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Determining the ecohydrological character of aquatic refugia in a dryland river system: the importance of temporal scale

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Abstract

Aquatic refugia are important features of riverine landscapes; providing habitat for biota during extremes and facilitating the recovery of biota from disturbance. The persistence and quality of aquatic refugia is intricately linked to the hydrological regime of their parent rivers. Knowledge of the influence of hydrology on refugia is essential for understanding their role in the functioning of riverine ecosystems. A hierarchical framework is used to investigate the hydrological character of refugial waterholes in a dryland river system at multiple temporal scales. The study demonstrates that temporal variability is matched by a high level of spatial variability in hydrological character and that spatial patterns in hydrological character varied according to the temporal scale at which hydrological characterisation was made. The findings of this study have important implications for dryland river ecosystems because of the fundamental importance of hydrology as a driver of riverine ecosystems.

Key words: ecohydrology, refugial waterholes, hierarchical framework, dryland rivers.

1. Introduction

Aquatic refugia play an important ecological role in riverine systems that experience variable hydrological regimes (Lancaster, Belyea 1997; Lake 2003). During disturbances such as high flows, low flows and no-flow periods, persistent aquatic floodplain habitats and in-channel waterholes remain and serve as important refugia that provide habitat, shelter and protection for water-dependent biota (Morton *et al.* 1995; Magoulick, Kobza 2003) and contribute to the recovery of river-floodplain ecosystems following such disturbances (Poff, Ward 1990; Sedell *et al.* 1990). Extended periods of no flow are common in dryland river systems (Graf 1988) and the utilisation of refugia by aquatic organisms is often the key to the survival of populations (Balcombe *et al.* 2006), and strongly influences the capacity of populations and ecosystem processes to recover (Lake 2003; Arthington *et al.* 2005).

The persistence and quality of refugial waterholes is intricately linked to their hydrological regime which governs their connectivity with other refugia within the riverine landscape (Lake 2003), provides water and renews waterhole resources. Knowledge of the influence of hydrology on refugia is essential for understanding their role in the functioning of riverine ecosystems (Lancaster, Belyea 1997; Magoulick, Kobza 2003). However, the highly variable and unpredictable hydrological nature of dryland rivers means that it is difficult to determine their hydrological character (McMahon, Finlayson 2003). Moreover, hydrological processes operate at a variety of spatial and temporal scales, all of which have the potential to generate different ecological responses (Poff *et al.* 1997; Dollar *et al.* 2007). In light of this, a temporal flow hierarchy has been proposed to meet the challenges of characterising hydrology in dryland river systems (Puckridge *et al.* 1998; Puckridge *et al.* 2000; Thoms, Sheldon 2000). Three temporal scales are recognised in the hydrological hierarchy as being important for river ecosystem function: flow regime, flow history and flow pulse. Regime-scale hydrology operates over hundreds of years and represents the long-term statistical generalisation of flow behaviour. History-scale hydrology operates between one and one hundred years and incorporates the sequence of floods and dry-spells during that time. Finally, the pulse-scale represents conditions at the scale of single flow events.

Although low-flow periods and no-flow events are characteristic of dryland ecosystems and are essential to the long-term functioning of these ecosystems (Graf 1988; Walker *et al.* 1995; Humphries, Baldwin 2003), water resource development has significantly changed their hydrological character (Kingsford 1999; Thoms, Sheldon 2000; Bunn *et al.* 2006b). Climate change is predicted to further increase the intensity and frequency of low and no-flow periods in these regions, and with continued water resource developments, the pressure on aquatic refugia will become even more influential on the continued resilience of aquatic ecosystems (Lake 2003). For this reason, the role of the entire hydrological regime in maintaining refugia, especially in relation to low-flow periods and no-flow events, need serious consideration (Lancaster, Belyea 1997; Bunn *et al.* 2006a).

This study uses the hierarchical framework of Dollar *et al.* (2007) and James and Thoms (2010) to investigate the hydrological character of refugial waterholes in a dryland river system. The knowledge gained from this study provides the hydrological context for further studies that examine how hydrology across a range of temporal scales influences ecosystem character and food web structure.

2. Materials and methods

2.1. Study Area and Methods

A series of waterholes located in the Lower Balonne Floodplain region of the northern Murray-Darling Basin, SE Australia were utilised for this study. The Lower Balonne Floodplain ecosystem extends from St George in Queensland (QLD) to the Barwon-Darling River in northern NSW and covers an area of 19 800 km^2. It is an extensive floodplain wetland complex (Thoms *et al.* 2002) comprised of four principal channels – the Culgoa, Birrie, Bokhara and Narran rivers – as well as a maze of smaller channels, flood runners, numerous permanent and ephemeral billabongs, swamps and waterholes. The region has been categorised by Thoms and Sheldon (2002) as the anastomosing zone of the Condamine-Balonne. Low-level private weirs along the Culgoa, Birrie, Bokhara and Narran provide stock and domestic supply. River regulation for mostly cotton irrigation, controls approximately 30% of the Condamine-Balonne river channel and Jack Taylor Weir (10,100 ML) at St George controls flow to the Lower-Balonne (Thoms, Parsons 2003). Water is also pumped from the rivers and distributary channels of the Lower Balonne during flow events and flood overflows are diverted to storages by levees and drains on the floodplain (Cullen *et al.* 2003).

Discharges of the five main channels in the Lower Balonne differ. A large proportion of average flows occur in very wet years and during major floods. Variability in flow is also high: coefficients of variation (CVs) for annual flows range from 103 to 200 and median annual flows can be less than 30% of mean annual flow. Flows (both annual volumes and flood peaks) generally decrease downstream towards the end of the system because of a lack of tributary contributions and high evaporation, a characteristic feature of Australian inland river systems (Thoms, Sheldon 2002). There have been changes in the hydrological regime of the Lower Balonne over the last 100 years, with the period prior to the 1900s and since the mid-1940s being wetter, on average. This has been associated with greater runoff and flood activity than for the period 1900 to 1945. These changes reflect the shift in the geographical pattern of correlation between precipitation and the Southern Oscillation Index (SOI) for the years before the 1950s compared with the years since the 1950s.

Potential refugial waterholes on the Lower Balonne were identified through examination of aerial photographs and topographic maps, and consultation with local communities and landholders.

As a result of this process 22 refugial waterholes were identified and confirmed by ground survey during November 2007 after a 44 month dry period in which the system had not experienced complete hydrological connection. After complete connection was experienced in the Lower Balonne in December 2007, 16 of the 22 waterholes were selected for assessment; 4 on each of the Culgoa, Birrie, Bokhara and Narran rivers (Fig. 1, Table I).

Daily discharge data for 11 gauging stations, located across four rivers (Fig. 1, Table I), were used to characterise the hydrology of the 16 refugial waterholes identified in the system (Fig. 1).

These data (1965-2008) were used to calculate 32 hydrological variables for each gauging station at each of the three temporal scales: flow regime, flow history and flow pulse (Table II). The relatively short period of flow data used to calculate flow regime variables meant that the derived variables may not provide a true characterisation of flow regime and must be treated with caution; however, this limitation is imposed by the availability of historical flow data and hence could not be avoided.

Table I. Refugial waterholes and their corresponding gauging stations. Waterhole names are based on the properties where they are located.

River	Waterhole	Gauge #	Map ID #
Culgoa	Brenda	422015	1
	Caringle	422017	2
	Westmunda	422011	3
	Gurrawarra	422006	4
Birrie	Kookaburra	422013	5
	Talawanta	422010	6
	Eurah		
	Twin Rivers		
Bokhara	Dumble	422014	7
	Willoh	422005	8
	Warranilla		
	Bokhara Plains		
Narran	Eulreul	422012	9
	Angledool		
	Bangate	422016	10
	Narran Park	422029	11

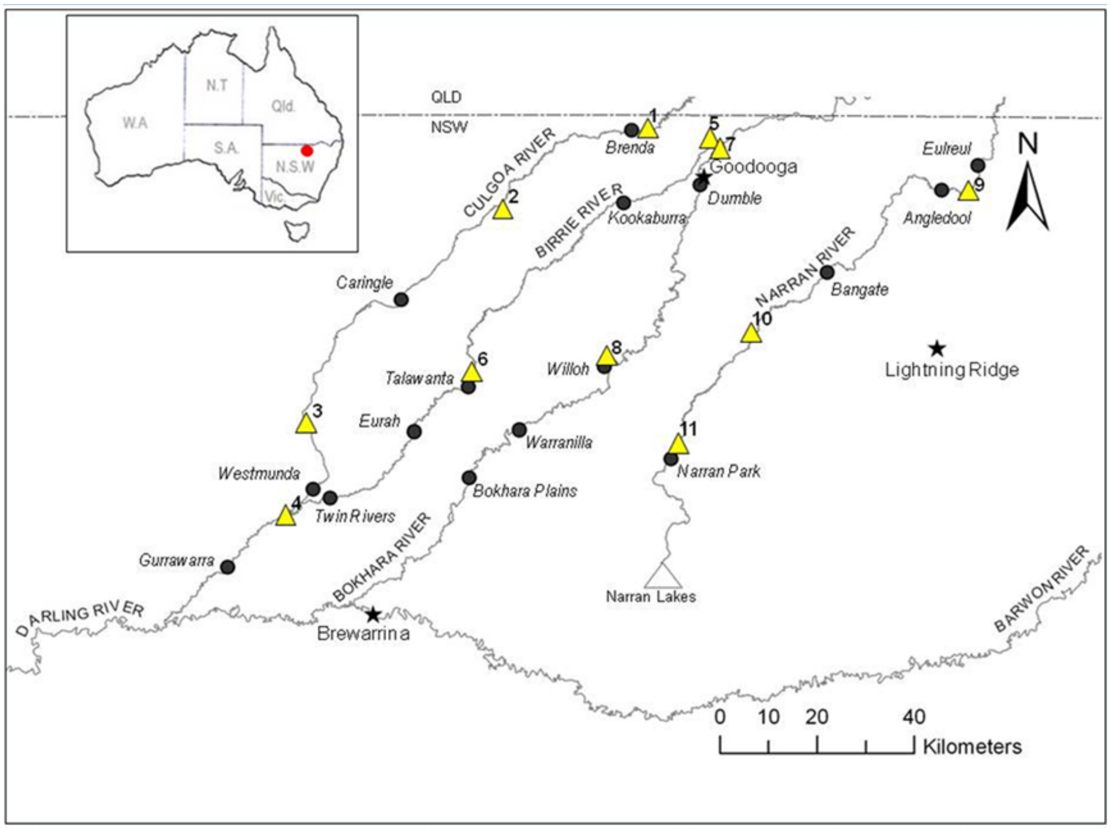

Fig. 1. Study area situated in the New South Wales section of the Lower Balonne floodplain. Triangles represent gauging stations that correspond to information in Table 1; refugial waterhole locations are indicated by filled circles with italicised labels.

Table II. Hydrology variables used to describe the hydrological character of waterholes at the regime, history and pulse scales.

	Variable description	**Variable code**
Flow Regime variables	Median annual flow	Med
	Coefficient of variation in flow	CV
	Variation in flow	Var
	Number of no flow days	No flow
	Lane's index of variability	Lane
Flow history variables	Number of connection events	HSNum
	Average magnitude of connection events	HSMag
	Mean duration of connection events	HSMeanDur
	Total duration of connection events	HSTotDur
	Total of periods between connection events	HSTotPerBetw
	Mean period between connection events	HSMPerBetw
	Longest period between connection events	HSMaxPerBetw
	Base Flow Index	BFI
	Flood Flow Index	FFI
	Colwell's index of Predictability	P_MedM
	Colwell's index of Constancy	C_MedM
	Colwell's index of Contingency	M_MedM
	Partial series 1Yr ARI	PS1YrARI
	Partial series 2Yr ARI	PS2YrARI
	Annual series 5Yr ARI	AS5YrARI
	Annual series 10Yr ARI	AS10YrARI
	Annual series 15Yr ARI	AS15YrARI
	Annual series 20Yr ARI	AS20YrARI
Flow pulse variables	Frequency of threshold exceedence	TotalEvents
	Frequency of local connection	LocalConn
	Frequency of upstream connection	U/sConn
	Frequency of downstream connection	D/sConn
	Frequency of either upstream or downstream connection	AnyConn
	Frequency of total longitudinal connection	RiverConn
	Total volume of water above connection threshold	TotalVol
	Duration of threshold exceedence (%)	%ExceedDur
	Days since last flow above threshold	LastEvent

Any gaps in the daily flow data were infilled using regional correlations, as outlined by Gordon *et al.* (1992). In addition, daily discharge data for the two years prior to this study (January 2006 to December 2007) were used to characterise the hydrological regime at the flow-pulse scale; here a Spell Analysis (Thoms, Parsons 2002) was undertaken to analyse the frequency, duration and magnitude of hydrological connection experienced by each waterhole.

All variables associated with hydrological connectivity of waterholes were based on a flow connection threshold established for each waterhole. This was established using rating curves and channel cross-sectional data for the various gauging stations. The minimum discharge at which a flow connection is made between waterholes to allow a sufficient water depth for fish movement (in this case a 30 cm water depth to allow the common top predators *Macquaria ambigua* to move between sites) was calculated using the method of Thoms *et al.* (2005). The selection of this threshold ensures that flows experienced at each site include only those that are ecologically significant, since this work has been used in further studies exploring the relationship between hydrological character, fish communities and food web structure. For pulse-scale connectivity, several forms of connection were recognised:

1. exceedence of the connection threshold (threshold exceedence);
2. exceedence of the connection threshold without exceedence at either upstream or downstream gauges (local connection)
3. exceedence of the connection threshold synchronous with exceedence at an upstream gauging station (upstream connection);
4. exceedence of the connection threshold synchronous with exceedence at a downstream gauging station (downstream connection);
5. exceedence of the connection threshold synchronous with exceedence at all gauging stations in the river (total longitudinal connection).

These additional variables were used to distinguish between increases in stage height associated with local rainfall and those associated with larger scale events.

2.2. Data analysis

The hydrological character of gauging stations was compared at each temporal scale through the use of resemblance matrices calculated using each set of hydrology variables (i.e, variables at the regime, history and pulse scales). The resemblance matrices were based on Gower dissimilarity measures, in which between sample similarities are based on calculations that incorporate range-standardisation to allow for the use of variables with differing scales and ranges (Belbin 1993). The resemblance matrices derived for regime, history and pulse scales were used in hierarchical classifications to determine groups of gauging stations that were hydrologically similar at each temporal scale. Non-metric multi-dimensional scaling ordinations were also carried out on each matrix to provide a further visual representation of the hydrological character of gauging stations in ordination space. The influence of each hydrology variable on the ordination of gauging stations was examined using a Principal Component Correlation (PCC) which carries out multiple linear regressions of ordination coordinates with the hydrology variables. The correlation value (r^2) produced for each hydrology variable is an indication of the strength of the association between the variable and the position of the stations in ordination space (Thoms, Parsons 2003). Variables with an r^2 value equal or greater than 0.75 were considered to have a strong influence on the position of stations in ordination space. All multivariate analyses were performed using the PATN analysis package (Belbin, 1993).

3. Results

Each of the four river systems within the Lower Balonne has a distinct general hydrological character. Mean annual discharges are substantially greater in the Culgoa River compared to the Bokhara, Birrie and Narran Rivers, while flow variability, as measured by the coefficient of variation of daily flows, also differs between the four rivers and along each river system. Along the Culgoa River, flows at the upper and lower gauging stations have higher co-efficients of variation compared to stations in the mid-sections (Table III). Similarly, flows in the lower Narran River are less variable in comparison to flows in the mid and upstream sections (Table III). The between-river variation shows that flows in the Birrie and Bokhara Rivers are more variable in comparison to the Culgoa and Narran Rivers. Overall, there is a tendency for flow variability to decrease slightly downstream in each river (Table III).

Hierarchical classifications of the 11 gauging stations according to their hydrological character at the regime, history and pulse scales are shown in the dendrograms of Fig. 2. Groups of gauging stations that emerge from the classifications based on regime- and history-scale variables are essentially the same ((a) and (b)). Accordingly, for both the flow regime and flow history scale, three groups of gauging stations can be identified; the first being the gauging stations on the Birrie and Bokhara Rivers, the second consisting of gauging stations on the Narran River and the third consisting of the gauging stations on the Culgoa River. Because the classifications based on flow regime and flow history variables are essentially the same, the groups resulting from these classifications are hereafter described collectively as the Longer-term hydrology Groups or LT Groups.

Principal component correlations reveal that 14 of the 22 longer-term hydrology variables are strongly associated ($r^2 > 0.80$) with the positions of each of the 11 gauging stations in ordination space

Table III. Statistics for annual discharge (ML) at the 11 Lower Balonne Rivers gauging stations included in the study. Rivers are in order from west to east and from upstream to downstream. Map ID numbers correspond to gauging station locations in Figure 1.

Map ID	River and gauge name	Gauge	Record	Median	Mean	Max	Min	CV
1	Culgoa @ Brenda	422015	1965-2008	206842	391288	3941766	1329	174
2	Culgoa @ Weilmoringle	422017	1965-2008	176052	268989	1902608	266	134
3	Culgoa @ Mundiwa	422011	1965-2008*	179565	223791	964828	3626	94
4	Culgoa @ Kenebree	422006	1965-2008	223813	454014	3660165	4316	160
5	Bokhara @ Goodooga	422014	1965-2008	11595	54648	724605	0	221
6	Bokhara @ Bokhara Plains	422005	1965-2008**	13015	59744	610283	0	204
7	Birrie @ Goodooga	422013	1965-2008	22074	79559	1052444	0	217
8	Birrie @ Talawanta	422010	1965-2008	19471	67156	522959	0	167
9	Narran @ Angledool	422012	1965-2008	68986	145256	1135833	0	144
10	Narran @ Belvadere	422016	1965-2008	69440	136576	1078031	0	143
11	Narran @ Narran Park	422029	2001-2008	173	13914	40976	0	130
			*data missing from 1985-1992 **data missing from 1993					

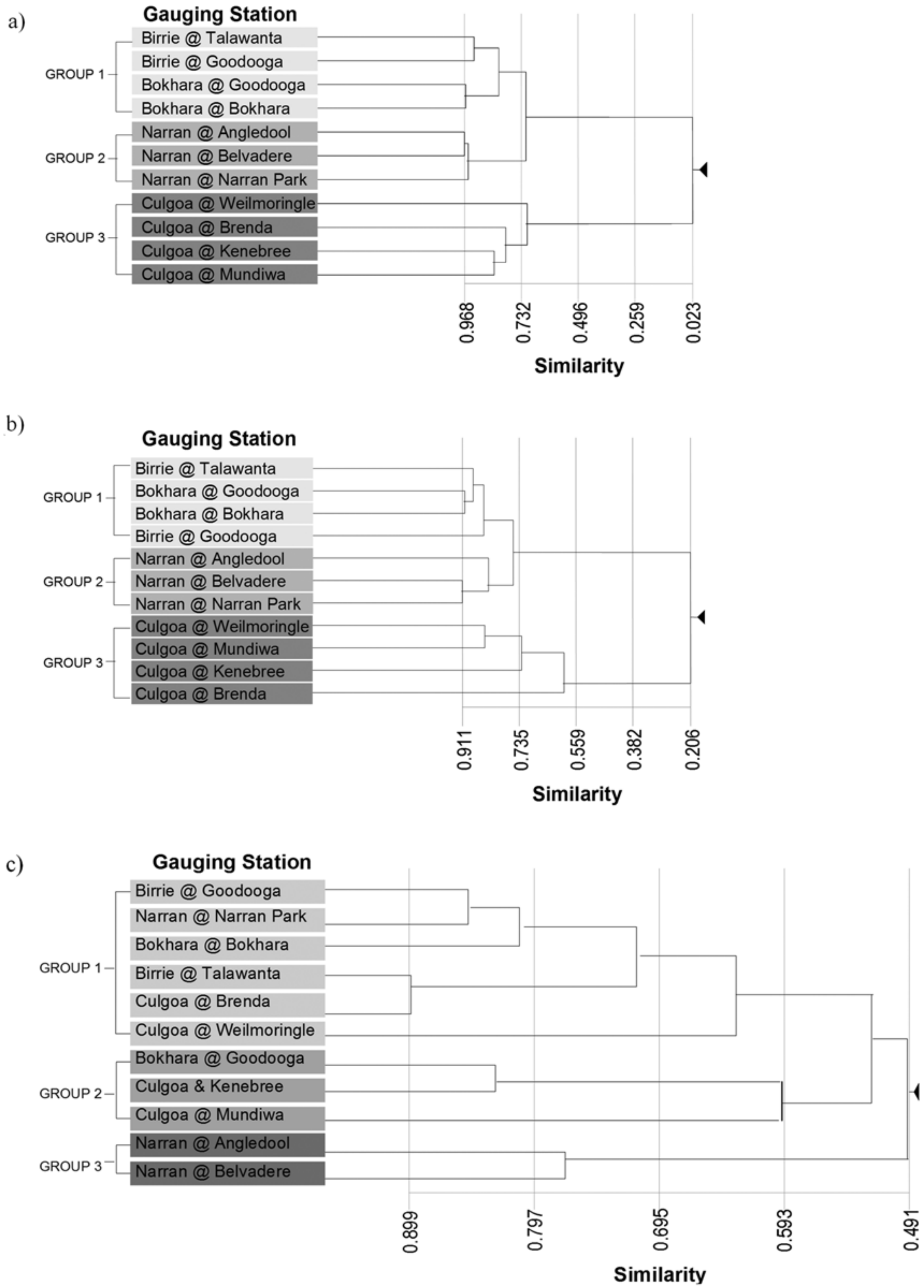

Fig. 2. Hierarchical classification of Lower Balonne gauging stations based on (a) flow regime-scale hydrology variables, (b) flow history-scale hydrology variables and (c) flow pulse-scale hydrology variables. Groups indicate gauging stations with similar hydrological character.

(Table IV, Fig. 3). These include variables describing the duration and magnitude of connection events, the duration of periods of disconnection and no flow, the magnitudes of medium to large floods, overall flow variability and low-flow variability as well as measures of predictability and constancy (Table IV). Gauging stations in LT Group 1 (Birrie and Bokhara Rivers) are characterised by low frequencies and durations of connection events and by long periods of disconnection and no flow (Table IV, Fig. 3). Flow predictability and constancy and low flow variability (Lane Index) are lowest at LT Group 1 gauging stations. Flood magnitudes at these gauging stations are also substantially lower than at the remaining gauging stations. LT Group 2 gauging stations (Narran River) are also characterised by short durations of connection, long periods of disconnection and no flow and low predictability and constancy; they are distinguished from those of LT Group 1 by a greater frequency of connection events, by higher magnitude floods and by greater low-flow variability (Table IV, Fig. 3). Finally, LT Group 3 gauging stations (Culgoa River) experience more frequent, longer and larger magnitude connection events and a correspondingly lower frequency and duration of disconnection and no-flow periods (Table IV, Fig. 3). The relatively short duration of low-flow periods for LT Groups 3 gauging stations is reflected in the high low-flow variability. In contrast overall flow predictability and constancy are relatively high for LT Group 3 gauging stations. Flood magnitudes at LT Group 3 gauging stations are greater than at gauging stations in LT Groups 1 and 2; however, flood magnitudes are also more variable among LT Group 3 gauging stations than is the case for LT Group 1 and 2 gauging stations (Table IV).

Three groups of gauging stations emerge from the flow pulse classification and these groups differ to those groups which emerged from the longer-term classification. The flow pulse classification results in grouping of gauging stations across rivers with no clear association between the four rivers or their longitudinal position in the Lower Balonne drainage network. Thus, Flow Pulse (FP) Group 1 includes the two gauging stations on the Birrie River, one each of the Bokhara (Bokhara) and Narran (Narran Park) gauging stations and two of the Culgoa gauging stations (Brenda and Weilmoringle), FP group 2 consists of the remaining two Culgoa gauging stations (Kenebree and Mundiwa) and the remaining Bokhara gauging station (Goodooga), while FP group 3 is made up of the remaining Narran gauging stations (Angledool and Belvadere).

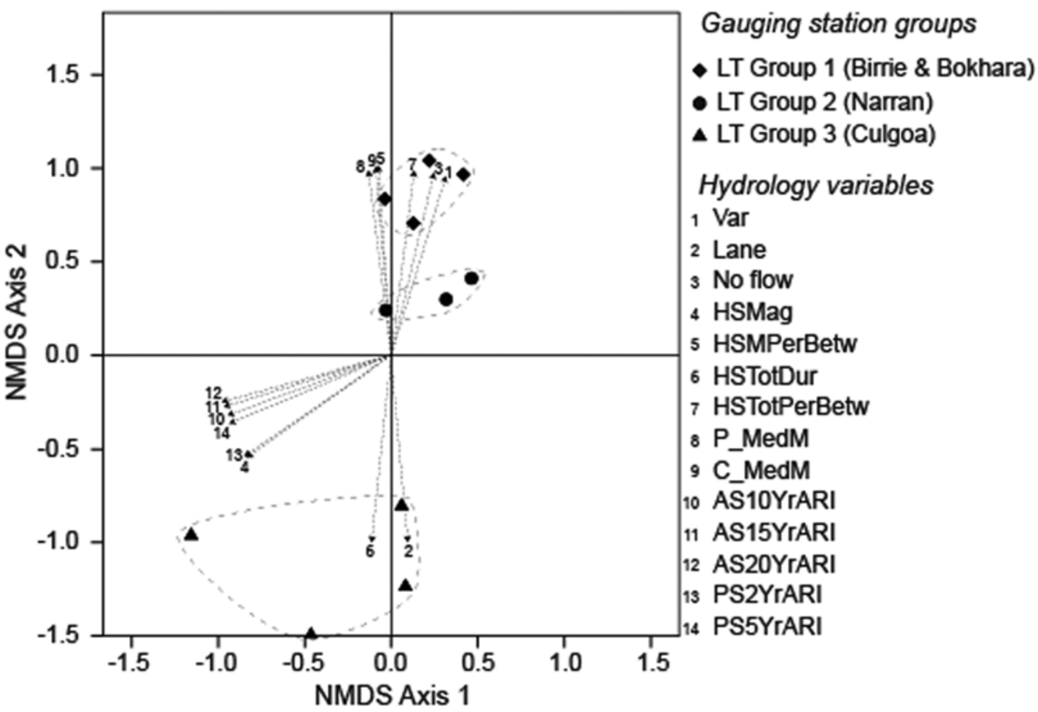

Fig. 3. Non-metric multi-dimensional ordination of gauging stations based on longer-term hydrology variables. Stations are classed by longer-term hydrology group and longer term hydrology variables with a strong influence on the ordination based on PCC analysis ($r^2 > 0.80$) are plotted as vectors.

Table IV. Longer-term hydrology variables summarised by LT Group and the corresponding r^2values derived for each variable in PCC analysis. Hydrology variables returning r^2 values greater than 0.8 are considered to have a strong influence on the distribution of gauging stations in ordination space.

	r^2	LT Group											
		1				2				3			
		Mean	**Median**	**Max**	**Minimum**	**Mean**	**Median**	**Maximum**	**Minimum**	**Mean**	**Median**	**Maximum**	**Minimum**
HSTotDur (days)	0.95	3281.50	3241.50	3668.00	2975.00	3441.00	3475.00	3519.00	3329.00	6191.25	6196.00	6558.00	5815.00
AS10YrARI (ML/d)	0.95	6537.75	5851.77	9353.65	5093.83	8489.66	8128.05	10839.42	6501.49	24759.45	22457.19	37473.05	16650.36
HSTotPerBetw (days)	0.94	12007.00	12014.50	12306.00	11693.00	11926.00	11903.00	12063.00	11812.00	9147.75	9153.00	9518.00	8767.00
AS15YrARI (ML/d)	0.94	8451.52	7692.32	12118.24	6303.19	8942.89	8405.73	11914.67	6508.28	29605.32	27124.15	45551.49	18621.51
C_MedM	0.94	0.49	0.49	0.52	0.47	0.46	0.47	0.47	0.45	0.27	0.26	0.30	0.23
P_MedM	0.93	0.55	0.54	0.58	0.53	0.52	0.52	0.53	0.51	0.33	0.32	0.37	0.29
AS20YrARI (ML/d)	0.93	9880.79	9085.12	14186.48	7166.43	9185.98	8519.04	12525.87	6513.02	32798.38	30329.83	50820.84	19713.01
Var	0.93	1000.00	1000.00	1000.00	1000.00	1000.00	1000.00	1000.00	1000.00	193.69	137.30	388.35	111.79
PS5YrARI (ML/d)	0.93	3855.73	3438.09	5877.48	2669.25	6674.97	6230.67	7590.70	6203.54	14746.58	13262.06	22455.27	10006.93
Lane	0.89	1.08	1.09	1.14	1.02	1.26	1.26	1.27	1.26	1.41	1.40	1.44	1.39
HSMag (ML/d)	0.89	1366.80	1272.52	1785.93	1136.24	2629.95	2597.04	2831.45	2461.35	4830.35	4574.65	6671.06	3501.05
HSMPerBetw (days)	0.88	149.45	149.39	159.82	139.20	134.45	129.38	154.65	119.31	95.08	95.33	110.67	78.98
PS2YrARI (M L/d)	0.84	1903.74	1761.77	2924.76	1166.68	5214.76	4961.22	5724.42	4958.63	8433.70	7486.64	12308.71	6452.82
No flow (days)	0.84	9947.50	10010.50	10586.00	9183.00	10197.67	9998.00	10765.00	9830.00	6085.00	5941.00	6867.00	5591.00
HSMeanDur (days)	0.77	40.31	40.65	44.76	35.20	38.23	37.37	42.14	35.19	63.00	63.16	67.14	58.55
PS1YrARI (ML/d)	0.74	460.04	420.71	691.76	306.98	3103.56	3053.74	3342.64	2914.29	3901.83	3906.88	4036.68	3756.87
HSNum (events)	0.58	81.50	81.50	85.00	78.00	90.67	93.00	100.00	79.00	99.00	98.50	112.00	87.00
CV	0.57	4.37	4.48	4.72	3.79	3.27	3.20	3.42	3.19	3.27	3.25	3.81	2.79
M_MedM	0.27	0.06	0.06	0.06	0.05	0.06	0.06	0.06	0.06	0.06	0.06	0.07	0.05
BFI	0.15	0.13	0.13	0.14	0.12	0.12	0.12	0.12	0.10	0.13	0.13	0.15	0.11
FFI	0.15	0.87	0.87	0.88	0.86	0.89	0.88	0.90	0.88	0.87	0.87	0.89	0.85

Principal component correlations reveal that of the 8 flow pulse hydrology variables are strongly associated with positions of gauging stations in ordination space (r^2 > 0.75) (Table V, Fig. 4). These variables describe the frequency and duration of connections over the period from January 2006 to December 2007. Highest connectivity over this period occurred at FP Group 2 gauging stations (Table V, Fig. 4) and lowest connectivity occurred at the FP Group 3 gauging stations (Table V, Fig. 4). Connectivity at FP Group 1 gauging stations was intermediate (Table V, Fig. 4).

4. Discussion

The hydrological character of 11 gauging stations and hence 16 refugial waterholes in the Lower Balonne distributary network is complex. Although there is a clear and fundamental similarity between the refugial waterholes in this study in that each persists as a viable aquatic habitat even after a long period without flow, the results of this study show clear spatial variability in their hydrological character across the lower Balonne at both short and longer-term temporal scales. This variability demonstrates that, even among persistent refugial water holes, there is substantial diversity in hydrological character across the landscape. Given the fundamental role of hydrology as a driver of ecosystem pattern and process, it is reasonable to assume that this hydrological diversity is an important factor underlying the biological diversity that is frequently observed in waterholes and billabongs in Australian floodplain river systems (Hillman 1986; Shiel *et al.* 1998; Quinn *et al.* 2000; Hillman, Quinn 2002; Reid, Ogden 2009). The corollary of this is that loss of hydrological diversity among refugial waterholes is likely to result in a corresponding decline in biological diversity across the floodplain landscape.

Importantly, the spatial patterns in hydrological character differ depending upon the temporal scale considered. Classifications based on regime and history-scale hydrology reveal the same groupings of gauging stations. Gauging stations characterised at these two scales reflect their parent rivers; that is, those on the Birrie and Bokhara were hydrologically similar, but differed from those on the Narran and Culgoa rivers. Pulse-scale hydrological character on the other hand, displayed a patchy configuration, with classifications containing gauging stations from different rivers and from various positions in the Lower Balonne.

The spatial arrangement of longer-term hydrological groups indicates that these patterns are influenced by processes that operate at larger spatial scales, unifying hydrological character at the river reach scale. This is entirely consistent with fundamental understanding of river structure and function. In the absence of significant gains or losses from the river, or changes in slope and substrate, the longer-term hydrological character of rivers within the Lower Balonne are consistent along their length (Thoms 2003). The lack of a clear spatial pattern with respect to river or longitudinal position in relation to flow pulse-scale hydrological character is more perplexing; it suggests that in addition to operating over shorter time-scales, pulse-scale hydrology also operates at smaller spatial scales (Biggs *et al.* 2005). Small

Table V. Flow pulse hydrology variables summarised by FP Group and the corresponding r^2 values derived for each variable in PCC analysis. Hydrology variables returning r^2 values greater than 0.75 are considered to have a strong influence on the distribution of gauging stations in ordination space.

	r^2	FP Group											
		1				2				3			
		Mean	Median	Maximum	Minimum	Mean	Median	Maximum	Minimum	Mean	Median	Maximum	Minimum
AnyConn	0.90	4	5	6	2	6	6	7	6	3	3	4	2
TotalEvents	0.84	7	6	10	5	7	6	8	6	3	3	4	2
%ExceedDur	0.80	13	13.1	16.3	10.4	16	16.8	18.6	12.7	4.4	4.4	6.2	2.6
U/sConn	0.75	0	0	1	0	2	3	3	1	2	2	3	1
LocalConn	0.57	2	3	4	0	0	0	1	0	0	0	0	0
TotalVol (ML/d)	0.57	46884	44316	108303	16828	148846	185548	245986	15005	22970	22970	23550	22389
RiverConn	0.41	4	4	5	2	3	3	3	3	1	1	1	1
D/sConn	0.40	0	0	1	0	1	0	4	0	1	1	1	0
LastEvent (days)	NA	9	0	38	0	14	0	41	0	6	6	12	0

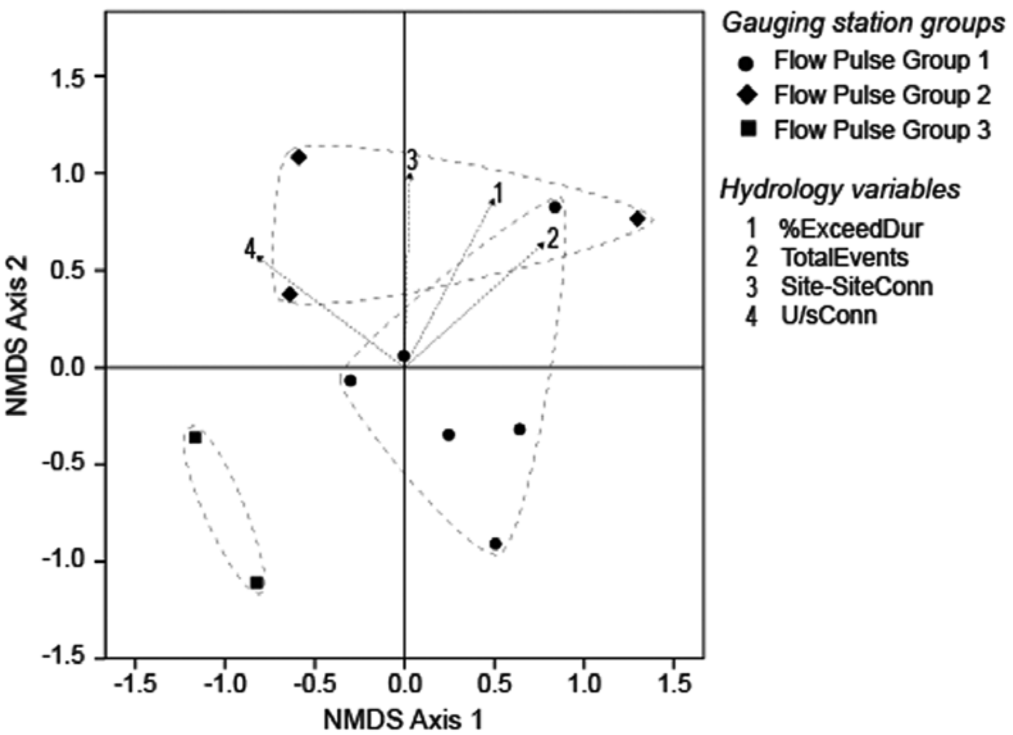

Fig. 4. Non-metric multi-dimensional ordination of gauging stations based on flow pulse hydrology variables. Stations are classed by flow pulse hydrology group and flow pulse hydrology variables with a strong influence on the ordination based on PCC analysis ($r^2 > 0.75$) are plotted as vectors.

scale variations in hydrological character reflect variations in geomorphology and associated flow transmission as demonstrated by Thoms and Parsons (2002) for the four river systems in the study area. Moreover, Knighton and Nanson (1994) described three features that influence flow transmission: evaporation and evapotranspiration, infiltration and drainage diffusion in the dryland river system of the adjacent Cooper Creek system in central Australia. Differences in channel dimensions and soil texture can affect rates of evaporation and infiltration, thus controlling variation in transmission losses across a system. All of these factors could be contributing to differences in hydrological character at the pulse-scale of individual waterholes across the Lower Balonne. It is important to note, however, that if constant overtime, such small-scale spatial variation would translate to similar spatial patterns in longer-term hydrological character; this is not the case, as the clear spatial patterns in longer-term hydrological character demonstrate. Thus, for this explanation to hold requires that these spatial patterns vary over time. Such temporal variation could arise from variation in the process of flow through the system and/or in the underlying physical template. In the case of the process of flow through the system, different magnitude events may result in different flow paths and spatial patterns in transmission losses; for example, with increased discharge, smaller channels and floodplains could become inundated and act as sumps for flood waters, increasing transmission losses. In the case of the underlying physical template, different antecedent conditions and/or small-scale temporal variation in microtopography could potentially also affect flow paths and transmission rates.

An alternative explanation for the observed pattern at the pulse-scale is that it is a consequence of water resource development (WRD). Flow regulation and water abstractions have been shown to increase the frequency and duration of low-flow conditions and reduced the frequency of medium sized pulses in dryland rivers (Thoms, Sheldon 2000). As a consequence this changes the nature of hydrological connectivity throughout a system by decreasing reliability of connection events and increasing hydrological fragmentation (Kingsford, Thomas 1995; Thoms, Sheldon 2000; Thoms, Parsons 2003). Using simulated flow data, Thoms (2003) demonstrated a clear distinction between the ‘natural’ hydrological character of the Lower Balonne system and the ‘current’ hydrological character that is the result of recent water resource development. Because water resource development in the Lower Balonne system is relatively recent (since the mid 1990s), it is likely that the spatial pattern revealed by the classifications based on 44 years of data in this study, reflects more the ‘natural’ hydrological character than the ‘current’, post-water resource development character. Conversely, this studies’ flow pulse hydrological characterisation, based on the two years from January 2006 to December 2007, is clearly a reflection of the post-water resource development hydrological character of the Lower Balonne system.

Further analysis is required to determine which of these mechanisms best accounts for the observed patterns of the flow pulse scale hydrology in the Lower Balonne. If the pattern reflects interaction between spatial variability in flow paths and transmission rates, and temporal variation in flow and the underlying template, we would expect that a different set of flow data from another 2-year period would yield a different spatial pattern through the same classification process. Alternatively, if the observed patterns in flow pulse scale hydrology reflects recent water resource development, we would expect the spatial patterns that emerge from flow pulse classifications carried out on post-WRD periods to be similar to the patterns found in this study, while classifications carried out on pre-WRD periods would be expected to match the patterns found in this study when hydrological character was classified based on longer-term hydrology.

Conclusions

Dryland river systems are widely recognised as being highly temporally variable (Puckridge *et al.* 1998). This study has demonstrated that this temporal variability is matched by a high level of spatial variability in hydrological character. This has important implications for dryland river ecosystems because, given the fundamental importance of hydrology as a driver of riverine ecosystems (Walker *et al.* 1995), this spatial variation in hydrological character is likely to contribute greatly to spatial variation in the physical habitat template and hence support biodiversity. Importantly, the results of this study support the conceptual frameworks that stress the need for hydrology to be considered at several temporal scales. Analysis of hydrological character at multiple temporal scales allowed for temporal and spatial patterns to emerge at different scales of observation. Results showed that hydrological character differed at two temporal scales, rather than the three temporal scales proposed by other researchers (Puckridge *et al.* 1998; Thoms, Sheldon 2000), although the significance of this finding is difficult to gauge because the hydrological record is limited to the past 44 years, meaning that flow regimes may not have been adequately characterised.

The findings of this study have important implications for ecohydrological studies. Given the strong influence hydrology has on ecosystems and their hierarchical nature (Power *et al.* 1995; Wu, Loucks 1995; Tockner *et al.* 2000; Robinson *et al.* 2002), we can expect that hydrological character at different temporal scales will influence ecosystem structure and function at corresponding levels of ecological organisation (Biggs *et al.* 2005). Accordingly, searching for patterns between biota and hydrology will be futile if hydrology is characterised at the wrong scale (James, Thoms 2010). Biotic components with long lifecycles and slow colonisation rates will respond to hydrological drivers that act over long timescales, while those with short life cycles and rapid colonisation rates will respond to hydrological drivers acting over shorter timescales (James, Thoms 2010). Even for individual biotic components there is likely to be variation in the temporal scale of hydrological influence depending on the level of biotic organisation. For example, the diversity of fish communities within a river system is likely to be more strongly associated with the long-term hydrological character of that system than the nature of recent flow events because diversity reflects the cumulative effects of colonisation, local extinctions and recruitment success over many generations; conversely, the size or age structure of individual fish populations is likely to be more strongly linked to the nature of recent flow events because these provide cues for breeding and control access to habitats and resources that influence recruitment success and growth rates.

The importance of scale has been widely recognised in hydrology (Jewitt 1998; Janauer 2000; Grayson, Blöschl 2001) but multi-scalar studies of the hydrological character of riverine ecosystems are relatively limited. Hydrological similarity between groups of gauging stations and hence refugial waterholes is shown to exist within the Lower Balonne. However, the composition of waterholes in the various statistical groups differs between levels of the hydrological hierarchy, as does their spatial organisation within the river network. This variable assemblage of waterhole composition, at the different levels of organisation, will be important when attempts are made to link hydrological character with ecological functioning in this river system. Rivers are complex hierarchical systems whereby their hydrological character influences components of their structure and functioning at predetermined levels of organisation (James, Thoms 2010). Often significant mismatches of scale exist in hydroecology/ecohydrology approaches because of the limited appreciation of scale, different levels of application, an emphasis on different temporal and spatial variabilities and also the disciplinary homes of the respective practitioners involved. Improving our understanding of the relationships between hydrological scales may be facilitated through a construct of hierarchical levels of organisation (Dollar *et al.* 2007). Hierarchical frameworks, such as that employed in this study, provide an approach to dissecting spatial and temporal domains of hydrological influence in river ecosystems (O'Neill 1989).

Environmental flow management thus needs to be cognizant of the spatial and temporal complexity of hydrological character and understand that flow management needs to address hydrological character across long and short-term scales in order to achieve ecological outcomes (Thoms, Parsons 2003).

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