GRIFFITH UNIVERSITY

Dry-season changes in macroinvertebrate assemblages of highly seasonal rivers: responses to low flow, no flow and antecedent hydrology

Author

Leigh, Catherine

Published

2013

Journal Title

Hydrobiologia

DOI

Rights statement

Downloaded from

Griffith Research Online

Title

Dry season changes in macroinvertebrate assemblages of highly seasonal rivers: responses to low flow, no flow and antecedent hydrology

Author

Catherine Leigh

Affiliations and contact details

Australian Rivers Institute, Griffith University, 170 Kessels Road, Nathan, Queensland, Australia

c.leigh@griffith.edu.au

Abstract

Highly seasonal rivers can experience extended low flow, and often dry, periods. Macroinvertebrate and flow data were used to explore hypotheses on the effects of antecedent hydrology and the low-flow, dry-season period on macroinvertebrate assemblages in northern Australia. Composition differed between early and late dry seasons. Taxa were more sensitive to water quality and more rheophilous in the early dry season when their habitats were lotic than when habitats later became lentic. As flow magnitudes in the antecedent dry season and on the sampling day increased, the habitats became more oxygenated and, in turn, macroinvertebrate richness increased. Higher wet-season flow magnitudes, flow variability and rates of fall were correlated with lower richness in the following dry season. Alteration of the flow-disturbance regime that increases the likelihood of flow cessation in macroinvertebrate habitats, or extends the dry-season period beyond that previously experienced in these highly seasonal systems, may alter the resistance and resilience of assemblages such that the seasonal decline and recovery of biodiversity may no longer be so reliable. Given the projected increase in low-flow incidence in many regions of the world, future research needs to examine the effects of reduced flow, flow cessation and stream drying as multiple, interacting stressors on stream biota.

Key Words

Low flow, macroinvertebrates, streams, seasonality, disturbance

Introduction

Highly seasonal streams and rivers of the low latitudes play an important role in the global hydrological cycle (Cotner et al., 2006), with some of these systems having the largest discharges in the world (Latrubesse et al., 2005; Boulton et al., 2008). In Australia, for example, the wet-dry tropical rivers of the Gulf of Carpentaria and Timor Sea drainage divisions, which make up approximately15% of the land area, transport approximately 50% of the continent's annual average runoff to the ocean (AWRC, 1976). This high discharge, however, occurs during a relatively short wet season with the rivers experiencing extended dry periods each year due to seasonally low rainfall. Low and zero flows therefore constitute a significant component of the rivers' flow regimes (McMahon & Finlayson, 2003). While the combined consideration of low flows and biotic response within river systems is growing (e.g., Dewson et al., 2007; Stubbington et al., 2009; Walters and Post, 2011), there is a need for more-detailed understanding given scenarios of altered discharge under a changing climate and increased water use by humans (Milly et al., 2005; Stevenson & Sabater, 2010; Ledger et al., 2011). This is as important for the highly seasonal rivers of the tropics as it is for temperate systems (Boyero et al., 2009).

Composition and diversity of biota within highly seasonal streams and rivers reflect patterns of within- and among-season variation in abiotic and biotic conditions, as well as evolutionary constraints (Arrington & Winemiller, 2006; Bonada et al. 2007; Leung & Dudgeon, 2011). Rain-induced spates during the wet season alter water chemistry and shape the channel, floodplain and biotic responses, which through the falling water period transform into the dry-season responses to reduced discharge and more localised changes in abiotic and biotic conditions. Transition into the next wet season then completes the cycle (Leigh & Sheldon, 2008; Warfe et al., 2011). Seasonal patterns of variation in populations and assemblages of aquatic biota have been noted in the highly seasonal systems of the neotropics (Nolte et al., 1997; Montoya et al., 2006) and monsoonal Asia (Leung et al., 2012) and in tropical rivers draining to Australia's east coast (Perna & Pearson, 2008; Rayner et al., 2008). Maximum density and biomass of aquatic insects has been found, for example, during the dry season in tropical lowland streams that have a relatively benign dry season (Ramierez et al., 2006), and highest richness and abundance of invertebrates occurs during the relatively short dry season in highland, neo-tropical streams (Jacobsen & Encalada, 1998). Highly seasonal, lowland rivers are found across the world's wet-dry tropics, in Africa (north and south of the Congo), South America (in the Cerrado, Llanos and Chaco), in southern Asia and across northern Australia (Latrubesse et al., 2005), and for many of these systems extended dry seasons with little to no rainfall are the norm. Much of our understanding, however, on the seasonal trends within populations

and assemblages of in-stream biota in these types of tropical rivers comes from studies within only a few systems (e.g., Douglas et al., 2005; Pettit et al., 2011; Leigh et al., 2012).

Our understanding of seasonal dynamics of macroinvertebrate assemblages in lowland streams of the wet-dry tropics, including the biotic responses to natural periods of extended low and zero flow during the dry season, draws heavily on studies of the Alligator Rivers Region in northern Australia, and in particular from Magela Creek in the East Alligator River basin (Garcia et al., 2011). In this system, macroinvertebrate richness and abundance of shallow pool assemblages were examined over a one year period and found to peak around the late wet to early dry season, declining to minima by the end of the dry season (Marchant, 1982). Patterns in the deeper, main-channel pools were comparable but less pronounced. The observed changes reflected patterns of growth in macrophytes during the wet season, which were thought to provide food and shelter for the macroinvertebrates. Similar patterns were found in a later study that included some of the same sampling locations: macroinvertebrate diversity decreased over the course of a dry season but showed rapid recovery in the early wet season with the resumption of flow (Outridge, 1988). Richness and abundances were again associated with the presence of macrophytes. Organic detritus delivered to sites on the early wet season flows, however, was considered a more important food source than the macrophytes, and, as such, was proposed to support diverse assemblages at that time of year. Diversity metrics were also correlated with habitat characteristics (waterbody depth, water temperature, turbidity, conductivity and chlorophyll), indicative of the multiple and potentially interrelated factors that vary seasonally with climate and river flow. Paltridge et al. (1997) studied the post-dry season recolonisation of macroinvertebrate assemblages in the ephemeral main stem of Magela Creek and found that richness and abundance tended to increase early on in the wet season. These trends resulted from macroinvertebrate recolonisation via drift with the onset of flow and the re-emergence of taxa from their dry-season refuges in the substrata.

The spatial prevalence and temporal persistence of a dry-season decline in macroinvertebrate diversity, a wet season recovery in response to seasonal flow patterns, and concomitant changes in water quality and biophysical habitat across the wet-dry tropics is unknown. However, responses are likely to differ between flow regime classes, such as perennial versus intermittent systems, and between habitat types, such as lotic versus lentic (e.g., Humphrey et al., 2008; Leigh & Sheldon, 2009). Flow data and macroinvertebrate presence/absence data, collected over two years as part of the Australian Rivers Assessment Scheme (AUSRIVAS) from undeveloped streams and rivers across the wet-dry tropics of northern Australia, were used to explore the effects

of antecedent flow and the low-flow, dry-season period on assemblage characteristics of composition, diversity and biological traits. I hypothesized that in the sampled edge and sand habitats (i) there would be differences in assemblage characteristics, water quality and habitat-scale environmental characteristics between early (immediate post-wet) and late dry seasons, (ii) these assemblage characteristics would be associated with the habitat characteristics, and (iii) antecedent flow characteristics of the most recent dry and wet seasons would be associated with dry-season macroinvertebrate diversity and biological traits. I expected that time since the last wet-season peak flow would correlate negatively with macroinvertebrate richness, that low-flow magnitude at the time of sampling would correlate positively with macroinvertebrate richness, and that late dry-season assemblages would be less rich than early dry-season assemblages, particularly if habitats became lentic in the late dry season.

Materials and Methods

Study region

River systems across much of northern Australia's wet-dry tropics are unregulated. River flow in the wet season is primarily event driven in the summer months (~November-April, depending on location). Low flows, including zero flows, are natural phenomena of the long dry season, although groundwater discharge ensures that some rivers (e.g., the Daly) flow throughout the year (Petheram et al., 2008; Kennard et al., 2010a). This study examined streams and rivers within the Northern Territory that discharge into the Timor Sea and Gulf of Carpentaria (Fig. 1). Systems in this region have been classified as stable baseflow (perennial), predictable summer highly intermittent (summer-dominated runoff; 100-200 zero flow d y^{-1}) and variable summer extremely intermittent (summer-dominated runoff; > 250 zero flow d y^{-1}) (Kennard et al., 2010a).

Data collation and preparation

AUSRIVAS uses standardised and rapid approaches to monitor and assess the biological health of rivers in the Australian States and Territories and is based on predictive modelling. For the present study, I used AUSRIVAS data collected from multiple river basins in the Northern Territory (Lloyd & Cook, 2001) in the early (May and June) and late (September and October) dry seasons of 1995 and 1996. These data form the basis of the predictive models that are now used to assess the biological health of streams near Darwin, Northern Territory (Fig.1) but have not previously been used to explore hypotheses on seasonal patterns or flow-ecology relationships. Samples and data were collected from edge and/or sand habitats within each site, these being the two most dominant habitat types in the region. Sites were defined as reaches of approximately 100 m in length.

For each site, between-season sampling dates were separated by at least three months. Edge habitats were near vertical edges of rivers and streams, preferably with abundant root material and usually an associated pool. Sand habitats were sand beds that did not have a thick cover of detritus or algae.

Macroinvertebrates were collected from a total length of 10 m of edge or sand habitat using hand nets (250-μm mesh), preserved in 70% aqueous ethanol and then identified in the laboratory (excluding Cnidaria, Nematophora, Nematoda, Ostracoda, Copepoda, Cladocera and Collembola) to the family level of taxonomic resolution except for Oligochaeta (Class), Acarina and Conchostraca (Order) and Chironomidae (Subfamily). In accordance with AUSRIVAS protocol, samples were subsampled using a modified sub-sampling box (Marchant, 1989) until all (if < 200) or 200 animals were identified, with adults and larvae of the same taxon being combined numerically. In some cases, however, more than 200 individuals had been identified and counted, so for the present study sampling effort was standardised across samples by generating random subsamples of 200 individuals, without replication, using the vegan package (Oksanen et al., 2012) in R (R Core Development Team). This ensured that the maximum total individual count for any sample used in data analysis was 200. From this data, several metrics were calculated for each sand and edge sample: total richness (S), EPT richness (Ephemeroptera + Plecoptera + Trichoptera, although note that no sample contained Plecoptera), and the mean SIGNAL grade, dispersal capacity, rheophily and thermophily of taxa present. For context, SIGNAL grades for the Northern Territory macroinvertebrate taxa range from 1 to 9, where higher grades indicate taxa that are more sensitive to poor water quality and pollutants (Chessman, 2003). Rheophily and thermophily trait values for all taxa included in the Northern Territory AUSRIVAS training manual range from 0 to 3.39, and from 0.77 to 1.19, respectively, where higher values are more indicative of rheophilous and thermophilous taxa, respectively (Chessman, 2009). The dispersal capacity trait of Schäfer et al. (2011) ranges from low (1) to high (4). These traits were chosen because habitat preferences and dispersal capacities may give insight into the mechanisms by which assemblages respond to, or are affected by, hydrology, including low flows (e.g., Chessman et al., 2010; Brooks et al., 2011) and they were among the few with trait data available for the majority of taxa found in the study region.

At each site, mean water depth (m), stream width (m) and current speed (m s^{-1}) at the habitat-scale were also measured along with spot-measures of electrical conductivity (μS cm^{-1}), dissolved oxygen (DO, mg L^{-1}), temperature (°C), total nitrogen (TN, as total oxidised plus total Kjeldahl nitrogen, mg L^{-1}) and total phosphorus (TP, mg L^{-1}). Edge and sand habitats within the sampled reaches were often lentic (current speed = 0), even

though the relevant streams or rivers may have been in flow at the time. For the first two hypotheses, which concerned assemblage and habitat characteristics of the early and late dry seasons, data were therefore grouped by habitat (edge or sand) and by the early versus late dry-season flow status of the habitat types (Table 1). This produced three groups of data on which separate analyses were performed: sand habitats that were lotic in the early dry season but lentic in the late dry season; edge habitats that were lotic in the early dry season but lentic in the late dry season; and edge habitats that were always lentic (Table 1). To explore the third hypothesis, which concerned antecedent hydrology, data were collated only from those sites in close proximity to flow gauging stations (within ~4 km of the edge and sand sampling locations) (Fig. 1; Table 1). I compiled mean daily flow data ($m^3 s^{-1}$) from these gauging stations to calculate antecedent flow metrics relative to the dates on which the early and late dry-season samples had been collected. Flow metrics that described ecologically-relevant aspects of hydrology (e.g., magnitude, duration and rates of change; Poff et al., 1997) were calculated in RAP v3.0.3 (Marsh et al., 2003) for the most recent wet and dry seasons relative to samples, i.e., within one year of the macroinvertebrate sample date (Table 2). The antecedent dry period was defined from the beginning of May in the same year of sampling through to the date of sampling, and the antecedent wet season from the start of December in the year prior to sampling through to the end of April in the year of sampling. These dates aligned with end of the dry season and start of the wet season as indicated by hydrographs of river discharge across the 1995 to 1996 period (Fig. 2).

Data analysis

Difference in assemblage composition between the early and late dry seasons (hypothesis one) was tested by Permutational Multivariate Analysis of Variance (PERMANOVA) (Anderson, 2001), based on the Bray-Curtis similarity measure between sample pairs of presence/absence data and using 9999 permutations to generate *P*-values for the PERMANOVA test-statistic, the pseudo-*F*. This *F* ratio is similar to that in traditional ANOVA except that the pseudo-*F* does not have a known distribution under a true null hypothesis (Anderson et al., 2008). Year (1995, 1996) as well as river basin and all interaction terms were included as random factors in models when samples were collected from more than one river basin and there were enough samples to provide adequate degrees of freedom for analyses. If the estimate of a term's component of variation in the model was negative, the term's variance component was considered to be zero and was removed from the model by pooling its degrees of freedom and sums of squares with another term. Pooling was done sequentially and followed methods outlined in Anderson et al. (2008). Bray-Curtis similarity matrices, based only on groups of samples for which there was a significant effect of season ($P < 0.05$), were then ordinated using Principal Coordinate

Analysis (PCoA), which maximises the total variation among samples in the space identified by the relevant similarity measure. Vectors of taxonomic presence/absence, diversity and trait metrics and habitat-scale environmental and water quality variables were overlain on the PCoA ordinations to provide insight as to which taxa and habitat characteristics were associated with the dissimilarity between seasons. Vector overlays can be useful as an explanatory tool when the vectors identify variables that align along the same axis as do groups of similarity data (Anderson et al., 2008). A Spearman correlation cut-off of ± 0.35 was used as an indication of strong association between the variables and the pattern of assemblage dissimilarity between seasons (e.g., Brooks et al., 2011). Difference in habitat characteristics, and in macroinvertebrate diversity and trait metrics between the early and late dry season (hypothesis one) was tested using one-way ANOVA. Associations between habitat characteristics and macroinvertebrate metrics (hypothesis two) were described by the Pearson correlation coefficient (r). This coefficient was also used to explore associations between antecedent flow metrics (Table 2) and the macroinvertebrate (S, EPT richness, mean SIGNAL grade, dispersal capacity, rheophily and thermophily) and habitat metrics (mean stream width, mean water depth, mean current speed, conductivity, temperature, DO, TN and TP) (hypothesis three). Variables were log transformed where appropriate to meet assumptions of the parametric analyses. Univariate analyses were performed in R v2.13.1 (R development Core Team, 2011, Vienna) with $\alpha = 0.05$. All multivariate analyses were performed in PRIMER v6.1.13 with the PERMANOVA+ 1.0.3 add-on package (PRIMER-E, 2009, Plymouth).

Results

Hypotheses one and two: there are differences in assemblage composition and habitat characteristics between early (immediate post-wet) and late dry seasons, and assemblage characteristics are associated with habitat characteristics

Season had a significant effect on similarity in assemblage composition among samples for sand habitats that were lotic in the early dry season but lentic in the late dry season (pseudo-$F_{1, 12} = 2.30$, $P = 0.0347$). These samples were collected from streams and rivers in the Daly River basin only (Table 1). For edge habitats that were lentic in the early and late dry seasons, river basin alone had a significant effect on similarity in assemblage composition among samples (pseudo-$F_{4, 30} = 2.22$, $P = 0.0011$), indicating that assemblage composition in these habitats differed among river basins. For the sand habitats that changed flow status between seasons, the first two axes of the PCoA explained 56.9% of the variation in assemblage similarity. The split between early and late dry-season samples aligned well with the first axis such that early dry-season samples from lotic habitats aligned positively and the late dry-season samples from lentic habitats aligned

negatively along the axis (Fig. 3). The vector overlay of macroinvertebrate presences/absences suggested that the presence of Ceratopogonidae, Orthocladiinae, Pyralidae and the EPT taxa Hydrospychidae, Leptophlebiidae and Philopotamidae (mean SIGNAL grade = 5.5, mean rheophily = 1.72) was more strongly associated with the sand habitats in the early dry season that were lotic (r > 0.35 for all), than with the same habitats under lentic conditions in the late dry season, which were more strongly associated with the presence of Corbiculiidae, Lymnaeidae, Oligochaeta, Palaemonidae, Atyidae, Dytiscidae, Elmidae, Hydrophilidae and Ecnomidae (mean SIGNAL grade = 3.2, mean rheophily = 0.81) (r < -0.35 for all). Diversity and trait metrics and habitat-scale environmental and water quality variables that aligned positively along the first PCoA axis (such that higher values of these variables were associated with the lotic, early dry-season assemblages) included mean SIGNAL grade, mean rheophily, mean water depth, DO and TP (r > 0.4 for all). Mean current speed was zero in lentic habitats of the late dry season and this variable, therefore, also aligned positively along the first PCoA axis. Temperature and conductivity aligned negatively along the first PCoA axis (p < -0.4) such that higher water temperatures and conductivities were associated with the lentic, late dry-season assemblages in these sand habitats.

Season also had significant effects on habitat and assemblage characteristics of these sand habitats, supporting the results from multivariate analyses. The late dry-season (lentic) habitats had significantly higher water temperatures ($F_{1, 12} = 21.6$, $P = 0.0006$) and TN concentrations ($F_{1, 12} = 5.0$, $P = 0.0458$) but lower DO ($F_{1, 12} = 5.9$, $P = 0.0319$) than the same (but lotic) habitats in the early dry season (Fig. 4). The assemblages in the lentic sand habitats had lower SIGNAL grades ($F_{1, 12} = 10.6$, $P = 0.0069$) and rheophily ($F_{1, 12} = 5.3$, $P = 0.0405$) in the late compared with the early dry season when the sand habitats were lotic (Fig. 4). Strong correlations were detected between habitat characteristics and macroinvertebrate metrics of the sand habitat samples. Temperature correlated negatively, and current speed positively, with EPT richness, SIGNAL grade and rheophily; DO correlated positively with SIGNAL grade; and TN correlated negatively with both SIGNAL grade and rheophily ($P < 0.05$; Fig. 5).

In edge habitats, temperature was also significantly higher in the late than early dry season for habitats that changed from lotic to lentic ($F_{1, 16} = 5.7$, $P = 0.0298$) and for those that were always lentic ($F_{1, 34} = 13.5$, $P = 0.0008$) (Fig. 4). For the edge habitats that changed from lotic to lentic between seasons, DO was also lower in the late dry season ($F_{1, 16} = 13.2$, $P = 0.0022$), as was the assemblage SIGNAL grade ($F_{1, 16} = 15.0$, $P = 0.0013$) and rheophily ($F_{1, 16} = 7.3$, $P = 0.0155$) (Fig. 4). As water temperature increased and as mean current speed

decreased in these habitats, the assemblage SIGNAL grade and rheophily declined ($P < 0.05$; Fig. 6). Rheophily

also declined, but taxonomic richness increased, as water conductivity increased ($P < 0.05$; Fig. 6). EPT

richness declined as dissolved oxygen concentration decreased ($P < 0.05$; Fig. 6). The same relationships

between conductivity and overall richness, and between DO and EPT richness, were also found in the edge

habitat samples that were lentic in both the early and late dry seasons ($P < 0.05$). In these habitats, DO also

correlated positively with overall richness, rheophily and SIGNAL grade, and dispersal capacity increased with

mean water depth ($P < 0.05$; Fig 6).

Hypothesis three: antecedent flow characteristics of the most recent dry and wet seasons are associated with

dry-season macroinvertebrate characteristics

        In sand habitats (Fig. 7), macroinvertebrate richness (S) was negatively correlated with average and

high flow magnitudes and the mean rate of fall in the antecedent wet season (WeMax: $r = -0.58$; WeP90: $r = -$

0.63; WeMDF: $r = -0.64$; WeMRateFall: $r = -0.55$). The mean SIGNAL grade and rheophily of assemblages

declined as the number of days since the wet season peak flow ($r = -0.46$ and -0.48, respectively) and since the

end of the wet season increased ($r = -0.44$ and -0.43, respectively), and the SIGNAL grade also declined as flow

variability in the antecedent dry season increased (DrCV: $r = -0.51$) (Fig. 7). EPT richness declined as average

and high flows in the antecedent wet season increased in magnitude (WeP90 and WeMDF: $r = -0.51$) (Fig. 7). In

edge habitats (Fig. 7), assemblage richness declined as flow variability in the antecedent wet season increased

(WeCV: $r = -0.52$). As duration since the end of the wet season lengthened, the SIGNAL grade and dispersal

capacity of the edge habitat assemblages declined ($r = -0.51$ in both cases).

        For both the sand and edge habitats, assemblage diversity and biological traits were also correlated

with habitat-scale environmental and water quality characteristics, which themselves were correlated with the

antecedent flow metrics (Fig. 7). Overall richness in edge habitats increased with DO ($r = 0.51$), which

increased as flow magnitudes in the antecedent dry season and on the day of sampling all increased (DrP10,

DrMDF, DrP90 and FlowOnDay: $r > 0.55$). In sand habitats, the assemblage SIGNAL grade declined as water

temperature and TN concentration both increased ($r = -0.72$ and -0.53, respectively) and assemblage rheophily

and EPT richness also declined as water temperatures increased ($r = -0.69$ and -0.45, respectively). Water

temperature and TN concentration both became higher as flow variability in the antecedent dry season increased

(DrCV: $r > 0.71$ for sand; $r > 0.60$ for edges), and as the duration since the wet season peak flow

(DsinceWeMax: $r > 0.46$ for sand; $r > 0.65$ for edges) and the end of the wet season lengthened (DsinceEndWet:

r > 0.44 for sand; r > 0.59 for edges). In sand habitats, TN concentration increased as the average (DrMDF: r = -0.72) and high flow magnitudes (DrP90: r = -0.51) in the antecedent dry season declined.

Discussion

The late dry-season assemblages of the highly seasonal systems in the wet-dry tropics study region were expected to be less rich than the early dry-season assemblages, particularly when habitats became lentic towards the end of the dry season. Between-season differences, however, were associated with macroinvertebrate rheophily and sensitivity to water poor quality rather than richness. It is possible that richness varied during the course of the dry season, following the typical trajectory of a peak in richness with the initial onset of reduced flow and habitat contraction, with subsequent reduction in richness as habitat conditions deteriorated with time (e.g., Boulton & Lake, 1992). However, the early and late dry-season assemblages may have been sampled at points in time along this trajectory when dramatic differences in richness were not apparent. Taxonomic replacement of lotic taxa by lentic taxa between the early and late dry seasons may also have occurred, thereby preventing a decline in richness (Bogan & Lytle, 2007). The differences found between seasons in the composition and trait characteristics of assemblages, despite the comparable numbers of taxa, therefore reflect a taxonomic turnover similar to that observed in other systems in which relatively long periods of reduced flow or stream drying occur (Bogan & Lytle, 2012).

Macroinvertebrate assemblages of the studied river systems consisted of taxa that were, on average, more sensitive to water quality and more rheophilous in the early dry season when their habitats were in flow than in the late dry season when the habitats had become lentic. In addition, the waters of the sand and edge habitats harbouring the macroinvertebrates were cooler and more oxic in the early dry season than towards the end of the dry season. In the sand habitats, the waters were also more nutrient rich in the late dry season, which parallels findings of other tropical river studies in which nutrient concentrations are greatest during the low-water period (Cotner et al., 2006). There were also significant changes in assemblage composition between the early and late dry seasons when sand habitats were in flow during the early dry season but lentic during the late dry season. Together, these findings supported the first hypothesis that there would be differences in assemblage and habitat-scale environmental characteristics of sites between the early and late dry seasons, even though patterns of richness did not match the prediction. Similar shifts in assemblage composition in response to extended dry periods have been observed elsewhere in Australia, even in systems with flow regimes quite dissimilar to those in the wet-dry tropics. For example, in Victorian streams (southeast Australia), Rose et al.

(2008) found that edge assemblages shifted during an extended dry period that was characterised by reduced flow and increased lentic habitat. Paralleling findings of the present study, the shift resulted from the replacement of water quality sensitive and rheophilous taxa with taxa more tolerant to pollution and typically associated with still waters.

Contrary to the first hypothesis, however, assemblage composition between seasons could not be differentiated when habitats were lentic in both the early and late dry seasons (water temperature was the only habitat-scale characteristic that was discernibly different between seasons for these lentic habitats). The lack of seasonal structure may have been in part affected by biogeochemical variation across river basins and interannual variation in habitat and flow characteristics that produced variation in assemblages not directly attributable to season. Interannual variation in discharge has been related to deviance from typical seasonal patterns of assemblage structure in Sycamore Creek, a North American desert stream (Boulton et al., 1992) and, in the present study, hydrological characteristics in the year antecedent to sample collection were shown to affect assemblage characteristics (as discussed below). In the wet-dry tropics' study region, large-scale variation in factors such as geology, climate and groundwater supply, which affect stream geomorphology, flow permanence and water quality among other things (Townsend & Padovan, 2005), likely plays a role in distinguishing the macroinvertebrate assemblages of different river basins, particularly when temporal change in flow status of macroinvertebrate habitats does not occur. This is despite previous research finding little biogeographic structuring of family-level macroinvertebrate data across northern Australia (Kay et al., 1999, Cook et al., 2010).

The sand habitats that experienced a change in flow status from lotic to lentic between the early and late dry season were in the Daly River basin, the major rivers of which are perennial and supplied by groundwater discharge that maintains baseflow in the dry season (Webster et al., 2005). The edge habitats that changed from lotic to lentic were located across multiple river basins, yet the changes in water quality (temperature, DO) and macroinvertebrate assemblage characteristics (SIGNAL grade and rheophily) in these edge habitats matched those in the sand habitats of the Daly River basin. This suggests that habitats in the study region that change from lotic to lentic through the course of a dry season may be the most likely to exhibit pronounced seasonal changes in their physical and chemical characteristics and macroinvertebrate assemblages, regardless of the river basin (and thus baseflow water source) in which they reside. Strong spatial effects of dry-season flow status, above those of river basin, on macroinvertebrate assemblages have been found among

waterbodies in the Australian wet-dry tropics in systems east of the present study region (Leigh & Sheldon, 2009). The present study suggests that *temporal* change in dry-season flow status of habitats may also be a strong driver of assemblage structure, including trait composition.

Previously proposed relationships between seasonal patterns in macroinvertebrate assemblages and the wet-season growth of macrophytes, flow-delivered supply of organic detritus (Marchant, 1982; Outridge, 1988) or post-dry season recolonisation of habitats from drift or hyporheic refugia (Paltridge et al., 1997) were not explored directly in this study. Therefore, the importance of these factors to temporal change during the dry season in assemblage characteristics across the study region cannot be commented on specifically. However, the reduced rheophily and water quality sensitivity of assemblages in the late dry-season habitats may have been due to active dispersal of taxa sensitive to water quality changes or with flowing-habitat preferences. These taxa may have actively sought refuge elsewhere in response to physical and chemical changes in their dry-season habitats that occurred as a result of flow cessation (when lotic habitats convert to lentic ones) or declining flow magnitudes as the dry season progressed (Lake, 2003). For example, TN concentration increased as dry-season flow magnitudes declined and as the dry-season period lengthened, and higher TN concentrations were associated with lower sensitivity grades and rheophily trait values of assemblages. Also, the overall dispersal capacity of edge assemblages became lower as the dry-season period to which they were exposed lengthened. This suggested that as the dry season progressed, the taxa that found the changes in habitat conditions unsuitable and could escape these habitats probably did so (e.g., Lytle et al., 2008).

Reduced flows are known to affect physical and chemical characteristics of refugial waterbodies, in particular the conductivity and diel temperature ranges usually increase, and dissolved oxygen concentrations usually decrease as the waterbodies dry out (Boulton & Suter, 1986; Sheldon & Fellows, 2010). Many macroinvertebrates are sensitive to these water quality parameters (Chessman, 2003) and it is therefore not surprising that pollution-tolerant and nonrheophilic taxa are favoured by low-flow conditions, and particularly when flow ceases for extended periods of time. Thus, low-flow events and their duration are likely to elicit both direct and indirect responses in macroinvertebrate assemblages (Lake, 2003). As such, the simple dichotomy of flow status (lotic versus lentic, as proposed above) is unlikely to explain all flow-related changes in macroinvertebrate assemblage characteristics or the physical and chemical conditions of their habitats during the naturally low-flow periods of the dry season. For example, direct negative responses of rheophilous taxa to long periods of zero flow may be accompanied by negative responses of sensitive taxa to the changes in water quality

associated with cease-to-flow events. The patterns observed in the present study are therefore likely to be related to effects of flow-mediated changes in habitat and water quality characteristics, such as habitat size contraction and concentration of particulates, reduced water turbulence and decreased oxygenation, and increased water temperatures, that result from antecedent as well as contemporary hydrology and climate (Lake, 2003).

Along with the duration of low-flow or cease-to-flow events, other aspects of low-flow hydrology (e.g., magnitude, variability, rate of change), in relation to both the dry-season sample date and the flow events occurring in the antecedent wet season, played a role in structuring the dry-season assemblages in the present study. These findings supported the third hypothesis that antecedent flow characteristics of the most recent dry and wet seasons would be associated with dry-season macroinvertebrate characteristics. As the time between sampling and the wet season peak or the end of the wet season lengthened, the duration of the dry-season low-flow period that the assemblages had experienced increased. The longer this duration, the more tolerant (less water quality sensitive) and less rheophilic were the dry-season assemblages. This supports research on drought, low flows and water withdrawals in other systems throughout Australia (Marsh et al., 2012) and across the world, whereby the cumulative duration of low-flow events has had major effects on the ecological responses of aquatic biota (Dewson et al., 2007; Miller et al., 2007; Finn et al., 2009). In the present study, evidence was also found to support the expectations that macroinvertebrate richness in the dry season would correlate negatively with time since the antecedent wet-season peak flow, and positively with flow magnitude at the time of sampling. As flow magnitudes in the antecedent dry season and on the day of sampling increased, the waters in macroinvertebrate habitats became more oxic, and as the habitats became more oxygenated, macroinvertebrate richness increased. Overall and EPT richness were also related to antecedent wet season hydrology. Higher wet season flow magnitudes, flow variability and rates of fall were correlated with lower richness in the dry season. Although the macroinvertebrate fauna of these highly seasonal streams and rivers are no doubt well-adapted to regular and naturally extended periods of low flow (Kennard et al. 2010b; Leigh et al. 2010), the current findings suggest that particularly short and high wet-season flows (pulse disturbances) may have sustained effects on assemblage richness through the comparatively long dry season (press or ramp responses; Lake, 2000). Furthermore, alteration of the flow disturbance regime that increases the likelihood of flow cessation in macroinvertebrate habitats or extends the dry-season period beyond that previously experienced in these highly seasonal systems may alter the resistance and resilience of assemblages (Boulton, 2003) such that cyclic decline and recovery of biodiversity, as both observed (e.g., Outridge, 1988) and expected in these systems (Leigh & Sheldon, 2008; Leigh et al., 2012), may no longer be such a reliable pattern.

Observational studies, including the present study, provide insight on the effects of low flow, water drawdown and seasonality on river ecosystems and their biota, as has been demonstrated in Australia and New Zealand (Jowett et al., 2005; Chessman et al., 2008; Leigh, 2012), Europe (Bonada et al. 2007; Wood et al., 2010; Datry, 2012) and the Americas (Miller et al., 2007; Zeug & Winemiller, 2008). Yet our mechanistic understanding of ecological responses to reduced flow, flow cessation and stream drying still requires expansion (Dewson et al., 2007; Rolls et al., 2012). For example, the ability to draw conclusions about causal mechanisms of assemblage responses to low flows and the dry season in this study was likely restricted by confounding effects of river basin and multiple stressors (e.g., baseflow hydrology and physical and chemical changes to habitat) on assemblage characteristics. Future research may need to examine dry-season– and low-flow–ecology relationships within particular river basins or use a filters approach (e.g., Brooks et al., 2011) to control for variation in the physical and chemical environment among streams, providing that sufficient data are available. The use of experimental stream channels to determine biotic and ecosystem responses to coincident change in more than one aspect of the low-flow disturbance regime (duration, magnitude, frequency, timing and rate of change; cf. McCabe & Gotelli, 2000) may also improve our ability to predict responses to flow-regime changes (perennial to intermittent; intermittent to ephemeral) associated with climate change and the projected increase in demand on the world's freshwater resources.

Acknowledgements

References

Anderson, M. J., 2001. A new method for nonparametric multivariate analysis of variance. Austral Ecology 26: 32-46.

Anderson, M. J., R. N. Gorley & K. R. Clarke, 2008. PERMANOVA+ for PRIMER: Guide to Software and Statistical Methods. PRIMER-E, Plymouth, United Kingdom.

Arrington, D. A., & K. O. Winemiller, 2006. Habitat affinity, the seasonal flood pulse, and community assembly in the littoral zone of a Neotropical floodplain river. Journal of the North American Benthological Society 25: 126-141.

AWRC (Australian Water Resources Council), 1976. Review of Australia's Water Resources 1975. Department of Natural Resources. Canberra, Australia.

Bogan, M. T., & D. A. Lytle, 2007. Seasonal flow variation allows 'time-sharing' by disparate aquatic insect communities in montane desert streams. Freshwater Biology 52: 290-304.

Bogan, M. T., & D. A. Lytle, 2012. Severe drought drives novel community trajectories in desert stream pools. Freshwater Biology 56: 2070-2081.

Bonada, N., M. Rieradevall, & N. Prat. 2007. Macroinvertebrate community structure and biological traits related to flow permanence in a Mediterranean river network. Hydrobiologia 589:91-106.

Boulton, A. J., 2003. Parallels and contrasts in the effects of drought on stream macroinvertebrate assemblages. Freshwater Biology 48: 1173-1185.

Boulton, A. J., L. Boyero, A. P. Covich, M. Dobson, S. Lake, & R. Pearson, 2008. Are tropical streams ecologically different from temperate streams? In D. Dudgeon (ed), Tropical Stream Ecology. Elsevier, London: 257-284.

Boulton, A. J., & P. S. Lake, 1992. The ecology of two intermittent streams in Victoria, Australia. III. Temporal changes in faunal composition. Freshwater Biology 27: 123-138.

Boulton, A. J., & P. J. Suter, 1986. Ecology of temporary streams - an Australian perspective. In P. De Deckker & W. D. Williams (eds), Limnology in Australia. Council for Scientific and Industrial Research, Junk, Melbourne, Australia: 486-496.

Boulton, A. J., C. G. Peterson, N. B. Grimm, & S. G. Fisher, 1992. Stability of an aquatic macroinvertebrate community in a multiyear hydrologic disturbance regime. Ecology 73: 2192-2207.

Boyero, L., A. Ramírez, D. Dudgeon, & R. G. Pearson, 2009. Are tropical streams really different? Journal of the North American Benthological Society 28: 397-403.

Brooks, A. J., B. C. Chessman, & T. Haeusler, 2011. Macroinvertebrate traits distinguish unregulated rivers subject to water abstraction. Journal of the North American Benthological Society 30: 419-435.

Chessman, B. C., 2003. New sensitivity grades for Australian river macroinvertebrates. Marine and Freshwater Research 54: 95-103.

Chessman, B. C., 2009. Climatic changes and 13-year trends in stream macroinvertebrate assemblages in New South Wales, Australia. Global Change Biology 15: 2791-2802.

Chessman, B. C., H. A. Jones, N. K. Searle, I. O. Growns, & M. R. Pearson, 2010. Assessing effects of flow alteration on macroinvertebrate assemblages in Australian dryland rivers. Freshwater Biology 55: 1780-1800.

Chessman, B. C., M. J. Royal, & M. Muschal, 2008. Does water abstraction from unregulated streams affect aquatic macrophyte assemblages? An evaluation based on comparisons with reference sites. Ecohydrology 1: 67-75.

Cook, B., B. Pusey, J. Hughes, & M. Kennard, 2010. Delineation of freshwater bioregions in northern Australia. In M. J. Kennard (ed), Identifying High Conservation Value Aquatic Ecosystems in Northern Australia. Final Report for the Department of Environment, Water, Heritage and the Arts and the National Water Commission. Charles Darwin University, Darwin, Australia: 57-74.

Cotner, J. B., J. V. Montoya, D. L. Roelke, & K. O. Winemiller, 2006. Seasonally variable riverine production in the Venezuelan llanos. Journal of the North American Benthological Society 25: 171-184.

Datry, T. 2012. Benthic and hyporheic invertebrate assemblages along a flow intermittence gradient: effects of duration of dry events. Freshwater Biology 57:563-574.

Dewson, Z. S., A. B. W. James, & R. G. Death, 2007. A review of the consequences of decreased flow for instream habitat and macroinvertebrates. Journal of the North American Benthological Society 26: 401-415.

Douglas, M. M., S. E. Bunn, & P. M. Davies, 2005. River and wetland food webs in Australia's wet-dry tropics: general principles and implications for management. Marine and Freshwater Research 56: 329-342.

Finn, M. A., A. J. Boulton, & B. C. Chessman, 2009. Ecological responses to artificial drought in two Australian rivers with differing water extraction. Fundamental and Applied Limnology/ Archiv für Hydrobiologie 175: 231-248.

Garcia, E., P. Dostine, C. Humphrey, M. Douglas, B. Pusey, & B. Cook, 2011. Aquatic Invertebrates. In B. J. Pusey (ed), Aquatic Biodiversity in Northern Australia: Patterns, Threats and Future. CDU Press, Darwin: 51-70.

Humphrey, C., J. Hanley, & C. Camilleri, 2008. Report 6: Aquatic invertebrates. In G. P. Lukacs & C. M. Finlayson (eds), A Compendium of Ecological Information on Australia's Northern Tropical Rivers. Sub-project 1 of Australia's Tropical Rivers - An Integrated Data Assessment and Analysis (DET18). A Report to Land & Water Australia. National Centre for Tropical Wetland Research, Townsville, Australia.

Jacobsen, D., & A. Encalada, 1998. The macroinvertebrate fauna of Ecuadorian highland streams in the wet and dry season. Archiv Fur Hydrobiologie 142: 53-70.

Jowett, I. G., J. Richardson, & M. L. Bonnett, 2005. Relationship between flow regime and fish abundances in a gravel-bed river, New Zealand. Journal of Fish Biology 66: 1419-1436.

Kay, W. R., M. J. Smith, A. M. Pinder, J. M. McRae, J. A. Davis, & S. A. Halse, 1999. Patterns of distribution of macroinvertebrate families in rivers of north-western Australia. Freshwater Biology 41: 299-316.

Kennard, M., B. Pusey, J. Boyden, D. Burrows, C. Leigh, C. Perna, P. Bayliss, & A. Georges. 2010b. Compilation of species distribution datasets for use as biodiversity surrogates. In M. J. Kennard (ed), Identifying High Conservation Value Aquatic Ecosystems in Northern Australia. Final Report for the Department of Environment, Water, Heritage and the Arts and the National Water Commission. Charles Darwin University, Darwin, Australia: 48-56.

Kennard, M. J., B. J. Pusey, J. D. Olden, S. J. Mackay, J. L. Stein, & N. Marsh, 2010a. Classification of natural flow regimes in Australia to support environmental flow management. Freshwater Biology 55: 171–193.

Lake, P. S., 2000. Disturbance, patchiness, and diversity in streams. Journal of the North American Benthological Society 19: 573-592.

Lake, P. S., 2003. Ecological effects of perturbation by drought in flowing waters. Freshwater Biology 48: 1161-1172.

Latrubesse, E. M., J. C. Stevaux, & R. Sinha, 2005. Tropical rivers. Geomorphology 70: 187-206.

Ledger, M. E., F. K. Edwards, L. E. Brown, A. M. Milner, & G. Woodward, 2011. Impact of simulated drought on ecosystem biomass production: an experimental test in stream mesocosms. Global Change Biology 17: 2288-2297.

Leigh, C., 2012. Macroinvertebrate Responses to Dry Season and Antecedent Flow in Highly Seasonal Streams and Rivers of the Wet-Dry Tropics, Northern Territory. National Water Commission, Canberra, Australia.

Leigh, C., & F. Sheldon, 2008. Hydrological changes and ecological impacts associated with water resource development in large floodplain rivers in the Australian tropics. River Research and Applications 24:1251-1270.

Leigh, C., & F. Sheldon, 2009. Hydrological connectivity drives patterns of macroinvertebrate biodiversity in floodplain rivers of the Australian wet /dry tropics. Freshwater Biology 54: 549-571.

Leigh, C., M. A. Burford, F. Sheldon, & S. E. Bunn. 2010. Dynamic stability in dry season food webs within tropical floodplain rivers. Marine and Freshwater Research 61:357-368.

Leigh, C., B. Stewart-Koster, F. Sheldon, & M. A. Burford, 2012. Understanding multiple ecological responses to anthropogenic disturbance: rivers and potential flow regime change. Ecological Applications 22: 250-263.

Leung, A. S. L., & D. Dudgeon, 2011. Scales of spatiotemporal variability in macroinvertebrate abundance and diversity in monsoonal streams: detecting environmental change. Freshwater Biology 56: 1193-1208.

Leung, A. S. L., A. O. Y. Li, & D. Dudgeon, 2012. Scales of spatiotemporal variation in macroinvertebrate assemblage structure in monsoonal streams: the importance of season. Freshwater Biology 57: 218-231.

Lloyd, J., & S. Cook, 2001. Northern Territory AUSRIVAS: Australian River Assessment Scheme Sampling and Processing Manual. Natural Resources Division, Department of Lands, Planning and Environment, Northern Territory, Australia.

Lytle, D. A., J. D. Olden, & L. E. McMullen, 2008. Drought escape behaviours of aquatic insects may be adaptations to highly variable flow regimes characteristic of desert rivers. The Southwestern Naturalist 53: 399-402.

Marchant, R., 1982. Seasonal variation in the macroinvertebrate fauna of billabongs along Magela Creek, Northern Territory. Australian Journal of Marine and Freshwater Research 33: 329-342.

Marchant, R., 1989. A subsampler for samples of benthic invertebrates. Bulletin of the Australian Society for Limnology 12: 49-52

Marsh, N., F. Sheldon, & R. Rolls, 2012. Synthesis of case studies quantifying ecological responses to low flows. National Water Commission, Canberra, Australia [available on internet at http://archive.nwc.gov.au/library/waterlines/76]. Accessed 18 Oct 2012.

Marsh, N. A., M. J. Stewardson, & M. J. Kennard, 2003. River Analysis Package. Cooperative Research Centre for Catchment Hydrology, Monash University Melbourne, Australia.

McCabe, D. J., & N. J. Gotelli, 2000. Effects of disturbance frequency, intensity, and area on assemblages of stream macroinvertebrates. Oecologia 124: 270-279.

McMahon, T. A., and B. L. Finlayson, 2003. Droughts and anti-droughts: the low flow hydrology of Australian rivers. Freshwater Biology 48: 1147–1160.

Miller, S. W., D. Wooster, & J. Li, 2007. Resistance and resilience of macroinvertebrates to irrigation water withdrawals. Freshwater Biology 52: 2494-2510.

Milly, P. C. D., K. A. Dunne & A. V. Vecchia, 2005. Global pattern of trends in streamflow and water availability in a changing climate. Nature 438: 347–350.

Montoya, J. V., D. L. Roelke, K. O. Winemiller, J. B. Cotner, & J. A. Snider, 2006. Hydrological seasonality and benthic algal biomass in a neotropical floodplain river. Journal of the North American Benthological Society 25: 157-170.

Nolte, U., M. J. de Oliveira, & E. Stur, 1997. Seasonal, discharge-driven patterns of mayfly assemblages in an intermittent Neotropical stream. Freshwater Biology 37: 333-343.

Oksanen, J., F. G. Blanchet, Roeland Kindt, P. Legendre, P. R. Minchin, R. B. O'Hara, G. L. Simpson, P. Solymos, M. H. H. Stevens, & H. Wagner, 2012. Vegan: Community Ecology Package. R package version 2.0-3 [available on internet at http://CRAN.R-project.org/package=vegan]. Accessed 18 Oct 2012.

Outridge, P., 1988. Seasonal and spatial variations in benthic macroinvertebrate communities of Magela Creek, Northern Territory. Australian Journal of Marine and Freshwater Research 39: 211-223.

Paltridge, R. M., P. L. Dostine, C. L. Humphrey, & A. J. Boulton, 1997. Macroinvertebrate recolonization after re-wetting of a tropical seasonally-flowing stream (Magela Creek, Northern Territory, Australia). Marine and Freshwater Research 48: 633-645.

Perna C., & R. G. Pearson 2008, Temporal dynamics of fish assemblages in small seasonal streams in the Queensland tropics. Australian Journal of Zoology 56: 65–73.

Petheram, C., T. A. McMahon, & M. C. Peel, 2008. Flow characteristics of rivers in northern Australia: implications for development. Journal of Hydrology 357: 93-111.

Pettit, N. E., P. Bayliss, P. M. Davies, S. K. Hamilton, D. M. Warfe, S. E. Bunn, & M. M. Douglas, 2011. Seasonal contrasts in carbon resources and ecological processes on a tropical floodplain. Freshwater Biology 56: 1047-1064.

Poff, N. L., J. D. Allan, M. B. Bain, J. R. Karr, K. L. Prestegaard, B. D. Richter, R. E. Sparks, & J. C. Stromberg, 1997. The natural flow regime: a paradigm for river conservation and restoration. BioScience 47: 769-784.

Ramirez, A., C. M. Pringle, & M. Douglas, 2006. Temporal and spatial patterns in stream physicochemistry and insect assemblages in tropical lowland streams. Journal of the North American Benthological Society 25: 108-125.

Rayner, T. S., B. Pusey, & R. G. Pearson, 2008. Seasonal flooding, instream habitat structure and fish assemblages in the Mulgrave River, north-east Queensland: towards a new conceptual framework for

understanding fish-habitat dynamics in small tropical rivers. Marine and Freshwater Research 59: 97-116.

Rolls, R. J., C. Leigh, & F. Sheldon. Mechanistic effects of low flow hydrology on riverine ecosystems: ecological principles and consequences of alteration. Freshwater Science 31:1163-1186.

Rose, P., L. Metzeling, & S. Catzikiris, 2008. Can macroinvertebrate rapid bioassessment methods be used to assess river health during drought in south eastern Australian streams? Freshwater Biology 53: 2626-2638.

Schäfer, R. B., B. J. Kefford, L. Metzeling, M. Liess, S. Burgert, R. Marchant, V. Pettigrove, P. Goonan, & D. Nugegoda, 2011. A trait database of stream invertebrates for the ecological risk assessment of single and combined effects of salinity and pesticides in South-East Australia. Science of the Total Environment 409: 2055-2063.

Sheldon, F. & C. S. Fellows. 2010. Water quality in two Australian dryland rivers: spatial and temporal variability and the role of flow. Marine and Freshwater Research 61: 864-874.

Stevenson, R. J., & S. Sabater, 2010. Understanding effects of global change on river ecosystems: science to support policy in a changing world. Hydrobiologia 657: 3-18.

Stubbington, R., P. J. Wood, & A. J. Boulton, 2009. Low flow controls on benthic and hyporheic macroinvertebrate assemblages during supra-seasonal drought. Hydrological Processes 23: 2252-2263.

Townsend, S. A., & A. V. Padovan, 2005. The seasonal accrual and loss of benthic algae (*Spirogyra*) in the Daly River, an oligotrophic river in tropical Australia. Marine and Freshwater Research 56: 317-327.

Walters, A. W., & D. M. Post, 2011. How low can you go? Impacts of a low-flow disturbance on aquatic insect communities. Ecological Applications 21: 163-174.

Warfe, D. M., N. E. Pettit, P. M. Davies, B. J. Pusey, S. K. Hamilton, M. J. Kennard, S. A. Townsend, P. Bayliss, D. P. Ward, M. M. Douglas, M. A. Burford, M. Finn, S. E. Bunn, & I. A. Halliday, 2011. The 'wet–dry' in the wet–dry tropics drives river ecosystem structure and processes in northern Australia. Freshwater Biology 56: 2169-2195.

Webster, I. T., N. Rea, A. V. Padovan, P. Dostine, S. A. Townsend, & S. Cook, 2005. An analysis of primary production in the Daly River, a relatively unimpacted tropical river in northern Australia. Marine and Freshwater Research 56: 303-316.

Wood, P. J., A. J. Boulton, S. Little, & R. Stubbington, 2010. Is the hyporheic zone a refugium for aquatic macroinvertebrates during severe low flow conditions? Fundamental and Applied Limnology 176: 377-390.

Zeug, S. C., & K. O. Winemiller, 2008. Relationships between hydrology, spatial heterogeneity, and fish recruitment dynamics in a temperate floodplain river. River Research and Applications 24: 90-102.

Tables

Table 1 Data used to explore the three hypotheses examined in this study (n = sample size), as grouped by habitat type and early versus late dry-season flow status of the habitats (hypotheses 1 and 2), or by habitat type and site proximity to flow gauging stations (hypothesis 3)

Hypothesis	Habitat	Drainage basins	Years of available data	Number of sites (total n)	Early dry season status (n)	Late dry season status (n)	Total (family) richness
1 and 2	Sand	Daly	1995	7 (14)	Lotic (7)	Lentic (7)	35
1 and 2	Edge	Daly, East Alligator, Finniss, Melville Island, Roper	1995	9 (18)	Lotic (9)	Lentic (9)	55
1 and 2	Edge	Adelaide, Daly, Finniss, Melville Island, Roper	1995, 1996	9 (36)	Lentic (18)	Lentic (18)	61
3	Sand	Daly, Mary, South Alligator, Victoria	1995, 1996	7 (21)	Lentic (2), Lotic (8)	Lentic(6), Lotic(5)	40
3	Edge	Daly, Mary, Victoria	1995, 1996	6 (16)	Lentic (2), Lotic (5)	Lentic (3), Lotic (6)	56

Table 2 Flow metrics calculated for different antecedent periods relative to each sample analysed under hypothesis three

Period	Code	Unit	Type	Description
Dry	DrP10	m^3s^{-1}	Magnitude	10th percentile of MDF (low flow threshold)
	DrP90	m^3s^{-1}	Magnitude	90th percentile of MDF (high flow threshold)
	DrMDF	m^3s^{-1}	Magnitude	Mean mdf
	DrCV		Variation in magnitue	CV (standard deviation/mean) of MDF
Wet	WeMax	m^3s^{-1}	Magnitude	Maximum MDF
	WeP90	m^3s^{-1}	Magnitude	90th percentile of MDF (high flow threshold)
	WeMDF	m^3s^{-1}	Magnitude	Mean MDF
	WeCV		Variation in magnitude	CV (standard deviation/mean) of MDF
	WeMRateFall	m^3s^{-2}	Rate of change	Mean rate of fall
General	FlowOnDay	m^3s^{-1}	Magnitude	MDF on sampling date
	DsinceWeMax	d	Duration	Number of days between WeMax and sampling date
	DsinceEndWet	d	Duration	Number of days between 1 May and sampling date

Figure captions

Fig. 1 River basins in the wet-dry tropics from which macroinvertebrate samples were collected, Northern Territory, Australia. The Finniss basin also includes smaller catchments of the Howard and Darwin Harbour rivers. Open triangles and closed squares show macroinvertebrate sampling sites, with closed squares indicating those with nearby flow gauging stations (within ~4 km). Closed circle, city of Darwin

Fig. 2 Mean daily flow (m^3 s^{-1}) recorded at gauging stations in close proximity to the macroinvertebrate sampling sites, with macroinvertebrate sample dates at edge (E) and sand (S) habitats indicated by arrows

Fig. 3 Principal Coordinate Analysis (PCoA) ordinations of macroinvertebrate assemblage similarities among samples collected from sand habitats that were lotic in the early dry season (open triangles) but lentic in the late dry season (closed triangles). Vector overlays show (A) taxa and (B) assemblage and habitat characteristics that correlate strongly with either the first and second axis (Spearman correlations > |0.35|). The circle represents a vector correlation of 1

Fig. 4 Box and whisker plots of sand and edge habitat and assemblage characteristics that were significantly different between early and late dry seasons. Left column plots (A-D) and plot I show sand habitats that changed from lotic to lentic; middle column plots (E-H) show edge habitats that changed from lotic to lentic; plot J shows edge habitats that remained lentic
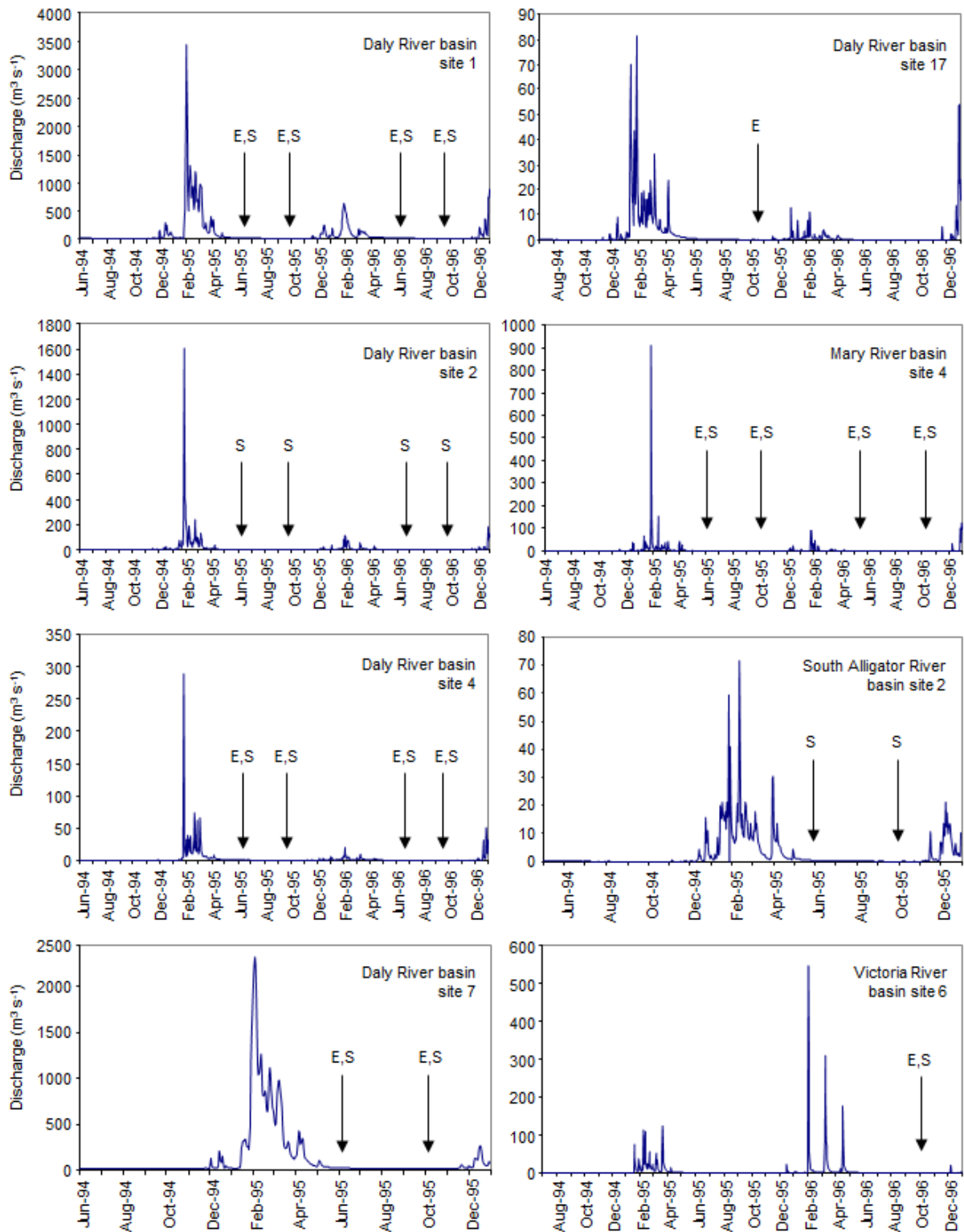
Fig. 5 Scatterplots of habitat versus assemblage characteristics for sand habitats from the Daly River basin that were lotic in the early dry season but lentic in the late dry season of 1995

Fig. 6 Scatterplots of habitat versus assemblage characteristics for edge habitats from multiple streams and rivers that were lotic in the early dry season but lentic in the late dry season of 1995 (A-G), or that were lentic in both the early and late dry seasons (H-K)
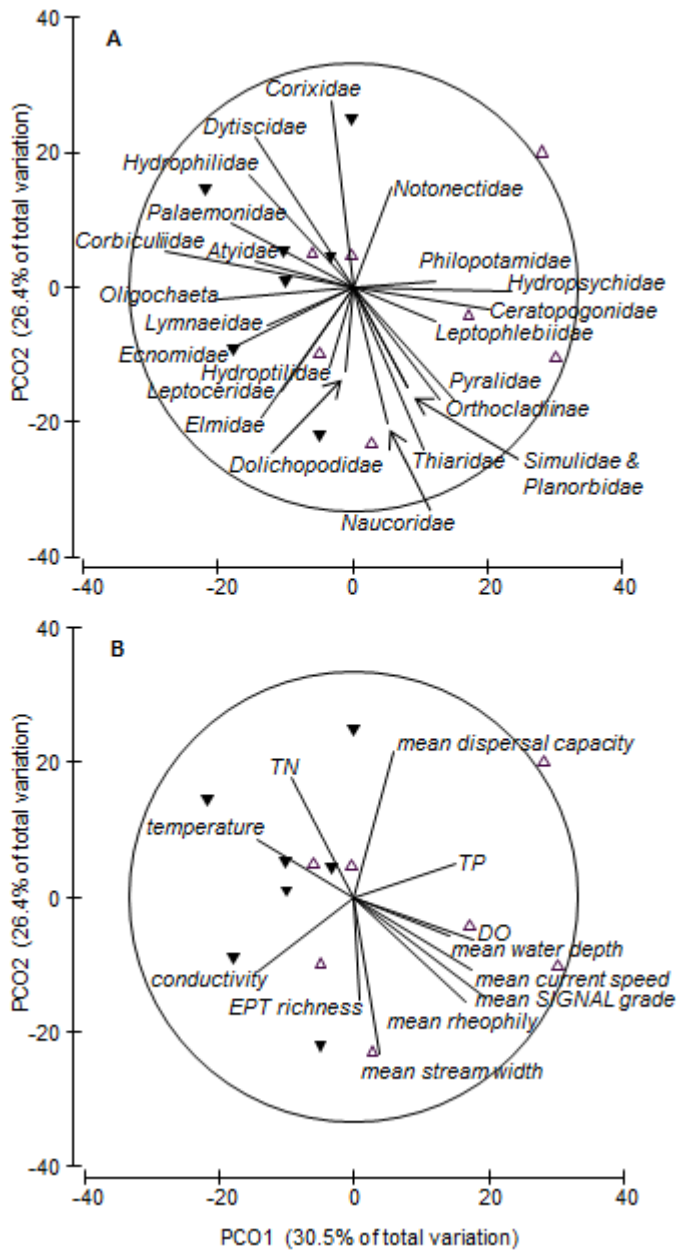
Fig. 7 Schematic of significant correlations ($P < 0.05$) between antecedent hydrology and the dry-season macroinvertebrate and habitat characteristics of (A) sand and (B) edge habitats from multiple streams and rivers. See Table 2 for flow-metric codes
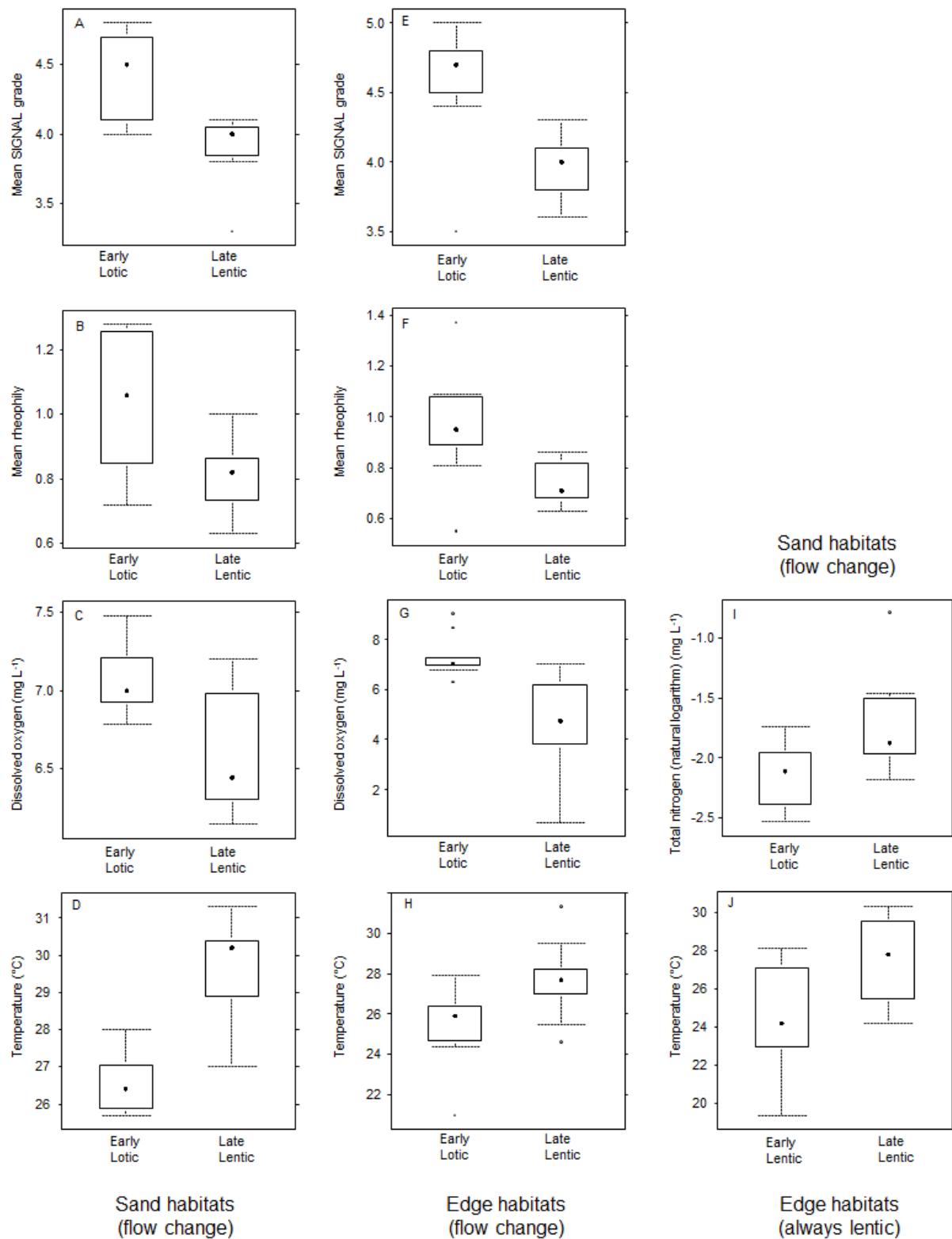
Fig. 1 River basins in the wet-dry tropics from which macroinvertebrate samples were collected, Northern Territory, Australia. The Finniss basin also includes smaller catchments of the Howard and Darwin Harbour rivers. Open triangles and closed squares show macroinvertebrate sampling sites, with closed squares indicating those with nearby flow gauging stations (within ~4 km). Closed circle, city of Darwin
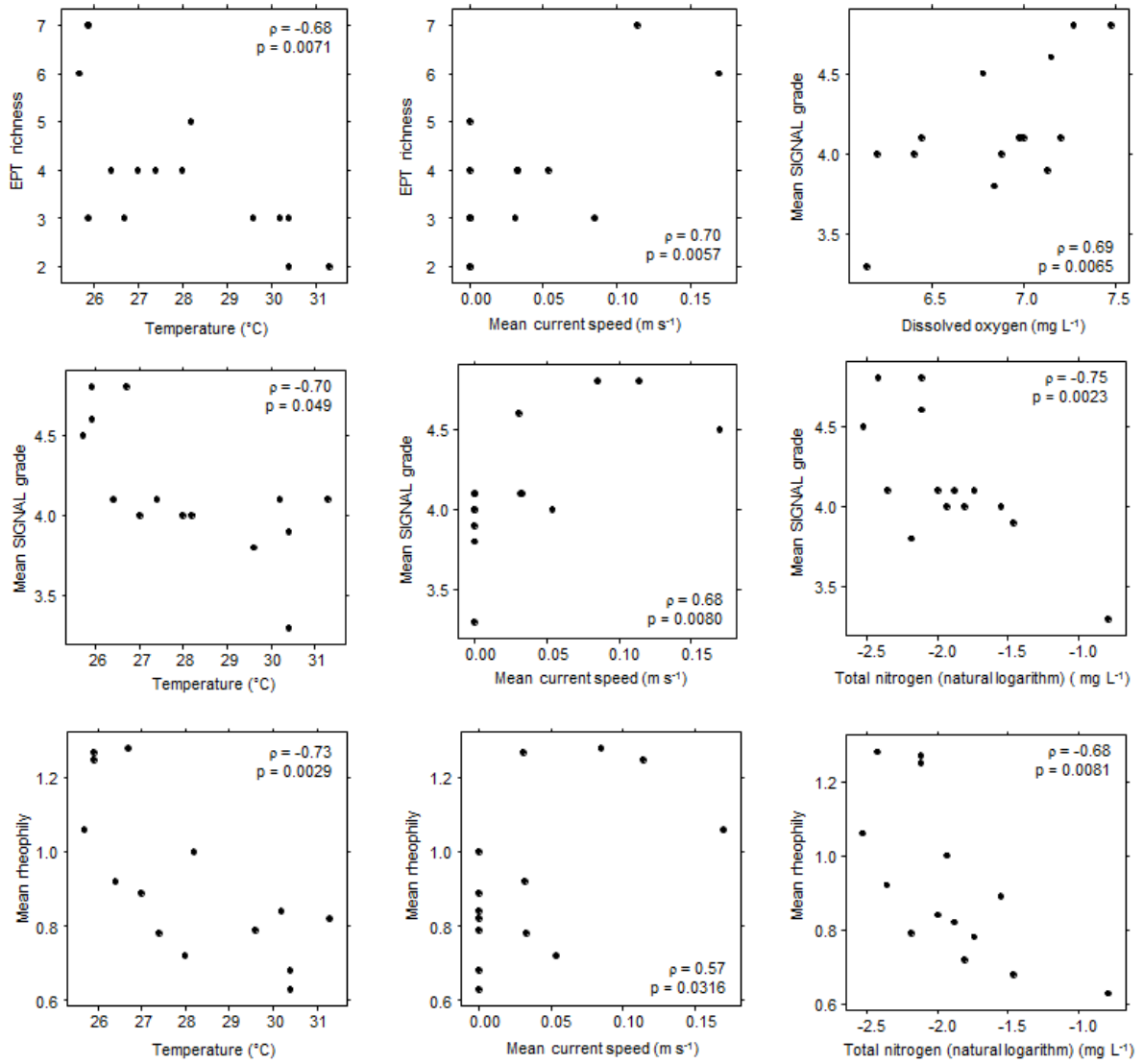
Fig. 2 Mean daily flow (m^3 s^{-1}) recorded at gauging stations in close proximity to the macroinvertebrate sampling sites, with macroinvertebrate sample dates at edge (E) and sand (S) habitats indicated by arrows
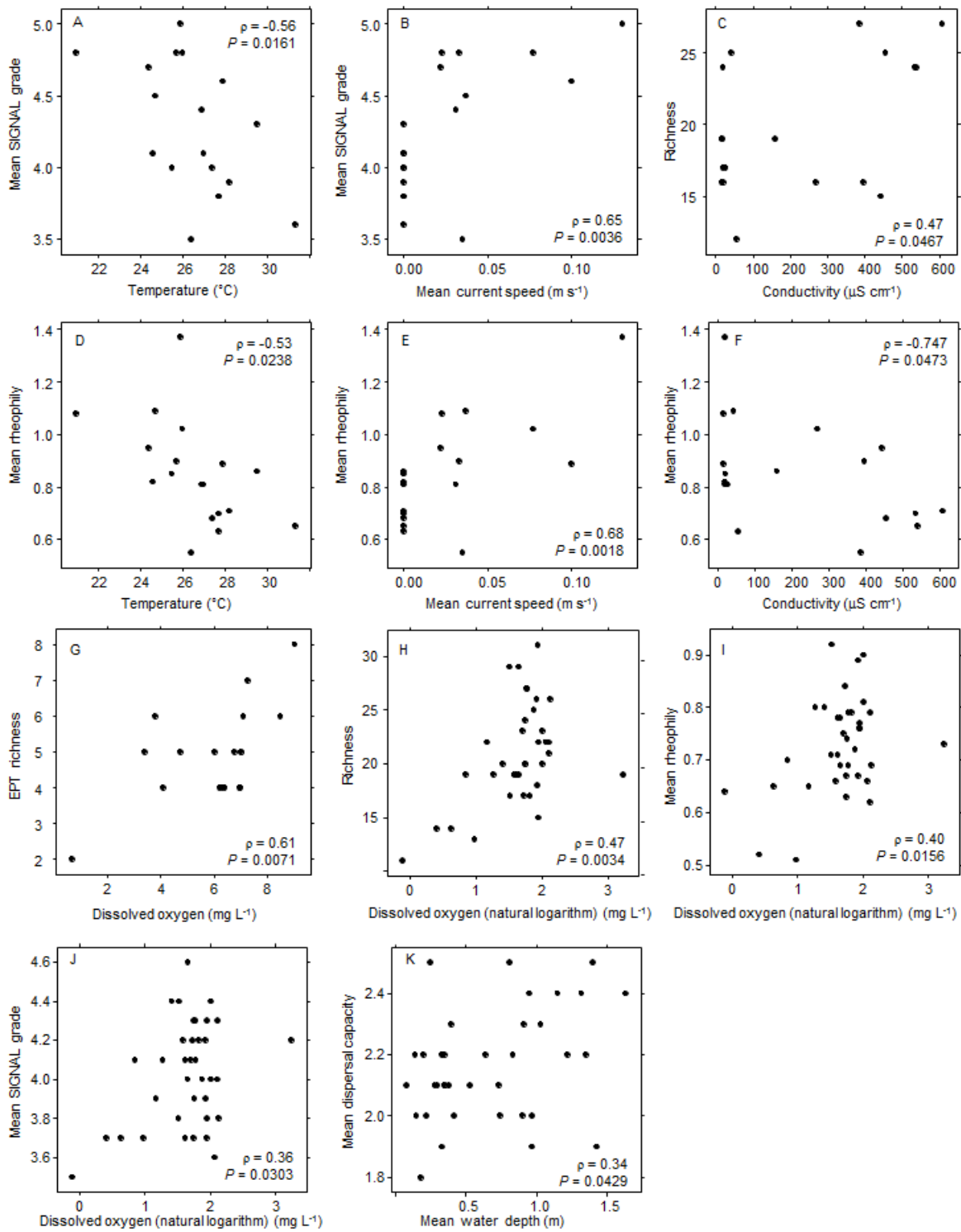
Fig. 3 Principal Coordinate Analysis (PCoA) ordinations of macroinvertebrate assemblage similarities among samples collected from sand habitats that were lotic in the early dry season (open triangles) but lentic in the late dry season (closed triangles). Vector overlays show (A) taxa and (B) assemblage and habitat characteristics that correlate strongly with either the first and second axis (Spearman correlations > |0.35|). The circle represents a vector correlation of 1

Fig. 4 Box and whisker plots of sand and edge habitat and assemblage characteristics that were significantly different between early and late dry seasons. Left column plots (A-D) and plot I show sand habitats that changed from lotic to lentic; middle column plots (E-H) show edge habitats that changed from lotic to lentic; plot J shows edge habitats that remained lentic
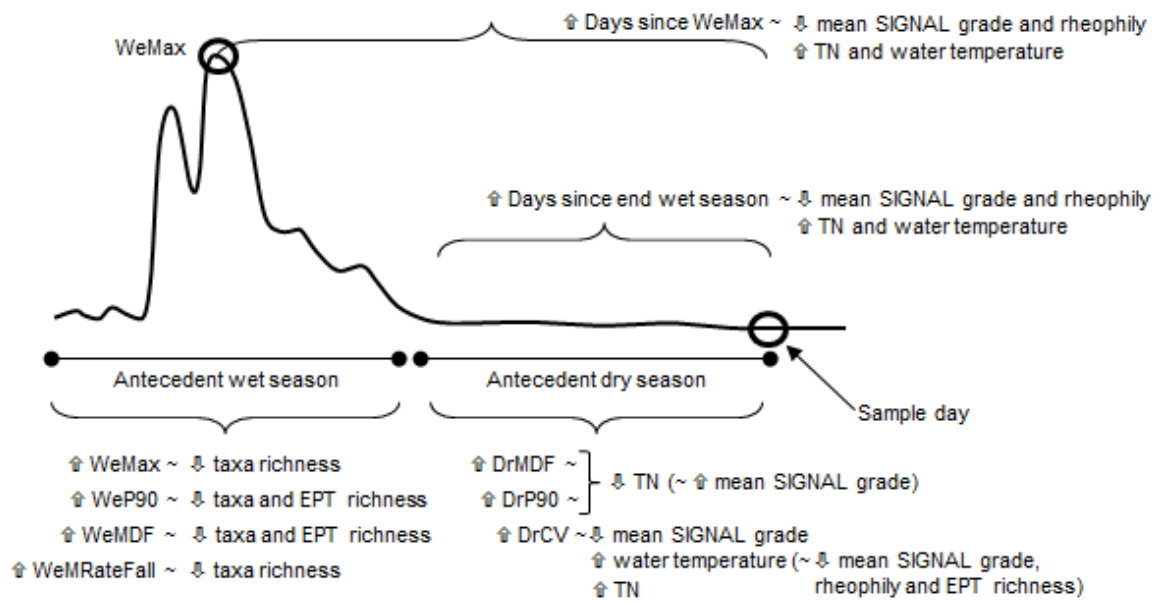
Fig. 5 Scatterplots of habitat versus assemblage characteristics for sand habitats from the Daly River basin that were lotic in the early dry season but lentic in the late dry season of 1995
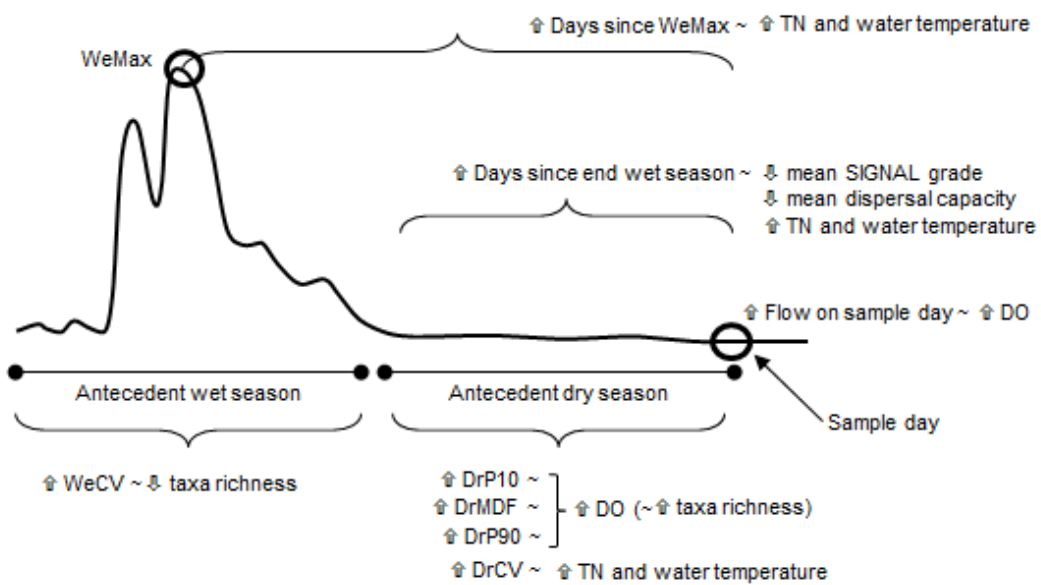
Fig. 6 Scatterplots of habitat versus assemblage characteristics for edge habitats from multiple streams and rivers that were lotic in the early dry season but lentic in the late dry season of 1995 (A-G), or that were lentic in both the early and late dry seasons (H-K)

Fig. 7 Schematic of significant correlations (*P* < 0.05) between antecedent hydrology and the dry-season macroinvertebrate and habitat characteristics of (A) sand and (B) edge habitats from multiple streams and rivers. See Table 2 for flow-metric codes