, at the time of sampling, they had lost significant water to evaporation during flow through the system, although they were less influenced by evaporation than the waterholes and pools we sampled. Therefore, the intersection of the waterhole LEL and the LMWL should be a better indicator of the isotopic composition of the waters that reached the waterholes than these river samples. Water samples were not collected during the period of river flow through the waterholes.

Two of the four Noonbah waterholes appeared distinct in their isotopic composition and LEL slopes; therefore, all four waterholes in that group were considered separately. The LEL for two of the Noonbah waterholes (Pelican and Waterloo) indicates an isotopic starting point (-4.7% for $\delta^{18}O$) and slope that are similar to those of the rest of the sites, but the LEL based on the other two waterholes (Top and Bottom) intersects the LMWL at -14.8% for $\delta^{18}O$ and at -102% for δD .

The two samples of windmill waters plot close to the LMWL and are relatively depleted, although they may show some evaporation influence. Inputs of this deeper ground-

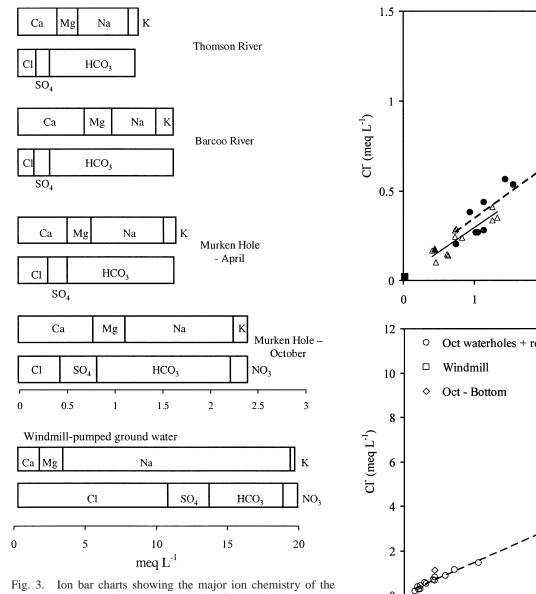


Fig. 3. Ion bar charts showing the major ion chemistry of the Thomson and Barcoo Rivers (sampled when flow had nearly ceased in April 2002), a representative waterhole in April and October 2002, and windmill-pumped groundwater from near Windorah (note different scale).

water cannot produce the progressive isotopic enrichment observed in the waterholes, which concurs with the evidence from Na^+ and Cl^- .

The evaporation pan experiment showed the expected isotopic enrichment as its water volume was reduced by evaporation (Fig. 6). Following the approach outlined by Gibson et al. (1999), these data were used, together with temperature (mean = 28.4°C) and relative humidity (mean = 0.31) from the meteorological station, to estimate a mean δ^{18} O of atmospheric moisture (δ_{Δ}) of -17.71‰.

Evaporative water loss and persistence time—The V_f/V_0 ratios calculated for the January–October period were combined with the stage–volume relation for each waterhole to estimate evaporation rates and persistence times (Table 3;

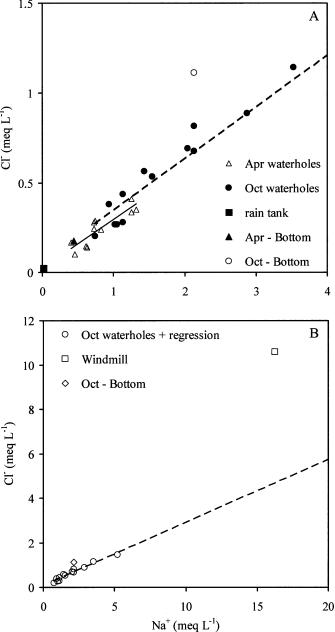


Fig. 4. (A) Concentrations of Na⁺ and Cl⁻ in the waterholes in April and October 2002, with separate regression lines fit to data from each sampling date (Bottom Waterhole was excluded from the regressions). Concentrations in water from a rain tank are included for comparison. (B) Comparison of Na⁺ and Cl⁻ in the waterholes in October 2002 with concentrations in windmill-pumped groundwater from near Windorah (note different scale).

Fig. 7). Evaporation rates deviated considerably from the pan evaporation rate of 2.51 m yr⁻¹ observed at Windorah from February to October 2002, being lower in all but four cases and substantially greater in one waterhole (Bottom Waterhole; Table 3).

Persistence-time estimates are mostly >1 yr, reflecting the selection of sites based on the criterion that they usually contained water throughout the dry season. Some waterholes

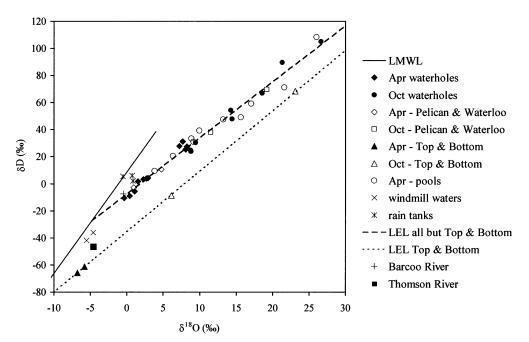


Fig. 5. Stable isotope ratios of water in the waterholes (April and October 2002) as well as in the floodplain pools, windmill-pumped groundwaters, rivers, and rain tanks in their vicinity (April only). The local meteoric waterline (LMWL) is for rain events at Alice Springs >100 mm, and the local evaporation lines (LELs) are based on regressions for the April and October measurements in waterholes and pools. A distinct LEL was fit to Top and Bottom Waterholes.

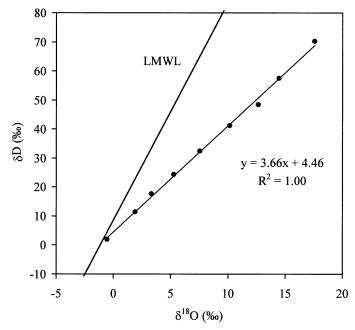


Fig. 6. Stable isotope ratios in an evaporating pan of rainwater, showing progressive enrichment for 32 d from an initial isotopic composition close to the local meteoric waterline (LMWL; solid line); the enrichment trend is shown by the regression line. The LMWL is for rain events >100 mm at Alice Springs.

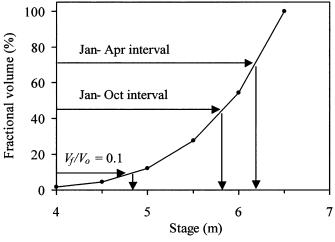


Fig. 7. Estimation of persistence time using the unique stage-volume relation for each waterhole demonstrated using Murken Hole as an example. Waterholes were assumed to be at bankfull stage (100% volume) when the river flow ceased in January. The δ^{18} O-based V_f/V_0 estimates for April and October showed the concomitant decrease in stage (evaporation rate) during the January-October period of no river flow. This rate of decrease in stage was then extrapolated forward in time to determine the persistence time, defined as how long it would take for the waterhole to evaporate to a stage corresponding to 10% of its bankfull volume ($V_f/V_0=0.1$).

were estimated to have markedly longer persistence times than others, and this does not appear to be a simple function of either basin morphology or evaporation rates alone. Pearson correlations between morphometric parameters (area and mean depth) and fractional water loss, evaporation rates, and persistence times showed no significant relationships at the p=0.05 level for waterhole area and only one positive relationship (r=0.56, p=0.04 between mean depth and the January–October V_f/V_0). Persistence times are not significantly correlated (p=0.05) with evaporation rates, which, in turn, are not significantly correlated with the January–October V_f/V_0 estimates.

Discussion

Waterhole hydrology—Evidence from major solute and stable isotopic tracers indicates that during the isolation phase, the hydrology of waterholes in the Cooper Creek system is dominated by evaporative water loss. Therefore, the interval between flows that fill the waterholes to bankfull level dictates whether they persist as refuges for aquatic biota. This finding concurs with two studies of similar waterholes in other Australian river systems, one based on an analysis of water level changes (Costelloe et al. 2003) and the other based on an observation of the evaporative concentration of solutes (Townsend 2002).

The variable evaporation rates we measured may be influenced in part by waterhole size, but other factors are also likely to be important, such as the effective fetch for wind action, the height and width of riparian vegetation, and the degree of channel incision below the levees, which affect wind-induced turbulence at the water surface, exposure of the water surface to solar heating, and convective air circulation above the water surface (Brutsaert 1982). Prediction of persistence times from basin morphometry and channel and riparian-zone features, which are potentially observable on broader scales using remote sensing, would be desirable to extend these results to other waterholes.

The use of major solutes as tracers of evaporation requires that they behave nearly conservatively in solution. Na+ and Cl- are often chosen because these ions are little affected by mineral precipitation, ion exchange reactions, or biotic uptake and release. Na+ could conceivably be added to solution by mineral weathering (e.g., feldspar), but there was no evidence in this study for substantial increases in Na+ relative to Cl-. Other alternative explanations for the increase in Na+ and Cl- concentrations, besides evaporative concentration, include inputs of groundwater or dry deposition of solids containing Na+ and Cl- in the same proportions as the river water. Samples of pumped groundwater had markedly different ratios of these ions, however. Rates of dry deposition of dust are high in this semiarid climate (Leys and McTainsh 1999), but if dry deposition were a major source of these ions, the rain tanks would have been markedly enriched in Na+, Cl-, and other solutes due to leaching from the rooftop collection surfaces, and yet this was not observed (Fig. 4A).

Two waterholes—Top and Bottom—clearly differed from the rest in their isotopic composition (Fig. 5). Information

from a local resident (Angus Emmott of Noonbah Station) indicates that these waterholes are connected by almost any flow event, whereas nearby Pelican and Waterloo Waterholes are connected only at higher river flows. Therefore, the distinct isotopic composition of the source water for Top and Bottom Waterholes might reflect the last flow event of the Thomson River in the first week of March, which was likely too small to influence the other waterholes (Fig. 2). The distinct isotopic composition of the Thomson River in April (Fig. 5) supports this interpretation. However, despite accounting for the difference in isotopic composition of the source water, Bottom Waterhole is also distinctive in its high apparent evaporation rate of ~ 5 m yr⁻¹, far exceeding openpan rates measured at the Windorah meteorological station. We found nothing in the data or calculations to invalidate this evaporation rate estimate for Bottom Waterhole, although we acknowledge that it appears to be erroneously high. It is plausible that this waterhole received inputs of water that were elevated in Na+ and Cl-, as suggested by its departure in the direction of windmill-pumped groundwater in Fig. 4A, but those inputs would also have to be highly enriched in ¹⁸O and ²H, in contrast to what we found in the two samples of windmill waters closer to Windorah. Furthermore, there would have to have been simultaneous outputs of water as well as inputs, because the water level observed in October fit the persistence-time estimate that it should have been close to 10% of bankfull by that time. An alternative explanation involves the unusual basin morphometry of this waterhole, which has a deep hole and broad shallow area; if the water column stratifies over the hole, then the volume exposed to evaporation would be less than we assumed. Thermal profiles were not available to test this hypothesis.

Stage monitoring could provide similar information on rates of drawdown by evaporation (Costelloe et al. 2003). Ideally, stage data would be accompanied by the examination of tracers of groundwater inputs to ensure that the changes observed are largely driven by evaporation. Unfortunately, no stage data were available for the waterholes of the Cooper Creek system.

Caveats—Assumptions of the present analysis include (1) groundwater inputs would resemble the windmill-pumped waters of the underlying aquifer, or at least they would differ geochemically from surface waters; (2) the short-term evaporation pan experiment represented atmospheric conditions during the January–October study period; and (3) the period of this study represented conditions for longer periods for the extrapolations to reliably estimate persistence times. We also assumed no significant water withdrawals for human use.

The timing of this study is also important. The drier and hotter conditions of 2002 were discussed above and presumably produced higher evaporation rates and thus shorter persistence-time estimates, although the relative differences among waterholes should not have changed. Antecedent flows were moderate and thus probably representative of most annual flow events; much larger floods that inundate more of the floodplain could conceivably result in greater infiltration and movement of water along local groundwater

flow paths, effectively causing a temporary storage of floodwaters that slowly return to the waterholes. In that case, the chemical and isotopic composition of the groundwater returning to the waterholes may differ relative to the river water from which it originated, with the degree of change dependent on the residence time of the water on the surface, where it would be subject to evaporative fractionation of isotopes, and underground, where its ionic composition would be more strongly influenced by chemical interactions with soil minerals.

The results that we report regarding the predominant influence of evaporation on waterhole drawdown should not be assumed to apply to every waterhole in the region without a more widespread survey. There are climatic, hydrogeologic, and geomorphic variations across the Cooper Creek system that may influence surface—groundwater exchanges. If there are some waterholes that are indeed groundwater dependent, they could be exceptionally important aquatic refugia during the most extended dry periods, unless the groundwater is saline. Future surveys should be designed to identify whether such sites exist.

Human impacts on refugia in dryland rivers—The importance of frequent but modest river flows in maintaining aquatic refugia in this dryland river has implications for the conservation of the river biota. Human activities potentially affect the amount of water in these refugia and the duration that they persist between flow pulses. River flow regimes can be altered by upstream impoundments or capture of runoff for agricultural use (water harvesting), and water can be withdrawn directly from waterholes during intervals between flows (Thoms and Sheldon 2000). Relative amounts of river flow through various channels in an anabranched system can readily be altered by small impoundments, raised roads or other interferences with the geomorphological structure of the channels. Such impacts should be carefully considered because hydrological modifications that result in increased frequency and extent of waterhole desiccation could have deleterious ecological impacts, including a reduction or local extirpation of aquatic animals such as fishes and turtles as well as reduced water availability for riparian trees, floodplain wildlife, and livestock.

The absence of significant groundwater inputs to the waterholes during the isolation phase underscores the importance of managing river flows across the range of flow events to conserve these ecosystems (Richter et al. 1997). Alterations in the frequency and duration of river through-flow may, in turn, change the duration of the ensuing isolation phase. From the standpoint of managing waterholes as discrete ecosystems, the size of the flow event may be less important than the frequency of events that refill them; modest discharges that produce flow through the channels could maintain waterholes in dry years, even if they do not inundate the adjacent floodplains. These more frequent flow events may act together with occasional major flows in maintaining the geomorphology of waterhole basins (Knighton and Nanson 1994a) and in providing connectivity across the region for the movement of aquatic animals between refugia (Sheldon et al. 2002). River water withdrawals for human use tend to disproportionately affect the more modest flows rather than the largest ones (Thoms and Sheldon 2000). Although the natural flow regime seems critical to the maintenance of waterholes as refugia, the results of this study suggest that the exploitation of groundwater in the aquifers underlying the waterholes has little impact on their hydrology and ecology, as long as that groundwater is not discharged into the waterholes, where it could alter the hydrochemistry. Hydrological modifications in the headwaters of the river system, such as groundwater and river water extraction, construction of dams, and deforestation, are likely to be produce more important impacts on aquatic refugia through changes in the natural flow regime (Poff et al. 1997).

References

- BAILEY, V. 2001. Western streams water quality monitoring project. Queensland Department of Natural Resources and Mines.
- Brutsaert, W. 1982. Evaporation into the atmosphere: Theory, history, and applications. Reidel.
- Bunn, S. E., S. R. Balcombe, P. M. Davies, C. S. Fellows, and F. J. McKenzie-Smith. In press. Aquatic productivity and food webs of desert river ecosystems. *In* R. T. Kingsford [ed.], Changeable, changed, changing: The ecology of desert rivers. Cambridge Univ. Press.
- ——, P. M. DAVIES, AND M. WINNING. 2003. Sources of organic carbon supporting the food web of an arid zone floodplain river. Freshwater Biol. **48:** 619–635.
- COOK, B. D., S. E. Bunn, And J. M. Hughes. 2002. Genetic structure and dispersal of *Macrobrachium australiense* (Decapoda: Palaemonidae) in western Queensland, Australia. Freshwater Biol. 47: 2098–2112.
- COSTELLOE, J. F., R. B. GRAYSON, AND T. A. McMahon. 2003. Hydrological characteristics of arid zone river waterholes. Proc. 2nd Internat. Hydrol. Water Resources Symp., The Institution of Engineers (Australia).
- DAVIES, B. R., M. C. THOMS, K. F. WALKER, J. H. O'KEEFE, AND J. A. GORE. 1994. Dryland rivers: Their ecology, conservation and management, p. 537–600. *In* P. Calow and G. E. Petts [eds.], The rivers handbook, V. 2. Blackwell.
- EUGSTER, H. P., AND L. A. HARDIE. 1978. Saline lakes, p. 237–293. In A. Lerman [ed.], Lakes—chemistry, geology, physics. Springer-Verlag.
- GAT, J. R. 1995. Stable isotopes of fresh and saline lakes, p. 139–165. *In* A. Lerman, D. M. Imboden, and J. R. Gat [eds.], Physics and chemistry of lakes. Springer-Verlag.
- GIBLING, M. R., G. C. NANSON, AND J. C. MAROULIS. 1998. Anastomosing river sedimentation in the Channel Country of central Australia. Sedimentology **45:** 595–619.
- GIBSON, J. J., T. W. D. EDWARDS, AND T. D. PROWSE. 1999. Panderived isotopic composition of atmospheric water vapour and its variability in northern Canada. J. Hydrol. 217: 55–74.
- GONFIANTINI, R. 1986. Environmental isotopes in lake studies, p. 113–168. *In* P. Fritz and J. C. Fontes [eds.], Handbook of environmental isotope geochemistry, V. 3. Elsevier.
- HATTON, T., AND R. EVANS. 1998. Dependence of ecosystems on groundwater and its significance to Australia. LWRRDC Occasional Paper 12/98. Land and Water Resources Research and Development Corporation.
- HUGHES, J. M., AND M. J. HILLYER. 2003. Patterns of connectivity among populations of *Cherax destructor* (Decapoda: Parastacidae) in western Queensland, Australia. Mar. Freshwater Res. 54: 587–596.
- KINGSFORD, R. T., A. J. BOULTON, AND J. T. PUCKRIDGE. 1998. Challenges in managing dryland rivers crossing political

boundaries: Lessons from Cooper Creek and the Paroo River, central Australia. Aquat. Conserv. Mar. Freshwater Ecosyst. 8: 361–378.

- ——, A. L. CURTIN, AND J. L. PORTER. 1999. Water flows on Cooper Creek determine 'boom' and 'bust' periods for waterbirds. Biol. Conserv. 88: 231–248.
- KNIGHTON, A. D., AND G. C. NANSON. 1994a. Waterholes and their significance in the anastomosing channel system of Cooper Creek, Australia. Geomorphology 9: 311–324.
- ——, AND ——. 1994b. Flow transmission along an arid zone anastomosing river, Cooper Creek, Australia. Hydrol. Proc. 8: 137–154.
- LESACK, L. F. W., AND J. M. MELACK. 1995. Flooding hydrology and mixture dynamics of lake water derived from multiple sources in an Amazon floodplain lake. Water Resour. Res. 31: 329–345.
- LEYS, J. F., AND G. H. McTAINSH. 1999. Dust and nutrient deposition to riverine environments of south-eastern Australia. Z. Geomorph. N.F., Suppl.-Bd. **116:** 59–76.
- MERTES, L. A. K. 1997. Documentation and significance of the perirheic zone on inundated floodplains. Water Resour. Res. **33:** 1749–1762.
- POFF, N. L., AND OTHERS. 1997. The natural flow regime: A paradigm for conservation. BioScience 47: 769–784.
- Puckridge, J. T., F. Sheldon, K. F. Walker, and A. J. Boulton. 1998. Flow variability and the ecology of large rivers. Mar. Freshwater Res. **49:** 55–72.
- ——, K. F. WALKER, AND J. F. COSTELLOE. 2000. Hydrological persistence and the ecology of dryland rivers. Regul. Rivers Res. Manag. **16**: 385–402.

- RICHTER, B. D., J. V. BAUMGARTNER, R. WIGINGTON, AND D. P. BRAUN. 1997. How much water does a river need? Freshwater Biol. 37: 231–249.
- ROSHIER, D. A., A. I. ROBERTSON, AND R. T. KINGSFORD. 2002. Responses of waterbirds to flooding in an arid region of Australia and implications for conservation. Biol. Conserv. **106**: 399–411.
- Rust, B. R., and G. C. Nanson. 1986. Contemporary and palaeo channel patterns and the late Quaternary stratigraphy of Cooper Creek, southwest Queensland, Australia. Earth Surf. Proc. Landforms 11: 581–590.
- Sheldon, F., A. J. Boulton, and J. T. Puckridge. 2002. Conservation value of variable connectivity: Aquatic invertebrate assemblages of channel and floodplain habitats of a central Australian arid-zone river, Cooper Creek. Biol. Conserv. 103: 13–31.
- THOMS, M. C., AND F. SHELDON. 2000. Water resource development and hydrological change in a large dryland river: The Barwon-Darling River, Australia. J. Hydrol. 228: 10–21.
- Townsend, S. A. 2002. Seasonal evaporative concentration of an extremely turbid water-body in the semiarid tropics of Australia. Lake Reservoir Manag. 7: 103–107.
- WALKER, K. F., F. SHELDON, AND J. T. PUCKRIDGE. 1995. A perspective on dryland river ecosystems. Regul. Rivers Res. Manag. 11: 85–104.
- WETZEL, R. G., AND G. E. LIKENS. 2000. Limnological analyses, 3rd ed. Springer-Verlag.

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