Fish assemblage patterns across a gradient of flow regulation in an Australian dryland river system

FISH ASSEMBLAGE PATTERNS ACROSS A GRADIENT OF FLOW REGULATION IN AN AUSTRALIAN DRYLAND RIVER SYSTEM

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ABSTRACT

Hydrological regime, physical habitat structure and water chemistry are interacting drivers of fish assemblage structure in floodplain rivers throughout the world. In rivers with altered flow regimes, understanding fish assemblage responses to flow and physico-chemical conditions is important in setting priorities for environmental flow allocations and other river management strategies. To this end we examined fish assemblage patterns across a simple gradient of flow regulation in the upper Murray-Darling Basin, Australia. We found clear separation of three fish assemblage groups that were spatially differentiated in November 2002, at the end of the winter dry season. Fish assemblage patterns were concordant with differences in water chemistry, but not with the geomorphological attributes of channel and floodplain waterholes. After the summer-flow period, when all in-channel river sites received flow, some floodplain sites were lost to drying and one increased in volume, fish assemblages were less clearly differentiated. The fish assemblages of river sites did not increase in richness or abundance in response to channel flow and the associated potential for increased fish recruitment and movement associated with flow connectivity. Instead, the more regulated river's fish assemblages appeared to be under stress, most likely from historical flow regulation. These findings have clear implications for the management of hydrological regimes and the provision of environmental flows in regulated rivers of the upper Murray-Darling Basin.

KEY WORDS: geomorphology, water chemistry, fish assemblage structure, environmental flows

INTRODUCTION

Water resource development in many of the world's floodplain rivers has led to changes in fish diversity, community structure and productivity, and assisted the establishment of exotic species (Rodriguez and Lewis 1997; Bunn and Arthington, 2002; Welcomme *et al*., 2006). The Murray-Darling Basin (MDB), Australia's largest catchment (with an area of 1.06 mkm^2) is no exception with most of its rivers altered since the 1960s by dams and water abstraction to support agricultural and rural

development (Arthington, 1996; Thoms *et al*., 2005). Fish stocks of Murray-Darling Basin rivers have been documented as severely stressed and in decline as a result of river regulation (Walker and Thoms, 1993; Gehrke *et al*., 1995; MDBC, 2004).

In the northern MDB, rainfall and runoff are highly variable and unpredictable such that many rivers exist as strings of disconnected waterholes apart from times of irregular flow. The impacts of water resource development on aquatic biota, especially fish assemblages, are likely to be severe in these dryland river systems (Davies *et al*., 1994; Kingsford, 2006). Fish living in dryland rivers maintain populations through prolonged "bust" periods by means of resistance traits and low-flow recruitment processes (Arthington *et al*., 2005; Balcombe and Arthington, 2009). Given that water resource development and allocation to irrigated agriculture tends to remove low flow pulses (Bunn *et al*., 2006), the potential for fish populations and assemblages to recover during "boom" conditions may be limited if they do not retain sufficient numbers to take advantage of higher flow conditions. Furthermore, changed natural patterns of flow, and hence connectivity potential among waterholes, are likely to limit the resistance of fish to low flow disturbances and also their resilience, as they rely on connectivity among waterholes to maintain populations through movement and recruitment processes (Junk *et al*., 1989; Puckridge *et al*., 2000; Balcombe *et al*., 2006; 2007; Balcombe and Arthington, 2009).

In order to manage these altered river systems by strategies such as the allocation of environmental flows, it is important to understand the main drivers of fish distribution and abundance patterns, especially the significance of modified flow regimes (Arthington *et al*., 2006; Welcomme *et al*., 2006; Poff *et al*., 2009). To this end, we compared fish assemblages across 15 waterholes within the Border Rivers, Moonie River and Barwon River catchments of the northern MDB that were grouped *a priori* based upon antecedent hydrology and levels of hydrological alteration. Our primary hypothesis was that waterhole geomorphology interacting with hydrological conditions and water chemistry (cf. Arthington *et al*., 2005; Balcombe *et al*., 2006) would be the primary drivers of differences in fish abundance, species richness and assemblage structure across the gradient of flow regulation.

MATERIALS AND METHODS

Waterholes were located on the floodplains and within the channel of the Macintyre-Barwon River and in-channel of the Moonie and Weir Rivers. The Macintyre and Barwon Rivers are subject to highly regulated river flows via a number of impoundments upstream of Goondiwindi which regulate 88% of inflows (CSIRO, 2007). Water storage in impoundments has decreased the average frequency of flows that connect anabranches and billabongs of the Macintyre river floodplain by about 22 percent and has reduced the volume of individual events by about 8 percent (CSIRO, 2007). Furthermore, Thoms *et al*., (2005) report that three headwater dams and 15 main channel weirs in the Macintyre catchment have significantly reduced the mean annual flow volume of the Macintyre River by as much as 38.5% at Goondiwindi.

In contrast, river flows in the much smaller Moonie and Weir Rivers remain unregulated by large storage impoundments, and contain comparatively fewer weir structures (Biggs *et al*., 2005). In these two catchments existing surface water extraction are small, and at present, groundwater development is considerably lower in comparison to the Macintyre and Barwon systems (Biggs *et al*., 2005). The low

level of water resource development in the Moonie and Weir Rivers differentiates them from the much larger and heavily impacted Macintyre and Barwon Rivers.

Waterholes were selected to represent the natural range of size, shape, connectivity and water permanence throughout the Barwon catchment by selecting up to four waterholes in four regions (Goondiwindi, Talwood, Mungindi and Collarenebri) of this catchment (Fig. 1). Four waterholes were studied in the first three regions, although only three were included at Collarenebri due to the loss of one waterhole to drying prior to our first sampling occasion. All fifteen waterholes were sampled for fish in November 2002 and thirteen were sampled in April 2003, due to the loss of a further two waterholes through drying. Waterholes included main channel regulated river sites (the Barwon or Macintyre River, BAR), smaller, unregulated river channel sites (the Weir or Moonie Rivers, MW) and floodplain sites (waterholes on the Barwon/Macintyre floodplain, FP).

Thirty-four physical floodplain and waterhole variables were measured in November 2002 at three spatial scales (Table I) 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). Water samples were collected from the surface at each site and analysed in the laboratory for ionic composition and nutrient concentration following standard methods (APHA 1975). Water chemistry was analysed on the two fish sampling occasions: November 2002 and March 2003.

The fish assemblage within each of the fifteen waterholes was 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 19h with the wing entrance 10m in width and one seine haul standardised to a $50m^2$ area. Fyke nets (13 mm mesh) captured both small and large-bodied individuals of all species. Fish were identified and counted and all native species were returned live to the water at the point of capture.

Data Analysis – geomorphology and water chemistry

Similarities and differences in waterhole geomorphology and water chemistry were analysed using ordination based upon hybrid non-metric multi-dimensional scaling (MDS). MDS plots were generated from Normalised Euclidean distance similarity matrices produced from $\log_{10}(x + 1)$ abundance and species presence/absence data. One-way analyses of similarities (ANOSIM), based upon the same similarity matrices, were used to identify differences among the three waterhole groups (BAR, MW and FP) in relation to their geomorphology and water chemistry. Geomorphological features were measured and analysed for one occasion only, November 2002, at two spatial scales: macro-scale (landscape and whole waterhole) features and meso-scale (within waterhole) features (Table I).

Univariate analysis of fish abundance and richness

Variations in fish species presence/absence and assemblage structure across waterholes and sampling times were analysed using the combined fyke and seine net CPUE data. These CPUE 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 upon the data collected by both sampling methods. One-way analysis of variance (ANOVA) was used to test the predictions that waterhole group (fixed factor) influences total fish CPUE and species richness amongst

waterholes for each of the two sampling occasions. To meet the assumptions of ANOVA all CPUE data were normalised by $\log_{10}$ (x) transformations; these transformations also improved homogeneity of variances among waterhole groups. Statistical significance was accepted at $P \leq 0.05$. Tukeys HSD *post-hoc* tests were used to establish the nature of any differences in CPUE or species richness among each possible pair of waterhole groups.

Multivariate analysis of fish abundance and richness

Fish species CPUE and presence/absence data were analysed using SIMPER to identify the main species driving differences in each waterhole group for each of the two sampling times. Assemblage patterns were subsequently analysed using ordination based upon hybrid non-metric multi-dimensional scaling (MDS). MDS plots were generated from Bray-Curtis similarity matrices produced from $\log_{10}$(CPUE + 1) and species presence/absence data. One-way analyses of similarities (ANOSIM) based upon the same similarity matrices were used to identify assemblage differences among the three waterhole groups (Barwon River, BAR; Moonie/Weir River, MW; floodplain, FP) during the November 2002 and March 2003 sampling occasions. SIMPER was used to describe the main species contributing to differences among each pairwise comparison.

BIO-ENV (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 (Clark and Ainsworth, 1993). Autocorrelated floodplain and waterhole variables were removed prior to the BIO-ENV procedure, using Spearman rank correlations ($r_s > 0.8$) to identify redundant variables. The environmental similarity matrices were based upon normalised Euclidean distance rather than Bray-Curtis similarity as per Clarke and Warwick, (2001). BIO-ENV analysis was performed on the November 2002 and March 2003 datasets. All multivariate analyses were undertaken in the PRIMER version 5 software package (Clarke and Gorley, 2001).

Associations between individual species and water chemistry parameters were examined using Spearman rank correlation. Due to the large number of tests undertaken, significant correlations were accepted at $p < 0.001$ to protect against Type I error (Keppel, 1991). All univariate analyses were performed using Systat for Windows 11.00.01 (SSI, 2004).

RESULTS

Hydrology and water chemistry

Prior to the first sampling occasion (November 2002), most waterholes were on a trajectory of decreasing volume as most had not received any inflows since March - April 2002 (Figure 2). The exception to this was that the two Moonie River waterholes had received a 300 $MLday^{-1}$ flow in October 2002. All Macintyre and Barwon River sites experienced periods of flow between the first and second (March 2003) sampling trips, hence they experienced channel connectivity among the main river sites. The two Weir River sites had a minor in-channel flow event approximately

two weeks prior to sampling in March 2003, while a flow pulse was passing through the Moonie River sites at the time of sampling in March 2003.

Although there were no gauging stations at the floodplain sites, landholder information revealed that all floodplain sites had received water inputs during the autumn prior to the first sampling occasion in November 2002. After this time and prior to the second sampling occasion (March 2003), Punbougal Lagoon was the only floodplain site that had received any significant in-flow from local rains, resulting in water level retraction at Maynes and Wirrabilla Lagoons and Gnungarah Creek (Figure 2). Furthermore, this drying event resulted in the complete drying of two sites, Whalan Creek and Wolonga Lagoon, by the second sampling occasion in March 2003.

Water chemistry variables tracked the hydrological patterns and differences among waterholes, as indicated by high levels of conductivity and dissolved ions across most waterholes in November 2002 following the dry period (Table II). This trend was not apparent in the MW sites, particularly the two Moonie River sites, where low conductivity and dissolved ions and high turbidity were associated with the recent flows in the Moonie River. In contrast, FP sites were at the opposite extreme, with low turbidity, high conductivity and dissolved ions. Water chemistry in BR sites sat in between the MW and FP sites, with intermediate values for most components measured.

The three waterhole groups formed three distinct water chemistry groups in multidimensional space (Figure 3a). MW and BAR waterholes formed distinct clusters, while FP sites comprised a looser aggregation (Figure 3a). ANOSIM revealed that water chemistry factors were significant in differentiating waterhole groups and pair-wise differences between the three waterhole groups were also significant (Table III).

In March 2003, water chemistry was generally less differentiated across sites due to the effects of recent flows (Figure 3b). FP waterholes were particularly spread in ordination space, suggesting that each waterhole within the group changed along its own temporal trajectory. Even though BAR and MW sites had received inflows prior to March 2003, these two waterhole groups still sat apart and formed reasonably distinct groups in ordination space (Fig 3b). Waterhole chemistry was significantly different in relation to waterhole group in March 2003, and all pair-wise comparisons were also significant (Table III).

Geomorphology

The 15 waterholes overlapped in their basic dimensions, although the Moonie and Weir River (MW) waterholes tended to be smaller in area and volume than either the floodplain (FP) or the Barwon and Macintyre River (BAR) waterholes (Table II). FP waterholes also tended to be surrounded by a wider floodplain than the other two groups, while BAR waterholes tended to have the largest surface area of the three types.

Ordination of the macro-scale physical data revealed a broad spread of waterholes (Figure 4a). The only significant separation of waterhole groups was between the FP and MW sites (Fig 4a, Table III). Similarly, at the meso-scale, FP and MW waterholes formed relatively tight groups, without overlap, while BAR waterholes showed greater within-group variation (Figure 4b). Meso-scale physical factors were significantly different in relation to waterhole group, and pair-wise comparisons revealed that only FP and BAR sites were significantly different to each other (Table III).

Fish assemblages

We collected a total of 13 species across the 15 sites and two sampling occasions, comprising nine native species from eight families and three exotic species from two families (Table IV). Throughout the course of this study we recorded a total catch per unit effort of 2151 fish (Table V). Bony bream was the most abundant species, accounting for 68% of fish caught across all sites and sampling times. It was found in all waterholes sampled on at least one occasion and was most abundant in FP waterholes across both time periods. The next most abundant species were yellowbelly (11%), carp gudgeons (10%) and common carp (5%). Of these three species, carp gudgeons were the least distributed across sites, being restricted mostly to FP sites, particularly Punbougal Lagoon where 81% of their total was captured. Few yellowbelly were caught in floodplain sites, with the majority caught in MW sites. This pattern was also largely reflected in the distribution of common carp.

Total fish CPUE and species richness showed limited variability among the three waterhole groups in both sampling periods (Figure 5). In November 2002 after the dry period, CPUE was significantly different in relation to waterhole group (ANOVA: $F_{2,12} = 16.3$, Figure 5a). Tukey's pairwise comparisons revealed that FP waterholes had significantly higher CPUE than both BAR and MW waterholes. Although there was still a tendency for CPUE to be highest in FP waterholes compared to the other two groups (Figure 5b) in March 2003, there was no significant difference in CPUE in relation to waterhole group (ANOVA: $F_{2,12} = 2.7$). In November 2002, although species richness was generally lower in MW sites than others (Figure 5c), waterhole groups were not significantly different (ANOVA: $F_{2,12} = 3.7$). In March 2003 there was a tendency for MW sites to have greater species richness than other sites (Fig 5d), although this difference was also non-significant (ANOVA: $F_{2,12} = 3.7$).

Fish assemblage patterns

SIMPER analysis revealed that similarities in fish assemblages within both FP and BAR sites based upon CPUE data were largely due to the abundance of bony bream, accounting for between 52 and 99% of the similarity across sites and times (Table VI). In contrast, the similarity among MW waterholes based upon CPUE was due to the abundances of yellowbelly and the exotic common carp and goldfish in November 2002 and yellowbelly, bony bream and common carp in March 2003 (Table VI).

Similarities in fish assemblages among waterhole groups based on species presence/ absence were less clear than for assemblages based on CPUE (Table VI) with high variability in the species that accounted for most of the patterns. In November 2002, 72 % of the similarity in BAR sites was due to the presence/absence of rainbowfish and yellowbelly while 6% of the similarity in March 2003 was driven by bony bream and yellowbelly. Bony bream and carp gudgeon presence/absence had the greatest influence on FP site similarities (61%) in November 2002, while in March 2003 bony bream dominated the assemblage patterns (78% similarity). MW site similarities were largely due to carp presence/absence in November 2002 (60%), while in March 2003 presence/absence assemblage patterns were due to the combined patterns of five species (Table VI).

Ordination plots of fish assemblage structure based on CPUE revealed a clear separation of assemblages along the three waterhole groups (Figure 6). This was especially so in November 2002 when there were three clear assemblage groups. These patterns were also supported by ANOSIM, with fish assemblage structure

significantly different across all pairs of groups (Table VII). SIMPER revealed that the differences in assemblage structure between FP and the other two waterhole groups were due largely to the high abundances of bony bream and, to a lesser extent, carp gudgeons in FP waterholes (Table VI and VII). In contrast, the difference in assemblage structure between MW and BAR waterholes was influenced by the abundances of a wider array of species: higher numbers of bony bream and rainbowfish in BAR waterholes, and more yellowbelly, carp and goldfish in MW waterholes.

In March 2003 some waterholes had received in-flows prior to sampling while others had decreased in volume since November 2002, hence, the fish assemblages in waterhole groups formed looser aggregations in multidimensional space than in November 2002 (Fig 6b). FP and BAR sites were particularly loosely arranged towards the left half of the plot, while MW sites sat in the right half. While waterhole group was significant for overall fish assemblage structure, only MW sites were significantly different to the other two groups (Table VII). These differences in assemblage structure were largely due to the higher numbers of yellowbelly and lower numbers of bony bream in MW waterholes compared to the other two waterhole groups (Tables VI and VII).

Patterns of assemblage structure based upon species presence/absence again revealed a strong and significant influence of waterhole group in November 2002 (Fig 7a; Table VII). MW sites formed a clear grouping to the right of the MDS plot, FP waterholes sat toward the top middle to left, while BAR sites tended to sit mid-bottom of the plot. All pair-wise comparisons among waterhole groups were significant and these differences reflected a much more even spread of species than for the CPUE patterns, with at least seven species contributing to more than 82% of the pair-wise differences (Table VII). In addition to the common species found to influence CPUE assemblage patterns, the remaining species (such as spangled perch, carp gudgeons, catfish and smelt) also contributed to the presence/absence assemblage patterns. In March 2003, fish assemblage patterns based upon species presence/absence were less clear than in November 2002, with sites largely spread within the MDS plot (Figure 6b). While all MW waterholes remained within a tight group, both FP and BAR waterholes followed separate trajectories and, hence, waterhole group was not a significant factor explaining patterns in assemblage structure (Table VII).

Bio-Env analysis revealed no concordance between fish assemblage structure and the geomorphological variables measured in November 2002. Some clear relationships were, however, apparent between fish ordination patterns and water chemistry variables. Turbidity was most consistently associated with spatial patterns in fish CPUE (Table VIII). Fish species presence/absence patterns were less clear showing the strongest association with the three combined variables TC, NO_3 and SO_4 in November 2002, while the associations with water chemistry were weak in March 2003 (Table VIII).

While there was no association between geomorphological factors and fish assemblage structure, there were significant correlations between some of these factors and individual species abundances (Table IX). For example, the abundance of *M. ambigua* was negatively correlated with both area (A) and wetted perimeter (WP) of waterholes on both sampling occasions. In addition to these results, there was also a consistent pattern of waterhole scale factors being correlated with fish species abundance, with A, ACS (area of cross section) and WP being significantly correlated with one or more of bony bream, yellowbelly and common carp on both sampling occasions. Similarly, conductivity and turbidity were also consistently associated

with the abundance of one or more of the same three fish species on both sampling occasions.

DISCUSSION

Fish assemblage structure in the waterbodies of large floodplain rivers can be predicted from hydrological, physical and water chemistry factors, particularly where these factors vary predictably from year to year (Junk *et al*., 1989; Rodriguez and Lewis, 1997). This predictability is important when floodplain rivers are regulated and it becomes desirable to recommend environmental water allocations that will enhance and restore fish populations and assemblages (Welcomme *et al*., 2006). In highly variable river systems, our capacity to predict fish assemblage and population characteristics is more problematic, and exacerbated when flow regimes are regulated. Yet, the search for patterns of ecological response to flow regime change is essential to support environmental flow management (Poff *et al*., 2009). In this study, we sought to identify the main drivers of fish assemblage and abundance patterns across a simple gradient of flow regulation in three dryland floodplain rivers.

The physical attributes of the fifteen waterholes were highly variable and did not separate strongly into distinctive groups. The Moonie, Weir, Macintyre and Barwon River waterholes were most similar and could not be differentiated at either of the two spatial scales of physical assessment (large scale and within waterhole scale). If physical features of waterholes were key drivers of fish distribution and abundance patterns then we would expect that the fish assemblages of MW and BAR waterholes would be most similar, and FP assemblages to be differentiated from the other two types. However, the three waterhole groups were more strongly differentiated by their water chemistry, in both November 2002 and March 2003. Hence, if water chemistry was a key driver of fish assemblage attributes then we would expect the three waterhole groups to have strongly differentiated fish assemblages on both sampling occasions.

Total abundance and species richness of fish assemblages did not meet our predictions in relation to the three waterhole groups, with little variability evident apart from FP waterholes having higher fish abundances than either the MW and BAR waterholes in November 2002. Given the dominance of bony bream to total abundance in the catchment, and the low species richness (approx. four species on average per waterhole for all samples collected), these results are perhaps not so surprising. Bony bream is a habitat generalist and arguably the most widely distributed Australian dryland fish species (Pusey *et al*., 2004). We would, therefore, not expect bony bream or total fish abundance to be particularly sensitive to habitat, hydrological or water chemistry differences among waterhole groups. While we detected 13 species in total, the low species richness in any one site would also reduce the likelihood of detecting large diversity differences among the waterhole groups. The aspect of fish assemblages that should be more detectable across differing environmental conditions among waterhole groups would be differences in the actual species make-up and their relative abundances (Arthington *et al*., 2005; Balcombe *et al*., 2006).

By contrast, fish assemblage structure did show significant differences among waterhole groups, as predicted, particularly in November 2002. At that time, the three waterhole groups were significantly differentiated in terms of both CPUE and presence/absence patterns. This differentiation appeared to be driven by the

differential effects of the degree of water loss and/or time elapsed since flow among waterhole groups, as evidenced by their differentiation in relation to the suite of water chemistry characteristics measured. Such differentiation of fish assemblages in relation to antecedent hydrology and to a lesser extent, water chemistry, has also been found in fish assemblages of the Warrego River, upper Murray-Darling Basin and in Cooper Creek, a dryland river within the Lake Eyre Basin (Arthington *et al*., 2005; Balcombe *et al*., 2006; Balcombe and Arthington, 2009).

In contrast to the assemblage patterns found in Novemeber, fish assemblage structure based on relative abundance of species in March 2003 were less distinct, with only MW waterholes differentiated from BAR and FP. Nevertheless, this differentiation was not evident from the species presence/absence data. After periods of flow, waterhole groups still remained differentiated by their water chemistry, presumably due to the differences in flow inputs to some waterholes (e.g BAR and MW sites) and drying in others (FP sites). However, there was a surprising lack of response in fish abundance in BAR sites, in that all had received significant flow pulses prior to March 2003, and yet were not differentiated from fish assemblages in FP sites. Given that only one FP site had received any incoming flow (Punbougal), we would have predicted the FP group to have had depressed abundances and species richness in comparison to in-channel waterhole groups that had received significant inflows. This result may indicate the poor condition of the Macintyre and Barwon River fish populations in our study area, in that we did not detect a strong assemblage change due to increased numbers of fish and species that might have resulted from flow-induced immigration and juvenile recruitment (cf. King *et al.*, 2003; Arrington and Winemiller, 2004; Balcombe and Arthington, 2009). Poor fish assemblage response to flow in the BAR waterhole group contrasts with increased abundance and species richness in the MW sites and Punbougal Lagoon in March 2003 following flow inputs.

The lack of response in yellowbelly abundance in March 2003 following flow in the Barwon River may present a specific indicator of the generally depressed condition of the fish assemblages in this regulated river. At the same time, there was a strong recruitment response in both Moonie and Weir rivers. Increased abundance of yellowbelly has been shown to correspond strongly to flow pulses in the northern MDB via high juvenile recruitment (Balcombe *et al*., 2006; Sternberg, 2008). The closely related Lake Eyre yellowbelly (*Macquaria* sp.) also shows a strong recruitment response to flow (Arthington *et al*., 2005; Balcombe and Arthington, 2009).

Initially we had expected that waterhole physical factors would be strong determinants of differences in fish assemblages among the three waterhole groups. However, the morphological differences among the three waterhole groups, most notably MW and FP waterholes, were not strongly reflected in patterns of fish assemblage structure. The BIO-ENV analysis indicated that fish assemblages patterns were not associated with physical waterhole/habitat variables, with no significant relationships present. However, BIO-ENV did demonstrate a link between fish assemblage structure and water chemistry, particularly turbidity in relation to species abundances in both November 2002 and March 2003.

Although differences in the physical features among waterhole groups were not concordant with patterns in fish assemblage structure, there were some significant correlations between individual species abundances and particular physical factors. Yellowbelly abundance was negatively correlated with both waterhole area and wetted perimeter on both sampling occasions, while carp numbers were also

negatively correlated with cross-sectional area on both occasions. These relationships appear to reflect the higher abundances of yellowbelly and carp in MW waterholes rather than these species seeking out or persisting in particular waterholes based upon their size, basin shape or wetted perimeter. Similarly for water chemistry variables, the most consistent relationships were the positive correlations between bony bream and conductivity level, and turbidity and the abundance of carp.

The analytical approach we used appears to have merit, particularly its ability to categorise patterns of fish assemblage structure among waterhole groups based on hydrological history/flow disturbance. These patterns were strongest in November 2002, when all waterholes within each 'group' had experienced the most similar conditions, i.e. several months without inflow and gradual drying. This pattern largely disintegrated due to the fish assemblages in the FP waterholes following different trajectories, including two completely drying, two drying down severely, one drying to a lesser extent and one (Punbougal) actually increasing in volume. It must be noted that for both MW and BAR waterholes, the fish assemblages (based on CPUE and presence absence) remained within distinct groups on both sampling occasions. Most notably, the BAR waterholes were species and abundance poor, possibly due to the long history of flow regulation in the Macintyre – Barwon River system (> 60 years; Thoms and Sheldon, 2000) which may have depressed the potential for pulses of recruitment to occur even after flow events and improvements in water chemistry.

In summary, this study demonstrates several important features of fish assemblages in unregulated and regulated dryland rivers. Geomorphological parameters alone do not enable clear categorisation of waterhole types in dryland rivers and their floodplains in this part of the Murray-Darling Basin. We cannot expect to be able to predict fish assemblage richness and species abundances largely from basic morphological features, as shown for Cooper Creek (Arthington *et al*., 2005). The drivers of differences in fish assemblage patterns appear more complex than simple morphological typologies can reveal, evidently being associated more strongly with the water chemistry, which may reflect differences in antecedent hydrology and connectivity.. These factors also drive spatial variations in the fish assemblages in other floodplain river systems (Rodriguez and Lewis, 1997). However in the highly variable hydrological environment of our study area, distribution patterns of individual fish species appeared to be unpredictable apart from a few instances such as the ubiquity of bony bream and the association of yellowbelly with waterholes in the MW sites.

Overall, our results strongly suggest that the largely unregulated rivers of the upper Murray-Darling Basin are in better ecological condition and able to support recruiting populations, whereas fish recruitment (e.g. yellowbelly) in the regulated rivers may have been suppressed by successive years without strong flood pulses that enable populations to remain resilient even after natural dry periods (cf Warrego R., Cooper Creek, Arthington *et al*., 2005; Balcombe *et al.*, 2006).

These findings have implications for the management of hydrological regimes and the provision of environmental flows in regulated rivers of the upper Murray-Darling Basin. They extend evidence of the deleterious effects of flow regulation in rivers of the Murray-Darling Basin (Gherke *et al*., 1995; MDBC, 2004; King *et al*. 2009) and support the need for environmental water allocations to enhance fish recruitment, particularly for species of fisheries significance such as the yellowbelly. As in many other floodplain rivers, the primary threat to fish diversity and population processes is reduced flood frequency, intensity and duration caused by upstream

impoundments (Thomaz *et al*., 2004). Our finding that the fish assemblages of relatively undisturbed Moonie and Weir Rivers are in better ecological condition, and support recruiting populations of yellowbelly, provides a sound ecological rationale for flow restoration and other ecologically beneficial water management strategies in the more regulated Macintyre and Barwon rivers.

ACKNOWLEDGEMENTS

The authors would like to thank the various Dryland River Refugia project team members and volunteers who provided field support, and the numerous landholders for their property access and support. Our research was conducted under Queensland Fisheries Permit PRM00157K and Griffith University Animal Experimentation Ethics Committee permit AES/03/02.

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Table I. Waterhole geomorphology and habitat variables (and abbreviations) measured at three spatial scales in the Macintyre, Barwon and Border Rives catchments.

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

Table II. Variation in waterhole geomorphology and water chemistry parameters between the three waterhole groups. Data are reported as medians and ranges.

	BAR		FP		MW	
Basic Geomorphology						
Total Floodplain width (km)	15.9	9.79-56.1	59.0	6.71-640	48.0	1.98-61.3
Area (m^2 x 10^3)	58.8	47.3-173	158	19.6-511	10.7	8.38-17.2
V (m^3 x 10^3)	448	336-2250	779	123-2900	59.9	43.4-1130
P (m)	2734	2369-7511	5605	1314-8460	1091	728-10110
L	1320	1079-3607	2500	614-4133	503	341-5039
November 2002 water chemistry						
Conductivity @ 25^0C(µScm^{-1})	360	275-385	473	325-990	200	150-260
pH	7.7	7.55-7.75	7.75	7.5-5.25	7.2	7.15-7.25
Turbidity (NTU)	83	8-105	285	28-2000	1475	1000-2000
Alkalinity as $CaCO_3$ (mg L^{-1})	130	105-145	200	110-330	68	56-81
Silica (mg L^{-1})	6	3-10	17	4-29	27	19-33
Total suspended solids (mg L^{-1})	60	30-90	220	5-1000	635	250-1700
Total Nitrogen as N (mg L^{-1})	0.8	0.4-0.9	1.7	1.1-4.2	2.7	1.7
3.6Total Phosphorus as P (mg L^{-1})	0.08	0.06-0.09	0.42	0.09-1.0	0.9	0.57-1.5
Sodium (mg L^{-1})	31	18-34	54	39-135	22	18-27
Potassium (mg L^{-1})	4.0	2.9-4.3	12	8.4-16	7.1	6.1-8.2
Calcium (mg L^{-1})	22	16-24	25	14-42	8.1	5.9-12
Magnesium (mg L^{-1})	14	12-15	12	7.1-32	3.7	2.4-7.1
Bicarbonate (mg L^{-1})	160	130-175	243	130-390	83	69-98
Carbonate (mg L^{-1})	0.5	0.3-0.5	0.9	0.2-4.5	0.1	0.1-0.1
Chloride (mg L^{-1})	25	16-29	30	24-150	14	7.9-20
Flouride (mg L^{-1})	0.2	0.1-0.2	0.4	0.3-1.0	0.15	0.1-0.2
Nitrate (mg L^{-1})	1.0	0.5-2.0	2.0	1.2-6.7	3.1	1.7-9.1
Sulfate (mg L^{-1})	13	2.2-15	12	6.4-65	5.7	4.9-12
March 2003 water chemistry						
Conductivity @ 25^0C(µScm^{-1})	230	220-290	273	115-1300	493	150-790
pH	7.5	7.5-8.2	7.8	7.3-8.8	7.7	7.2-8.4
Turbidity (NTU)	245	47-360	738	14-1450	298	76-960
Alkalinity as $CaCO_3$ (mg L^{-1})	75	70-115	101	46-440	189	54-365
Silica (mg L^{-1})	16	15-18	13	3-18	21	14-22
Total suspended solids (mg L^{-1})	150	40-330	165	20-270	190	80-290
Total Nitrogen as N (mg L^{-1})	1.3	0.6-1.4	2.3	1.2-2.6	1.9	1.6-2.8
Total Phosphorus as P (mg L^{-1})	0.26	0.15-0.31	0.70	0.44-0.83	0.67	0.38-0.78
Sodium (mg L^{-1})	19	18-22	34	15-230	52	18-120
Potassium (mg L^{-1})	3.7	3.2-4.0	8.6	5-22	11.7	4.4-19
Calcium (mg L^{-1})	14	13-18	12	4.7-28	28	5.9-42
Magnesium (mg L^{-1})	8.6	8.3-13.5	7.4	2.2-30	13	3-23
Bicarbonate (mg L^{-1})	91	86-135	124	55-495	228	66-430
Carbonate (mg L^{-1})	0.2	0.1-1.3	0.7	0.1-20	1.0	0.1-7.3
Chloride (mg L^{-1})	18	16-21	19	5.9-125	32	9.4-61
Flouride (mg L^{-1})	0.2	0.2-0.2	0.35	0.1-0.6	0.5	0.2-0.7
Nitrate (mg L^{-1})	2.3	0.6-2.5	2.2	2.1-3.0	2.9	2.3-5.4
Sulfate (mg L^{-1})	11	8.4-12	6.9	2.7-99	11	5.2-15

640 Table III. Summary of ANOSIM results comparing the three waterhole groups based on geomorphology and water quality. Note: Waterhole group: BAR = Macintyre and Barwon rivers, FP = floodplain, MW = Moonie/Weir rivers

Factor	**Global R**	**P**	**Significant pairwise tests**
Large scale geomorphology	0.197	0.04	MW-FP (0.04)
Waterhole scale geomorphology	0.379	0.001	BAR-FP (0.002), MW-FP (0.005)
Water chemistry-November 2002	0.61	0.001	BAR-FP (0.004), BAR-MW (0.008), MW-FP (0.01)
Water chemistry-March 2003	0.709	0.001	BAR-FP (0.008), BAR-MW (0.008), MW-FP (0.03)

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Table IV. Fish species (and code) caught in waterholes in the four study rivers and nearby floodplains, November 2002 and March 2003.

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Family/species	**Common name**	**Species code**
Indigenous species		
Ambassidae		
Ambassis agasizzii Steindachner, 1867	olive perchlet	AMB
Clupeidae		
Nematolosa erebi (Günther, 1868)		NEM
Atherinidae		
Craterocephalus stercusmuscarum fulvus	fly-specked hardyhead	CRA
Gobiidae		
Hypseleotris spp.	carp gudgeons	HYP
Melanotaeniidae		
Melanotaenia fluviatilis (Castelnau, 1878)	crimson-spotted rainbowfish	MEL
Percichthyidae		
Maccullochella peeli peeli	Murray cod	MPP
Macquaria ambigua (Richardson, 1845)	golden perch	MAC
Plotosidae		
Tandanus tandanus Mitchell, 1838	eel-tailed catfish	TAN
Retropinnidae		
Retropinna semoni (Weber, 1895)	Australian smelt	RET
Terapontidae		
Leiopotherapon unicolor (Günther, 1859)	spangled perch	LEI
Alien species		
Cyprinidae		
Carassius auratus (Linnaeus, 1758)	goldfish	CAR
Cyprinus carpio (Linnaeus, 1758)	common carp	CYP
Poeciliidae		
Gambusia holbrooki (Girard, 1859)	mosquitofish	GAM

Table V. Fish catch per unit effort (CPUE) for individual species in the 15 study waterholes, November 2002 (Time 1) and March 2003 (Time 2). Species codes are given in Table IV.

Waterhole	Reach	Group	Time	AMB	CRAT.	NEM	MEL	HYP	MPP	MAC	TAN	RET	LEI	CAR	CYP	GAM	TOTAL CPUE	RICHNESS
Ironbark Wh.	G	BAR	1	8	0	0	9	1	1	1	0	0	0	0	0	0	20	5
Ironbark Wh.	G	BAR	2	4	1	8	2	1	0	5	0	1	0	0	0	0	22	7
Whalan Ck.	G	FP	1	0	0	50	0	5	0	0	0	0	6	3	2	0	66	5
Whalan Ck.	G	FP	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Maynes Lg.	G	FP	1	0	0	76	0	0	0	0	0	0	0	0	0	0	76	1
Maynes Lg.	G	FP	2	0	0	130	0	0	0	0	0	10	0	1	1	0	142	4
Punbougal Lg.	G	FP	1	0	0	109	2	34	0	0	0	0	10	0	0	0	155	4
Punbougal Lg.	G	FP	2	0	0	306	10	136	0	0	0	0	1	2	0	0	455	6
Wolonga Lg.	T	FP	1	0	0	35	0	1	0	8	0	0	3	2	14	0	63	6
Wolonga Lg.	T	FP	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Newinga Wh.	T	MW	1	0	0	0	0	0	0	3	0	0	0	6	6	0	15	3
Newinga Wh.	T	MW	2	0	0	15	0	0	0	9	0	0	0	5	2	4	35	5
Mill Wh.	T	MW	1	0	0	0	0	0	0	3	0	0	0	0	3	0	6	2
Mill Wh.	T	MW	2	0	0	28	1	11	0	96	2	0	2	2	4	0	146	8
Kanowna Wh.	T	BAR	1	0	0	10	8	0	0	2	0	2	0	0	0	0	22	4
Kanowna Wh.	T	BAR	2	0	0	100	0	0	0	2	0	0	0	3	0	0	105	3
Goondoobluie Wh.	M	MW	1	0	0	0	0	0	0	0	1	0	0	6	8	0	15	3
Goondoobluie Wh.	M	MW	2	0	0	10	0	0	0	25	1	0	1	1	8	0	46	6
Tchuringa Wh.	M	MW	1	0	0	0	0	0	0	9	0	0	0	0	19	0	28	2
Tchuringa Wh.	M	MW	2	0	0	1	0	0	0	32	0	0	1	2	6	1	43	6
Rocky Wh.	M	BAR	1	0	0	10	6	1	0	1	2	0	0	0	1	0	21	5
Rocky Wh.	M	BAR	2	0	0	28	1	0	1	3	0	0	0	0	4	0	37	5
Saltbush Wh.	M	BAR	1	0	0	15	4	2	0	4	0	0	0	0	5	0	30	5
Saltbush Wh.	M	BAR	2	0	0	41	0	0	0	5	0	0	0	0	6	0	52	3
Wirrabilla Lg.	C	FP	1	0	0	172	1	12	0	2	0	1	0	0	2	0	190	6
Wirrabilla Lg.	C	FP	2	0	0	153	0	0	0	0	0	0	0	0	1	0	154	2
Gnungarah Ck.	C	FP	1	0	0	19	0	5	0	2	0	0	1	1	8	0	36	6
Gnungarah Ck.	C	FP	2	0	0	49	0	0	0	3	0	0	0	0	0	0	52	2
Devil's Wh.	C	BAR	1	0	0	15	3	0	0	1	0	0	0	5	0	0	24	4
Devil's Wh.	C	BAR	2	0	0	75	0	1	0	17	0	1	0	1	0	0	95	4
total CPUE				12	1	1455	47	210	2	233	6	15	25	40	100	5	2151	

Table VI.. Significant taxa contributing to the similarity patterns in three waterhole groups from SIMPER analysis. Species codes are given in Table IV.

Sampling Time	**transformation**	**Waterhole group**	**Significant taxa**
1	Log_{10} CPUE	BAR	AS = 52; *Nem* (52), *Mel* (38), *Mac* (9)
1	Log_{10} CPUE	FP	AS = 50; *Nem* (87), *Hyp* (5)
1	Log_{10} CPUE	MW	AS = 47; *Cyp* (64), *Mac* (22), *Car* (14)
1	Presence/absence	BAR	AS = 61; *Mel* (36), *Mac* (36), *Nem* (22)
1	Presence/absence	FP	AS = 58; *Nem* (40), *Hyp* (21), *Lei* (13), *Cyp* (12), *Car* (6)
1	Presence/absence	MW	AS = 68; *Cyp* (60), *Mac* (32)
2	Log_{10} CPUE	BAR	AS = 48; *Nem* (84), *Mac* (13)
2	Log_{10} CPUE	FP	AS = 50; *Nem* (99)
2	Log_{10} CPUE	MW	AS = 48; *Mac* (60), *Nem* (20), *Cyp* (12)
2	Presence/absence	BAR	AS = 55; *Nem* (43), *Mac* (43), *Cyp* (5)
2	Presence/absence	FP	AS = 40; *Nem* (78), *Cyp* (14)
2	Presence/absence	MW	AS = 78; *Nem* (21), *Cyp* (21), *Car* (21), *Mac* (21), *Lei* (10)

Table VII. Summary of ANOSIM results comparing waterhole fish assemblages based upon CPUE and presence/absence among waterhole groups. For significant pairwise comparisons, the taxa contributing to the differences are given from SIMPER analysis. Species codes are given in Table IV. Note: Waterhole group: BAR = Macintyre and Barwon rivers, FP = floodplain, MW = Moonie/Weir Rivers.

Sampling time	**Transformation**	**Factor**	**Global R**	**P**	**Significant pairwise tests and significant taxa (%)**
1	Log (CPUE +1)	Group	0.764	0.001	BAR-FP (p = 0.002) AD= 75%, *Nem* (64), *Hyp* (8), *Mel* (8), *Cyp* (7); BAR-MW (p = 0.008) AD=86%, *Nem* (30), *Cyp* (22), *Mel* (19), *Car* (9), *Mac* (8), *Amb* (5); FP-MW (p =0.005) AD = 88%, *Nem* (71), *Cyp* (8), *Hyp* (8)
1	Pres/abs	Group	0.503	0.001	BAR-FP (p = 0.03), AD= 51%, *Mel* (16), *Lei* (13), *Mac* (13), *Hyp* (12), *Cyp* (11), *Car* (10), *Ret* (7); BAR-MW (p = 0.008), AD= 63%, *Mel* (23), *Nem* (18), *Cyp* (14),*Car* (11), *Hyp* (9), *Tan* (8) *Mac* (5), *Ret* (5); FP-MW (p = 0.005) AD= 69%, *Nem* (23), *Hyp* (16), *Mac* (13), *Lei* (13), *Car* (11), *Cyp* (11) , *Mel* (7)
2	Log (CPUE +1)	Group	0.437	0.002	BAR-MW (p = 0.008), AD= 68% *Nem* (45), *Mac* (36), *Cyp* (5); FP-MW (p = 0.03), AD= 68% *Nem* (64), *Mac* (20), *Hyp* (9)
2	Pres/abs	Reach	0.148	n.s.	

Table VIII. Summary of BIO-ENV results based on Spearman rank correlations (r_s) between fish assemblage structure (CPUE and presence/absence) and water chemistry variables. Note: Results are only presented for the best possible solution.

Sampling time	**Transformation**	1 variable	2 variables	3 variables
Water Chemistry				
1	Log (CPUE +1)	Tur (0.52)	Con, Tur (0.58)	Con, Tur, SO_4 (0.61)
1	Pres/abs	pH (0.53)	Mg, SO_4 (0.59)	TC, NO_3, SO_4 (0.63)
2	Log (CPUE +1)	Tur (0.69)	Tur, TN (0.71)	Tur, TN, Fl (0.72)
2	Pres/abs	TSS (0.31)	TSS, TN (0.35)	TSS, TN, Fl (0.35)

Table IX. Significant Spearman rank correlations (r_s) between fish species abundance/diversity with geomorphological (codes given in Table 1) and water chemistry variables (Tur = turbidity, ConToH = total hardness, Sil = silicates, TC = total carbon, TSS = total suspended solids, N:P = nitrogen:phosphorus ratio). *p≤0.005 **p≤ 0.001

Sampling time	**Factor**	**Fish species, r_s (p)**
Geomorphology		
1	A	*Mac* -0.81**, *Cyp* -0.65 *
1	ACS	*Cyp* -0.68 *, *Mac* -0.66**
1	DCS	*Mel* 0.7 *
1	WP	*Mac* -0.65 *
1	SI	*Nem*, -0.7 * *Tot* –0.77**
2	A	*Nem* 0.71*, *Mac* -0.71**
2	ACS	*Cyp*, -0.76*
2	WCS	*Mac* -0.79 **
2	WD	*Mac* -0.8 **
2	WP	*Mac* -0.78 *
Water chemistry		
1	Con	*Nem* 0.86**, *Tot* 0.8**
1	pH	*Nem* 0.68*
1	Tur	*Cyp* 0.72*, *Mel* –0.81**
1	Alk	*Nem* 0.83**, *Tot* 0.75**
1	NO_3	*Mel* -0.71*
2	Con	*Nem* 0.82**, *Tot* 0.79**
2	Tur	*Nem* -0.71*, *Cyp* 0.82**, *Mac* 0.79**
2	TSS	*Cyp* 0.78**
2	Fl	*Nem* 0.79**, *Mac* -0.79**

Figure Captions

Figure 1 Simplified map of study site locations along the Macintyre, Barwon, Weir and Moonie River systems, upper Murray-Darling Basin. Note: Only rivers containing sites are shown for clarity.

Figure 2 Daily discharge data at six sites in proximity to study sites.

Figure 3. MDS plot of waterhole water chemistry based upon distance measures for a) November 2002 and b) March 2003.

Figure 4. MDS plot of waterhole geomorphology based upon distance measures for a) large scale morphology and b) within waterhole morphology.

Figure 3. MDS plot of waterhole geomorphology based upon distance measures for a) large scale morphology and b) within waterhole morphology.

Figure 4 Mean fish catch per unit effort (a. and b.) and mean species richness (c. and d.) grouped by waterhole group within the Barwon River catchment on two sampling occasions.

Figure 5 MDS plot of fish assemblage data for November 2002 and March 2003 combined based upon (a.) $\log_{10}$ transformed catch per unit effort and (b.) fish species presence/absence

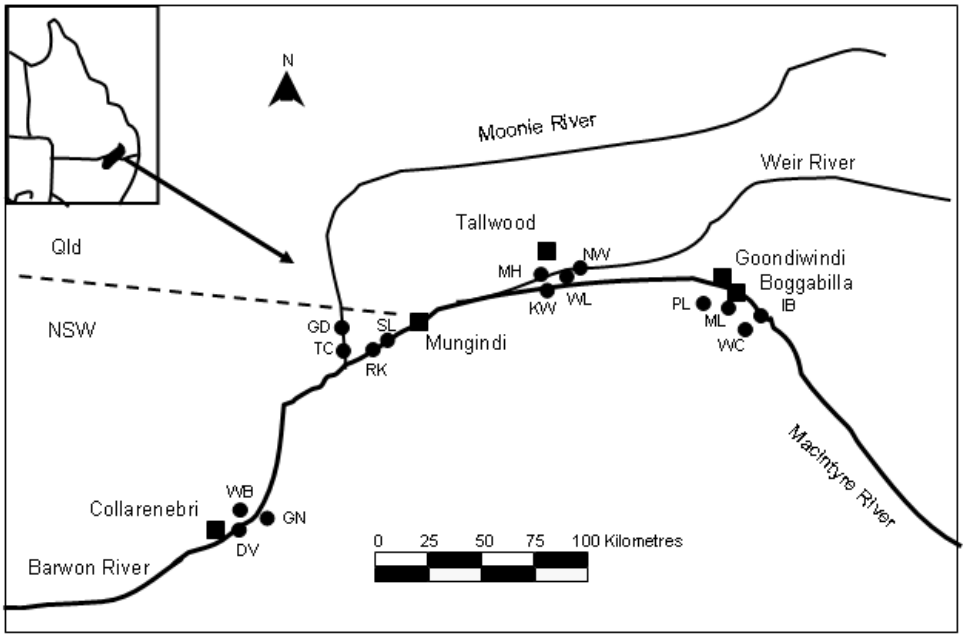

N
Moonie River
Weir River
Tallwood
Qld
NSW
NW
MH
KW
WL
Goondiwindi
Boggabilla
PL
ML
IB
WC
GD
TC
SL
RK
Mungindi
Macintyre River
WB
Collarenebri
GN
DV
Barwon River
0 25 50 75 100 Kilometres

Figure 1

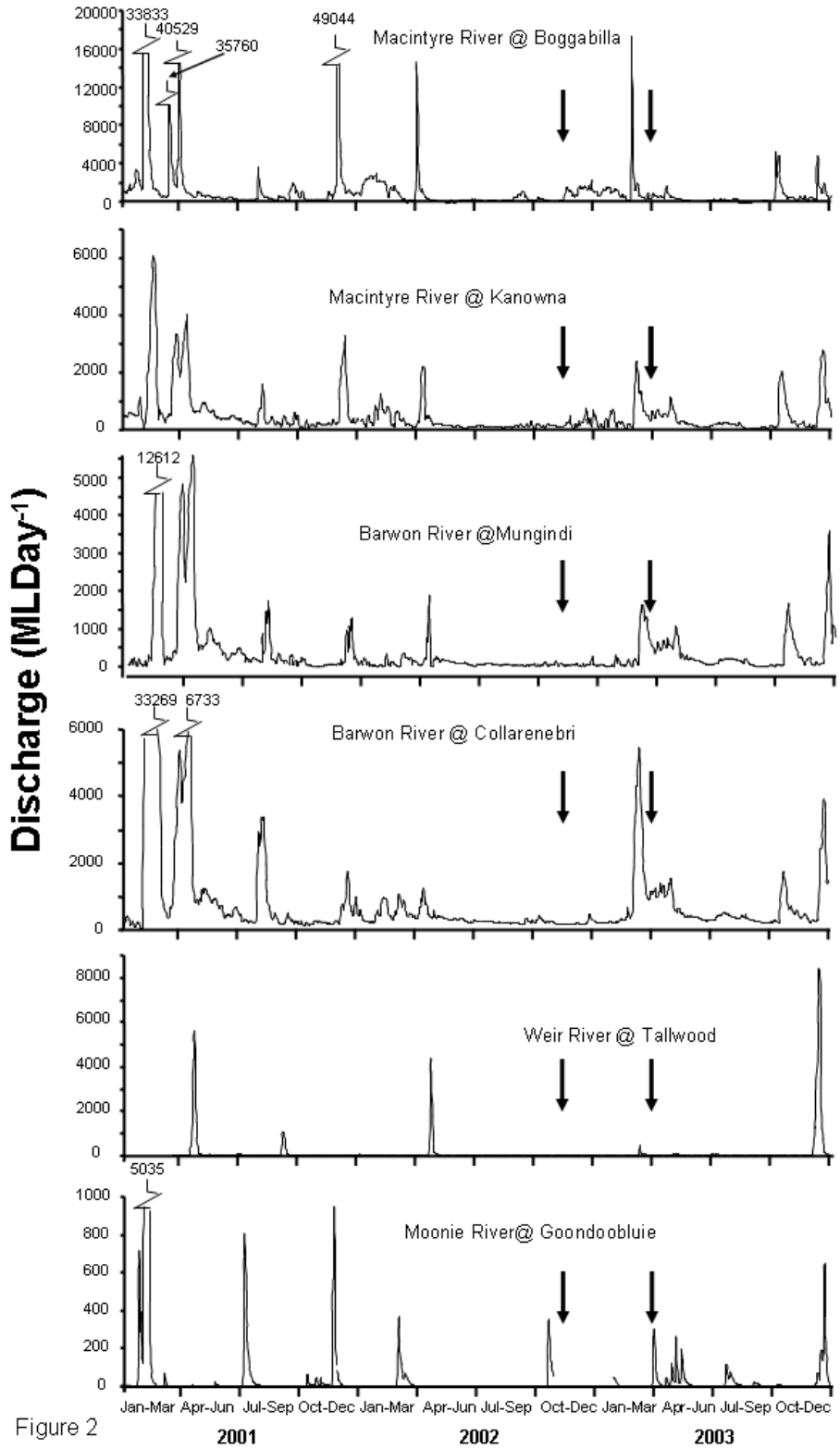

Discharge (MLDay-1)
Macintyre River @ Boggabilla
33833
40529
35760
49044
Macintyre River @ Kanowna
Barwon River @Mungindi
12612
Barwon River @ Collarenebri
33269
6733
Weir River @ Tallwood
Moonie River@ Goondoobluie
5035
Jan-Mar Apr-Jun Jul-Sep Oct-Dec Jan-Mar Apr-Jun Jul-Sep Oct-Dec Jan-Mar Apr-Jun Jul-Sep Oct-Dec
2001
2002
2003

Figure 2

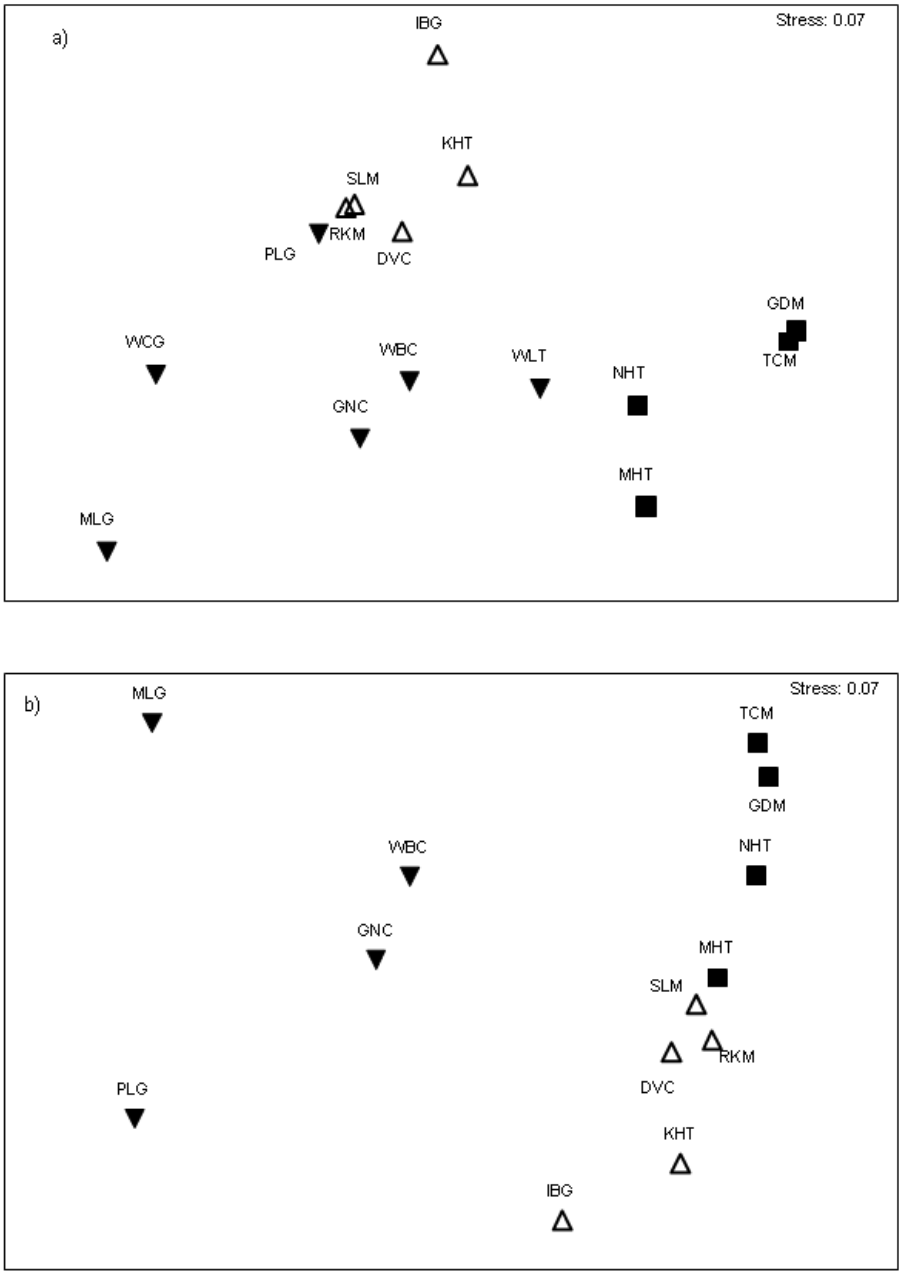
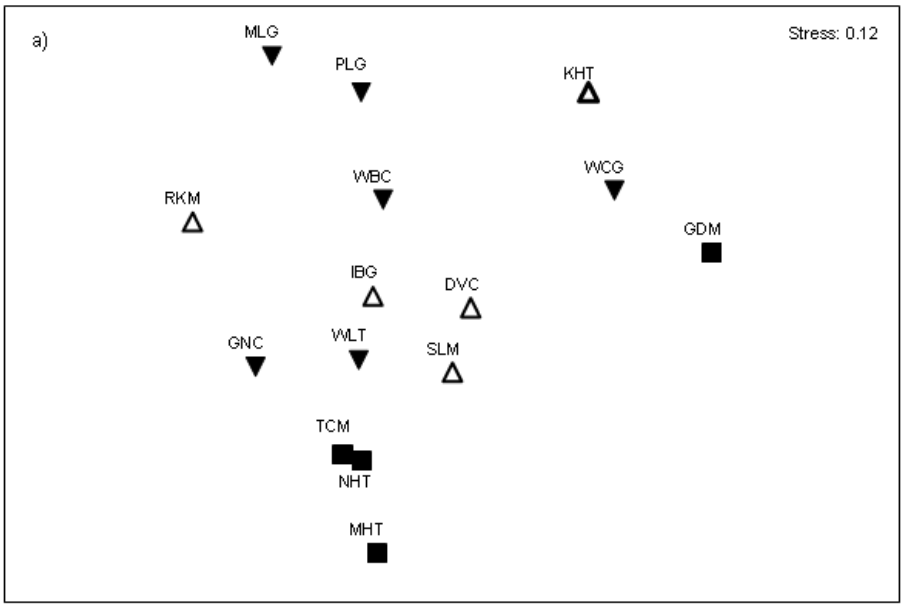
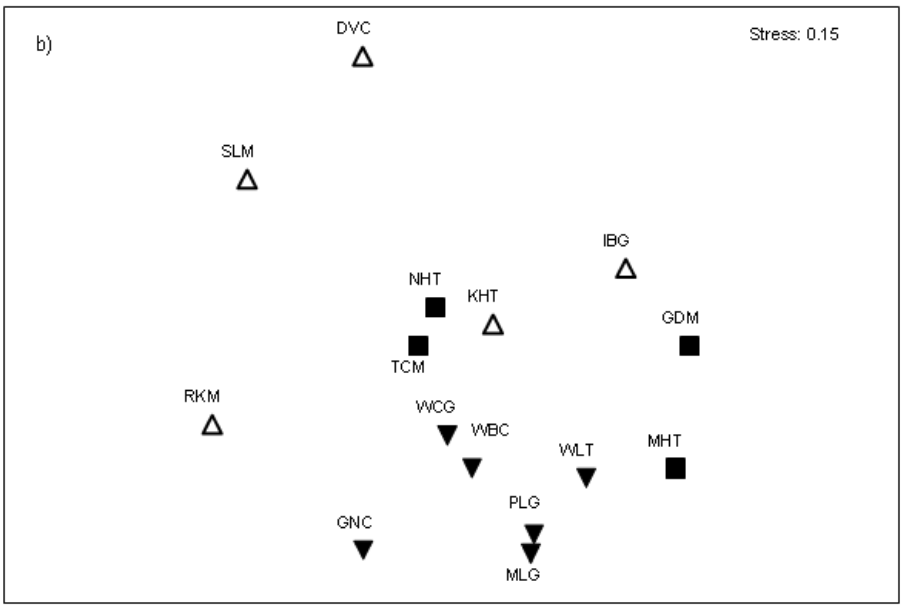

a)
Stress: 0.07
IBG
KHT
SLM
RKM
PLG
DVC
GDM
TCM
WCG
WBC
WLT
NHT
GNC
MHT
MLG
b)
Stress: 0.07
MLG
TCM
GDM
WBC
NHT
GNC
MHT
SLM
RKM
DVC
PLG
KHT
IBG
Waterhole Group: △ = BAR ▼ = FP ■ = MW

Figure 3





Waterhole Group: △ = BAR ▼ = FP ■ = MW

Figure 4

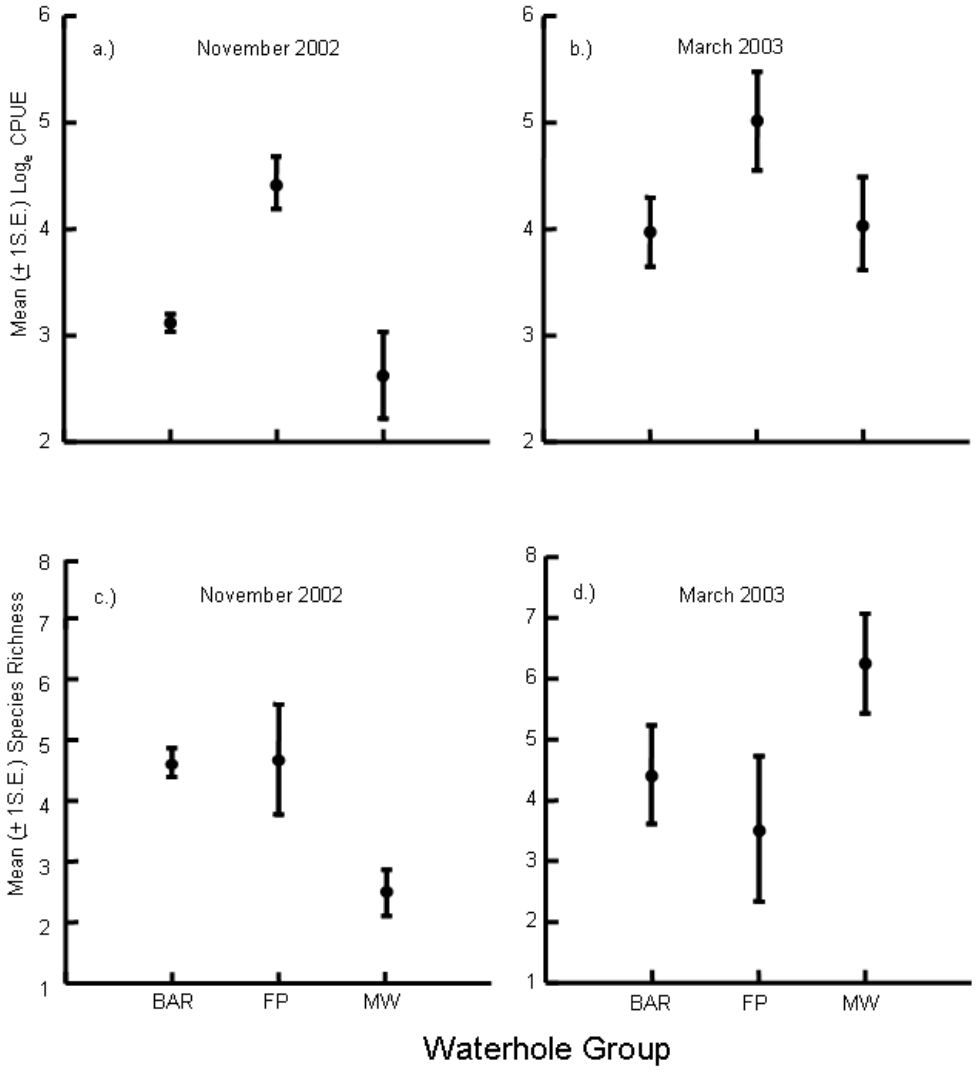
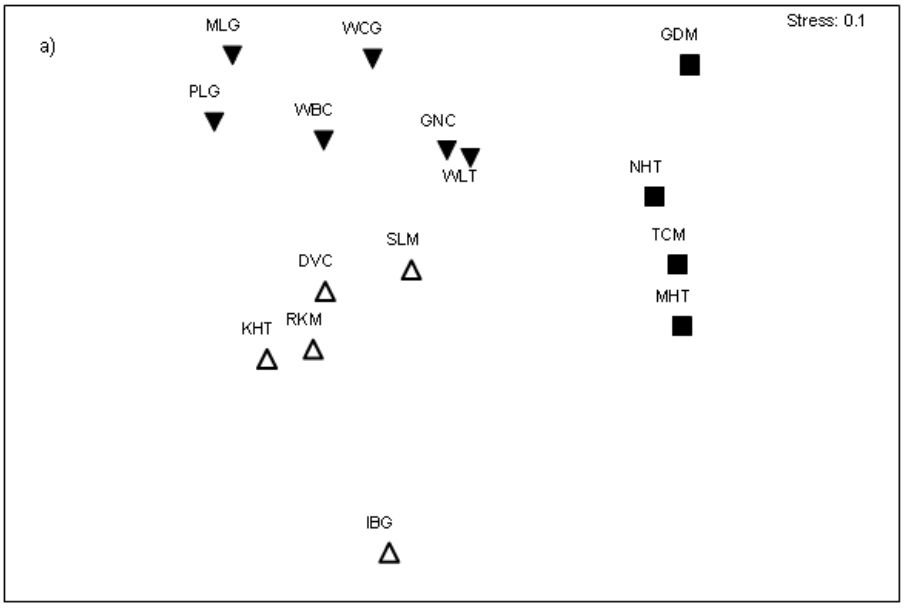
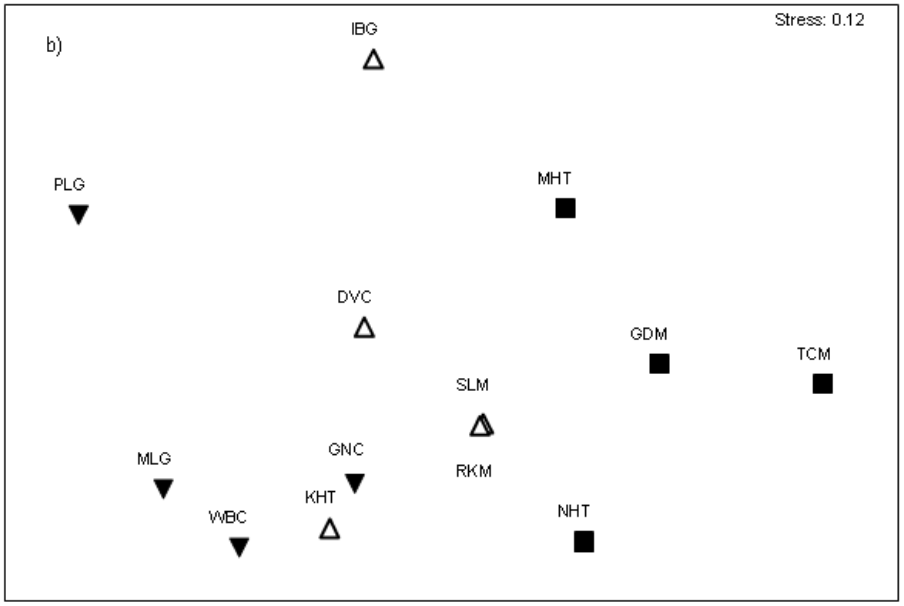

a.)
November 2002
b.)
March 2003
c.)
November 2002
d.)
March 2003
Mean (± 1S.E.) Log$_e$ CPUE
Mean (± 1S.E.) Species Richness
BAR
FP
MW
Waterhole Group

Figure 5





Waterhole Group: △ = BAR ▼ = FP ■ = MW

Figure 6

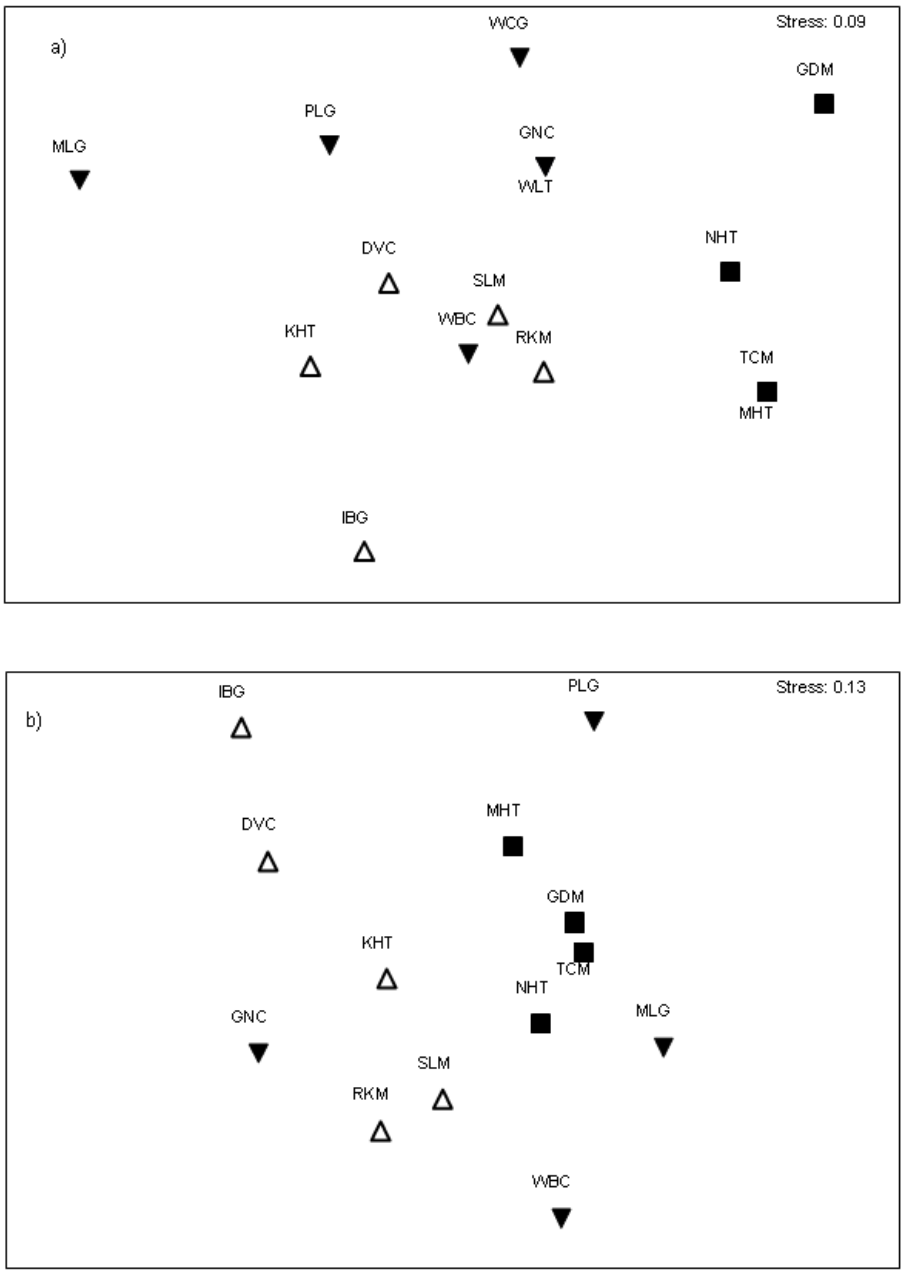

a)
Stress: 0.09
WCG
GDM
PLG
GNC
MLG
WLT
NHT
DVC
SLM
WBC
KHT
RKM
TCM
MHT
IBG
b)
Stress: 0.13
IBG
PLG
MHT
DVC
GDM
KHT
TCM
NHT
GNC
MLG
SLM
RKM
WBC
Waterhole Group: △ = BAR ▼ = FP ■ = MW

Figure 7