Spatial Variation in the Distribution and Abundance of Submersed Macrophytes in an Australian Subtropical River

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Abstract

Spatial variation in the distribution and abundance of submersed macrophytes in the Mary River, a subtropical Australian river, was examined at 29 sites on four occasions (116 samples) over a one year period. Thirteen submersed macrophyte taxa representing seven families were recorded during the study period. Submersed macrophyte cover was generally patchy and mean quadrat cover per sample was below 7% for every recorded taxon. Classification and ordination identified four distinct groups characterised by differences in submersed macrophyte abundance and associated environmental variables.

Three of the four groups were characterised by different abundances of three core taxa, Myriophyllum verrucosum, Vallisneria nana and Potamogeton crispus. The distribution of the four sample groups within the Mary River catchment was associated with two environmental gradients, the first gradient representing discharge intensity, discharge variability and total Kjeldahl nitrogen concentration and the second gradient representing discharge intensity, substrate composition, riparian canopy cover and total phosphorus concentration. Both environmental gradients were constrained by geomorphology at the catchment as well as the reach scale. Our findings are consistent with a general conceptual model that highlights the importance of major environmental gradients in structuring submersed macrophyte assemblages.

Keywords: Submersed macrophytes; distribution; abundance; spatial variation; environmental gradients; conceptual model

1. Introduction

Anthropogenic disturbance of riverine ecosystems has been cited as an important cause of degradation to lotic macrophyte assemblages, with responses including excessive macrophyte growth, loss of native species and invasion by exotic species (e.g. Litav and Agami, 1977; Schütz, 1995; French and Chambers, 1997; Bunn et al., 1998; Demars and Harper, 1998; King and Buckney, 2000). Conceptual and predictive models are seen as essential management tools for understanding and minimising anthropogenic impacts upon aquatic macrophyte assemblages, and ensuring the conservation of rare or endangered macrophyte taxa (e.g. Keddy, 1992; Carr et al., 1997; Hill et al., 1998). Development of predictive models requires an understanding of the relationships between aquatic

macrophyte assemblage structure and environmental parameters in undisturbed catchments (e.g. Hart and Finelli, 1999). The environmental parameters that control the distribution and abundance of aquatic macrophytes in unregulated Australian streams and rivers have received little attention compared to the effort focussed on lake and wetland macrophyte assemblages (e.g. Brock, 1991; Royle and King, 1991; Casanova, 1994; Rea and Ganf, 1994), thereby hindering the development of predictive models and appropriate management strategies for aquatic macrophytes in lotic systems.

Recent studies in Europe and elsewhere have emphasised the influence of multiple interacting environmental factors on the distribution and abundance of lotic macrophytes (Muotka and Virtanen, 1995; Biggs, 1996; Suren, 1996; Carr et al., 1997; Suren and Ormerod, 1998; Carr and Chambers, 1998; Riis et al., 2000). The relative importance of environmental factors to macrophyte assemblage structure has been shown to vary spatially and temporally (Sand-Jensen et al., 1989; Biggs, 1996; Suren, 1996; Suren and Ormerod, 1998) and over different scales of habitat resolution (Farmer and Adams, 1989; Hughes, 1990; Chambers et al., 1991; French and Chambers, 1996; Palmer and Poff, 1997). Consequently, it has been recommended that in situ studies of macrophytes in streams should simultaneously measure a suite of physical and chemical environmental variables to adequately characterise the abiotic environment of aquatic macrophytes (see Mitchell and Rogers, 1985; Farmer and Adams, 1989; Carr and Chambers, 1998).

In this paper we examine spatial variation in the composition of submersed macrophyte assemblages of the Mary River, a coastal river of southeast Queensland, Australia. Our objective is to relate spatial variation in the distribution and abundance of submersed macrophytes to environmental variables (catchment characteristics, discharge, water velocity, substrate composition, riparian cover and water quality). From these relationships we assess the applicability of a general conceptual model (Riis and Biggs

2001) that highlights the importance of major environmental gradients in structuring submersed macrophyte assemblages.

2. Methods

2.1. Study area

The Mary River catchment, with an area of 9 700 km^2 and approximate main channel length of 300 km (Bridges et al., 1990; Johnson, 1997), is one of the larger river systems of subtropical southeast Queensland, Australia (Fig. 1). The Mary River conforms to the general pattern of high hydrologic variability and low annual runoff noted for Australian rivers in comparison to northern hemisphere rivers (Finlayson and MacMahon, 1988; Puckridge et al., 1998). The mean annual runoff of the Mary River catchment is approximately 2.3×10^9 m^3 (Department of Primary Industries, 1993), much of which is supplied by tributaries draining the western part of the catchment (Pusey et al., 1993 and Fig. 1). Discharge is generally seasonal with summer maxima and winter-spring minima (Fig. 2). Tributaries (e.g. Amamoor Ck, Fig. 2) and upper reaches of the main channel may cease to flow during periods of low rainfall. The seasonal discharge pattern is to some extent obscured by the activity of tropical and temperate weather patterns that may produce winter spates (Fig. 2).

2.2. Sites

Sites were located where possible in tributary and river reaches considered to be relatively free of anthropogenic disturbance with respect to riparian habitat, water quality

(particularly nutrients, turbidity) and flow regulation. All major tributaries and representative main channel habitats within the freshwater reaches were included in the study in order to encompass as much natural environmental variation in the catchment as possible. Twenty-nine sites were surveyed on fourth to seventh order streams, at elevations of up to 160 m Australian Height Datum (AHD; Fig. 1). Only one site (site 30, Yabba Creek) was directly influenced by flow regulation (Borumba Dam, total capacity 4.6×10^7 m^3; SunWater, 2001). Each site was a distinct hydraulic unit (i.e. riffle, run or pool) between 20 and 60 m in length. In general, several sites were surveyed per stream reach (Fig. 1). Each site was surveyed on four separate occasions (May 1996, September 1996, January 1997, May 1997). This provided a total of 116 samples (i.e. 29 sites surveyed four times) describing submersed macrophyte composition and abundance and environmental parameters throughout the catchment.

2.3. Sampling methods

Submersed macrophyte abundance and environmental variables were quantified within 1 m^2 quadrats according to a standard survey protocol. Quadrat position within each site was determined from random number pairs representing quadrat position within the stream in terms of distance upstream (from a fixed point) and position on a transect placed perpendicular to the direction of flow. In general 20-30 quadrats were surveyed per site sample. Submersed macrophyte abundance (as percentage cover of individual taxa per quadrat) was estimated as the proportion of space, within a vertical projection of the quadrat to the water surface, occupied by plant material (Ward and Talbot, 1984). Water velocity within each quadrat was recorded at 0.6 times the stream depth with a Swoffer model 2100 flow meter. Water depth was recorded to the nearest centimetre. Substrate

composition was visually estimated using a modified Wentworth Scale as the proportion to the nearest 10% of mud (<0.063 mm diameter), sand (0.063-2 mm), fine gravel (2-16 mm), gravel (16-64 mm), cobble (64-128 mm), rock (128-512 mm) or bedrock (>512 mm) present per quadrat. Water slope over the site length was measured with a staff and Sokkia automatic level. Riparian canopy cover directly above each quadrat was measured using a spherical densiometer (Lemmon, 1956). Water quality data (DO, pH, conductivity, water temperature) for each quadrat were recorded in situ (Greenspan water quality sensors and Pacific Data Systems DT50 data logger). Turbidity was recorded at three locations within each site using a Hach model 16800 turbidimeter.

One water sample was collected from within each stream reach surveyed on each of the four sampling occasions for determination of major ions and nutrients (as total Kjeldahl nitrogen, TKN and total phosphorus, TP). One water sample per reach was considered sufficient as previous water quality sampling within the catchment has shown only minor differences in water quality between adjacent sites in the same reach (Mackay, Kennard and Arthington, unpublished). Water samples for major ion analysis were collected in 1 L detergent-washed polyethylene bottles and nutrient samples in 250 mL polyethylene bottles washed with reverse-osmosis purified water. Nutrient samples were frozen after collection (Queensland Department of Environment and Heritage, 1995) and analysed within five days of collection. All samples were analysed by the Queensland Government Chemical Laboratories using standard methods (American Public Health Association, 1995).

Catchment characteristics of individual sites (upstream catchment area, distance to river mouth, and elevation) were determined from Australia 1:100 000 topographic series maps. Submersed macrophytes were identified using keys (Stanley and Ross, 1983, 1986,

1989; Sainty and Jacobs, 1994; Jacobs and Frank, 1997) or by comparison with reference material verified by the Queensland Herbarium.

2.4. Statistical analysis

Discharge statistics for individual Mary River sites were calculated from modelled discharge data (expressed as total daily discharge, TDD, $m^3\ d^{-1}$) provided by the former Queensland Department of Natural Resources for the period 1994-1997. Defining discharge descriptors of most relevance to submersed macrophytes is not straightforward since very few studies have related specific discharge statistics to the distribution and abundance of submersed macrophytes. From the modelled data available we calculated seven discharge descriptors that were considered potentially relevant to submersed macrophytes and can be calculated easily without specialist software (Orchard, 1985; Poff and Ward, 1989; Biggs, 1996; Brock and Casanova, 1997). These variables were maximum and minimum total daily discharge, 10^{th} and 90^{th} percentiles of the total daily discharge, median total daily discharge, coefficient of variation (CV) of total daily discharge and number of zero flow days. Because of the limited temporal discharge data available (three years prior to sampling) we did not calculate flood frequencies, which may influence the structure of lotic communities (Poff and Ward, 1989). All discharge statistics were calculated from total daily discharge data for a time period defined by the 1095 days (365 days per year by 3 years) prior to the day of sampling, providing a short-term characterisation of the history of discharge events influencing submersed macrophytes and their habitat.

Spatial variation in submersed macrophyte species composition/abundance and relationships with environmental variables were examined by classification and ordination of samples using PATN (Belbin, 1995). All samples from each of the four surveys were

analysed concurrently. As rare taxa may obscure patterns produced by classification and ordination those species occurring in less than 5% of samples were omitted from multivariate analyses (Gauch, 1982; Clarke and Warwick, 1994). Removal of rare taxa did not reduce the number of samples available for multivariate analysis. Submersed macrophyte cover estimates (as mean quadrat cover per sample, calculated from all of the quadrat estimates taken for that sample including quadrats without macrophytes) were $\log(\underline{x}+1)$ transformed prior to analysis. A sample by sample association matrix was generated using the Bray-Curtis dissimilarity measure and used to generate an agglomerative hierarchical classification (Unweighted Pair-Group Method Using Arithmetic Averages, UPGMA) with $\beta = -1$ (Belbin, 1995). An appropriate number of sample groups was determined by inspection of the dendrogram structure and use of the Group Definition (GDEF) function in PATN (Belbin, 1995). Kruskal-Wallis tests were used to compare means for species cover and environmental variables between sample groups identified by UPGMA (Zar, 1996).

Sample groups identified by UPGMA classification were confirmed by ordination of the sample by sample association matrix using Semi-Strong-Hybrid Multidimensional Scaling (SSHMDS; Belbin, 1995). Where possible, ordination stress was held below 0.15 (Belbin, 1995) by manipulating the number of dimensions and changing cut levels and regression techniques used. Each ordination was rotated to simple structure (Varimax rotation) to simplify interpretation. Species cover and environmental variables were correlated with the ordination space by Principal Axis Correlation, which uses multiple regression to fit attributes to an ordination space as vectors of best fit (Belbin, 1995). The significance of correlation coefficients produced by Principal Axis Correlation was tested using a Monte-Carlo procedure (Monte-Carlo Attributes and Ordination procedure in PATN) and 100 randomisations (Belbin, 1995).

3. Results

3.1. Spatial variation in environmental variables

Pronounced spatial variation in environmental conditions occurred within the Mary River catchment (Table 1). Macroscale variables describing site position in catchment (upstream catchment area, distance to river mouth, elevation) were highly correlated with mesoscale and microscale variables describing physical (in-stream) habitat, discharge and water quality (Table 1). Water quality parameters were positively correlated with upstream catchment area and negatively correlated with site elevation (Table 1). Conductivity, pH, alkalinity, nutrient concentrations and turbidity increased as catchment area increased and site elevation decreased. Similarly, water velocity and measures of discharge magnitude (i.e. maximum and minimum daily discharge, percentile measures) increased as catchment area increased and elevation decreased. Furthermore, the CV of total daily discharge was positively correlated with elevation and distance to mouth, indicating higher elevation sites were subjected to “flashier” stream discharges than lower catchment sites (see also Fig. 2).

3.2. Submersed macrophyte assemblages

Thirteen submersed macrophyte taxa were recorded from 25 of 29 sites (77 of 116 samples) surveyed in the Mary River catchment (Table 2). Submersed macrophytes were not recorded from Kilcoy Creek (sites 1-3) and Tinana Creek (site 46) on any of the four sampling occasions (16 samples in total), and sites in Wide Bay Creek (sites 38 and 39)

were dry for the last two surveys in January and May 1997 (4 samples in total). Thirteen sites had submersed macrophytes present on each of the four sampling occasions.

Submersed macrophyte cover was generally patchy and mean cover per quadrat across all samples was below 7% for every taxon recorded (Table 2). However, extensive submersed macrophyte beds were present in Amamoor Creek (site 52), Booloumba Creek (site 6), Yabba Creek (site 30) and Wide Bay Creek (sites 38 and 39) where maximum cover values for some quadrats exceeded 50% (Table 2). Submersed macrophyte assemblages were dominated by Myriophyllum verrucosum, Vallisneria nana and Potamogeton crispus (Table 2), occurring in 34%, 30% and 30% of samples respectively. Myriophyllum variifolium, Chara spp., Nitella spp., Potamogeton perfoliatus, P. tricarinatus, Callitriche sp., Ceratophyllum demersum and Hydrilla verticillata were locally dominant taxa. Najas tenuifolia and P. ochreatus were rarely collected.

3.3. Sample classification and relationships with environmental variables

Nine common taxa (i.e. taxa occurring in more than 5% of samples, Table 2) were used in the classification of Mary River samples. UPGMA sample classification produced four clearly defined sample groups with the mean cover per quadrat of seven taxa found to be significantly different between groups (Table 3). Each group was characterised by taxa clearly dominant in terms of percentage cover and/or frequency of occurrence (Table 3). Group 1 samples were dominated by M. variifolium and Nitella spp., with M. verrucosum and P. crispus as co-occurring species (Table 3). M. variifolium and Nitella spp. were not exclusive to group 1 but occurred rarely outside of it. Group 2 samples were clearly dominated by V. nana. This species was often found in monospecific stands (41% of group 2 samples) or with H. verticillata or P. crispus as co-occurring species (Table 3). Group 3

samples were dominated by M. verrucosum with P. crispus and V. nana as commonly co-occurring species (Table 3). Group 4 samples were dominated by P. crispus and P. perfoliatus. These species were common within group 4 samples (93% and 40% of group 4 samples respectively) but were not abundant, as shown by estimates of mean cover (Table 3). V. nana and H. verticillata were common co-occurring species in this group.

Each of the four sample groups identified by UPGMA classification was associated with particular environmental conditions (Table 4). Group 1 samples (M. variifolium-Nitella spp.) were restricted to Amamoor Creek (sites 33, 52) and Booloumba Creek (sites 6, 7) at elevations ≥ 100 m AHD. These samples were collected from pools with relatively coarse substrata, discharges of relatively low magnitude and low variability relative to other parts of the catchment, and frequent periods of zero discharge (Table 4; Fig. 2). Group 1 samples were associated with low TKN and TP concentrations (Table 4). Group 2 samples (V. nana) were collected from sites characterised by shallow stream depths and low to medium water velocities, occurring at relatively low elevations (20-80 m AHD) in tributaries and the upper Mary River. Substrates were predominantly sand-gravel with very little coarse material (Table 4). Group 2 samples were subject to the most variable discharge conditions of the four sample groups identified, as indicated by the CV of mean daily discharge (816%, Table 4). These samples were associated with surface waters of low ionic concentration and low TP concentrations (Table 4).

Group 3 samples (dominated by M. verrucosum) occurred over a wide range of environmental conditions (Table 4) throughout the entire elevation range surveyed (0-160 m AHD) and were subjected to extremes of water velocity and discharge (Table 4). Median daily discharges were the highest amongst the four sample groups because group 3 samples were often collected from sites in the lower Mary River catchment, typically within the main channel (see Fig. 1). Substrates were generally coarser than for group 1

and group 2 samples. Mean TP concentration of group 3 samples was approximately twice that of sample groups 1, 2 and 4 but mean TKN concentrations were comparable to groups 2 and 4 (Table 4). Group 3 samples were collected from streams with a wide range of ionic concentrations (as shown by conductivity) and pH conditions (Table 4).

Group 4 samples (P. crispus-P. perfoliatus) occurred in similar habitats to group 3 samples but were more often found at higher elevations in lower water velocities (Table 4). Maximum total daily discharge for group 4 samples was relatively low but the median total daily discharge was relatively large (Table 4). The mean number of zero flow days was also relatively low. Group 4 samples occurred in surface waters of low to high ionic concentration (Table 4).

3.3 Sample ordination and relationships with environmental variables

Relationships between the four sample groups and environmental variables were further explored by ordination and correlation analyses (Fig. 3a-d). Macrophyte taxa and environmental variables that were significantly correlated with sample position in ordination space were consistent with taxa and environmental variables distinguishing UPGMA-defined sample groups (Tables 3 and 4, Fig. 3a-d). Elevation ($r = 0.595$), distance to mouth ($r = 0.580$) and maximum daily discharge ($r = 0.510$) were the variables most highly correlated with the position of samples in ordination space (Table 5). Elevation and distance to mouth produce a clear gradient within the ordination space along which group 1 samples (M. variifolium-Nitella spp.) are separated from samples dominated by V. nana, M. verrucosum and Potamogeton spp. (Fig. 3b). CV of total daily discharge, depth, water slope, TKN and pH also vary along the elevation gradient. Sample groups 2-4 are arrayed

over a more complex gradient of water velocity and discharge descriptors on axis 2 and substrate particle size (sand versus gravel) and riparian cover on axis 3 (Fig. 3c-d).

4. Discussion

This study has examined submersed macrophyte assemblage structure in the context of environmental heterogeneity and assessed the applicability of a general conceptual model of aquatic macrophyte growth in streams (Riis and Biggs 2001). Multivariate analysis revealed four distinct submersed macrophyte assemblages in the Mary River catchment that were structured by two major environmental gradients. The first gradient, representing discharge intensity, discharge variability and total Kjeldahl nitrogen concentration, separated group 1 samples from the remaining sample groups. The second gradient representing substrate composition, discharge intensity, riparian canopy cover and total phosphorus concentration, separated groups 2-4. The environmental gradients structuring submersed macrophytes assemblages in the Mary River are in general agreement with the conceptual model of Riis and Biggs (2001). Both environmental gradients are constrained by geomorphology at the catchment as well as reach scale, particularly site elevation. Elevation is often cited as an important factor influencing the structure of macrophyte assemblages (Suren, 1996; Suren and Ormerod, 1998; Ferreira and Moreira, 1999). In the Mary River catchment, elevation was correlated with meso- and microscale habitat variables (discharge measures, water quality, depth, substrate composition, water velocity; Table 1) that are more direct influences on macrophyte growth than elevation itself (e.g. Chambers et al., 1991; Suren, 1996; Statzner et al., 1988). Pronounced spatial variation in meso- and micro-scale habitat characteristics occurred over a relatively narrow elevation gradient (160 m) compared with the variation across elevation gradients reported

elsewhere (i.e. 750 m - Holmes et al., 1998; 3650 m - Suren and Ormerod, 1998). Discharge variations over the elevation gradient surveyed probably account for much of the environmental heterogeneity encountered at the meso- and micro-habitat scales in the Mary River catchment (see Table 4; Poff and Ward, 1989; Pusey et al., 1993; Mackay, Arthington and Kennard, unpublished data).

Macrophyte groups 1 and 3 were both dominated by amphibious species of Myriophyllum but appear at opposite ends of the hydraulic disturbance gradient. Both assemblages experience a considerable number of zero flow days. M. variifolium and M. verrucosum are both tolerant of fluctuating water levels, particularly where exposure may occur, through traits such as heterophylly (Brock, 1991; Orchard, 1985). Falling water levels are thought to trigger flowering responses in M. verrucosum (Orchard, 1985). Samples dominated by M. variifolium were associated with discharges of relatively low magnitude and variability, low water velocities and coarse substrates dominated by gravel and bedrock. Tolerance of M. variifolium to high flows has not been reported but this species is usually found in still to slow flowing water (Orchard, 1985). At the other extreme, M. verrucosum dominated those samples exposed to high magnitude stream discharges, high water velocities and coarse substrates composed of gravels and cobbles. Both M. variifolium and M. verrucosum possess pinnate submerged leaves which may reduce drag in flowing water (Willby et al., 2000; see also Sand-Jensen 2003). However, M. variifolium has larger leaves (11-20 mm long, 11-23 mm wide) and greater stem diameter (up to 5 mm) than M. verrucosum (leaves 6-12 mm long, 5-12 mm wide; stem diameter 1-1.5 mm; Orchard, 1985). Reduced surface area (i.e. smaller leaf area) and increased stem flexibility (i.e. reduced stem thickness) may allow M. verrucosum to tolerate greater drag forces than M. variifolium (e.g. Gordon et al., 1992; Usherwood et al.,

1997; Suren et al., 2000), which may explain the presence of the former species at high discharge sites.

V. nana (group 2) and P. crispus-P. perfoliatus (group 4) occupy intermediate positions on the disturbance axis relative to M. variifolium and M. verrucosum. These taxa can be considered obligate aquatics (Kadono, 1984; Brock and Casanova, 1997). V. nana occurred on sandy substrates at low-medium water velocities and should therefore be exposed to less intense hydraulic disturbance than M. verrucosum. P. crispus-P. perfoliatus (group 4) were associated with similar water velocity and substrate conditions as V. nana, but were more often associated with stream discharges of lower magnitude than V. nana (as indicated by maximum and minimum discharges and percentiles). We therefore assign V. nana to a higher position on the disturbance axis relative to P. crispus-P. perfoliatus.

Although V. nana and P. crispus-P. perfoliatus were associated with variable stream discharges they experienced relatively few days of zero flow. These species are not considered tolerant of repeated desiccation or exposure (Kadono, 1984; Preston, 1995; Preston and Croft, 1997; Blanch et al., 1999) but may survive in water several centimetres deep (Sainty and Jacobs, 1981; Preston and Croft, 1997). Myriophyllum spp. would therefore appear to have competitive advantages in habitats subject to periodic exposure.

The placement of submersed macrophyte taxa within the conceptual model of Riis and Biggs (2001) relative to resource availability is less straightforward since this axis constitutes several components. M. variifolium is allocated a lower position on the resource axis than the remaining taxa by virtue of its association with surface waters of low TKN and TP concentrations and low light environments (i.e. higher riparian canopy cover). In comparison, M. verrucosum was associated with waters of high TKN, TP and alkalinity (but low to intermediate light availability), suggesting that this species should be placed on the extreme of the resource axis. V. nana was associated with low TKN

concentrations, intermediate TP concentrations, low alkalinity and low riparian cover (high light availability). P. crispus-P. perfoliatus were associated with waters of low TP, high TKN, intermediate to low alkalinity and low riparian canopy cover. We therefore place these taxa in an intermediate position relative to M. variifolium and M. verrucosum on the resource supply axis. P. crispus and P. perfoliatus are often associated with mesotrophic and eutrophic waters or waters of high alkalinity (Spence and Maberley, 1985; Preston and Croft, 1997). The association of P. crispus-P. perfoliatus with surface waters of intermediate to low alkalinity is only relative to the ordination space, and does not imply an absolute requirement for waters of low alkalinity.

Implications of this study

In Australia, a commitment to Ecologically Sustainable Development of water resources and provision of environmental flows (Commonwealth of Australia, 1990; ARMCANZ and ANZECC, 1996) has prompted interest in establishing quantitative links between ecologically relevant hydrological descriptors and stream biota (Whittington, 2000). This study has shown that distinct submersed macrophyte assemblages are recognisable based on a small subset of taxa and that these assemblages can be associated with distinctive physical conditions in the Mary River catchment. It has also shown that the effects of hydrological and hydraulic parameters on submersed macrophytes cannot be considered in isolation from the effects of variations in resource availability, notably nutrients and light (Carr et al., 1997). The conceptual model for submersed macrophytes of the Mary River catchment includes both sets of variables and can be used to develop testable hypotheses predicting directions of change in assemblage structure for given changes in disturbance regimes and resource availability, as suggested by Riis and Biggs

(2001). Such models and predictions could have application in developing methods for the use of aquatic macrophytes as stream bioassessment tools in Australia, particularly in defining the reference condition for aquatic macrophytes (Ferreira and Moreira, 1999), and evaluating changes in macrophyte assemblage structure in relation to riparian vegetation loss, water quality impairment and alterations to stream flow regimes, and their mitigation.

Acknowledgements

Data presented in this paper were collected as part of Land and Water Resources Research and Development Corporation (LWRRDC) Project No. GRU-10. We thank Celia Thompson and Darren Renouf for assistance with field work. Garry Werren (James Cook University), Thorsten Mosisch (Australian Water Quality Unit, SA Water) and two anonymous referees kindly reviewed drafts of the manuscript. Discharge data and funding for water quality analyses were provided by the Queensland Department of Natural Resources. This paper represents a contribution to the Cooperative Research Centres for Freshwater Ecology and Tropical Rainforest Ecology and Management.

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Table 1

Spearman correlations for macroscale catchment descriptors (upstream catchment area, distance to river mouth, elevation) and meso- and micro-scale environmental variables. For clarity only significant correlations are shown ($p<0.01$). Range and median values for significant correlations also shown. NS = not significant. The number of samples is 112

Variable	Upstream Catchment Area	Distance to Mouth	Elevation	Range	Median
Catchment Descriptors					
Upstream catchment area (km^2)	1			26 – 4851	176
Distance to mouth (km)	0.938	1		10 – 211	34
Elevation (m)	-0.919	0.935	1	0 – 160	80
Discharge Descriptors					
Max. total daily discharge ($m^3\ s^{-1}$)	0.839	-0.762	-0.810	194 – 93165	4022
10^{th} percentile ($m^3\ s^{-1}$)	0.879	-0.797	-0.818	3.4 – 2573.8	35.4
90^{th} percentile ($m^3\ s^{-1}$)	ns	ns	ns	0 – 43.5	0.3
Median total daily discharge ($m^3\ s^{-1}$)	0.726	-0.591	-0.688	0.1 – 245.6	2.9
CV of total daily discharge (%)	-0.299	0.299	0.302	78 – 1314	629
Number of zero flow days	ns	-0.243	ns	0 – 512	44
Physical Habitat					
Width (m)	ns	ns	ns	0.8 – 40.1	7.5
Water Velocity ($m\ s^{-1}$)	0.311	-0.243	-0.307	0 – 0.8	0.05
Riparian Cover (%)	-0.638	0.407	0.516	1 – 97	50
Gravel (%)	0.410	-0.501	-0.501	0 – 82	38
Cobble (%)	-0.384	0.399	0.434	0 – 58	21
Rock (%)	-0.519	0.589	0.579	0 – 47	0
Water Quality					
Conductivity ($\mu S\ cm^{-1}$)	0.449	-0.629	-0.538	123 – 1903	509
Alkalinity ($mg\ L^{-1}$ as $CaCO_3$)	0.251	-0.411	-0.296	8.9 – 380.0	115.0
pH	0.327	-0.418	-0.372	6.38 – 8.70	7.82
Water Temperature (^oC)	0.310	-0.218	-0.258	15 – 29	19
Turbidity (NTU)	0.416	-0.485	-0.474	0.4 – 25	2.6
Total Kjeldahl Nitrogen ($mg\ L^{-1}$)	0.625	-0.644	-0.602	0.05 – 4.7	0.2
Total Phosphorus ($mg\ L^{-1}$)	0.530	-0.539	-0.553	0.001 – 0.520	0.015

Table 2

Submersed macrophyte taxa recorded from the Mary River catchment, May 1996-1997. Frequency of occurrence and mean taxon cover (± standard error) were calculated from all 112 samples (four samples from sites in Wide Bay Ck, which dried up for the final two surveys, were excluded from these calculations)

Taxon	Frequency of occurrence in samples (%)	Mean cover per quadrat (%)	Cover range (%)
Myriophyllum verrucosum Lindley	33.9	6.0 ± 1.2	0 - 57.7
Vallisneria nana R. Br.	30.4	6.8 ± 1.3	0 - 50.0
Potamogeton crispus L.	29.5	2.2 ± 0.5	0 - 30.0
Myriophyllum variifolium J. Hooker	12.5	3.1 ± 0.9	0 - 54.4
Hydrilla verticillata L.f. Royle	10.7	1.0 ± 0.4	0 - 30.0
Nitella spp.	8.9	0.8 ± 0.3	0 - 23.1
Potamogeton perfoliatus L.	7.1	1.9 ± 0.9	0 - 57.3
Chara spp.	6.3	0.7 ± 0.4	0 - 30.0
Potamogeton tricarinatus F. Muell. & A. Benn. ex A. Benn.	5.4	0.6 ± 0.3	0 - 25.0
Najas tenuifolia R. Br.	3.6	0.1 ± 0.1	0 - 5.7
Callitriche sp.	3.5	0.5 ± 0.3	0 - 24.6
Ceratophyllum demersum L.	2.7	0.2 ± 0.1	0 - 9.3
Potamogeton ochreatus Raoul	0.9	0.01 ± 0.01	0 - 0.9

Table 3

Mean cover (± standard error) of submersed macrophyte taxa occurring in sample groups defined by UPGMA classification of Mary River samples. Only taxa having significantly different cover (Kruskal-Wallis tests) between sample groups shown. For each taxon, the figure in brackets represents the percentage occurrence in samples in each UPGMA group

Taxon	Group 1 (n=13)	Group 2 (n=17)	Group 3 (n=32)	Group 4 (n=15)	p-value
Nitella sp.	5.6 ± 2.0 (69)	0.7 ± 0.7 (6)	0 (0)	0 (0)	0.000
M. variifolium	26.1 ± 3.5 (100)	0 (0)	0 ± 0.05 (3)	0 (0)	0.000
V. nana	0 (0)	30.0 ± 3.7 (100)	6.6 ± 2.0 (41)	2.6 ± 1.4 (27)	0.000
M. verrucosum	3.0 ± 1.3 (46)	0.4 ± 0.2 (18)	19.5 ± 2.8 (91)	0 (0)	0.000
P. tricarinatus	0 (0)	0 (0)	2 ± 1 (41)	0 (0)	0.029
P. crispus	1.1 ± 1.0 (15)	0.9 ± 0.6 (24)	2.0 ± 0.6 (41)	10.3 ± 2.3 (93)	0.000
P. perfoliatus	0 (0)	1 ± 0.5 (12)	0 (0)	14 ± 6 (40)	0.000

Table 4

Mean values (± standard error) for environmental variables determined by Kruskal-Wallis tests to be significantly different between UPGMA-defined macrophyte sample groups

Environmental Variable	Group 1	Group 2	Group 3	Group 4	p-value
Catchment Descriptors					
Elevation (AHD, m)	126 ± 6	49 ± 6	43 ± 7	85 ± 11	0.000
Upstream catchment area (km^2)	79 ± 9	730 ± 146	1870 ± 353	349 ± 93	0.000
Distance to mouth (km)	254 ± 7	182 ± 15	162 ± 9	225 ± 13	0.000
Discharge Descriptors					
Max. discharge ($m^3\ d^{-1}$)	$1.1\times10^6 \pm 3.3\times10^5$	$2.5\times10^7 \pm 5.9\times10^6$	$4.1\times10^7 \pm 7.0\times10^6$	$6.4\times10^6 \pm 3.3\times10^6$	0.000
90^{th} Percentile ($m^3\ d^{-1}$)	15418 ± 3850	90347 ± 16203	727569 ± 177679	61269 ± 13217	0.000
CV of total daily discharge (%)	452.4 ± 0.3	815.6 ± 0.7	594.1 ± 0.3	670.2 ± 1.4	0.000
Med. discharge ($m^3\ d^{-1}$)	1408 ± 210	5494 ± 544	65722 ± 16095	13727 ± 4701	0.001
10^{th} Percentile ($m^3\ d^{-1}$)	140 ± 53	280 ± 99	13310 ± 3275	4600 ± 1849	0.019
Number of zero flow days	193 ± 37	116 ± 23	155 ± 33	60 ± 24	0.041
Physical Habitat					
% Bedrock	1 ± 1	0 ± 0	0 ± 0	0 ± 0	0.000
Water slope (%)	0.01 ± 0	0.18 ± 0.07	0.60 ± 0.14	0.72 ± 0.23	0.000
% Cobble	22 ± 4	5 ± 4	21 ± 3	24 ± 5	0.000
Depth (cm)	62 ± 6	38 ± 6	32 ± 4	37 ± 7	0.003
% Rock	2 ± 1	0 ± 0	5 ± 2	5 ± 2	0.005
Water velocity ($m\ s^{-1}$)	0.01 ± 0.01	0.08 ± 0.03	0.24 ± 0.05	0.12 ± 0.05	0.014
% Sand	9 ± 5	34 ± 9	5 ± 2	15 ± 6	0.016
% Gravel	39 ± 3	33 ± 8	50 ± 3	33 ± 5	0.029
Water Quality					
Total Phosphorus ($\mu g\ L^{-1}$)	17 ± 10	18 ± 2	32 ± 5	13 ± 2	0.000
Total Kjeldahl Nitrogen ($mg\ L^{-1}$)	0.14 ± 0.02	0.30 ± 0.03	0.31 ± 0.02	0.26 ± 0.04	0.000
pH	7.81 ± 0.11	8.20 ± 0.14	8.27 ± 0.07	8.16 ± 0.05	0.029

Table 5

Principal Axis Correlation coefficients for submersed macrophyte taxa and environmental parameters significantly correlated with SSHMDS ordination of Mary River samples. Significance determined by Monte-Carlo randomisation. Significance *0.05<p<0.01; ** p<0.01

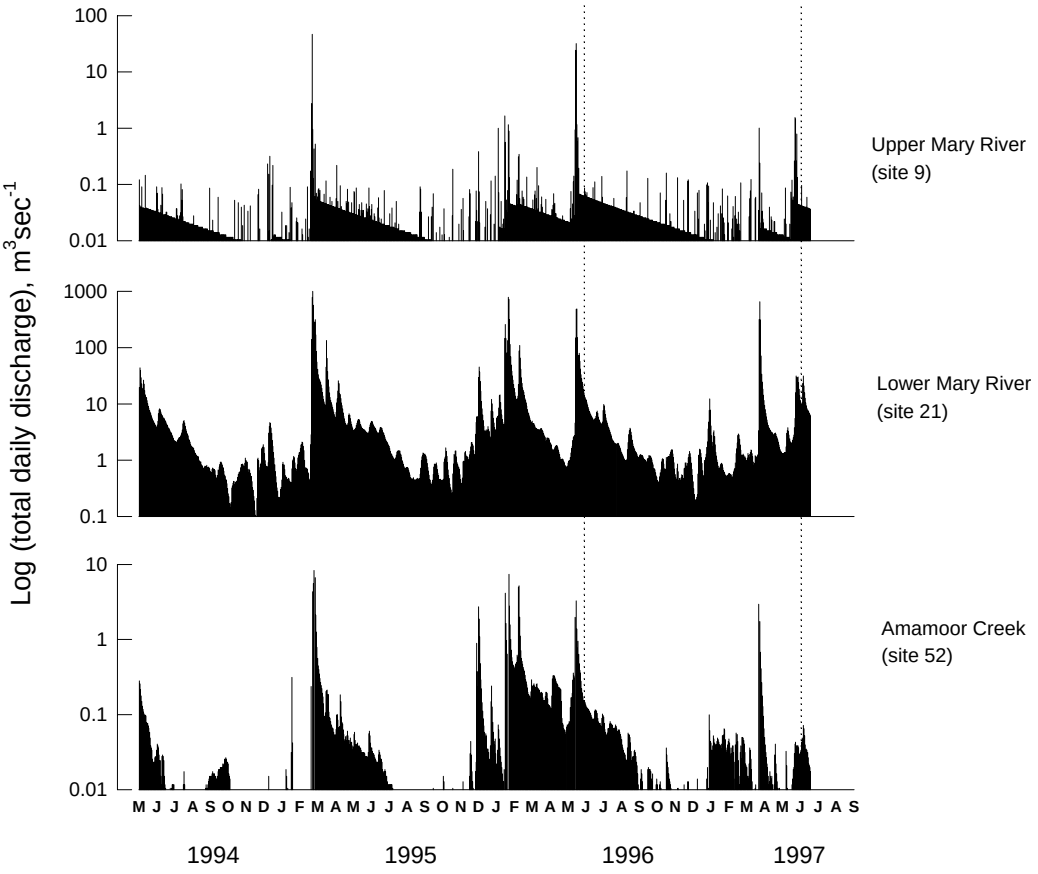
Taxa	**r**	**Environmental Variables**	**r**
V. nana	0.913 **	**Catchment Descriptors**	
P. crispus	0.849 **	Elevation	0.595 **
M. variifolium	0.837 **	Distance to mouth	0.580 **
M. verrucosum	0.803 **	Subcatchment area	0.450 **
Nitella spp.	0.694 **	**Discharge Descriptors**	
P. perfoliatus	0.506 **	Maximum daily discharge	0.510 **
P. tricarinatus	0.504 **	CV of daily discharge	0.457 **
H. verticillata	0.354 *	90^{th} Percentile of total daily discharge	0.369 **
		Median daily discharge	0.334 *
		Physical habitat	
		Riparian Cover	0.498 **
		% Sand	0.479 **
		% Gravel	0.409 **
		% Bedrock	0.404 **
		Water velocity	0.351 *
		Depth	0.328 *
		Water slope	0.323 *
		Water Quality	
		Total Hardness	0.503 **
		Conductivity	0.491 **
		Alkalinity	0.482 **
		pH	0.468**
		Total Kjeldahl Nitrogen	0.342 *
		Total Phosphorus	0.318 *

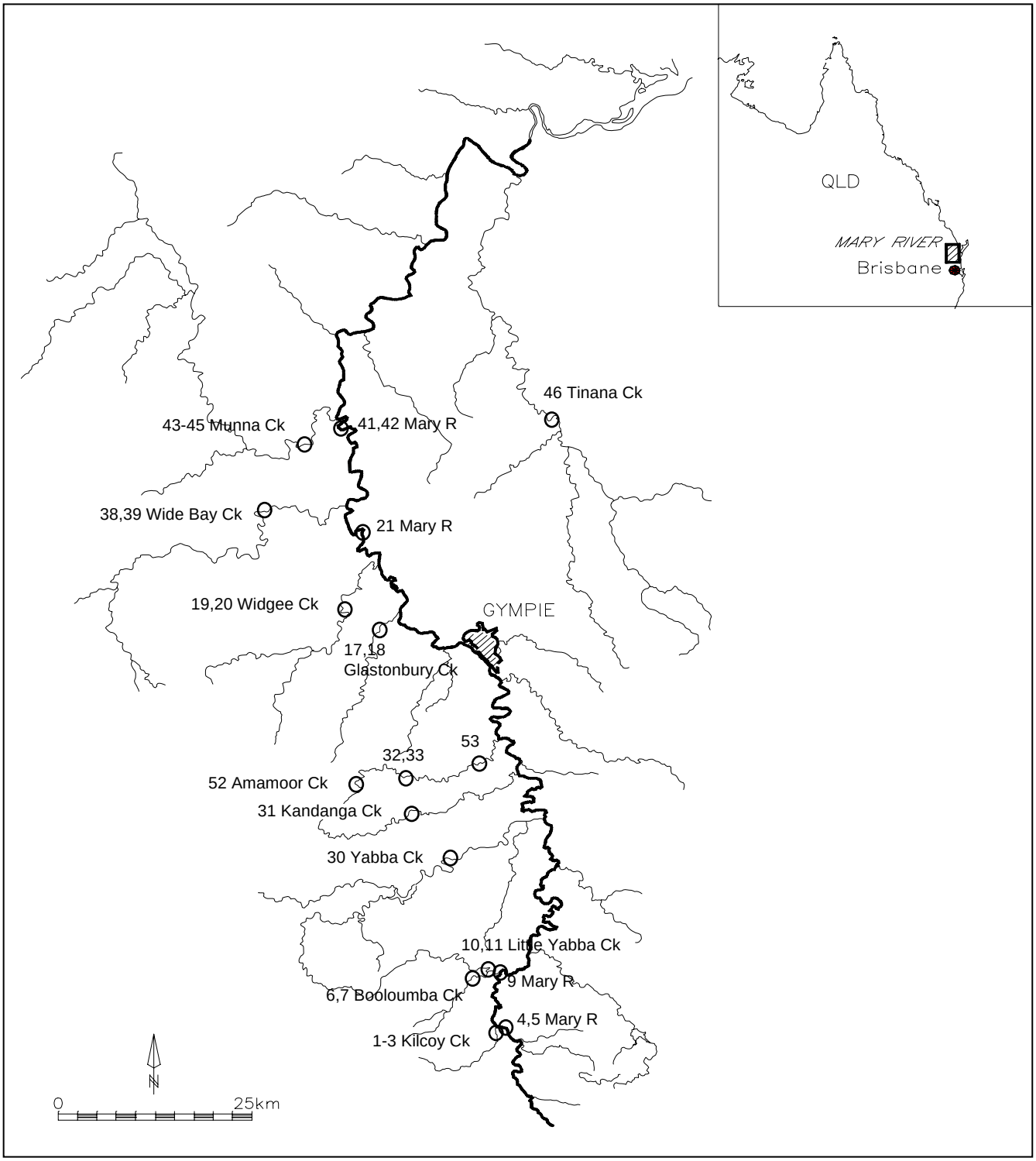
Figure Captions

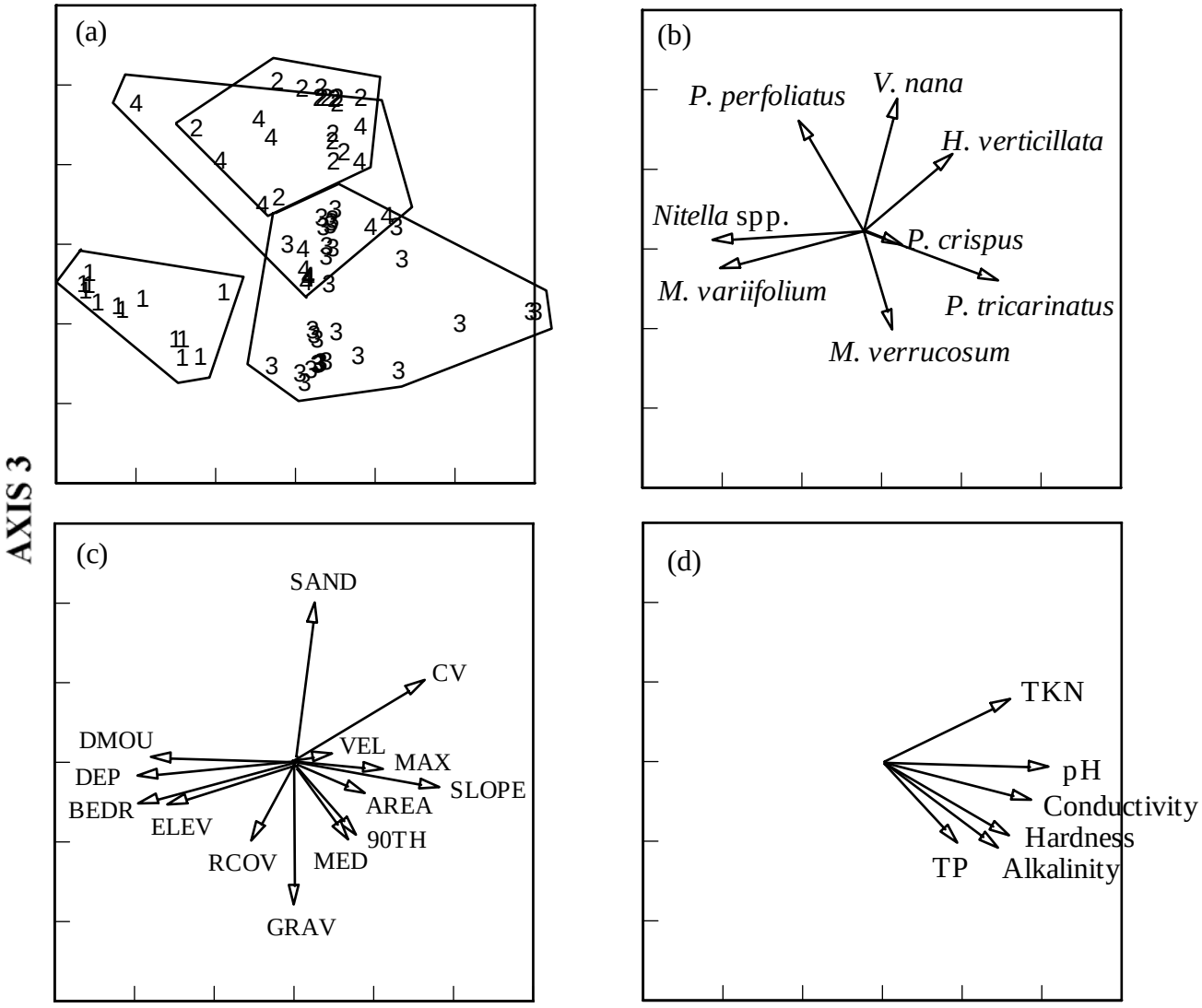
Figure 1. Location of the Mary River catchment and study sites (numbered 1-53). Note that site numbers are not indicative of the total number of sites included in this study. The main channel of the Mary River shown in bold.

Figure 2. Hydrographs for representative Mary River sites. The period of study is indicated by dashed vertical lines.

Figure 3. SSHMDS ordination of Mary River samples based on log($\underline{x}$+1) transformed species cover (common species only). Stress = 0.137, 3 dimensions (ratio regression). Variance explained by axes 2 and 3 = 67.3%. (a) Distribution of samples and UPGMA groups in ordination space. (b) Direction of significant correlations for submersed macrophyte taxa with the ordination. (c) Direction of significant correlations for physical habitat variables (including site position in catchment) with the ordination. (d) Direction of significant correlations for water quality variables with the ordination. Vectors labelled with abbreviations: DMOU, Distance to Mouth; ELEV, Elevation; AREA, Subcatchment area; DEP, Depth; BEDR, % Bedrock; RCOV, % Riparian cover; GRAV, % Gravel; MED, Median total daily discharge; 90TH, 90th percent of total daily discharge; SLOPE, Water slope; MAX, Maximum total daily discharge; VEL, Water velocity; CV, CV of total daily discharge; SAND, % Sand.


Log (total daily discharge), m3sec-1
100
10
1
0.1
0.01
Upper Mary River
(site 9)
1000
100
10
1
0.1
Lower Mary River
(site 21)
10
1
0.1
0.01
Amamoor Creek
(site 52)
M J J A S O N D J F M A M J J A S O N D J F M A M J J A S O N D J F M A M J J A S
1994
1995
1996
1997


QLD
MARY RIVER
Brisbane
46 Tinana Ck
43-45 Munna Ck
41,42 Mary R
38,39 Wide Bay Ck
21 Mary R
19,20 Widgee Ck
GYMPIE
17,18
Glastonbury Ck
53
32,33
52 Amamoor Ck
31 Kandanga Ck
30 Yabba Ck
10,11 Little Yabba Ck
9 Mary R
6,7 Booloumba Ck
4,5 Mary R
1-3 Kilcoy Ck
N
0
25km


(a)
(b)
P. perfoliatus
V. nana
H. verticillata
Nitella spp.
P. crispus
M. variifolium
P. tricarinatus
M. verrucosum
(c)
SAND
CV
DMOU
VEL
MAX
DEP
SLOPE
BEDR
AREA
ELEV
90TH
RCOV
MED
GRAV
(d)
TKN
pH
Conductivity
Hardness
TP
Alkalinity
AXIS 3
AXIS 2