

Fish assemblages of an Australian dryland river: abundance, assemblage structure and recruitment patterns in the Warrego River, Murray–Darling Basin

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Abstract. Fish in dryland rivers must cope with extreme variability in hydrology, temperature and other environmental factors that ultimately have a major influence on their patterns of distribution and abundance at the landscape scale. Given that fish persist in these systems under conditions of high environmental variability, dryland rivers represent ideal systems to investigate the processes contributing to and sustaining fish biodiversity and recruitment in variable environments. Hence, spatial and temporal variation in fish assemblage structure was examined in 15 waterholes of the Warrego River between October 2001 and May 2003. Fish assemblages in isolated waterholes were differentiated at the end of the dry 2001 winter but were relatively similar following high summer flows in January 2002 as a consequence of high hydrological connectivity among waterholes. Small, shallow waterholes supported more species and higher abundances than large-deep waterholes. Large, deep waterholes provided important refuge for large-bodied fish species such as adult yellowbelly, *Macquaria ambigua*, and the eel-tailed catfish, *Tandanus tandanus*. Recruitment patterns of bony bream (*Nematalosa erebi*), Hyrtl's tandan (*Neosilurus hyrtlii*) and yellowbelly were associated with high flow events and backwater inundation; however recruitment of yellowbelly and bony bream was also evident following a zero-flow period. Departures from typical flood-induced seasonal spawning patterns may reflect opportunistic spawning behaviours appropriate to the erratic patterns of flooding and dry spells in dryland rivers.

Extra keywords: alien species, connectivity, geomorphology, hydrology, refugia, spatial scale.

Introduction

Most Australian rivers flow through arid or semi-arid regions (Thoms and Sheldon 2000) and are characterised by highly variable and unpredictable flow regimes (Walker *et al.* 1995; Puckridge *et al.* 1998). Typically the fish assemblages of dryland rivers exhibit high variability in assemblage structure, often showing dramatic 'boom and bust' patterns of productivity corresponding to periods of flood and drought (Gehrke *et al.* 1995; Puckridge *et al.* 1998; Arthington *et al.* 2005). During dry periods, fish are confined to isolated floodplain and channel waterholes or 'refugia' (Morton *et al.* 1995; Magoulick and Kobza 2003), where assemblage structure is typically highly variable from one waterhole and river reach to another, as observed in many of the world's floodplain rivers (Rodriguez and Lewis 1997; Tejerina-Garro *et al.* 1998; Puckridge *et al.* 2000; Jackson *et al.* 2001; Welcomme 2001; Arthington *et al.* 2005). During floods, many

previously isolated waterholes become connected and fish can disperse over larger areas and utilise a range of newly inundated habitats (Balcombe *et al.* 2005). Thus spatial variability in floodplain fish assemblages is a consequence of number of interacting abiotic and biotic factors operating at various spatial scales (Arthington *et al.* 2005) such as hydrological and other influences on floodplain characteristics, waterhole morphology and connectivity, water quality, habitat structure and availability, competition for resources, and predation (Rodriguez and Lewis 1997; Welcomme 2001; Matthews and Marsh-Matthews 2003). Temporal variability in fish assemblages is driven by similar processes that impact on fish population dynamics via immigration, emigration, spawning, recruitment and mortality (King *et al.* 2003; Balcombe and Closs 2004; Welcomme and Halls 2004).

Studies on spatial and temporal patterns in fish assemblage structure in Cooper Creek, a large arid-zone river in the Lake

Eyre Basin, have shown that factors affecting fish assemblage structure in isolated floodplain waterbodies cannot be fully revealed by investigations conducted only at the waterhole scale. A hierarchical, multiscale approach was needed to reveal the influence of antecedent flooding, connectivity of waterholes and waterhole habitat structure on fish assemblage structure in dry season waterholes (Arthington *et al.* 2005). In that study, our temporal frame of reference was restricted to a single dry season in 2001 during which temporal patterns in waterhole fish assemblages were influenced primarily by water loss and changes in habitat structure, and opportunities for recruitment were negligible.

In the current paper, we examine spatial and temporal patterns in fish assemblage structure within isolated waterholes in the Warrego River catchment (a relatively undisturbed catchment of the upper Murray–Darling Basin, MDB) between 2001 and 2003. We selected this two-year timeframe in order to capture a wider range of temporal variation in hydrological conditions (channel flows, intermittent flooding, dry spells), waterhole connectivity and waterhole habitat structure, and to enhance the probability of documenting recruitment events and trends. Our aims were to: (a) document the range of natural variability in fish populations and assemblage structure in isolated waterholes, and the spatial and temporal scales of greatest variation; (b) determine the likely physical and chemical factors that regulate variations in waterhole fish assemblage structure at scales ranging from the individual waterhole to the river reach; and (c) determine how the recruitment patterns of four common fish species contributed to spatial and temporal variations in fish assemblage structure, and the potential influence of antecedent flow events on patterns of recruitment. The current study contributed to the Dryland River Refugia Project, a multidisciplinary investigation of the processes contributing to and sustaining aquatic biodiversity in dryland rivers of western Queensland (e.g. Bunn *et al.* 2003; Arthington *et al.* 2005; Marshall *et al.* 2006).

Materials and methods

Study area

The Warrego catchment, located in the north-west region of the MDB, has an area of $\sim 75\,000\text{ km}^2$. The headwaters of the Warrego River and 85% of the catchment are located in Queensland with the remainder, $12\,500\text{ km}^2$, in New South Wales (Fig. 1). The long-term average annual rainfall in the headwaters of the Warrego River is 650 mm and this decreases to $\sim 250\text{ mm}$ per annum in the lower regions of the catchment. Rainfall at Charleville in the upper catchment is also highly variable over time, ranging from 220 mm per annum in 1991 to 10 000 mm per annum in 1950. There is a marked seasonal distribution in rainfall with the majority of the catchment receiving 50% of its annual rainfall between December and March, whereas the lower regions of the catchment generally receive only 40% of annual rainfall during these summer months. The hydrological regime of the Warrego River is also highly variable in time and space. Peak discharges have exceeded $690\,000\text{ ML day}^{-1}$ ($79\,861\text{ m}^3\text{ s}^{-1}$) at Fords Bridge Gauge

(Fig. 1), and the longest period of no flow at this gauging station was 22 months during the late 1950s. Note that although all discharge figures are expressed in SI units of $\text{m}^3\text{ s}^{-1}$, they have been measured as daily totals.

Streamflow records from the Queensland Department of Natural Resources indicate that the mean annual discharge of the Warrego at Wyandra is $\sim 640\,000\text{ ML year}^{-1}$ ($202\text{ m}^3\text{ s}^{-1}$). Corresponding values derived from Fords Bridge, 350 km downstream of Wyandra, indicate that nearly 86% of flows diverge into Cuttaburra Creek and other distributaries and wetlands downstream of Wyandra.

The Warrego River displays complex channel morphologies. Its headwaters are generally confined within narrow valleys because of regional geological influences. Downstream of Cunnamulla, geological influences decrease and this is associated with marked increases in valley widths. In this region of the catchment the Warrego becomes a distributary river system with multiple channels, each channel displaying typical meandering characteristics – high sinuosity, low width to depth ratios and low bed slopes. Cuttaburra Creek, a relatively large distributary channel, can convey up to 40% of the Warrego River's flow (D. Green, personal communication, 2005) before returning flow to Yantabulla Swamp and then joining the Paroo River. The complex systems of channels in the lower Warrego system distribute episodic flows to numerous permanent and semi-permanent waterholes situated along the various channels. These waterholes may contain water for several years after the last flow event. Floodplain waterholes also occur in many reaches of the effluent system; however, little is known with respect to their hydrological characteristics, particularly in terms of wetting and drying regimes. Both floodplain and in-channel waterholes provide significant drought refuge for water birds and native animals during extended periods of no flow conditions within the catchment.

Fish assemblage structure was examined in four reaches of the Warrego River located at Quilberry, Glencoe, Binya and Thurulgoona (Fig. 1). Four waterholes were selected at each reach, to represent the natural range of size, shape, connectivity and water permanence, except Thurulgoona with only three being readily accessible. All fifteen waterholes were sampled for fish twice, in October 2001 and April 2002. The first sampling trip occurred during a relatively long dry spell when most waterholes had been disconnected for at least ten months, when the last significant flow was recorded at the Cunnamulla gauge. Four months previous to the first sampling occasion (16–23 October 2001) a small fresh of 500 ML day^{-1} ($58\text{ m}^3\text{ s}^{-1}$) occurred in the system (21 June 2001) and was detected at the Wyandra gauge. This flow would have provided some local minor filling of in-stream waterholes upstream of Cunnamulla (the Quilberry reach); however, as no flow was recorded downstream of Cunnamulla, no wetting was achieved at any of the other three reaches.

Prior to the second sampling occasion in April 2002, a flow of $54\,000\text{ ML day}^{-1}$ ($6250\text{ m}^3\text{ s}^{-1}$) was recorded at Cunnamulla on the 14 January 2002. This flow event would have provided substantial wetting of the river channel at all fifteen sites. A smaller peak of 3000 ML day^{-1} ($347\text{ m}^3\text{ s}^{-1}$) was recorded at Cunnamulla on 5 March 2002, providing some further wetting and filling of the larger in-channel waterholes on the Warrego River and Cuttaburra Creek (see Fig. 1). Thus the second sampling occasion followed a period of connectivity from channel and backwater flows in the summer of 2001–2002.

The four waterholes in the Binya reach were sampled on a further two occasions (October 2002 and May 2003) to extend our investigation of recruitment patterns in relation to flow history and flow events. Following the last recorded flow at Cunnamulla in March 2002, the system remained dry with no flow recorded at any of the gauges in the Warrego catchment before the third sampling occasion (8–10 Oct 2002). On the 16 February 2003 $\sim 80\,000\text{ ML day}^{-1}$ ($9259\text{ m}^3\text{ s}^{-1}$) was recorded at the Cunnamulla gauge, providing substantial wetting and filling of all Binya waterholes before the fourth sampling occasion.

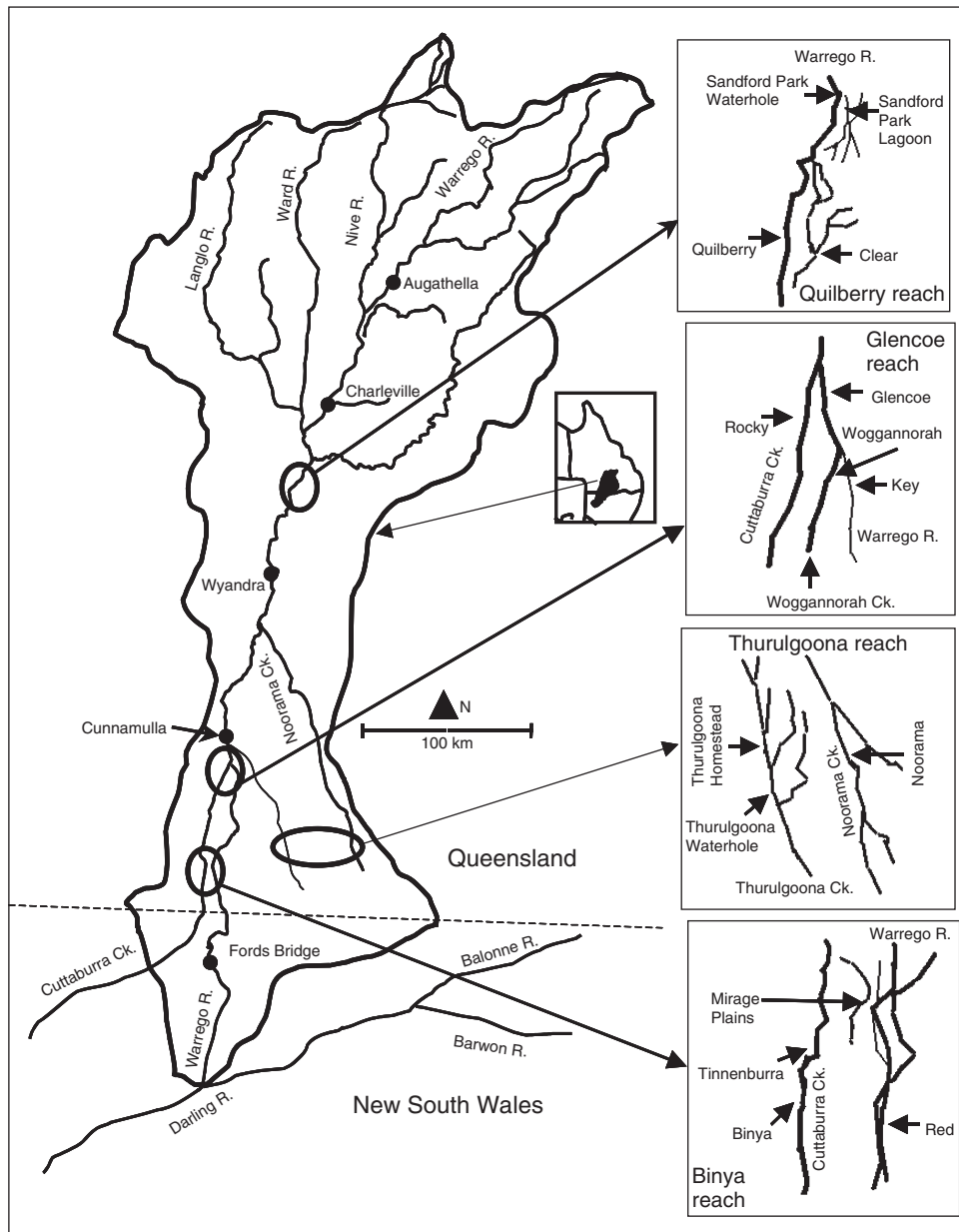


Fig. 1. The Warrego River catchment and four study reaches with insets showing waterhole configurations within each reach.

Survey methods

The fish assemblage within each of the fifteen waterholes was primarily sampled using three fyke nets and a single beach seine. Fyke wing width and sampling duration were recorded for each net for the subsequent calculation of catch per unit effort (CPUE), where CPUE represents the sum total of individuals collected from three fyke nets set for 19 h with the wing entrance 10 m in width. Fyke nets (13 mm mesh) captured both small and large-bodied individuals of all species. Beach seining (9.5 mm mesh) was used as an additional method to ensure that very small individuals, such as juvenile carp gudgeons (*Hypseleotris*) were not missed from species richness estimates. Further details of the sampling methods can be found in Arthington *et al.* (2005).

Fish were identified, and counted, and the standard lengths (SL) in mm of the four most abundant species – bony bream (*Nematalosa erebi*), Hyrtl’s tandan (*Neosilurus hyrtlii*), yellowbelly (*Macquaria ambigua*) and common carp (*Cyprinus carpio*) – were measured on all sampling trips. After counting and measurement, all native fish were returned alive to the water at the point of capture.

Thirty-eight physical floodplain and waterhole variables were measured in October 2001 at three spatial scales (Table 1) using remote aerial photography or on-ground surveying for each of the fifteen waterholes. The definition and collection of these variables was based on methods developed by Parsons *et al.* (2004) and elaborated in Arthington *et al.* (2005). Ten water chemistry variables were measured or water samples

Table 1. Warrego River waterhole geomorphology and habitat variables (and abbreviations) measured at three scales for BIO-ENV analysis

Highlighted variables were removed following redundancy analysis

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

^ABench measures refer to their placement in the channel, e.g. 0–1/3 means bench is in the bottom third of the channel.

collected at each waterhole on all sampling occasions when fish were sampled. These included conductivity, N:P, pH, sulphates (SO₄), silicates (Sil), total carbonates (TC), total hardness (ToH), total nitrogen (TN), total suspended solids (TSS) and turbidity (Tur). Water samples were collected at the surface and analysed using standard methods (APHA 1975).

Data analysis

Variations in fish assemblage structure and species richness across waterholes and sampling times were analysed using CPUE data based on fyke net catches. Catch per unit effort data were also used as a measure of total fish abundance (all species) and the abundance of individual species per waterhole. Species richness for each waterhole was based on the data collected by means of both sampling methods.

Assemblage patterns were analysed using ordination based on hybrid non-metric multidimensional scaling (MDS). Multidimensional scaling plots were generated from Bray–Curtis similarity matrices produced from $\log_{10}(\text{CPUE} + 1)$ and species presence/absence data. One-way analyses of similarities (ANOSIM) based on the same similarity matrices were used to identify assemblage differences among the four sampling reaches during the October 2001 and April 2002 sampling periods. Two-way crossed ANOSIMS were used to examine differences among reaches and sampling times for October 2001 and April 2002. One-way ANOSIMS were also used to examine differences among waterholes and sampling times in the Binya reach (October 2001, April and October 2002, May 2003). It was not possible to use two-way ANOSIMS on this dataset due to the low replication of waterholes and sampling times.

BIO-ENV function in Primer (Clarke and Warwick 2001) was used to investigate relationships between physical characteristics of the landscape (i.e. floodplain features), waterhole characteristics, water chemistry and fish assemblage structure/richness. BIO-ENV uses generalised Mantel tests to examine associations between faunal datasets and environmental data expressed as Spearman rank correlation coefficients for the association between the two matrices (Clarke and Ainsworth

1993). Autocorrelated floodplain and waterhole variables were removed before the BIO-ENV procedure, using Spearman rank correlations ($r_s > 0.8$) to identify redundant variables (see Table 1). The environmental similarity matrices were based on normalised Euclidean distance rather than Bray–Curtis similarity as per Clarke and Warwick (2001). BIO-ENV analysis was performed on the October 2001 and April 2002 datasets, representing the two sampling occasions where all fifteen waterholes were sampled. All multivariate analyses were undertaken in the PRIMER version 5 software package (Clarke and Gorley 2001).

To examine patterns of body length structure and possible recruitment in relation to sampling time and antecedent hydrological events, size frequency histograms were constructed for the four most common and abundant fish species. Recruitment patterns were examined only at the Binya reach (Fig. 1) over the period October 2001 to May 2003 (i.e. at the end of the dry season of 2001, after the wet season of 2002, after the dry season of 2002 and after the wet season of 2003).

Results

Fish assemblage patterns across four reaches on two sampling occasions

The fish fauna was composed of 10 indigenous species from eight families and three alien species from two families (Table 2). Considerable variation in total fish abundance was observed among waterholes and sampling times (Fig. 2). The most abundant and widespread species on the two sampling occasions when all fifteen waterholes were sampled, October 2001 (post dry) and April 2002 (post wet), was the bony bream, *Nematalosa erebi*. This species accounted for at least 40% of the catch on those occasions and was found in 14 of the 15 waterholes (Table 2). Other widespread species were yellowbelly (*Macquaria ambigua*) and Hyrtl's tandan (*Neosilurus hyrtlilii*) the latter also being the most abundant

Table 2. Fish species found in 15 waterholes of the Warrego River catchment in October 2001 and April 2002

Family and species	Common name	% of total catch per unit effort (CPUE) Oct 2001 (maximum no. of waterholes where present)	% of total CPUE Apr 2002 (maximum no. of waterholes where present)
Indigenous species			
Ambassidae			
<i>Ambassis agassizii</i> Steindachner, 1867	Olive perchlet	5 (2)	2 (1)
Clupeidae			
<i>Nematolosa erebi</i> (Günther, 1868)	Bony bream	53 (14)	40 (14)
Gobiidae			
<i>Hypseleotris</i> spp.	Carp gudgeons	<1 (9)	<1 (5)
Melanotaeniidae			
<i>Melanotaenia fluviatilis</i> (Castelnau, 1878)	Crimson-spotted rainbowfish	<1 (2)	<1 (4)
Percichthyidae			
<i>Macquaria ambigua</i> (Richardson, 1845)	Golden perch	7 (12)	6 (14)
Plotosidae			
<i>Neosilurus hyrtlui</i> (Steindachner, 1867)	Hyrtl's tandan	6 (9)	41 (12)
<i>Tandanus tandanus</i> Mitchell, 1838	Eel-tailed catfish	3 (7)	1 (6)
Retropinnidae			
<i>Retropinna semoni</i> (Weber, 1895)	Australian smelt	<1 (3)	<1 (2)
Terapontidae			
<i>Bidyanus bidyanus</i> (Mitchell, 1838)	Silver perch	<1 (1)	<1 (2)
<i>Leiopotherapon unicolor</i> (Günther, 1859)	Spangled perch	4 (6)	5 (14)
Alien species			
Cyprinidae			
<i>Carassius auratus</i> (Linnaeus, 1758)	Goldfish	5 (11)	1 (5)
<i>Cyprinus carpio</i> (Linnaeus, 1758)	Common carp	16 (11)	4 (7)
Poeciliidae			
<i>Gambusia holbrooki</i> (Girard, 1859)	Mosquitofish	0 (0)	<1 (1)

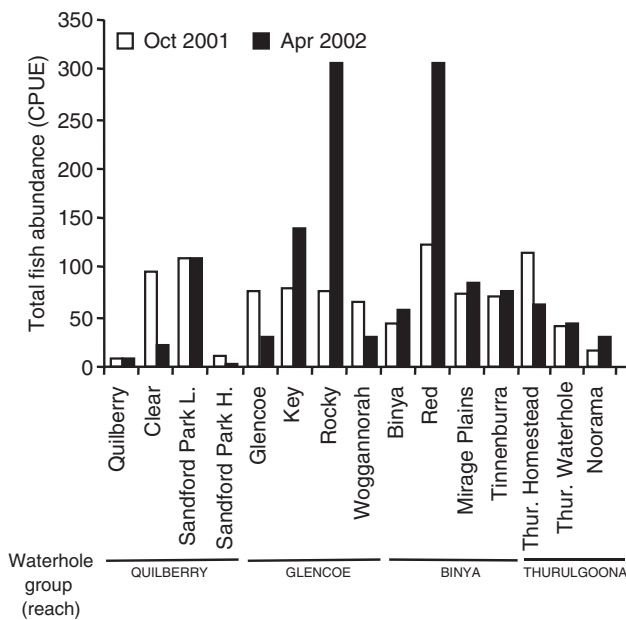


Fig. 2. Total fish abundance based on catch per unit effort (CPUE) derived from three standardized fyke nets per waterhole summed across four reaches and four sampling trips, October 2001 to April 2003.

species in April 2002, accounting for 41% of the total catch at that time. The exotic common carp (*Cyprinus carpio*) was also widespread and abundant, particularly in October 2001 when it was caught in 11 of the 15 waterholes and accounted for 16% of the total catch. The goldfish (*Carassius auratus*) was also found in 11 waterholes in October 2001 but comprised only 5% of total catch at that time.

Some waterholes had notably low fish catches, particularly Quilberry and Sandford Park Waterholes in the Quilberry reach, and Noorama in the Thurulgoona reach (Fig. 2). Catches varied considerably between October 2001 and April 2002 at most waterholes; however, there was no consistent temporal pattern within any one reach (Fig. 2). The main species contributing to large increases in abundance over this period (e.g. at Key, Rocky and Red waterholes) was Hyrtl's tandan (*N. hyrtlui*) (4,150% increase across the three waterholes). Observed decreases in fish abundance between October 2001 and April 2002 generally occurred in the medium-sized waterholes (e.g. Clear, Glencoe, Wogganorah and Thurulgoona Homestead). These were largely due to the reduced numbers of bony bream (*Nematolosa erebi*) in the three former waterholes (300%), while at Thurulgoona Homestead there was a large reduction in the number

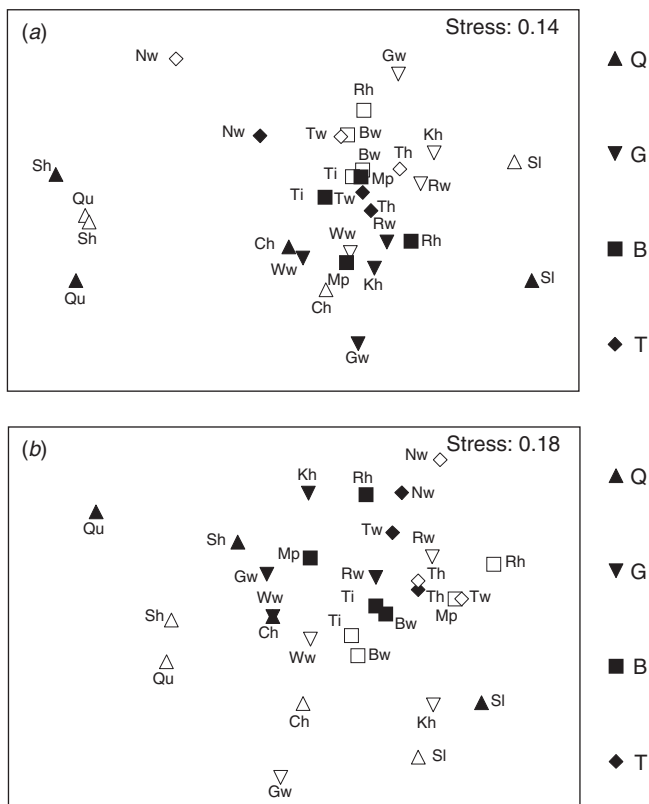


Fig. 3. (a) Non-metric multidimensional scaling plots based on $\log_{10}(x+1)$ transformed catch per unit effort (CPUE) data for sampling times 1 and 2 (b) and for presence/absence of species richness for sampling times 1 and 2. Open shapes = October 2001, closed = April 2002. Reaches and waterholes: Q = Quilberry: Quilberry (Qu), Clear (Ch), Sandford Park Lagoon (SI), Sandford Park Waterhole (Sh); G = Glencoe: Glencoe (Gw), Key (Kh), Rocky (Rw), Wogganorah (Ww); B = Binya: Binya (Bw), Red (Rh), Mirage Plains (Mp), Tinnenburra (Ti); T = Thurlugoon: Thurlugoon Homestead (Th), Thurlugoon waterhole (Tw), Noorama (Nw).

of native spangled perch (*Leiopotherapon unicolor*) and the exotic carp and goldfish (8,500% decrease combined across the three species).

Multivariate patterns of fish assemblage structure based on abundance (CPUE) and species richness showed no clear separation among waterholes with the exception of Sandford Park and Quilberry waterholes in the Quilberry reach (Fig. 3). Noorama waterhole in the Thurlugoon reach was also differentiated from the other waterholes in terms of fish assemblage structure but to a lesser extent than the two large Quilberry waterholes. There were significant differences in fish assemblage structure among some reaches in October 2001 based on CPUE data (Table 3).

In addition, reach differences were also apparent for patterns of both richness and CPUE based on the combined April and October dataset, particularly between Quilberry and Binya reaches (Table 3, Fig. 3). In contrast, fish assemblages

could not be differentiated between the two sampling times across all reaches for either CPUE or richness (Table 3).

No significant variation in multivariate patterns of fish CPUE or species richness across all waterholes could be explained by water chemistry. However, waterhole geomorphology and habitat structure explained some of the variability of CPUE and species richness patterns in both October 2001 and April 2002 (Table 4). The variable most commonly associated with these assemblage patterns was waterhole cross-sectional area (CSA). In combination with snags (SN) and overhanging vegetation (OV), CSA explained up to 45% of variation in the spatial patterns of waterhole fish assemblages expressed in terms of CPUE and species richness (Table 4). The strong association between fish relative abundance and species richness with CSA is consistent with the distributional data showing very low fish numbers and species at waterholes with the highest CSA values (Quilberry, Sandford Park Waterhole and Noorama). Conversely, waterholes with the smallest CSA values (Rocky and Red) had the highest fish abundances (Fig. 2).

Associations between individual species and geomorphological and habitat variables measured at three spatial scales revealed that landscape-scale factors were not in general correlated with the abundance of individual fish species (Table 5). The one exception to this was a significant negative association between total floodplain width and goldfish abundance in October 2001.

The variables most commonly associated with the abundance of each fish species were those measured at the waterhole scale. For example, a significant amount of the variation in eel-tailed catfish (*Tandanus tandanus*) abundance on both sampling occasions was explained by waterhole shape. The positive correlation for this catfish with CSA and depth of cross section (DCS) and negative association with width to depth ratio (WD) suggest that this species was more likely to be found in higher abundance in large, deeply incised waterholes (Table 5). In contrast, the abundances of bony bream (*Nematolosa erebi*) and Hyrtl's tandan (*Neosilurus hyrtlilii*) were negatively associated with CSA, suggesting that large, deeply incised waterholes were unlikely to support high numbers of these species. Apart from CSA, DCS and WD, other waterhole features correlated with individual species abundances were surface area (A) and wetted perimeter (WP) (Table 5).

Within waterholes, geomorphological factors associated with species abundances were off-take channels (OC), mid-channel bars (MCB) and anabranches (AN). These associations were only evident in April 2002 following summer rains and subsequent river runs when off-take channels would have provided additional wetted habitat for *T. tandanus*. In contrast, bony bream and Hyrtl's tandan showed a negative association with mid-channel bars and anabranches. Although inundation of these features increased physical complexity, such features may not be important for these two species.

Table 3. Summary of ANOSIM results comparing Warrego River fish assemblages based on catch per unit effort (CPUE) and presence/absence among reaches, times and waterholesReaches and waterholes: B = Binya, G = Glencoe, Q = Quilberry, t = Thurulgoona; Sampling trip: 1 = October 2001, 2 = April 2002, 3 = October 2002, 4 = May 2003. n.s., Not significant at $P < 0.05$

Sampling trip	Transformation	Factor	Global R	P	Significant pairwise tests
1	Log(CPUE + 1)	Reach	0.283	0.009	Q-B (0.03), G-B (0.03), G-T (0.03)
1	Presence/absence	Reach	0.162	n.s.	
2	Log(CPUE + 1)	Reach	0.121	n.s.	
2	Presence/absence	Reach	0.154	n.s.	
1 & 2 combined	Log(CPUE + 1)	Reach	0.202	0.003	Q-B (0.005), G-T (0.01)
1 & 2 combined	Log(CPUE + 1)	Time	0.094	n.s.	
1 & 2 combined	Presence/absence	Reach	0.158	0.02	Q-B (0.005), Q-T (0.02)
1 & 2 combined	Presence/absence	Time	0.102	n.s.	
1, 2, 3, 4 Binya	Log(CPUE + 1)	Waterhole	-0.028	n.s.	
1, 2, 3, 4 Binya	Log(CPUE + 1)	Time	0.51	0.001	1-4 (0.03), 2-4 (0.03), 3-4 (0.03)
1, 2, 3, 4 Binya	Presence/absence	Waterhole	0.06	n.s.	
1, 2, 3, 4 Binya	Presence/absence	Time	0.439	0.001	1-2 (0.03), 1-4 (0.03), 3-4 (0.03)

Table 4. Summary of BIO-ENV results based on Spearman rank correlations (r_s) between fish assemblage structure (catch per unit effort (CPUE) and richness) and geomorphological and water chemistry variables

Results only presented for best possible solution

Sampling time	Transformation	Best variable combination
1	Log(CPUE + 1)	CSA, SN, OV (0.68)
1	Presence/absence	CSA, SN (0.60)
2	Log(CPUE + 1)	CSA, SN, OV (0.68)
2	Presence/absence	CSA, OC, B2, OV (0.42)
		CSA, B2, BOU, OV (0.42)

Fish assemblage patterns at Binya reach on four sampling occasions

The longer term fish data collected from the most downstream (Binya) reach, showed that fish assemblages in the four waterholes were consistently similar to each other on all four sampling occasions, with no significant influence of waterhole on the multivariate patterns of CPUE and richness (Table 3). There was, however, significant variation in assemblage structure among sampling occasions for both CPUE and richness (Table 3, Fig. 4). Fish assemblages were most different on the fourth and final sampling occasion, May 2003, as shown by the position of May fish assemblages in the lower right areas of ordination space in Fig. 4a,b.

Length-frequency data indicate some periods of recruitment by the three most abundant indigenous species and common carp. There was, however, a lack of consistency in the recruitment patterns among the four species and across the Binya waterholes, and to a lesser extent in relation to the time of sampling.

Bony bream (*Nematolosa erebi*) showed likely periods of recruitment in three of the four waterholes, particularly in Red Hole in April 2002 and Mirage Plains and Tinnenburra holes in May 2003 (Fig. 5). A large proportion of the fish

collected were in size classes ≤ 60 mm SL at these times suggesting successful spawning leading to juvenile recruitment by late summer. Similar to the temporal patterns in size structure observed in bony bream, Hyrtl's tandan (*Neosilurus hyrtl*) also showed some definite periods of recruitment in the same three waterholes, although these were most obvious in April 2002 (Fig. 6) and coincided with the highest catches of this species in the Binya reach across all sampling times. There was also obvious recruitment of juvenile tandans in May 2003; however, the numbers caught were very low suggesting a very weak spawning response or low survival of larvae and juveniles of *N. hyrtl*.

Yellowbelly (*Macquaria ambigua*) also appeared to have several juvenile recruitment periods, particularly in Mirage Plains and Red holes in October 2002 and May 2003 (Fig. 7). There was also some obvious recruitment by May 2003 in the other waterholes, as evidenced by the dominance of fish ≤ 30 mm SL (Fig. 7).

The size structure plots for carp (*C. carpio*) indicate that larger-bodied individuals tended to dominate fish assemblages within the Binya waterhole group with only a few juveniles present (Fig. 8). Juvenile carp (< 100 mm SL) were collected in May 2003 following the largest flood recorded

Table 5. Significant Spearman rank correlations (r_s) between fish species abundance/diversity with geomorphological (codes given in Table 1) and water chemistry variables (Tur = turbidity, ToH = total hardness, Sil = silicates, TC = total carbon, TSS = total suspended solids, N:P = nitrogen:phosphorus ratio)

Sampling trip	Factor	Fish species, r_s (P)
Geomorphology		
1	TFW	<i>Carassius auratus</i> , -0.66 (0.007)
1	A	<i>Nematolosa erebi</i> , -0.73 (0.002)
1	CSA	<i>Tandanus tandanus</i> , 0.86 (0.00004)
1	DCS	<i>Tandanus tandanus</i> , 0.89 (0.00001)
2	A	<i>Neosilurus hyrtlii</i> , -0.74 (0.002)
2	CSA	<i>Nematolosa erebi</i> , -0.74 (0.002)
		<i>Neosilurus hyrtlii</i> , -0.70 (0.004)
2	WD	<i>Tandanus tandanus</i> , -0.65 (0.009)
2	WP	<i>Nematolosa erebi</i> , -0.66 (0.007)
2	OC	<i>Tandanus tandanus</i> , 0.66 (0.007)
2	AN	<i>Neosilurus hyrtlii</i> , -0.82 (0.0002)
2	MCB	<i>Nematolosa erebi</i> , -0.78 (0.0007)
Water chemistry		
1	Tur	<i>Tandanus tandanus</i> , 0.80 (0.0005)
1	ToH	<i>Nematolosa erebi</i> , 0.65 (0.009)
1	Sil	<i>Nematolosa erebi</i> , -0.74 (0.002)
1	TC	<i>Nematolosa erebi</i> , -0.83 (0.0001)
1	TSS	<i>Tandanus tandanus</i> , -0.70 (0.003)
1	N:P	<i>Nematolosa erebi</i> , 0.81 (0.0003)
1	NO ₃	<i>Tandanus tandanus</i> , -0.67 (0.006)
2	Tur	<i>Neosilurus hyrtlii</i> , -0.67 (0.006)
2	ToH	<i>Nematolosa erebi</i> , 0.57 (0.03)
2	TN	<i>Nematolosa erebi</i> , -0.66 (0.008)

during the Warrego study period. However, our data suggest a weak juvenile recruitment event.

Discussion

Fish assemblage structure in the Warrego River catchment reflected several processes operating across a range of spatial scales. There was a high degree of similarity in fish assemblages among waterholes and reaches with the only significant pairwise reach differences apparent in October 2001 and no evidence of differentiation from then until April 2002. This finding suggests that there was high connectivity potential among all waterholes and reaches between October and April, i.e. the early to late summer of 2001–2002. Flow events during this period included an overland flood in January 2002, three months before the second sampling occasion (April 2002) and an in-channel flood pulse two months following this flood. This degree of hydrological connectivity among waterholes during the wet summer months of 2002 appears to underpin the spatial patterns found in the fish assemblage. By the end of a wet period, fish assemblages would tend to show low differentiation in terms of species composition and relative abundances, providing the most common fish species present have high vagility, which is likely (Bishop *et al.* 1995; Pusey *et al.* 2004; Arthington *et al.* 2005). Summer

flooding in the Warrego study area appears to have ameliorated the influence of biophysical processes that typically operate within individual, isolated waterholes during dry periods, and drive fish assemblages along independent trajectories of change (Bishop and Forbes 1991; Bishop *et al.* 1995; Magoulick and Kobza 2003; Arthington *et al.* 2005).

In the context of rivers in the MDB the role of hydrological connectivity is an important factor to consider given the poor current condition of MDB fish assemblages (Schiller and Harris 2001; Koehn and Nicol 2004). Much of the impact on fish stocks in the MDB has been attributed to hydrological and associated land management changes to support agriculture, changes that ultimately impact on connectivity among waterbodies, reaches and even sub-catchments. Factors that threaten connectivity include: river regulation and associated construction of weirs and levee banks, the release of water from dams to accommodate irrigation demands thereby disrupting natural seasonal flow patterns, and floodplain alteration to facilitate the capture of flood flows in off-channel storages, often severing natural pathways of connection between floodplains and river channels (Walker *et al.* 1995; Balcombe and Closs 2004; Koehn and Nicol 2004). The Warrego generally does not suffer from these disturbances to natural patterns of stream flow and connectivity

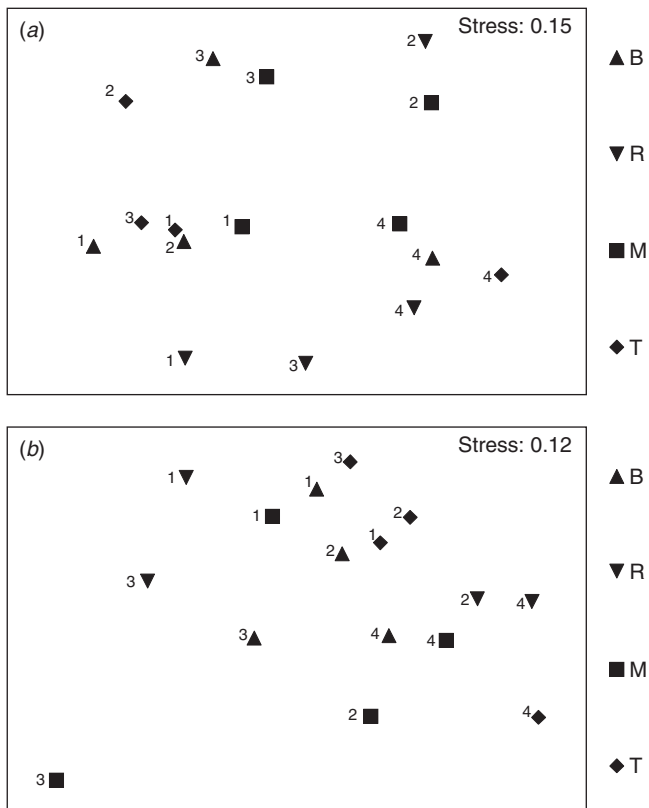


Fig. 4. Non-metric multidimensional scaling plots based on $\log_{10}(x + 1)$ transformed catch per unit effort (CPUE) data for the Binya reach on sampling dates 1, 2, 3 and 4 (a) and for presence/absence of species richness for sampling dates 1, 2, 3 and 4 (b). See Table 3 caption for sampling dates and reach codes.

and this relative lack of disturbance appears to be reflected in the condition of the fish fauna. Compared with other Murray–Darling rivers, Warrego catchment waterholes support higher abundances and richer assemblages than other sub-catchments of this river system (Gehrke *et al.* 1995). Furthermore, in the Warrego study, the low proportion of alien fish relative to total fish abundance (100 native to alien ratio) contrasts with the findings of Gehrke *et al.* (1995) in two Upper Murray–Darling rivers – the Paroo (~1.6) and the Darling River (~13). Given its present condition, the Warrego River may serve as a model dryland river for the further investigation of ecological processes sustaining fish in variable environments in both the MDB and other similar systems.

The average number of species and fish abundances in Warrego waterholes were somewhat lower than those found by Arthington *et al.* (2005) in another dryland river, Cooper Creek, within the Lake Eyre basin. Differences in species richness must be a reflection, to some extent, of the smaller fish species pool in the Warrego catchment (total of 10 indigenous species in 8 families) compared with the Cooper Creek system (total of 12 indigenous species in 8 families). The

reasons for marked differences in fish abundance per waterhole are unclear, but could be associated with higher rates of primary production in Cooper Creek waterholes compared with the Warrego River (Bunn *et al.* 2003, 2006). The higher fish abundances recorded in Cooper Creek waterholes in 2001 could also be related to the energy subsidies provided by extensive antecedent flooding in the summer of 2000 (Arthington *et al.* 2005; Balcombe *et al.* 2005).

October 2001 and April 2002 datasets revealed Quilberry reach to be most differentiated from the Binya reach in both fish abundance and species richness. These two reaches are the most distant in the catchment (see Fig. 1), which could suggest that physical distance may influence fish assemblage characteristics or even that the Cunnamulla Weir may impede fish movement between Quilberry and Binya reach. However, two distance measures were used in the BIO-ENV analyses (channel and straight-line distance to nearest waterholes) and neither influenced fish abundance and species richness among waterholes. A better explanation of the observed pattern is the major influence of having the two largest and most deeply incised waterholes in the study area – Quilberry and Sandford Park Waterholes in the Quilberry reach. These two waterholes supported the lowest numbers of individuals and species on both sampling occasions. It must also be noted that the other Quilberry waterholes, Clear and Sandford Park Lagoon, supported average abundances and no fewer species than downstream waterholes. This suggests that patterns of waterhole morphology and habitat structure at the landscape scale are more important drivers of fish assemblage structure than physical distance and degree of separation *per se*. This is consistent with evidence that waterhole scale factors exerted a strong influence on fish diversity and abundance in the Warrego catchment, particularly CSA and the presence of woody material (snags) derived from riparian vegetation. Thus at the waterhole scale, geomorphology and habitat structure largely explain variations in fish assemblage structure. Large deep waterholes supported fewer fish species and lower abundances, yet may act as key refugia for large-bodied fish such as adult yellowbelly and the catfish, *T. tandanus*. This could be particularly important under conditions of extended drought (up to 22 months in the Warrego catchment) when smaller waterholes may dry completely and large waterholes provide the only habitat sustaining aquatic species during dry spells between wet periods. Small populations of maturing and adult fish would be significant sources for juvenile recruitment when flows replenish and rejoin isolated waterholes.

Conversely, small, shallow waterholes of the Warrego River supported more species and higher abundances per unit area than large, deep waterholes, a pattern that could be driven largely by a greater amount of productive littoral zone and hence, significant potential for increased production of aquatic food resources (Bunn *et al.* 2003, 2006; Balcombe and Closs 2004; Medeiros 2005). Evidence of the importance of snags as a waterhole feature associated with

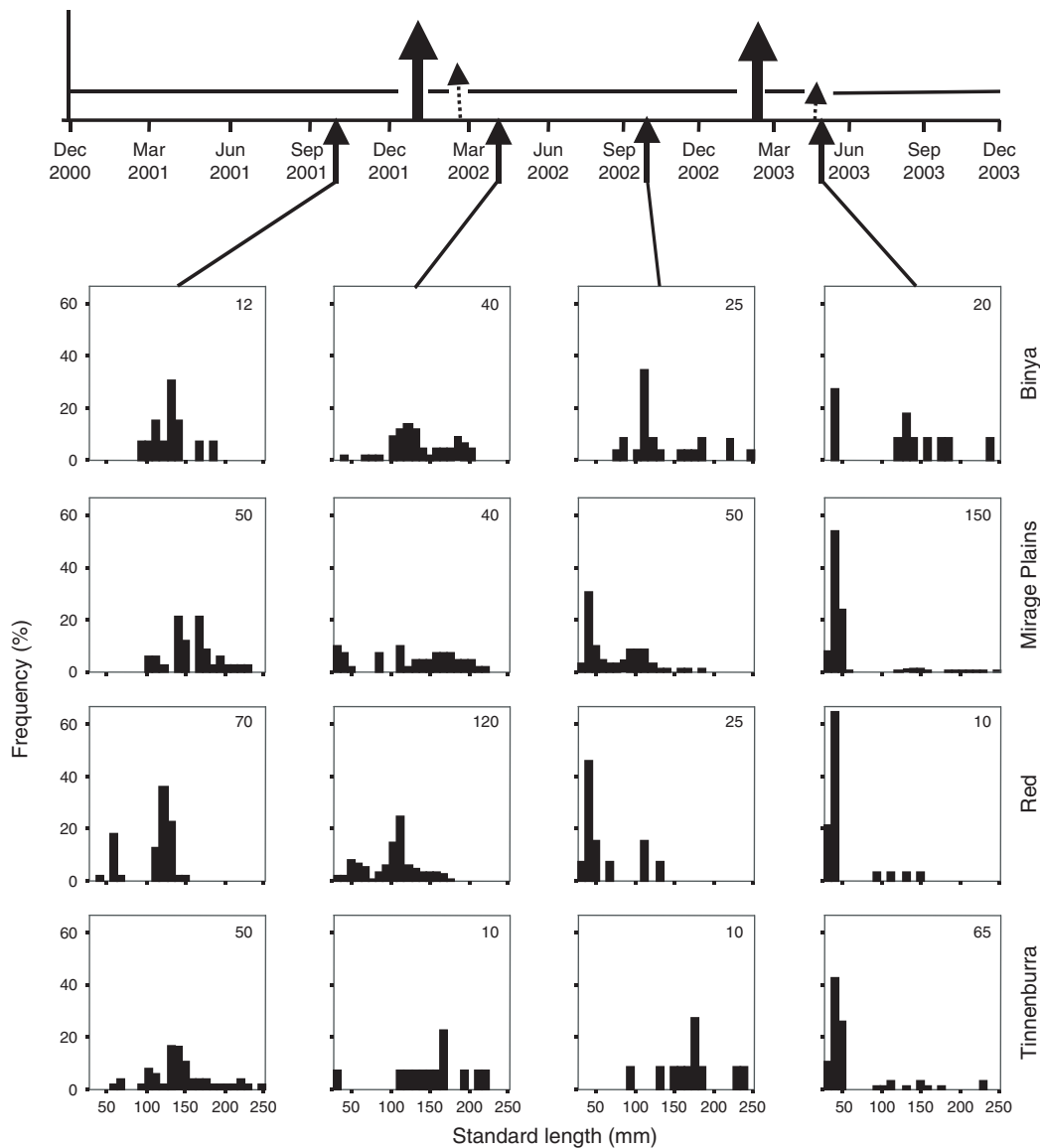


Fig. 5. Size-frequency distributions for *Nematalosa erebi* in four waterholes in the Binya reach of the Warrego River catchment on four sampling occasions. Note 1: Schematic of flow events provided at the top of figure, where wide arrows = overland flood events, dashed arrows = flow pulses, horizontal lines = periods of no flow. Note 2: numbers of fish (approximately equal to total catch per unit effort) measured for each plot appear at the top right of each individual plot.

variations in fish assemblage structure is also not surprising given that undercut root masses, large fallen logs and smaller woody material represent one of the few ubiquitous aspects of structural heterogeneity in these waterholes. These structural features probably provide significant sites for the production of food resources for fish and also predator refuges for smaller-bodied fish (Crook and Robertson 1999; Wright and Flecker 2004). The low abundance of small-bodied fish in the large, deeply incised waterholes may also be explained in part by higher rates of predation from larger predators (fish and birds) due to the relative lack of physical refugia per unit area.

Riparian protection to achieve natural delivery of timber and small woody material to waterholes should be an important consideration in the management of this catchment.

Temporal data for Binya reach waterholes show a high degree of similarity in fish assemblage structure among the four waterholes in both October 2001 and May 2003. In contrast there was little concordance in the fish assemblages among the four waterholes in both April and October 2002. The large difference between April and October 2002 can be explained by the high numbers of juvenile tandans (*Neosilurus hyrtlui*) in Red Hole, Mirage Plains and Tinnenburra

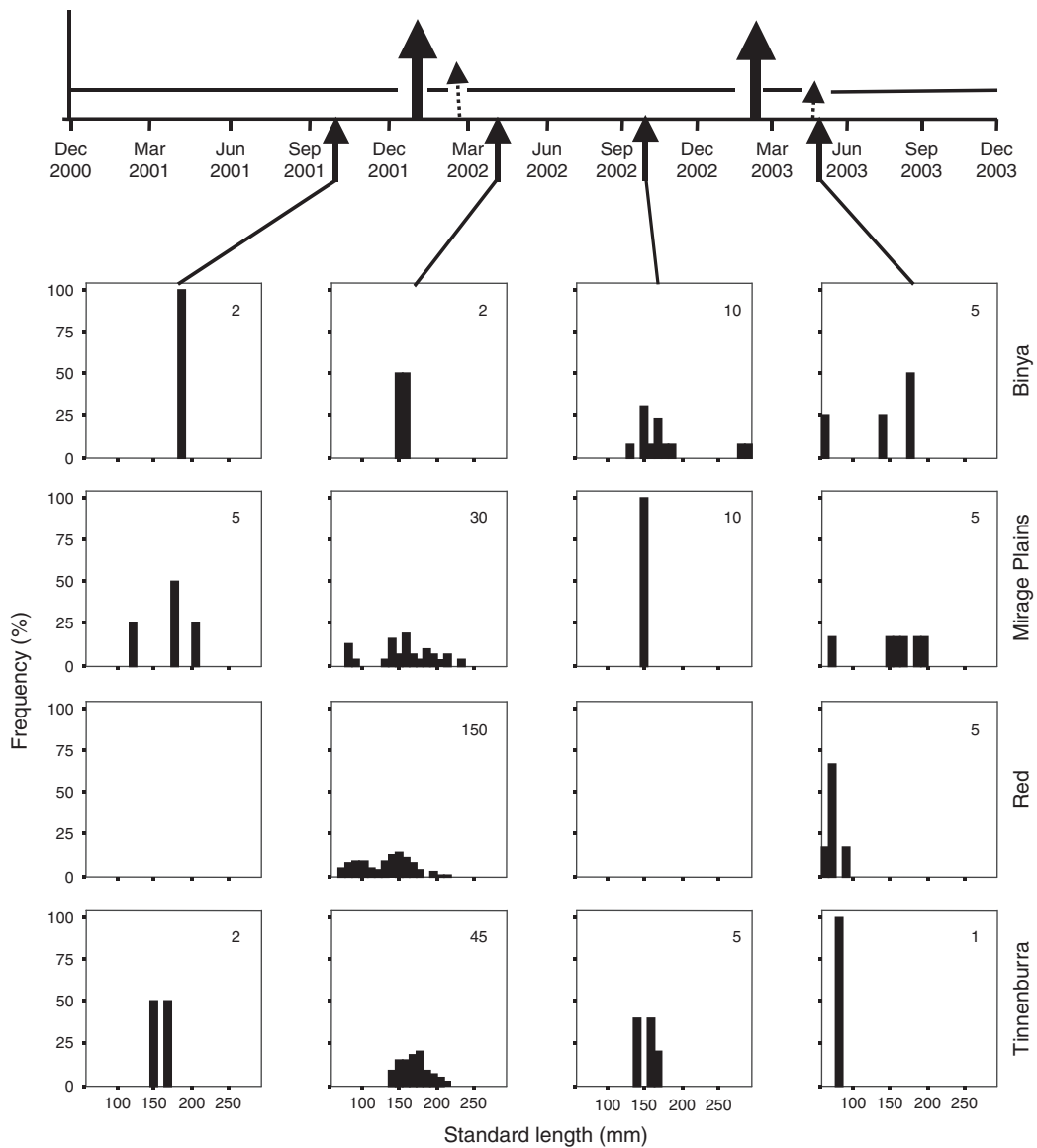


Fig. 6. Size-frequency distributions for *Neosilurus hyrtlii* in four waterholes in the Binya reach of the Warrego River catchment on four sampling occasions. Note: see caption for Fig. 5.

waterholes in April, with only a few individuals of this species captured in October. In Red Hole, there was also a large decrease in the abundance of bony bream (*Nematolosa erebi*) between April and October 2002. Hence, stochastic patterns of juvenile recruitment among the four waterholes largely influenced temporal variations in fish assemblage structure in the Binya reach. This suggests that non-uniform processes of recruitment operated across these three waterholes. Such variability could be driven primarily by subtle differences in hydrology within this waterhole group, given that within the Binya reach the waterholes we studied were located in three sub-catchments – Mirage Plains Creek, Cuttaburra Creek and Warrego River (see Fig. 1).

Recruitment of *Neosilurus hyrtlii* was particularly variable among waterholes, with high numbers of juveniles found only in Rocky, Red and to a lesser extent, Tinnenburra waterholes in April 2002. There is no obvious explanation for this result, apart from the similarity between Red and Rocky holes in that they are small in area, but relatively deep with very hard substrata. Little is known about the breeding biology of this tandan, particularly in the MDB (Pusey *et al.* 2004). Hence, it is not known whether this species spawns preferentially in these peculiar waterholes, or whether larvae/juveniles preferentially move into them during periods of flow, or achieve higher survivorship in such habitats. Recruitment of yellowbelly (*M. ambigua*) appeared to be associated with summer

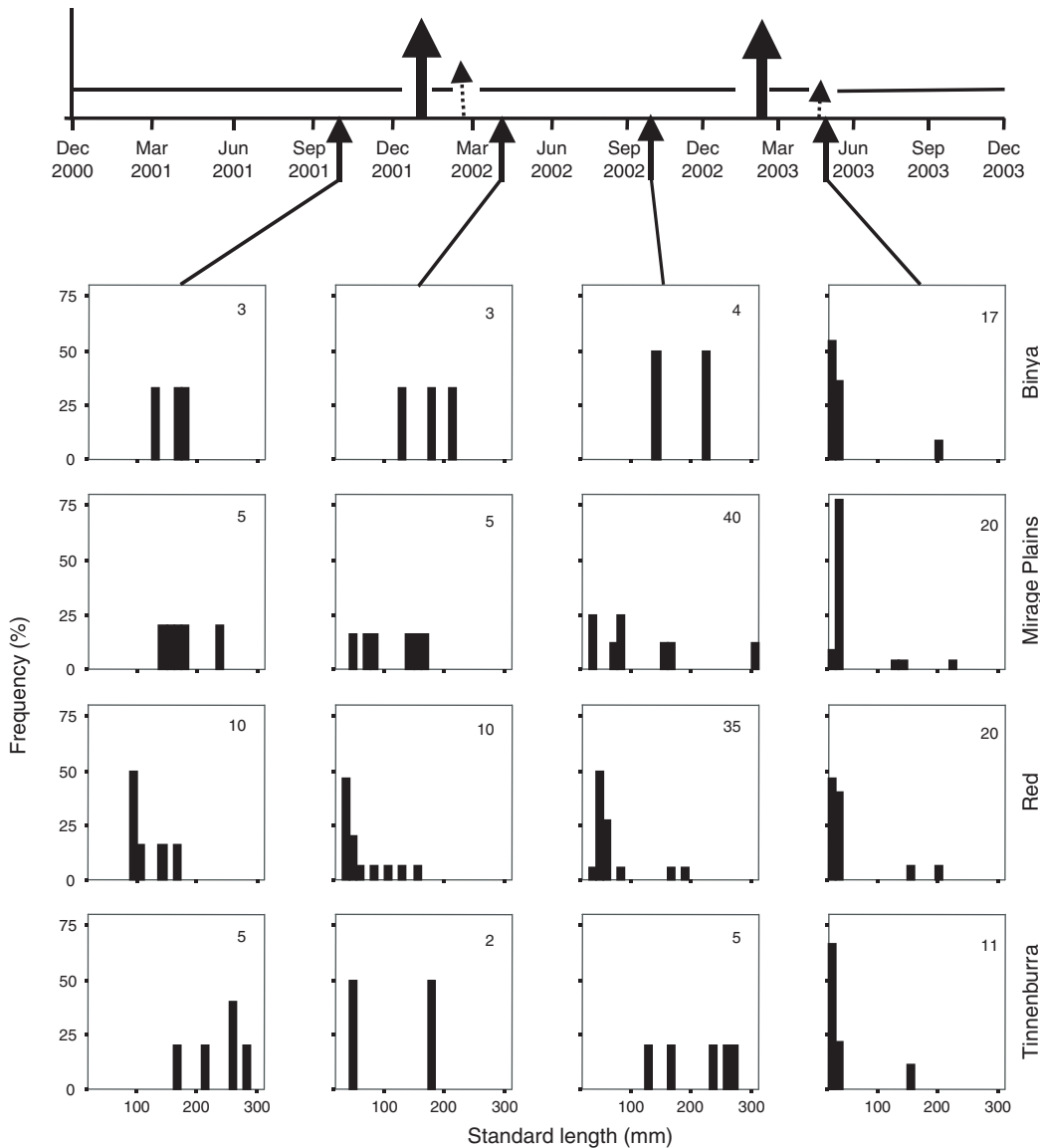


Fig. 7. Size-frequency distributions of *Macquaria ambigua* in four waterholes in the Binya reach of the Warrego River catchment on four sampling occasions. Note: see caption for Fig. 5.

flows given that juveniles were found mostly following summer flow events, although only in small numbers. However, juvenile yellowbelly were also present in Mirage Plains and Red Hole in October 2002 after a dry winter and spring period without any channel flows. Thus it would appear that spawning of this species is not solely dependent on flow events as proposed by King *et al.* (2003) in the Ovens River (a Murray River tributary) but has a much more opportunistic breeding strategy (see Mallen-Cooper and Stewart 2003 and Pusey *et al.* 2004 for review and discussion). Bony bream (*N. erebi*) recruitment also appeared to be linked to flow events, especially given the high numbers of smaller size classes caught in April 2002 and May 2003 following high flows (see Fig. 5). It seems that the bony bream is also not an obligate flood

spawner in this catchment as juveniles were also present in October 2001 and 2002 (at the end of dry spells) in at least two waterholes, albeit in low abundance.

Known as flood spawners, carp (*C. carpio*) did not produce the huge numbers of juveniles following floods that are often reported in more southern reaches of the MDB (King *et al.* 2003; Driver *et al.* 2005). Floods tend to occur between late winter and spring in the lower MDB, whereas floods occur later in the northern parts of the basin, principally in the summer and early autumn. Juvenile carp (<100 mm SL) were collected in May 2003 following the largest flows recorded during the Warrego study period (80 000 ML day⁻¹ (9259 m³ s⁻¹) at the Cunnamulla gauge). It is possible that only the February 2003 flood was sufficient in magnitude and

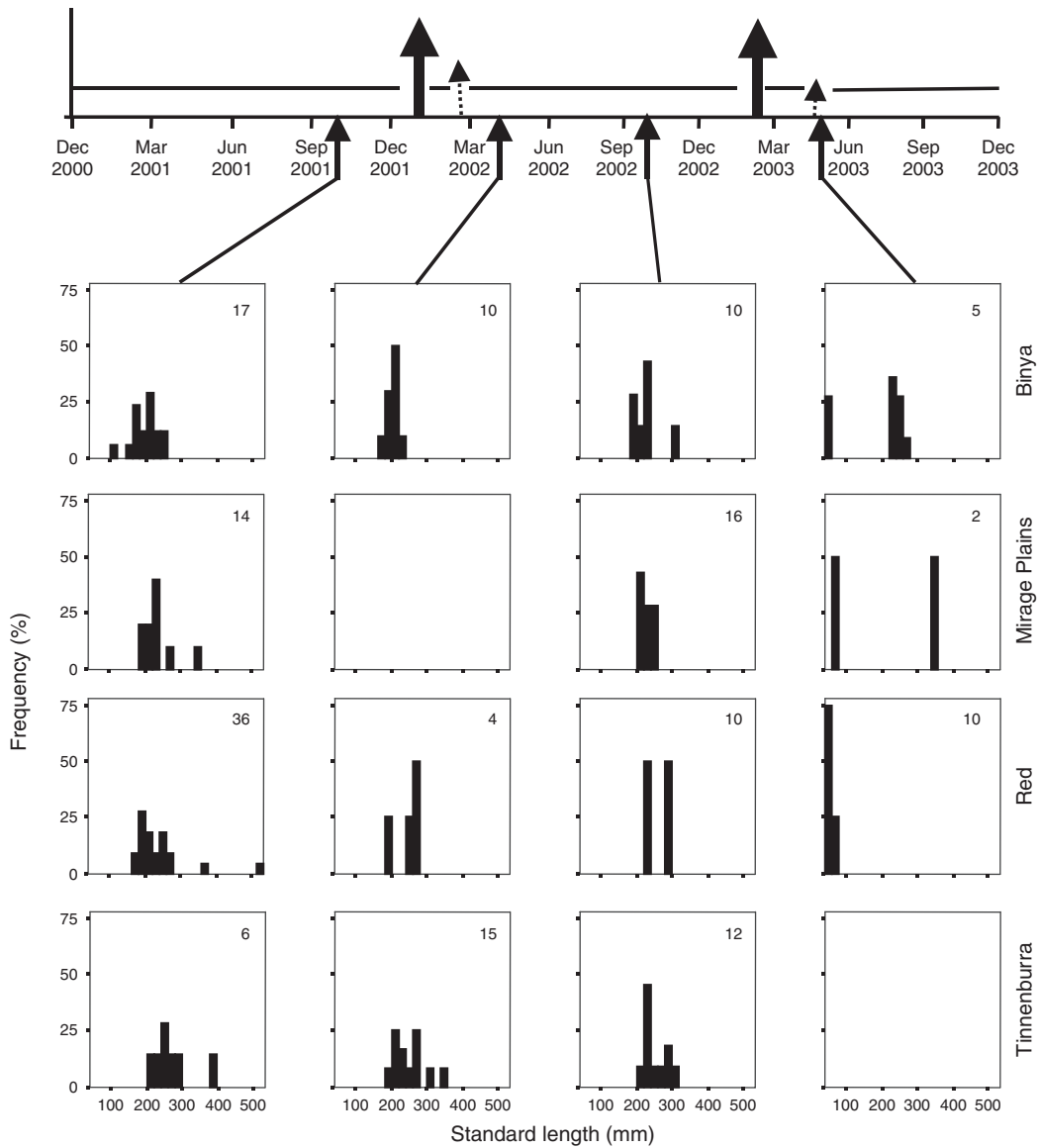


Fig. 8. Size-frequency distributions of *Cyprinus carpio* in four waterholes in the Binya reach of the Warrego River catchment on four sampling occasions. Note: see caption for Fig. 5.

duration to produce successful recruitment of carp through to juvenile stages. Brown *et al.* (2005) suggested that although increased river flow in the mid-Murray River resulted in carp spawning, it had to be of a great enough magnitude and duration to inundate wetlands to result in successful juvenile recruitment. Although the later flows in the Warrego system may not inhibit spawning, impacts on juvenile carp recruitment and/or survival could be felt as temperatures fall in late autumn. King (2005) found early stage larval carp fed on algae and small-bodied cladocerans, moving on to more epibenthic prey (such as chironomids, chydorid cladocerans and hemipterans) as juveniles. These prey resources could become limited as temperatures fall in late autumn and early winter resulting in low net juvenile carp recruitment.

To examine the role of flood timing on carp recruitment we would have needed to measure larval recruitment of the species, a requirement beyond the scope of the current study.

High flows occurred during the summer months of 2002 and 2003 and the recruitment patterns of common and abundant species (bony bream, *Nematolosa erebi*, catfish, *Neosilurus hyrtl*, and yellowbelly, *M. ambigua*) were associated with these events and backwater inundation, particularly after the high summer flows recorded in February 2003. However, recruitment levels were typically low for species known to respond to high flows and floodplain inundation (e.g. yellowbelly) and did not achieve levels recorded in the southern MDB. Furthermore, yellowbelly and bony bream showed evidence of recruitment in October 2002

following a winter period without any channel flows. We suggest that these departures from typical flood-induced seasonal spawning patterns may reflect opportunistic spawning behaviours appropriate to life in a dryland river system that only occasionally experiences high summer flows and extensive floodplain inundation, and one that may on occasion experience elevated flows during normally dry, winter months (e.g. June 2001). Conjecture still surrounds the stimuli required for spawning and the roles of flow and other factors in juvenile recruitment of the yellowbelly, as discussed in Humphries *et al.* (1999), Mallen-Cooper and Stewart (2003) and Pusey *et al.* (2004). Further work on spawning and recruitment of *Macquaria ambigua*, and the ambiguities of its breeding biology in relation to flow, is clearly warranted to protect this iconic species and to inform land and water management planning in the Warrego catchment.

Conclusions

The management of rivers with highly variable flow regimes is a particular challenge in dryland areas of Australia (Boulton *et al.* 2000). The current paper contributes new information and insight into the factors influencing the structure and diversity of Warrego River fish assemblages, and importantly, the influence of intermittent channel flows and minor flooding on patterns of recruitment during a relative dry period between October 2001 and May 2003. We have shown that fish assemblages in isolated waterholes at the end of the 2001 dry season were differentiated in terms of species richness, total abundance and the abundance of individual species but tended towards similarity of composition after summer channel flows and flooding of low-level backwaters had restored connectivity among isolated reaches and waterholes. Connectivity fosters fish movement, colonisation of previously isolated waterholes, and processes associated with 'boom and bust' cycles of recruitment and productivity (Junk *et al.* 1989; Closs and Lake 1996; Puckridge *et al.* 1998; Amoros and Bornette 2002; Fausch *et al.* 2002; Sheldon *et al.* 2002; Arthington *et al.* 2005). We conclude that it will be particularly important to maintain the natural quantities and timing of channel freshes and higher flow events that inundate backwaters, as these flows evidently achieve hydrological connectivity and drive ecological processes that sustain the diversity, recruitment and population dynamics of native fish species in the Warrego catchment. Furthermore, as it is part of a relatively undisturbed catchment, the Warrego River may serve as a model for further investigation of ecological processes sustaining native fish in variable environments.

Acknowledgments

The authors would like to thank the various Dryland Refugia team members and volunteers who provided field

support, and the following landholders for property access: Cecil Adcock, Gordon Cuff, Bill Fisher, Michael Gardiner, Hugh Miller, Ronald McIntosh, and John O'Sullivan. Our research was conducted under Queensland Fisheries Permit PRM00157K and Griffith University Animal Experimentation Ethics Committee permit AES/03/02.

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Manuscript received 8 February 2006; revised 9 May 2006; and accepted 19 July 2006.