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Replacement of littoral native vegetation with the ponded pasture grass *Hymenachne amplexicaulis*: effects on plant, macroinvertebrate and fish biodiversity of backwaters in the Fitzroy River, Central Queensland, Australia

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Running Title: Changes to fauna of backwaters following *Hymenachne* invasion

Abstract

Changes in plant and macroinvertebrate communities were found following replacement of extensive zones of floating-attached/submergent native vegetation within Fitzroy River backwaters by the major environmental weed *Hymenachne amplexicaulis* (Poaceae). Impacts of *H. amplexicaulis* on native littoral flora and fauna (macroinvertebrates and fish) were assessed by comparing three sites previously supporting native vegetation and now invaded by *H. amplexicaulis* with nearby stands of native backwater vegetation. Plant biomass of *Hymenachne* plant beds was thirty-fold greater than Native plant beds whereas plant species diversity (richness) was significantly less. Macroinvertebrate communities of *Hymenachne* beds were significantly lower in abundance of insect orders Ephemeroptera, Hemiptera and Odonata while Coleoptera were more abundant in *Hymenachne* beds. Non-metric multidimensional scaling ordination of macroinvertebrate Family abundance and composition data showed that *Hymenachne* plant beds had a different assemblage to that in Native plant beds. In common with other studies of weed invasions, an increased abundance of some vertebrate fauna was observed (in this case an introduced fish species *Xiphophorus maculatus* comprised 75% of fish captured in *Hymenachne* beds compared with 0% in Native plant beds). Change in vegetation structure was implicated as an important factor influencing macroinvertebrate and fish faunal composition and with potential to impact on waterbird habitat values of wetlands. and decline in habitat value of *Hymenachne*-invaded wetlands are discussed.

Key Words: environmental weeds, wetlands, community structure, waterbirds, food chains, macrophytes, weed invasion, exotic, species richness

Introduction

Hymenachne amplexicaulis (olive hymenachne) (Rudge) Nees, a native of Central and South America introduced into Queensland in the late 1980s for production of cattle fodder in ponded pastures, is listed as one of the 20 worst environmental weeds in Australia (Williams and West 2000). Ecology, history of introduction and control measures of *H. amplexicaulis* were reviewed by Csurhes *et al.* (1999). *H. amplexicaulis* has colonized river/creek margins with fluctuating water level, permanently wet areas < 1.2 m deep in the dry season, seasonally inundated swamps, natural lagoons and margins of water storage facilities. The potential distribution of *H. amplexicaulis* in Australia corresponds to coastal northern Australia with an estimated potential cover similar to the area currently occupied by another ponded pasture species, *Urochloa mutica* (para grass) - 100,000 ha in Queensland and 40,000 ha in the Northern Territory. The ability of *H. amplexicaulis* to colonize deeper water than *U. mutica* suggests that its potential distribution may be even greater. In Central Queensland, the presence of *H. amplexicaulis* in the Fitzroy River was first noted in the early 1990s (Houston and McCabe 1996) but was not detected in extensive surveys of the Fitzroy catchment in 1989-90 (Duivenvoorden 1992). In the lower Fitzroy River, *H. amplexicaulis* has largely supplanted aquatic plant communities fringing the river and invaded river backwaters (defined as shallow sheltered portions of the river that retain a connection to the river at normal pool level (Boulton and Lloyd 1991)).

Backwaters comprise part of the nationally significant wetland aggregation - the 'Fitzroy River Floodplain' – recognized as retaining significant natural values for fauna (ANCA 1996).

Construction of a barrage at Rockhampton in the early 1970s on the Fitzroy River deepened the river above the barrage causing river backwaters to become more extensive and remain inundated for longer periods of time. Although such wetlands have been altered to some extent by human

activity (Walker 1985), lower Fitzroy River backwaters were found to provide roosting and feeding habitat for > 40 species of waterbirds and breeding habitat for at least 14 species (Longmore 1978; Houston and McCabe 1996). Backwaters are also important as reservoirs of fish biomass and as nursery areas for juvenile fish (Welcomme 1979; Sheaffer and Nickum
5 1986).

H. amplexicaulis domination of wetlands may cause changes to: (1) structure, floristic composition and biodiversity of native aquatic plant beds; (2) associated fauna assemblages and biodiversity; (3) water quality associated with changes in plant community metabolism; (4) flow
10 regimes and possible exacerbation of flooding; (5) ecosystem functioning, e.g. smothering of river banks and changes to recruitment, nutrient recycling and survival of riparian forests. The first two of these effects (changes to flora and fauna) were of interest to this study. Invasion of freshwater wetlands by exotic aquatic and semiaquatic weeds has caused loss of plant and faunal biodiversity (Keast 1984; Howard-Williams and Davies 1988; Madsen *et al.* 1991) although
15 Australian examples are few (Groves and Willis 1999). In south-eastern Queensland creeks, Arthington *et al.* (1983) found a significant association between the presence of exotic semiaquatic grasses and the absence of native aquatic macrophytes as well as a change in vegetation community structure and fauna. Braithwaite *et al.* (1989) reported a decline in plant species richness and change in vegetation structure and fauna of floodplain sedgeland following
20 displacement by *Mimosa pigra*.

To assess the impact of *H. amplexicaulis* on river backwater wetlands, this study compares plant, invertebrate and fish assemblages of native littoral vegetation with nearby sites where native vegetation was observed in 1993 but has since been replaced by *H. amplexicaulis*. Only one

native vegetation type (the floating-attached/submergent zone represented by *Nymphoides indica* and *Ceratophyllum demersum*) was evaluated in this study.

Methods

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Study Area

The Fitzroy River and its tributaries (the Dawson, Nogoa, Comet, Isaac and McKenzie Rivers) has a catchment of 140 000 km². The barrage impoundment supplies water for Rockhampton, a
10 large regional centre 30 km inland. Grazing is the dominant land use in the catchment.

Rockhampton has a subtropical sub-humid climate. Rainfall is markedly seasonal with > 50% of rain falling between December and March and little or no rain in August and September. Floods occur during the summer months. Sampling was undertaken in December 1997 and April 1998
15 with average minimum and maximum temperatures of 21 to 32°C and 17 to 28°C respectively. Rainfall over the months December to April was below average (350 mm compared to the average of 548 mm based on 1939 to 1996 data) and, although water levels rose 0.3 m between December and April, the river did not flood in the summer of 1997-98.

20 Vegetation of lower Fitzroy River backwaters is characterized by: (i) an emergent zone dominated by *Urochloa mutica* (para grass, a naturalized semiaquatic grass widely distributed in catchments of subtropical and tropical coastal Australian rivers and recognized as an environmental weed (Williams and West 2000)), *Polygonum attenuatum*, *Typha domingensis*, *Phragmites australis*, *Cyperus exaltatus* and *Nelumbo nucifera*; (ii) a floating-
25 attached/submergent zone dominated by *Nymphoides indica* and *Ceratophyllum demersum* – the

most extensive zone within lower Fitzroy River backwaters; (iii) a floating zone of *Azolla* spp. and sometimes *Eichhornia crassipes* may be present, and (iv) a submergent zone dominated by *Ceratophyllum demersum*, *Hydrilla verticillata* and *Vallisneria spiralis*. *E. crassipes* (Water Hyacinth) is the focus of a Rockhampton City Council aquatic weed management programme.

- 5 Extent of these zones may fluctuate seasonally, particularly the floating-attached/submergent zone which may decline in area following summer wet season floods and re-establish during the winter months.

Sampling

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- Three backwaters (23°19' S, 150°27' E, Fig. 1) on either side of the Fitzroy River (6 km upstream from the barrage) were sampled. A site was defined as 100 m of river edge dominated by one vegetation type, i.e. Native (N) or *Hymenachne* (H). Three pairs of sites (three N and three H) were sampled during one summer-autumn period: N1 and H1 (December 1997), N2 and H2 and 15 N3 and H3 (April 1998) (Fig. 1). Where possible, these paired sites were located within the same backwater (N2 and H2, N3 and H3) but this was not possible in December 1997 (N1 and H1) when relatively low water levels prevented boat access to some stands of vegetation.

- At each site, the 100 m of edge was subdivided into twenty 5 m lengths and four of these 5 m 20 lengths were randomly chosen (replicates). At each of these replicates, the following samples were taken: water quality, plant species (identified from Sainty and Jacobs (1994) and a voucher collection held at Central Queensland University), percentage cover of dominant plants within two 1 m² quadrats, the depth to which the plant bed extended, fish abundance from two fish traps and invertebrate abundance and family composition from a pond net. To reduce edge effects, 25 samples were taken at least 1 m from the plant community/open water interface.

Water quality measurements (temperature, pH, conductivity, dissolved oxygen and turbidity) were taken from 30 cm depth between 0800 and 1200 hours at each site with a Horiba Multi-parameter Water Checker. Turbidity was expressed as the percentage light transmission at 30 cm depth compared with surface readings.

Plant biomass was sampled at H3, N1 and N3. The difference in plant structure between Native and *Hymenachne* beds necessitated different sampling techniques. *H. amplexicaulis* was sampled with a small quadrat (20 cm x 20 cm) and the use of secateurs to progressively remove the biomass in a vertical column above the substratum. The emergent component was sampled separately from the submerged component. Native plant beds were sampled by rapidly lowering a drum (0.264 m² cross-sectional area) into the aquatic bed and shearing the stems; to remove the vegetation it was necessary to first cut around the edge of the base of the drum with a long-handled shovel. Replicate samples varied with vegetation type – four for Native and two for *Hymenachne*.

Depths at which common emergent, floating-attached and submergent plant species were growing were made on an opportunistic basis between 1993 and 1998.

Sampling macroinvertebrates required a method that was effective in dense littoral vegetation. Pond net samples have been used to describe aquatic macroinvertebrate community structure, including studies of heavily vegetated marshes (Furse *et al.* 1981; Olson *et al.* 1995; Boulton and Lloyd 1991; Cheal *et al.* 1993; Turner and Trexler 1997; Humphries *et al.* 1998). Following these studies, pond nets were used to sample macroinvertebrate assemblages in the two types of aquatic plant beds. Four nektonic and epiphytic macroinvertebrate samples were taken from each

site with a 300 x 900 µm mesh pond net (a triangular frame with a 35 cm base and 30 cm sides). The littoral vegetation of the top 50 cm of water column was vigorously sampled over a 1 min period within a band 2.5 m long by 0.4 m wide on each side of the boat. Samples were stored in 70% ethanol and sorted to family level by reference to the taxonomic keys in Williams (1980) and Dean (1991). Mesofauna such as Acarina, Copepoda and Ostracoda were not included in the analysis.

The following indices were calculated for each site: macroinvertebrate abundance, family richness, number of taxa within the insect orders Ephemeroptera, Plecoptera and Trichoptera (EPT index - Karr 1999; Resh *et al.* 1995), the Shannon-Wiener diversity index and the Simpson dominance index (Krebs 1972). The percentage dominance of the three most abundant families was also calculated from pooled abundance for each vegetation type (Karr 1999; Resh *et al.* 1995).

Fish traps (40 cm x 25 cm x 25 cm) were baited with dried fish food and set at 40 to 60 cm depth for 2 h during the morning at each site. Catches from eight traps at each site were pooled to give an index of relative fish abundance and species composition.

Statistical Analysis

Tests for differences attributable to vegetation type (Native or *Hymenachne*) were as follows.

Pooled site data (e.g. plant species richness, fish species richness, fish abundance, abiotic variables, macroinvertebrate indicators including diversity, dominance and EPT indices) were tested with paired T-tests. Invertebrate abundance, taxa richness (order or family) and

abundance of dominant invertebrate orders (four replicates for each site) were tested by analysis

of variance (ANOVA) with sites nested within vegetation type. As mean abundance of each macroinvertebrate taxon was proportional to the standard deviation, abundance data were log transformed prior to data analysis ($\log_{10}(X + 1)$, Zar 1999). Significance of statistical tests was assessed at the 5% probability level.

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A visual representation of relationships between macroinvertebrate assemblages of the two vegetation types based on family abundance of the six sites was made with Bray-Curtis similarity measure and fourth root transformation (Clarke and Warwick 1994) to remove the excessive influence on similarity measures of abundant species (Clarke 1993). Non-metric

10 multidimensional scaling ordination (NMDS) was undertaken to determine site relationships in two dimensions presented in the form of a scattergram in which sites closer together more closely resemble each other in terms of their biotic composition than do sites further away. The scattergram is considered interpretable in two dimensions if the stress level of the iterative process is < 0.20 (Clarke and Warwick 1994). The relative contribution of family abundance was
15 assessed by comparing the scattergram obtained from abundance data with a scattergram obtained from presence-absence data.

Analysis of similarity (ANOSIM) was applied to determine whether the macroinvertebrate assemblages of vegetation types (defined on an *a priori* basis – Native and *Hymenachne* beds)
20 were significantly different in family abundance (Clark and Warwick 1994). Sites were nested within vegetation type (Clarke 1993). This tests two hypotheses: (i) that there are no differences among sites within each vegetation type; and (ii) that there are no differences between vegetation types. These analyses used the statistical package *Primer* (Carr 1996).

25 **Results**

Habitat Characteristics

H. amplexicaulis colonized both the emergent and floating-attached/submergent zones of

- 5 backwaters and was found in depths comparable to native species occupying these zones (Table 1). In the main river channel, where *H. amplexicaulis* beds bordered deeper waters, it formed a floating mat over the water surface with possible shading effects on submergent vegetation.

Depth ranges of the outer edge of each vegetation type (Native or *Hymenachne*) were comparable
10 (Table 2) and there were no significant differences between physico-chemical characteristics of Native and *Hymenachne* beds (Table 2).

Plants

- 15 Plant species richness (Table 3) within the Native sites (mean of 9) was significantly greater than *Hymenachne* sites (mean of 5) (t-test, d.f. = 2, $p < 0.05$).

- Plant cover within *Hymenachne* sites was dominated by *H. amplexicaulis* (93% cover) while plant cover within the Native beds was dominated by *N. indica* (65% cover) and *C. demersum*
20 (16% cover) (Table 3). These differences were reflected in analysis of plant biomass (Table 4). *H. amplexicaulis* comprised 100% of the biomass in the *Hymenachne* beds while *N. indica* (range 62% to 78%) and *C. demersum* (range 14% to 31%) dominated plant biomass in the Native beds.

Invertebrates

Twelve invertebrate orders (or higher taxa), including eight insect orders were collected from the six sites (Table 5). Bivalvia, Hirudinea, Plecoptera and Trichoptera were rare representing less than 0.1% of the combined catch for all sites. Of these, Bivalvia and Plecoptera (a single individual) were only collected from single *Hymenachne* sites (H1 and H3 respectively) and Trichoptera only from Native sites (Table 5). Insects comprised approximately 80% of the total catch from Native sites compared with 60% of the *Hymenachne* catch (Table 5).

Dominant macroinvertebrate families (those comprising 5% or more of the pooled abundance within a vegetation type) were Chironomidae, Pleidae, Corixidae, Mesovelidae, Siphonuridae, Planorbidae and Atyidae for Native sites and Culicidae, Pleidae, Dytiscidae, Planorbidae, Hydrobiidae and Atyidae for *Hymenachne* sites (Table 5).

Site family richness ranged from 24 to 38 families with a cumulative total of 40 families from Native plant beds and 46 from *Hymenachne* beds (Table 5). Family-rich groups included Coleoptera (12), Diptera (12), Hemiptera (8), Odonata (7) and Gastropoda (5) (Table 5).

Hymenachne beds did not differ significantly from native beds in abundance, order richness or family richness or in the Shannon-Wiener diversity index, the Simpson dominance index or the EPT index. However, abundance and EPT index of all three Native plant sites were greater than *Hymenachne* sites (Table 5). Percent dominant taxa were similar, just under 50%, for the two vegetation types.

The dominant invertebrate higher taxa (i.e. Order or above and comprising more than 5% of the total catch within a vegetation type) were Hemiptera, Diptera, Ephemeroptera, Gastropoda, Decapoda and Odonata for Native vegetation and Diptera, Gastropoda, Decapoda, Coleoptera,

Hemiptera and Odonata for *Hymenachne*. The abundance of Coleoptera within *Hymenachne* beds was significantly greater than Native sites, while Ephemeroptera, Hemiptera and Odonata abundance within Native sites were significantly greater than in *Hymenachne* sites (Fig. 2) (analysis of variance, d.f. = 1,4, $p < 0.05$).

5

A two dimensional non-metric multidimensional scaling ordination of macroinvertebrate family abundance showed two distinctly separated groups – one comprised of the three Native sites and the other of the three *Hymenachne* sites (Fig. 3a). Sites within vegetation types differed significantly ($r = 0.828$, $p < 0.001$ based on 5000 random permutations). A high sample statistic ($r = 1.000$) was also obtained for differences between the two vegetation types but this was testable only at the 0.10 probability level due to the low level of replication (10 permutations only were possible) and cannot be tested at the 0.05 level. However, the vegetation types were clearly separated by the ordination (Fig. 3a) and this confirmed that Native and *Hymenachne* plant beds were characterized by distinct invertebrate assemblages at the family level.

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The two dimensional non-metric multidimensional scaling ordination of macroinvertebrate family presence-absence data showed two groups of sites based on vegetation type (Fig. 3b), although sites were more widely spaced than the family abundance ordination (Fig. 3a). This indicates that macroinvertebrate assemblages of *Hymenachne* beds and Native plant beds can be differentiated by family presence-absence composition alone.

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Fish

Ten species of fish were captured from the sample sites including two introduced species, *Gambusia holbrooki* and *Xiphophorus maculatus* (Table 6). *Hypseleotris galii* and *Neosilurus*

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hyrtlui were found only in the Native plant beds while *H. klunzingeri*, *Mogurnda adspersa* and *X. maculatus* were found only in the *Hymenachne* beds. There were no significant differences in total fish abundance, species richness or species diversity between Native and *Hymenachne* beds. Excluding introduced species from the between vegetation type comparisons did not alter the
5 result of the statistical comparisons of abundance and species richness.

X. maculatus was the most abundant fish species comprising over 75% of the fish caught within *Hymenachne* beds and over 60% of the total fish abundance. Relative abundance of introduced fish was much greater in *Hymenachne* than Native plant beds (50, 37 and 0 compared with 1, 0
10 and 0 respectively, i.e. 79% compared with 3% of the pooled total fish catch for each vegetation type).

Discussion

A fundamental change in vegetation structure following wetland invasion by *H. amplexicaulis* was observed with displacement of floating-attached/submergent native aquatic plant beds by dense emergent grass beds harbouring significantly less plant species and increasing 30-fold in plant biomass, mirroring findings of other studies investigating impacts of weed invasions on wetlands (Arthington *et al.* 1983; Howard-Williams and Davies 1988; Braithwaite *et al.* 1989; Madsen *et al.* 1991; Van der Valk *et al.* 1993). As in other studies of weed impacts on fauna, faunal change was evident within *Hymenachne* beds compared with native plant beds, conditions favouring some native faunal groups (e.g. Coleoptera in this study; some fish species in Canadian lakes invaded by *Myriophyllum spicatum* - Keast 1984; herbivorous waterbirds in New Zealand lakes invaded by *Lagarosiphon major* - Howard-Williams and Davies 1988; and small mammals following *Mimosa pigra* invasion of northern Australian sedgeland - Braithwaite *et al.* 1989). In contrast, other faunal groups were disadvantaged (e.g. Ephemeroptera, Hemiptera and Odonata in this study; Isopoda, Chironomidae, Trichoptera, Ephemeroptera and several native fish species in Canadian lakes - Keast 1984; native fish species in southeastern Queensland creek pools invaded by *Urochloa mutica* (para grass) – Arthington *et al.* 1983; and lizards and birds of northern Australian sedgeland - Braithwaite *et al.* 1989).

Factors that may alter wetland faunal assemblages include impacts on vegetation structure, food webs and physical conditions. The great changes observed in plant community structure observed in this study implicate this factor as an important contributor to the observed changes in faunal composition. Invertebrate assemblages of different vegetation types have been found to differ in abundance (Suren and Lake 1989; Boulton and Lloyd 1991; Olson *et al.* 1995) and, as in the present study, a greater abundance of macroinvertebrates was found in aquatic macrophyte

beds dominated by species with finely-divided leaves than in inundated grass (Boulton and Lloyd 1991). Although not investigated in this study, waterbird assemblages of backwaters may also be affected by simplification of habitat structure, particularly as relatively few waterbird species utilize dense emergent vegetation compared to more open mixed stands of emergent, floating-
5 attached and submergent macrophyte vegetation (Morton and Brennan 1991).

A greater relative abundance of introduced fish in *Hymenachne* beds (79% of fish were exotic, predominantly *X. maculatus*) compared with native plant beds (3%) was observed in this study. A similar pattern of greater abundance of introduced fish (*Gambusia affinis* and *Xiphophorus*
10 *helleri*) associated with another species of exotic grass (para grass *U. mutica*) was also found in creeks in subtropical south-east Queensland (Arthington *et al.* 1983). Factors thought to favour introduced fish in exotic grass beds were a change in habitat structure (greater stem densities within exotic grass beds provide more lateral concealment from predation than native vegetation) and an abundance of plant food. Other studies have reported similar findings (e.g. in Canadian
15 lakes invaded by *Myriophyllum spicatum*, concealment from predation or a reduction in predator efficiency within denser macrophytes was thought to favour certain fish species (Keast 1984); and Braithwaite *et al.* (1989) also identified concealment from predation as a key to conditions within the introduced *Mimosa pigra* stands leading to increased densities of small mammals compared with native sedgeland). It appears that weeds invading wetlands alter habitat
20 conditions and increase abundance of fauna (either native or exotic) favoured by these changed conditions.

This study has shown that replacement of native aquatic plant beds by *H. amplexicaulis* may have serious ramifications for conservation of wetland biodiversity in tropical regions of Australia. In
25 addition to loss of plant biodiversity, *Hymenachne* dominated beds differed in invertebrate and

fish assemblages from Native beds and this was attributed to change in plant community structure. Harbours exotic fish in greater abundance than native aquatic vegetation may prove to be one of the main impacts of introduced ponded pasture grasses such as *H. amplexicaulis*.

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Table 1: Maximum depths of common macrophytes in the lower Fitzroy River

Growth Habit and Species	Common Name	Maximum Depth in Fitzroy River (m)
Emergent		
<i>Hymenachne amplexicaulis</i>	Olive Hymenachne	
Attached		1.5
Floating mat		3.2
<i>Urochloa mutica</i>	Para Grass	
Attached		1.1
Floating mat		2.7
<i>Paspalum paspaloides</i>	Water Couch	
Attached		0.4
Floating mat		0.7
<i>Phragmites australis</i>	Common Reed	1.0
<i>Polygonum attenuatum</i>	Smartweed	1.1
<i>Ludwigia peploides</i>	Water Primrose	1.2
<i>Persicaria decipiens</i>	Slender Knotweed	1.0
<i>Cyperus exaltatus</i>	A sedge	0.7
Floating-attached		
<i>Nymphoides indica</i>	Water Snowflake	1.7
<i>Nymphaea gigantea</i>	Giant Water-lily	3.0
<i>Ottelia ovalifolia</i>	Swamp Lily	0.8
Submergent		
<i>Ceratophyllum demersum</i>	Hornwort	4.8
<i>Hydrilla verticillata</i>	Water Thyme	3.0
<i>Vallisneria gigantea</i>	Ribbon-weed	2.2

Table 2: Physico-chemical water quality characteristics of Native and *Hymenachne* sites (values are means of four samples per site, standard deviations are shown in brackets)

Site	N1	N2	N3	H1	H2	H3
Depth (cm)	116.2 (13.0)	167.9 (17.2)	81.2 (15.8)	82.5 (7.1)	150.9 (4.4)	81.9 (15.6)
Temperature ($^{\circ}\text{C}$)	28.6 (0.5)	25.9 (0.7)	23.4 (0.3)	30.9 (1.3)	25.8 (0.1)	26.3 (0.4)
pH	7.8	6.7	7.2	8.4	6.6	7.6
Dissolved Oxygen (mg l^{-1})	3.53 (1.00)	0.83 (0.24)	4.15 (1.00)	2.70 (1.31)	0.70 (0.29)	3.63 (1.47)
Conductivity ($\mu\text{S cm}^{-1}$)	370.0 (20.0)	270.8 (14.4)	281.0 (9.5)	297.5 (5.0)	270.5 (6.7)	237.8 (2.5)
Turbidity (%)	0.03 (0.03)	2.27 (1.97)	0.71 (0.89)	1.26 (2.11)	2.63 (2.68)	0.32 (0.38)

Table 3: Plant species composition (observations from four randomly selected 5 m locations at each site) and cover of dominant species at Native and *Hymenachne* sites (an average of eight samples per site)

Zone	Species	Cover (%)				Cover (%)			
		N1	N2	N3	Mean	H1	H2	H3	Mean
Emergent	<i>Hymenachne amplexicaulis</i>	-	<1	-	<1	95	94	90	93
	<i>Polygonum attenuatum</i>	<1	9	<1	3	-	<1	-	<1
	<i>Urochloa mutica</i>	-	<1	<1	<1	-	-	-	-
	<i>Cyperus exaltatus</i>	-	-	<1	<1	-	-	-	-
	<i>Nelumbo nucifera</i>	-	-	<1	<1	-	-	-	-
	Total	<1	9	<1	3	95	94	90	93
Floating-attached	<i>Nymphoides indica</i>	63	58	73	65	<1	-	<1	<1
	<i>Ludwigia peploides</i>	-	-	<1	<1	-	-	-	-
	Total	63	58	73	65	<1	-	<1	<1
Free-floating	<i>Azolla filiculoides</i>	1	1	<1	1	<1	-	<1	<1
	<i>Lemna</i> sp.	<1	-	-	<1	<1	-	-	<1
	Total	1	1	<1	1	<1	-	<1	<1
Submergent	<i>Ceratophyllum demersum</i>	29	10	8	16	<1	1	<1	<1
	<i>Utricularia</i> sp	<1	<1	-	<1	-	<1	-	<1
	<i>Potamogeton crispus</i>	-	-	<1	<1	-	-	-	-
	<i>Najas tenuifolia</i>	<1	<1	-	<1	-	-	-	-
	<i>Vallisneria spiralis</i>	<1	<1	<1	<1	-	<1	<1	<1
	Total	29	10	8	16	<1	1	<1	<1
Total cover		94	79	81	84	95	95	90	94
Species richness		8	9	10	9	5	5	5	5

Table 4: Mean plant biomass (g m⁻²) at selected Native and *Hymenachne* sites (values are means of 4 samples for N1 and N3 and 2 samples for H1 with standard deviation in brackets)

Site	N1	N3	H3
Detritus	17.7 (15.5)	7.8 (1.4)	0.0 (0.0)
Species			
<i>Vallisneria gigantea</i>	0.0 (0.0)	2.8 (5.6)	0.0 (0.0)
<i>Ceratophyllum demersum</i>	25.9 (38.2)	75.0 (79.3)	0.0 (0.0)
<i>Nymphoides indica</i>	141.6 (51.0)	150.3 (52.0)	0.0 (0.0)
Unidentified algae	0.0 (0.0)	13.9 (15.7)	0.0 (0.0)
<i>H. amplexicaulis</i> . (above)	0.0 (0.0)	0.0 (0.0)	1263.8 (153.8)
<i>H. amplexicaulis</i> . (below)	0.0 (0.0)	0.0 (0.0)	4956.3 (595.7)
Total living plant biomass	181.9 (63.1)	242.1 (119.2)	6220.0 (441.9)

Table 5: Family composition, mean abundance (4 samples per site), family richness, EPT index, diversity and dominance of macroinvertebrate assemblages at each site (total catch for each order/class in bold) (na=not applicable)

Taxon	Native Sites				Hymenachne Sites			
	N1	N2	N3	% Pooled Abundance	H1	H2	H3	% Pooled Abundance
Bivalvia	0.0	0.0	0.0	0.0	1.5	0.0	0.0	0.1
Sphaeriidae	0.0	0.0	0.0	0.0	1.5	0.0	0.0	0.1
Gastropoda	121.5	249.8	381.0	13.6	272.8	58.3	70.0	26.5
Ancylidae	0.0	0.0	0.0	0.0	0.0	0.0	0.3	0.0
Hydrobiidae	0.5	0.0	0.0	0.0	125.5	0.0	1.0	8.4
Lymnaeidae	0.0	1.8	3.8	0.1	1.8	3.5	5.3	0.7
Planorbidae	121.0	248.0	377.3	13.5	140.5	51.5	59.5	16.6
Thiaridae	0.0	0.0	0.0	0.0	5.0	3.3	4.0	0.8
Decapoda	165.5	124.3	69.5	6.5	131.3	15.5	54.8	13.3
Atyidae	165.5	124.3	69.5	6.5	131.3	15.5	54.8	13.3
Hirudinea	0.5	0.8	1.5	0.0	0.0	0.3	0.5	0.0
Unidentified family	0.5	0.8	1.5	0.0	0.0	0.3	0.5	0.0
Ephemeroptera	77.8	308.3	415.3	14.5	8.8	2.3	40.5	3.4
Caenidae	68.0	9.5	165.5	4.4	2.3	0.0	0.0	0.1
Leptophlebiidae	0.0	0.5	0.0	0.0	0.0	0.0	0.0	0.0
Siphonuridae	9.8	298.3	249.8	10.1	6.5	2.3	40.5	3.3
Odonata	144.3	91.8	127.8	6.6	40.8	28.3	11.3	5.3
Aeshnidae	0.0	1.3	2.5	0.1	0.0	0.0	0.5	0.0
Calopterygidae	0.0	0.0	0.0	0.0	0.3	0.0	0.0	0.0
Coenagrionidae	49.3	44.3	61.3	2.8	17.0	9.8	9.0	2.4
Corduliidae	0.0	0.0	0.0	0.0	0.0	0.3	0.3	0.0
Gomphidae	0.0	1.0	0.0	0.0	0.0	0.0	0.0	0.0
Libellulidae	70.3	42.3	63.3	3.2	23.3	18.0	1.5	2.8
Protoneuridae	24.8	3.0	0.8	0.5	0.3	0.3	0.0	0.0
Hemiptera	484.0	391.0	863.5	31.5	35.5	39.8	94.3	11.2
Corixidae	150.0	16.3	299.5	8.4	0.0	3.3	2.5	0.4
Gerridae	2.3	21.3	8.8	0.6	1.0	2.5	5.8	0.6
Hydrometridae	0.0	0.0	0.0	0.0	0.8	1.0	0.0	0.1
Mesovelidae	219.0	55.3	97.0	6.7	4.0	2.3	10.8	1.1
Naucoridae	34.8	9.5	58.3	1.9	25.8	14.0	8.5	3.2
Nepidae	0.0	0.3	5.0	0.1	0.8	0.3	2.5	0.2
Notonectidae	1.0	2.3	14.8	0.3	0.0	4.0	5.5	0.6
Pleidae	77.0	286.3	380.3	13.5	3.3	12.5	58.8	4.9
Diptera	335.8	813.3	307.5	26.4	113.3	268.0	22.3	26.7
Ceratopogonidae	7.8	63.3	12.0	1.5	2.0	0.0	0.0	0.1
Culicidae	99.8	7.0	36.8	2.6	43.5	245.5	8.3	19.7
Chironomidae	228.0	733.8	251.0	22.0	30.0	19.0	10.3	3.9
Dolichopodidae	0.0	0.0	0.0	0.0	1.8	0.0	0.3	0.1
Empididae	0.0	1.3	0.0	0.0	2.0	0.0	0.0	0.1
Ephydriidae	0.0	0.5	0.0	0.0	0.0	0.0	0.0	0.0
Psychodidae	0.0	0.0	0.0	0.0	0.0	0.3	1.3	0.1
Sciomyzidae	0.0	0.0	0.0	0.0	0.0	0.0	1.5	0.1
Stratiomyidae	0.0	4.8	7.5	0.2	34.0	3.0	0.3	2.5
Syrphidae	0.0	0.0	0.0	0.0	0.0	0.3	0.5	0.0
Tabanidae	0.0	2.8	0.3	0.1	0.0	0.0	0.0	0.0
Thaumaleidae	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Plecoptera	0.0	0.0	0.0	0.0	0.0	0.0	0.3	0.0
Notonemouridae	0.0	0.0	0.0	0.0	0.0	0.0	0.3	0.0
Lepidoptera	2.0	12.3	13.3	0.5	17.8	0.3	0.0	1.2
Pyalidae	2.0	12.3	13.3	0.5	17.8	0.3	0.0	1.2
Trichoptera	6.0	0.8	1.0	0.1	0.0	0.0	0.0	0.0
Ecnomidae	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Hydroptilidae	4.5	0.8	1.0	0.1	0.0	0.0	0.0	0.0
Leptoceridae	1.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0

Table 5 (cont.)

Coleoptera	0.8	3.5	5.8	0.2	84.3	30.3	69.8	12.2
Carabidae	0.0	0.8	0.0	0.0	0.5	0.8	1.5	0.2
Chrysomelidae	0.0	0.5	0.0	0.0	0.8	0.0	0.3	0.1
Curculionidae	0.0	0.0	0.0	0.0	0.3	0.0	0.3	0.0
Dytiscidae	0.8	1.3	0.0	0.0	52.0	10.5	17.8	5.3
Haliplidae	0.0	0.0	0.0	0.0	0.0	0.0	1.3	0.1
Heteroceridae	0.0	0.3	0.0	0.0	0.0	0.0	0.0	0.0
Hydraenidae	0.0	0.0	0.3	0.0	0.8	2.3	1.0	0.3
Hydrochidae	0.0	0.5	0.8	0.0	0.0	0.5	0.3	0.0
Hydrophilidae	0.0	0.3	3.3	0.1	16.0	5.5	17.3	2.6
Noteridae	0.0	0.0	1.5	0.0	5.5	3.5	12.0	1.4
Spercheidae	0.0	0.0	0.0	0.0	4.8	5.0	12.3	1.5
Staphylinidae	0.0	0.0	0.0	0.0	3.8	2.3	6.0	0.8
Pooled site replicates								
Class/Order richness	10	10	10	10	9	9	9	11
Family richness	24	34	28	40	34	32	38	46
EPT index	5	4	3	6	2	1	2	3
Shannon-Wiener diversity index	2.40	2.01	2.39	Na	2.47	1.87	2.70	Na
Simpson's dominance index	0.11	0.20	0.12	Na	0.12	0.339	0.10	Na
Mean of site replicates (and standard deviation)								
Mean abundance	1338.0	1995.5	2186.0	Na	705.8	442.8	364.3	Na
	(562.9)	(861.5)	(1315.4)		(244.6)	(299.9)	(177.4)	
Mean Class/Order richness	8.0	8.8	9.3	Na	8.5	7.5	7.5	Na
	(1.0)	(0.6)	(0.6)		(0.8)	(0.5)	(0.5)	
Mean Family richness	18.3	23.8	23.3	Na	25.5	24.3	26.0	Na
	(1.0)	(4.6)	(2.2)		(3.9)	(1.0)	(6.2)	

Table 6: Fish species, abundance, species richness and diversity (pooled data for eight bait-traps) within Native and *Hymenachne* sites

Species	N1	N2	N3	Mean (SD)	H1	H2	H3	Mean (SD)
<i>Ambassis agassizi</i>	5	5	0	3.3 (2.9)	0	5	0	1.7 (2.9)
<i>Gambusia holbrooki</i>	1	0	0	0.3 (0.6)	3	1	0	1.3 (1.5)
<i>Glossamia aprion</i>	3	3	1	2.3 (1.2)	2	0	1	1.0 (1.0)
<i>Hypseleotris compressus</i>	0	0	1	0.3 (0.6)	2	0	0	0.7 (1.2)
<i>Hypseleotris galii</i>	1	0	1	0.7 (0.6)	0	0	0	0.0 (0.0)
<i>Hypseleotris klunzingeri</i>	0	0	0	0.0 (0.0)	0	5	0	1.7 (2.9)
<i>Hypseleotris</i> sp.	1	1	5	2.3 (2.3)	2	0	0	0.7 (1.2)
<i>Mogurnda adspersa</i>	0	0	0	0.0 (0.0)	6	0	0	2.0 (3.5)
<i>Neosilurus hyrtlii</i>	1	0	0	0.3 (0.6)	0	0	0	0.0 (0.0)
<i>Xiphophorus maculatus</i>	0	0	0	0.0 (0.0)	47	36	0	27.7 (24.6)
Total fish abundance	12	9	8	9.6 (2.1)	62	47	1	36.7 (31.8)
Total native fish abundance	11	9	8	9.3 (1.5)	12	10	1	7.7 (5.9)
Species richness (all species)	6	3	4	4.3 (1.5)	6	4	1	3.7 (2.5)
Species richness (native species only)	5	3	4	4.0 (1.0)	4	2	1	2.3 (1.5)
Shannon-Wiener diversity index	1.54	0.94	1.07	1.18 (0.32)	0.92	0.76	0.00	0.56 (0.49)
Simpson's dominance index	0.26	0.43	0.44	0.38 (0.10)	0.59	0.61	1.00	0.73 (0.23)

Captions

Figure 1: Study area showing location of sites

- 5 Figure 2: A comparison of mean Native and *Hymenachne* macroinvertebrate order abundance (a difference in letter above each taxon indicates a significant difference between the two vegetation types)

- 10 Figure 3a: Two dimensional non-metric multidimensional scaling ordination of the macroinvertebrate family abundance (4th root transformed, Bray-Curtis similarity index) from Native and *Hymenachne* sites (stress=0.01)

- 15 Figure 3b: Two dimensional non-metric multidimensional scaling ordination of the macroinvertebrate family composition (presence-absence data, Bray-Curtis similarity index) from Native and *Hymenachne* sites (stress=0.00)