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Native submerged macrophyte distribution in seasonally-flowing, south-western Australian streams in relation to stream condition

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Abstract

Submerged macrophytes are important structural and biological components of many lowland streams with potential to support ecosystem processes in degraded streams, provided that growth is not excessive. In a low-gradient agricultural landscape, a survey was used to explore associations between submerged macrophyte growth, biodiversity and variables assessing stream condition in seasonally-flowing streams. These variables were sampled across fifty-three reaches on seven adjacent streams in the mediterranean climate region of south-western Australia. Native submerged macrophytes were present in 43% of sampled reaches, forming two distinct macrophyte assemblages dominated either by *Potamogeton* spp. together with *Ottelia ovalifolia*, or by *Cycnogeton* spp. The *Potamogeton*/*Ottelia* assemblage was present in degraded reaches with higher light availability and deposition of fine sediments, but did not show excessive growth, even under nutrient-enriched conditions. Conversely, *Cycnogeton* spp. were associated with shaded conditions and greater flow. Reaches with macrophytes present had significantly higher macroinvertebrate abundance and family richness than those without, although rarefied family richness was similar among reaches with and without submerged macrophytes. The more structurally complex *Potamogeton/Ottelia* assemblage supported a greater abundance of grazers, shredders and predators than the simpler *Cycnogeton* spp. In degraded agricultural streams, remnant and colonising populations of submerged macrophytes may compensate for loss of riparian-derived habitat and resources for macroinvertebrates, and thus the food supply for predatory species.

Introduction

Submerged macrophytes provide structural habitat and food sources for aquatic fauna, (Carpenter and Lodge 1986; Heck and Crowder 1991; Warfe and Barmuta 2006; Shupryt and Stelzer 2009), interact with flow and sediment dynamics (Sand-Jensen 1998), and influence nutrient cycling (Clarke 2002), but these plants are rarely studied in seasonally-flowing streams. However, many streams in mediterranean-climate regions have conditions of low flow velocity and pooling for several months of the year that are suitable for growth of submerged macrophytes, which potentially support important ecosystem processes. While processes relating to submerged macrophyte distribution have been widely studied in perennial temperate rivers, their growth and response to anthropogenic change in seasonally-flowing streams is not well-understood. Changes to hydrology, sediments and resource availability in agricultural landscapes has likely altered the distribution of submerged macrophytes, and their ecological role under these conditions warrants further investigation.

Submerged aquatic macrophyte distribution in perennial rivers is driven primarily by the interrelated factors of flow and substratum type (Sand-Jensen 1998; Gurnell et al. 2006; Franklin et al. 2008), and secondarily by light climate (determined by riparian vegetation cover, turbidity and colour) and nutrient availability (Barrat-Segretain 1996; Bornette and Puijalon 2011). Stream degradation affects each of these factors, with potential for both positive and negative impacts on macrophyte growth; and the presence of macrophytes within a stream also has feedback effects on the stream environment (Figure 3.1). Reduced base flow velocity resulting from drainage, abstraction and impoundment may improve physical conditions for growth, but also affect flow duration and shorten the growth season (Figure 3.1). Increased runoff from cleared lands and artificial drainage can intensify high-flow events and impact plant establishment and anchorage; but also create wider, well-lit environments, with more suitable substrata due to mobilisation and deposition of fine sediments (Figure 3.1). Increased availability of light (through riparian clearing) and nutrients in agricultural catchments can promote aquatic plant growth (Figure 3.1) (Canfield and Hoyer 1988; Mebane et al. 2014). In some cases this may cause excessive (prolific, spreading, high density) growth, with potential to impact aquatic fauna through altered assemblage structure (Schultz and Dibble 2012) and increased risk of anoxia

(Stiers et al. 2011). However, growth response is constrained by flow and substratum characteristics (Riis and Biggs 2001) (Figure 3.1) and will therefore vary between systems.
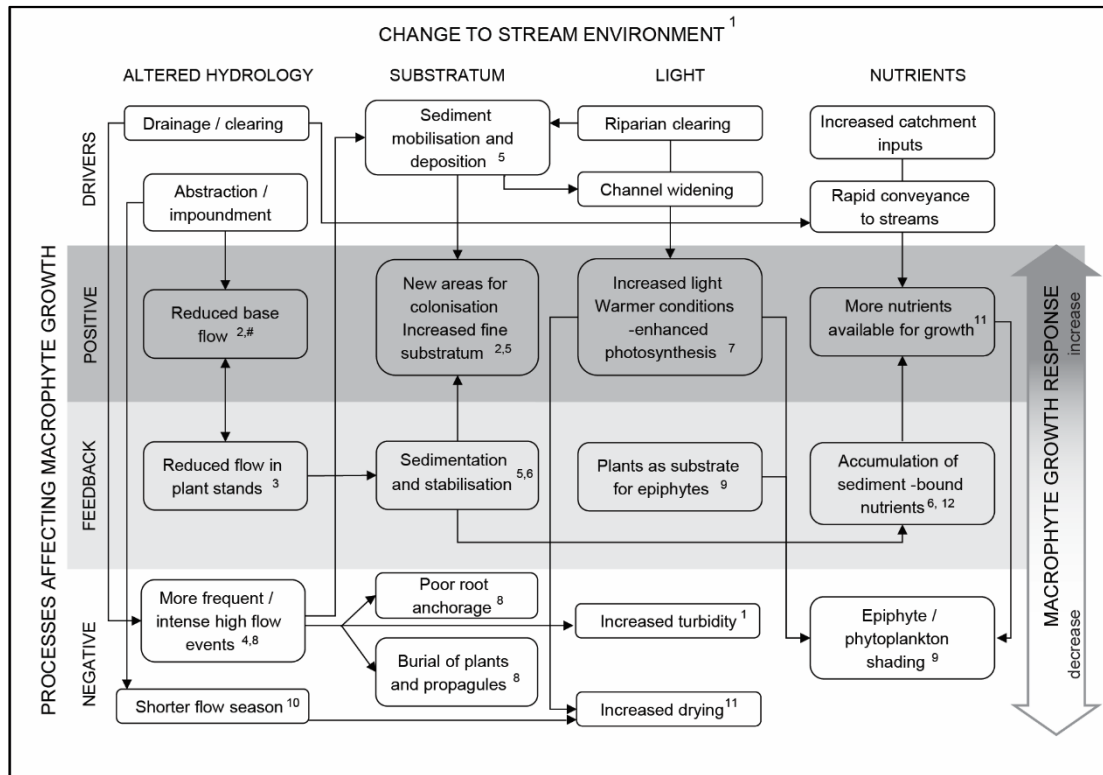
CHANGE TO STREAM ENVIRONMENT [1]

PROCESSES AFFECTING MACROPHYTE GROWTH

	ALTERED HYDROLOGY	SUBSTRATUM	LIGHT	NUTRIENTS
DRIVERS	Drainage / clearing	Sediment mobilisation and deposition [5]	Riparian clearing	Increased catchment inputs
	Abstraction / impoundment		Channel widening	Rapid conveyance to streams
POSITIVE	Reduced base flow [2,#]	New areas for colonisation Increased fine substratum [2,5]	Increased light Warmer conditions -enhanced photosynthesis [7]	More nutrients available for growth [11]
FEEDBACK	Reduced flow in plant stands [3]	Sedimentation and stabilisation [5,6]	Plants as substrate for epiphytes [9]	Accumulation of sediment -bound nutrients [6, 12]
NEGATIVE	More frequent / intense high flow events [4,8]	Poor root anchorage [8]	Increased turbidity [1]	Epiphyte / phytoplankton shading [9]
		Burial of plants and propagules [8]		
	Shorter flow season [10]		Increased drying [11]	

MACROPHYTE GROWTH RESPONSE (increase / decrease)

Figure 3.1. Conceptual model of native submerged macrophyte growth response to change in stream environment in an agricultural landscape. Interrelated changes to hydrology and resources (light and nutrients) create a suite of interacting processes with both positive and negative impacts of macrophyte growth, including feedback mechanisms as a result of the presence of plants ([1]Allan 2004; [2]Suren and Riis 2010; [3]Sand-Jensen 1998; [4]Riis and Biggs 2001; [5]Bornette et al. 2008; [6]Gurnell et al. 2006; [7]Bornett and Puijalon 2011; [8]Franklin et al, 2008; [9]Hilton et al 2006; [10]Deegan et al 2012; [11]Rea and Ganf 1994; [12]Mebane et al. 2014; [13]Clarke et al. 2002). [#]Flow reduction from abstraction/impoundment; excludes irrigation channels. The term 'growth response' is used in a general sense as it will vary with macrophyte community characteristics.

While flood disturbance is a fundamental driver of submerged macrophyte distribution in perennial temperate rivers (Riis and Biggs 2001), seasonal drying may be more important in mediterranean-climate streams and will influence the growth response to altered stream conditions. For example, macrophyte responses to nutrient enrichment may be limited either by drying of seasonal pools or by phytoplankton or epiphyte growth (under lentic conditions) if it reduces light availability (Hilton et al. 2006). Similarly, the reduced shading resulting from riparian clearing may exacerbate seasonal drying and create intolerably high temperatures for macrophyte persistence. So, although increased light availability, nutrients and fine sediment input to streams are a common consequence of catchment clearing and damaged riparian vegetation (Power et al. 2013, Figure 3.1), seasonal flow regimes may limit responses by macrophytes. Growth restrictions imposed by drying may prevent the excessive growth of macrophytes that is observed in perennial streams (Shultz and Dibble 2012).

Provided that growth is not excessive, submerged macrophytes may have an important ecological role in degraded stream reaches, particularly when habitat and food resources from riparian zones are limited. The heterogeneous habitat and refuge provided by macrophytes is well known to support aquatic fauna (Heck and Crowder 1991; Bell et al. 2013), and even small patches can contribute greatly to reach-scale populations of macroinvertebrates (Shupryt and Stelzer 2009). Furthermore, while river food webs in mediterranean-climate streams are generally assumed to be based on allochthonous and algal sources rather than macrophyte carbon (Power et al. 2013), there is increasing recognition that macrophytes may provide food resources, both directly (e.g. Watson and Barmuta 2011) and through supporting algal epiphytes (Warfe and Barmuta 2006).

This study investigated the ecological role of submerged macrophytes in degraded streams in an agricultural landscape, to evaluate their potential in river restoration. A survey of macrophytes, environmental variables and macroinvertebrates was conducted across seven adjacent seasonally-flowing river systems in the Geographe Bay Catchment (Western Australia). Specifically, the study aimed to (i) identify environmental variables associated with macrophyte occurrence; (ii) determine whether the presence of submerged macrophytes was associated with stream

degradation; and (iii) assess whether reaches with native macrophytes support a more abundant and diverse aquatic invertebrate assemblage than those without.

Methods

Study area

The study area included seven adjacent river systems in the Geographe Bay catchment, located approximately 250 km south of Perth, Western Australia (Figure 3.2): the Ludlow, Abba, Vasse, Sabina, Buayanyup, Carbunup and Marybrook Rivers. The region experiences a mediterranean climate of mild, wet winters and hot, dry summers. The catchment covers an area of approximately 2000 km^2, encompassing a series of short river systems (20 – 45 km in length) with headwaters in the lateritic Whicher Scarp, and traversing the Swan Coastal Plain to discharge into Geographe Bay. Swan Coastal Plain soils are characterised mainly by sandy-loam and deep sands with large areas of low-lying, seasonally inundated flats. Current land use is primarily dairy, livestock grazing, viticulture and horticulture. Stream modifications for drainage and impoundment are common, and surface water is extracted for agricultural and domestic water use. The catchment has been extensively cleared for agriculture, particularly coastal plain areas (37% of native vegetation remains, mainly in forested headwaters: Connell et al. 2000). Riparian vegetation has been impacted through direct clearing, livestock damage, and undermining of unstable banks. Natural riparian vegetation commonly includes an over-storey of *Eucalyptus* spp., *Corymbia calophylla*, *Agonis flexuosa* trees; mid storey of *Melaleuca* spp. and *Taxandria* spp.; and a mixed understorey of shrubs and rushes, with common emergent rushes including: *Baumea*, *Juncus* and *Leptocarpus* spp.
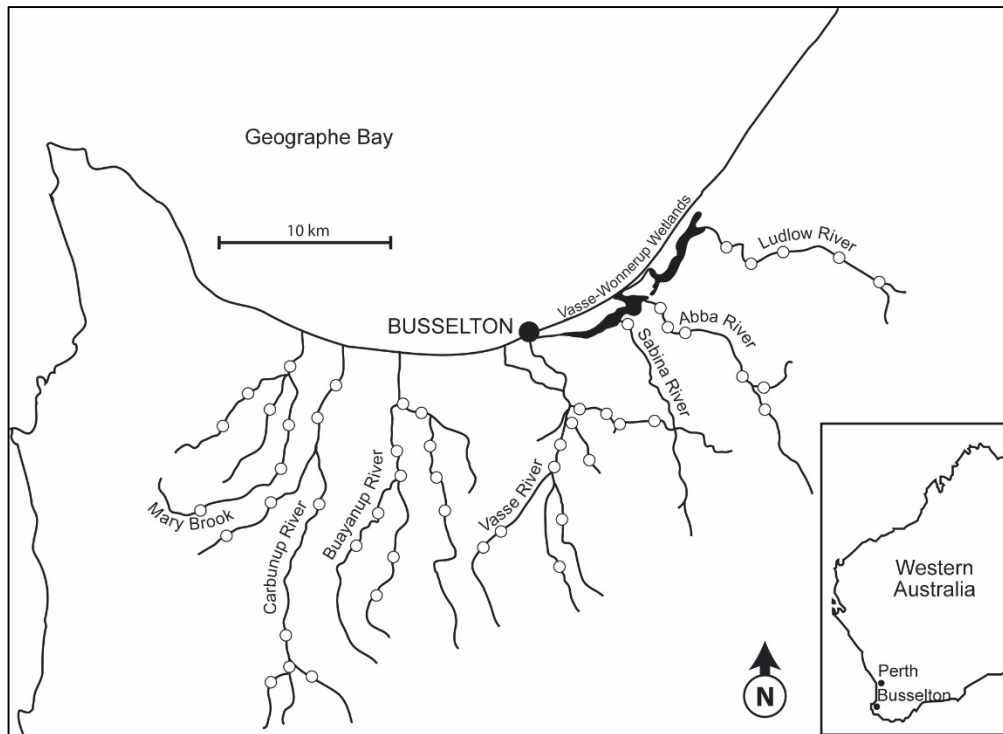
Figure 3.2. Location of the fifty-three study reaches (open circles) included in the survey. The location of Busselton is also shown with reference to the capital city of Perth in Western Australia.
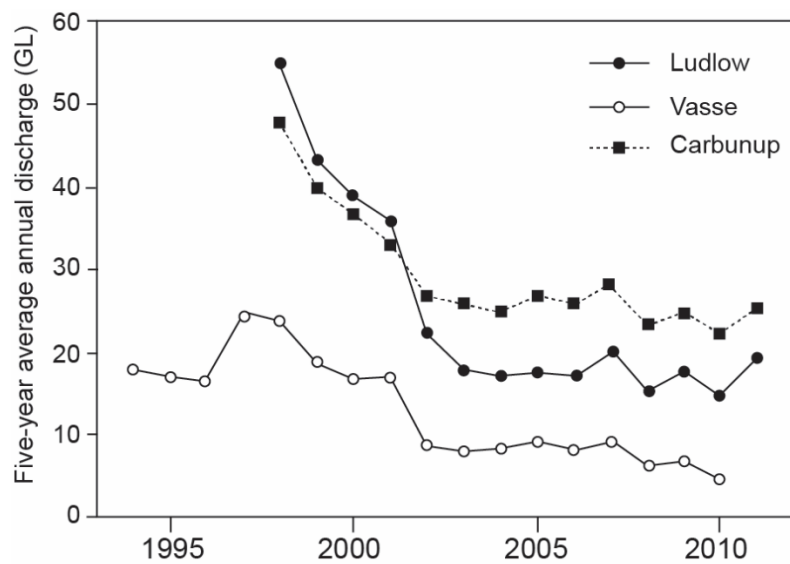

Figure 3.3. Mean annual discharge for the Ludlow, Vasse and Carbunup Rivers (only three rivers are gauged). Five-year average is calculated from the given year and the two years before and after (DOW 2015).

Average maximum temperature is 29 °C in summer and 17 °C in winter (BoM 2014). Average annual rainfall is 740 mm (1991-2010), but the 20-year average has declined by 15% over fifty years (1941-1960: 863 mm; BoM 2014). Seventy-five percent of rainfall occurs between May and September (DoW 2010) resulting in typical hydrographs of peak winter-spring flows and summer-autumn drying. Reduced rainfall and increased water extraction and impoundment have led to a substantial decline in river flows (Figure 3.3). Also, gauging data show a reduced frequency of high flow events and base flow rate (DoW 2015).

Sampling design and field methods

Fifty three reaches (20 m length) in seven seasonally-flowing river systems were surveyed in November 2013 (Figure 3.2) during spring base flow conditions. These included all accessible wadeable reaches with consistent flow (reaches on private land could not be accessed). Study reaches were upstream of road bridges where possible to exclude any influences, but in all cases, crossings were elevated bridges that did not impound or flow or influence substratum. When reaches were sampled downstream of bridges, they were located at a sufficient distance to reflect stream characteristics irrespective of the crossing. Most reaches were predominantly run (glide) habitat; riffles and pools were rare.

Native species of submerged (roots in sediment, all leaves submerged), floating-leaved (roots in sediment, some leaves submerged, some floating) and semi-emergent (roots in sediment but with some emergent leaves/stems) aquatic plants were recorded at each site. Identifications were confirmed by the Western Australian Herbarium. No native free-floating species were encountered and emergent rushes were not sampled. Cover for each native species, and for combined exotic species were assessed using the Braun-Blanquett scale: r = solitary plant, small cover; x = few plants, small cover; 2 = cover 5-25%; 3 = cover 25-50%; 4 = cover 50-75%; 5 = cover > 75%). Riparian condition assessment was completed using a method widely adopted in this region (WRC 1999) based on vegetation condition and stream stability, which grades each reach from pristine (A) to degraded (D), with three levels of condition within each grade (Table 3.1). Livestock access was noted as present or absent.

Table 3.1. Riparian condition assessment category descriptions (adapted from WRC 1999).

Category	Description	Level
A	Stable, with pristine to slightly disturbed riparian vegetation.	A1: Pristine condition.
		A2 Occasional weeds.
		A3: Localised disturbance.
B	Stable, with all components of riparian vegetation, but significant weed invasion.	B1: Native vegetation dominant.
		B2: Native vegetation and weeds co-dominant.
		B3: Weeds dominant.
C	Native understorey degraded, but some remnant vegetation; variable stability.	C1: Erosion prone, weeds maintain stability.
		C2: Some erosion.
		C3: Actively eroding.
D	Streams devoid of native vegetation; artificial drains	D1: Some areas of stability.
		D2: Extensive erosion and deposition.
		D3: Highly eroded, but fenced and colonised with weeds.

Physical stream characteristics (shading, periphyton growth, erosion, deposition, and substratum type) were scored using a scale of occurrence adapted from Chessman and Royal (2010): none (0) isolated (1), scattered (3), common (5) or abundant (7), with intermediate scores as appropriate. For substratum, scores were given for each of bedrock, boulders (> 256 mm diameter), cobbles (64-256 mm), pebbles (16-64 mm), granules (4-16 mm) and fines (< 4 mm) following Chessman and Royal (2010). Further classification of physical characteristic based on these scores for frequency analysis is described below.

Depth and velocity measurements taken at intervals along a cross section provided outputs of mean velocity, total discharge, depth, width and cross-sectional area for each reach (Flowtracker Handheld-ADV®). Cross sections were selected at a point which approximated average conditions for the reach, devoid of obstructions or pools, to maintain consistency across reaches. Reaches were visited monthly to determine the time of flow cessation because this is important in terms of length of growth season for macrophytes. Flow cessation was categorised as early-summer (December), mid-summer (January) or late summer (February). No reaches flowed after February. All reaches with late-summer flow retained pools which persisted beyond flow cessation, reflecting the local unconfined groundwater table, but these pools dried out during autumn.

Temperature, dissolved oxygen, conductivity, salinity and pH were measured *in situ* (YSI 556 MPS multiparameter probe). Turbidity was measured on site with a Hach

2100P turbidimeter. Samples were collected for laboratory analysis of total phosphorus (TP) and total nitrogen (TN) (Valderrama 1981); and colour (dissolved organic carbon) as gilvin (absorbance at 440 nm x 2.303 x 100, Kirk 1986).

Macroinvertebrate samples were initially taken from a random subset of twenty sites, including ten reaches with no macrophytes and ten with native macrophytes. When it became clear that two distinct macrophyte assemblages were present in these rivers, additional (randomly chosen) reaches were sampled. Aquatic invertebrates were sampled using a single ten-metre sweep (D-frame net, mesh size 250 µm) at twenty-five reaches: ten without macrophytes, eight with the *Cycnogeton* plant assemblage and seven with the *Potamogeton*/*Ottelia* plant assemblage (Braun-Blanquet score ≥ 2). Whole samples were preserved in ethanol in the field and invertebrates identified to family level (except Copepoda, Cladocera, Collembola, Clitellata, Hydracarina and Hirudinea, which were not identified further) and counted in the laboratory.

Data analysis

Two macrophyte assemblage types were identified, named by genus: *Potamogeton* and *Ottelia*; and *Cycnogeton*. A series of two-way contingency tables were constructed to test associations between occurrence of native macrophytes, stock access and physical reach characteristics. Frequency analysis was performed twice: once for macrophyte presence and absence categories; and secondly comparing absence, *Potamogeton*/*Ottelia*, and *Cycnogeton* categories. Riparian condition was collapsed into three categories: A and B condition reaches were grouped as there were only 4 reaches in A condition, and both these grades contain intact remnant riparian vegetation. Reaches were classified into three categories for stream shading, periphyton growth, erosion and deposition, based on the 0-7 scoring scale: none or isolated (0-1), scattered (2-4) and abundant (5-7). Substratum scores were used to derive three categories: mostly sandy, mixed substrate and mostly rocky. Braun-Blanquet scores for aquatic weed cover were pooled as either none or few (0, r, x) or common (2-5). Flow cessation categories of early- mid- and late-summer were used. Stream width was classified into three groups: < 2.5m, 2.5-4.5m and > 4.5m.

Where there were observed frequencies less than 5 within these categories, Fisher's exact tests were used in addition to Pearson's Chi-square, with the Freeman-Halton extension for tables larger than two by two (Quinn and Keogh 2003). Odds and

maximum likelihood (ML) odds ratios were calculated for tables where a significant association was found, with subdivision of larger tables into subsets of two by two tables. Where tables contained cells with zero observed frequencies, 0.5 was added to each cell for calculation of odds ratios (Quinn and Keogh 2003).

Multivariate analysis using all environmental variables was undertaken using canonical analysis of principal coordinates (CAP) to discriminate among reaches with *a priori* grouping based on macrophytes. Separate analyses were completed for presence and absence categories; and absence, *Potamogeton/Ottelia*, and *Cycnogeton* categories. A correlation matrix of environmental variables was constructed using Spearman's correlation coefficient.

Single factor ANOVA (SPSS version 21) was used to determine whether mean aquatic invertebrate abundance and mean family-level richness differed between macrophyte assemblage type (three levels, fixed: macrophytes absent, *Potamogeton/Ottelia*, *Cycnogeton*). All ANOVAs were checked for homoscedasticity (Levene's test) and normality (Shapiro-Wilk test) and abundance data was transformed ($\log_{10}(x+1)$) to meet the normality assumption. Planned contrasts compared differences among means for these two dependent variables between the presence or absence of each macrophyte type (*Potamogeton/Ottelia* and *Cycnogeton*). Because taxa richness is positively correlated with abundance (the well-known species-abundance relationship, Gotelli and Colwell 2001), mean rarefied family richness was calculated using the EcoSim program (Gotelli and Ensminger 2000). The ANOVAs and contrasts described above were repeated using the rarefied data.

Differences in invertebrate assemblage composition between reaches with and without macrophytes, and between reaches with different macrophyte assemblages, were examined using single-factor ANOSIM (analysis of similarity) based on a Bray-Curtis similarity matrix, using untransformed abundance data. SIMPER (similarity percentages) was used to identify the families responsible for the differences between reach groups and were presented using a graphical method developed by Lind et al. (2006). All multivariate analyses were completed using PRIMER-E 6 (Plymouth Routines in Multivariate Ecological Research: Clarke and Warwick 2001).

Results

Spatial variation in environmental characteristics

Seventy-five percent of reaches had poor riparian condition (C and D). Stream size varied considerably in terms of width, discharge and velocity (Table 3.2). Although velocity varied, all reaches had a part of the channel with low velocity, most commonly bank edges, and many reaches had areas with zero or negative velocity due to backwater areas at the bank edges. Average depth was variable (Table 3.2), but similar depth ranges were observed across all catchments. Wider stream reaches were found in the Vasse, Buayanyup, Carbunup and Marybrook systems, which had more reaches with good riparian condition and lower salinity (conductivity < 500 μScm^{-1}) (Table 3.2). The two most downstream reaches in the Sabina River were slightly brackish and likely influenced by the nearby Vasse Estuary. Nutrient concentrations, turbidity and colour were variable across the catchment (Table 3.2). Total phosphorus (TP) and total nitrogen (TN) in the Sabina and Vasse rivers were well above local guideline values for ecosystem protection, and TN was also high in the Abba and Buayanyup catchments. Both TN and TP were positively correlated with decreasing riparian condition (TP: $r = 0.44$, $P = 0.001$; TN: $r = 0.49$, $P < 0.001$).

Native macrophyte assemblages

Native submerged and semi-emergent macrophytes were observed at 23 of the 53 surveyed reaches (43%), with six species identified: *Cycnogeton huegelii* (Endl.)*, Liparophyllum lasiospermum* (F. Muell.) Tippery and Les, *Potamogeton drummondii* Benth., *Potamogeton ochreatus* Raoul, *Ottelia ovalifolia* (R. Br.) Rich. and *Isolepis* sp. (absence of inflorescences prevented identification). *Cycnogeton* species in this region (*C. huegelii* and *C. lineare* (Endl.) Sond.) are very similar (previously both *Triglochin procerum*, DPaW 2014) and both may have occurred but were not distinguishable due to a lack of fruiting material. A maximum of only three species were found in any reach. Cover of native macrophytes did not suggest excessive growth, with cover at most reaches below 25% and only one reach had more than 50% cover (of *Cycnogeton* spp., Figure 3.4).

Table 3.2. Site characteristics for each river system in the survey. Values shown are number of sites for riparian condition and macrophyte community categories; and mean values with standard error in parentheses for physical and water quality variables. Nutrient values in italics indicate results in excess of local guidelines for ecosystem protection (ANZECC and ARMCNZ, 2000). Extent of clearing from Pen (1999) (dash indicates no data available). In Mary Brook, one reach contained only *Isolepis sp.* and so did not fall into the three macrophyte community groupings.

River	Ludlow	Abba	Sabina	Vasse	Buayanyup	Carbunup	Mary Brook
Number of sites	5	6	4	10	11	9	8
Macrophyte Community:							
Potamogeton /Ottelia	0	2	0	4	4	0	1
Cycnogeton	1	1	2	0	0	5	2
None	4	3	2	6	7	4	4
Riparian condition:							
A/ B	0	0	0	2	3	5	3
C	5	4	2	3	3	3	4
D	0	2	2	5	5	1	1
Catchment area (ha)	21081	13763	7643	30582	17400	16516	10913
Extent of clearing (%)	25	80	30	65	-	55	-
Width (m) (min-max)	3.9-6.4	1.6-5.6	2.15-3.3	1.55-8.05	2.15-9.2	2.9-9.9	1.9-5.5
Max depth (m)	0.50	0.35	0.66	0.31	0.34	0.44	0.25
Min velocity (ms^{-1})	-0.003	-0.008	0.00	-0.004	-0.011	-0.002	-0.038
Max velocity (ms^{-1})	0.126	0.112	0.130	0.160	0.220	0.314	0.381
Discharge (m^{3}s^{-1})	0.041	0.026	0.045	0.072	0.102	0.300	0.129
Conductivity (µScm^{-1})	756 (49)	720 (66)	1227 (346)	445 (43)	418 (25)	389 (10)	479 (26)
pH	6.56 (0.3)	6.80 (0.2)	6.55 (0.2)	5.88 (0.5)	5.93 (0.2)	4.93 (0.3)	5.75 (0.4)
Colour (gilvin; g$_{440}$ m^{-1})	16.2 (2.5)	10.3 (1.9)	14.7 (6.0)	9.2 (2.5)	12.2 (2.1)	30.0 (18.5)	19.2 (5.7)
Turbidity (NTU)	6.1 (0.6)	5.6 (0.3)	11.0 (1.6)	14.8 (6.3)	3.2 (0.3)	11.2 (3.7)	5.1 (0.8)
TP (µgL^{-1})	38.0 (3.7)	27.8 (3.4)	179 (85.5)	110.4 (53.5)	32.27 (8.8)	17.33 (2.8)	21.71 (7.5)
TN (µgL^{-1})	874 (46)	1273 (546)	1925 (470)	1607 (350)	1635 (513)	610 (33)	804 (128)

Cycnogeton spp. occurred at thirteen sites, with *L. lasiospermum* also present at three of these. *Ottelia ovalifolia* and *Potamogeton* spp. often grew together, co-occurring at seven reaches and each growing alone at two reaches. Isolated *Cycnogeton* plants occurred in two reaches with *O. ovalifolia* and/or *Potamogeton* spp. *Isolepis* sp. occurred at four reaches, three of which had *O. ovalifolia* and/or *Potamogeton* spp. present. Thus two distinct macrophyte assemblages with differing distribution were identified, herein referred to as *Cycnogeton* and *Potamogeton/Ottelia*. These assemblages also differ in morphology (Figure 3.4): *Cycnogeton* is characterised by smooth strap-shaped leaves growing from the base of the plant; *Potamogeton/ Ottelia* has more complex structure, because *O. ovalifolia* and *P. drummondii* have both submerged and floating leaves and *P. drummondii* and *P. ochreatus* form dissected submerged canopies.
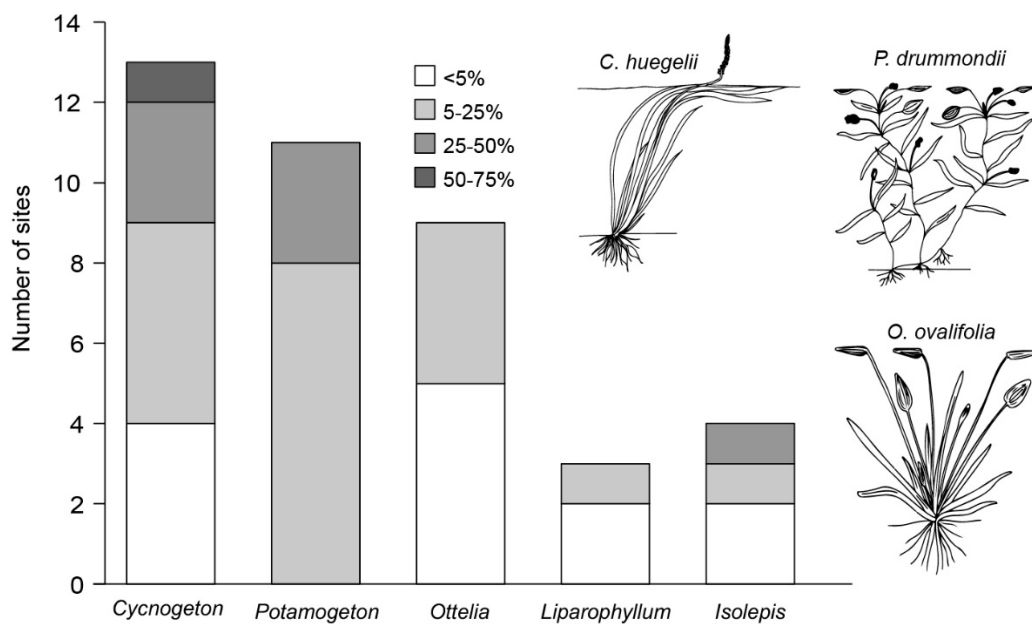

Figure 3.4. Number of sites within each Bran-Blanquette category for each genus of aquatic macrophyte. Macrophyte drawings show differing structural complexity of the two plant assemblages.

Introduced aquatic plants were present in 31 reaches (58%) including *Callitriche stagnalis* Scop., *Mentha pulegium* L., *Juncus microcephalis* Kunth, *Isolepis nodosa* (Rottb.) R.Br. and *Elodea canadensis* Michx. Grasses such as *Pennisetum clandestinum* Chiov. and various species of *Paspalum* L. also grew in some stream channels. Exotic species occurred mainly in poor condition reaches (28 C and D condition reaches) at varying levels of colonisation, and were also present at three B condition reaches. There was no significant association between native macrophyte and exotic aquatic plant presence in either frequency analysis or CAP.

Although macrophytes occurred at only three good (A or B) condition reaches (two with *Cycnogeton* and one with *Isolepis* sp.), presence/absence data did not indicate an association between riparian condition and macrophyte occurrence. Absence of macrophytes was significantly associated with stock access ($X^2_1 = 4.6$, $P = 0.034$), because macrophytes were present at only one reach that had stock access. Macrophytes were more likely to be present at reaches with no stock access compared to those with stock access (odds ratio = 8; CI_{95}: 0.92-69.44), however most reaches (83%) did not have direct stock access, and odds for presence and absence of macrophytes were equal (0.5) among reaches without access. Macrophyte presence/absence was not significantly associated with other categorical factors (riparian condition, shading, periphyton cover, aquatic weeds, erosion, deposition, substratum type, flow duration). Furthermore, sites without macrophytes were equally likely to be in D, C or A/B levels of riparian condition (Figure 3.5a).

Analysis of three groupings (absence, *Potamogeton*/*Ottelia*, and *Cycnogeton* categories) found a significant association between macrophyte assemblage type and both riparian condition ($X^2_4 = 10.0$, $P = 0.037$) and shading ($X^2_4 = 15.0$, $P = 0.005$). Results for these two variables were very similar (Figure 3.5) and highly correlated ($r = -0.693$, $P < 0.001$). Importantly, the two macrophyte assemblages responded differently, explaining the lack of association with macrophyte presence/absence categories. The odds of *Potamogeton/Ottelia* occurring were greater in C and D condition reaches with little or no shade, while odds of *Cycnogeton* occurring were greater in shaded C condition reaches (Table 3.3). Odds ratios also indicated that association with riparian condition was due mainly to the presence of *Cycnogeton* in C condition compared with D condition reaches; and the association with shading was due to the presence of *Potamogeton/Ottelia* in reaches with no or isolated shade (Table 3.3).
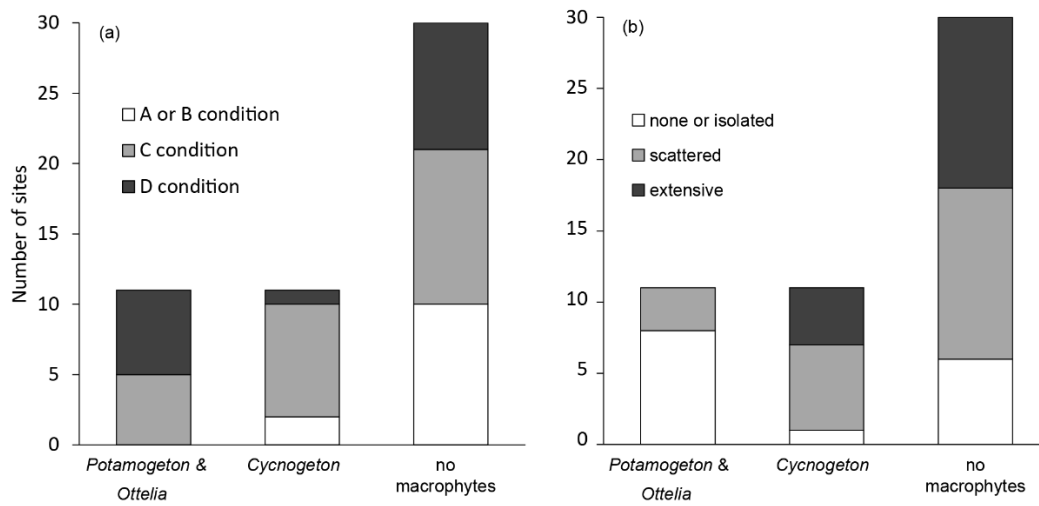
Figure 3.5. Distribution of each macrophyte assemblage group by riparian condition (a) and level of shading (b).

Table 3.3. Odds and odds ratios for riparian condition and shading.

Odds	Category	Potamogeton/ Ottelia	Cycnogeton
Foreshore condition	A or B	0.00	0.20
	C	0.45	0.73
	D	0.67	0.11
Shading	none or isolated (1)	1.33	0.17
	scattered (2)	0.25	0.50
	extensive (3)	0.00	0.33
Odds ratios	**Comparison**		
Foreshore condition	AB vs C	0.10 (0-2.03)	0.32 (0.06-1.66)
	AB vs D	0.07 (0-1.41)	1.51 (0.17-13.70)
	C vs D	0.70 (0.17-2.9)	4.68 (0.67-32.47)
Shading	2 vs 3	7.00 (0.33-150.06)	1.44 (0.34-6.07)
	1 vs 3	32.69 (1.62-660.28)	0.65 (0.08-5.11)
	1 vs 2	4.67 (0.98-22.33)	0.44 (0.06-3.32)

The three groupings of *Potamogeton/Ottelia*, *Cycnogeton* and macrophyte absence were clearly discriminated (axis correlations of 83% and 73%) on the basis of the measured environmental variables (Figure 3.6). Spearman rank correlation vectors indicated that presence of *Cycnogeton* was associated with increased shade and water colour; while *Potamogeton/Ottelia* was associated with higher temperatures and daytime dissolved oxygen (potentially resulting from plant photosynthesis), and inversely correlated with shade and colour (Figure 3.6). Plant absence was associated with substratum type and flow, having a positive correlation with pebbles and inverse correlation with fines, discharge velocity and flow season length (Figure 3.6). Turbidity and nutrients were not important determinants of macrophyte presence. Although the presence of neither plant assemblage was correlated with substratum variables, Braun-Blanquette scores did indicate a positive association with fine substrate. All reaches with macrophyte cover greater than 5% had at least scattered fines, and more than 85% of these reaches had common-abundant fine substratum particles.
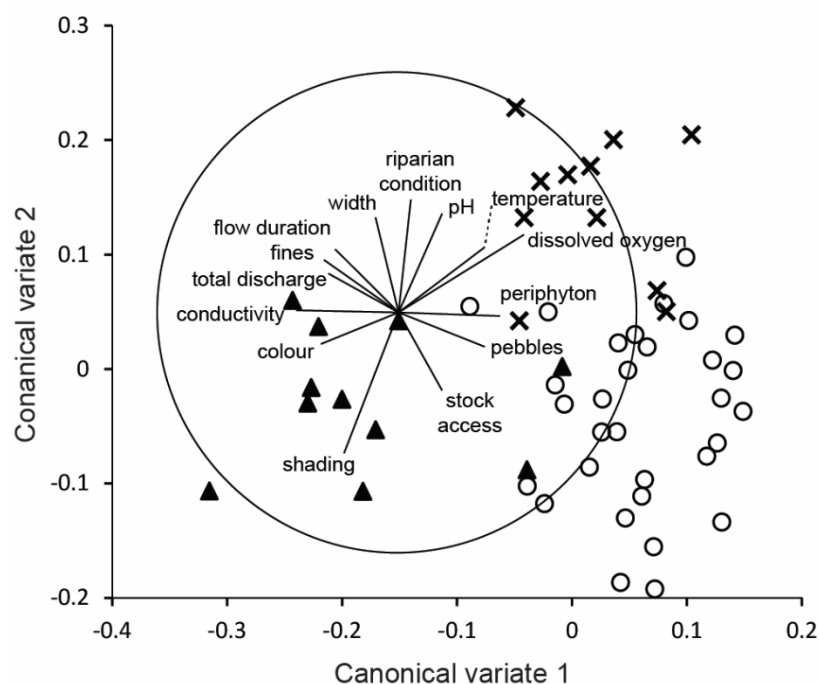

Figure 3.6. Canonical analysis of principal components (CAP) for macrophyte assemblage groups: *Cycnogeton* (triangles), *Potamogeton/Ottelia* (crosses) and no macrophytes (open circles).

Invertebrates

Mean aquatic invertebrate abundance ($F_{2,21} = 12.04$, $P < 0.001$) and mean family level richness ($F_{2,21} = 7.13$, $P = 0.004$) differed between macrophyte assemblage types. Macroinvertebrate abundance was greater in the presence of macrophytes overall ($t_{21} = 4.55$,

P < 0.001); and in each macrophyte assemblage compared with macrophyte absence (*Potamogeton/Ottelia*: t_{21} = -4.82, *p* < 0.001; *Cycnogeton*: (t_{21} = 2.84, *P* = 0.010) (Fig.7a). Mean abundance did not differ between *Potamogeton/Ottelia* and *Cycnogeton* due to high variation among reaches (Fig.7a; t_{21} = -1.83, *P* = 0.083). Family-level richness was also higher in reaches with *Potamogeton/Ottelia* (t_{21} = -3.27, *P* = 0.004) and *Cycnogeton* (t_{21} = 3.07, *P* = 0.006) compared with reaches with no macrophytes (Fig.7b), but did not differ between the two macrophyte assemblages (t_{21} = -0.18, *P* = 0.858). Mean rarefied taxa richness did not differ between reaches with or without macrophytes ($F_{2,21}$ = 1.57, *P* = 0.232) (Fig.7b), suggesting that increased family richness occurred as a consequence of higher invertebrate abundance amongst macrophytes. Reaches without macrophytes had seven fewer families than those with macrophytes, with Lestidae and Coenagrionidae (Zygoptera) notably absent. The only taxon exclusive to reaches without macrophytes was Ceratopogonidae (Diptera), but these were found in only one reach.
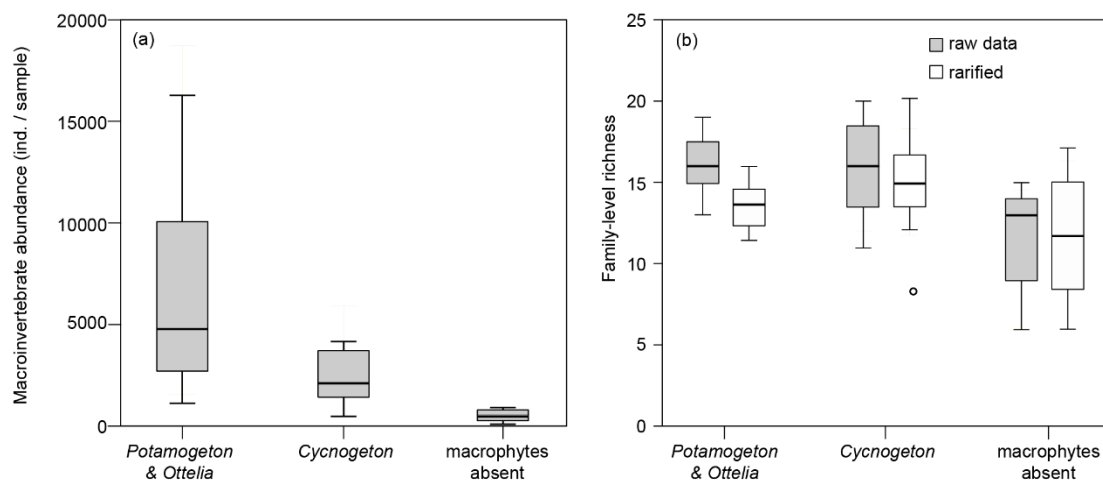

Figure 3.7. Macroinvertebrate abundance (a) and family-level richness (b) for each macrophyte assemblage. Boxplots show median (line), 25-75th percentile range (box), 5-25th and 75-95th percentile range (error bars) and outliers (o).

Invertebrate assemblage composition differed significantly between reaches with and without macrophytes (*R* = 0.29, *P* = 0.008) and between reaches with *Potamogeton/Ottelia* and those with *Cycnogeton* (*R* = 0.29, *P* = 0.002, Figure 3.8a). Reaches with macrophytes had much higher abundance of grazing taxa, with Cyprididae, Cladocera, Copepoda and Gastropoda accounting for 67% of dissimilarity (Figure 3.8b). Damselfly nymphs were only recorded in the presence of macrophytes and many other taxa were more abundant in their presence (Figure 3.8b). A few families occurred with approximately equal abundance regardless of macrophyte presence or absence: the generalist feeders Chironomidae and Copepoda,

predatory Dytiscidae and detritivorous caenid mayfly nymphs. Overall, some grazers (gastropods (excluding limpets), Curculionidae), suspension feeders (Simuliidae), shredders (Leptoceridae) and some predators (Odonata, Leptoceridae, aquatic mites) occurred more frequently in reaches with macrophytes than in those without (Figure 3.8b).

Reaches with *Potamogeton/Ottelia* had higher abundances of grazing Cyprididae, Cladocera and Gastropoda (except limpets) than those with *Cycnogeton*, and also of Culicidae, Corixidae, Curculionidae and Notonectidae. Hydroptilid caddisfly larvae, oligochaetes, Simuliidae larvae, freshwater limpets and crayfish were most abundant in reaches with *Cycnogeton* (Figure 3.8b). Amphipods (Perthidae) and Decapods (Palaemonidae, Parastacidae) were found only in reaches with *Cycnogeton* or with no macrophytes; although the two sites where Decapods occurred without submerged macrophytes did have good riparian condition together with emergent rushes.
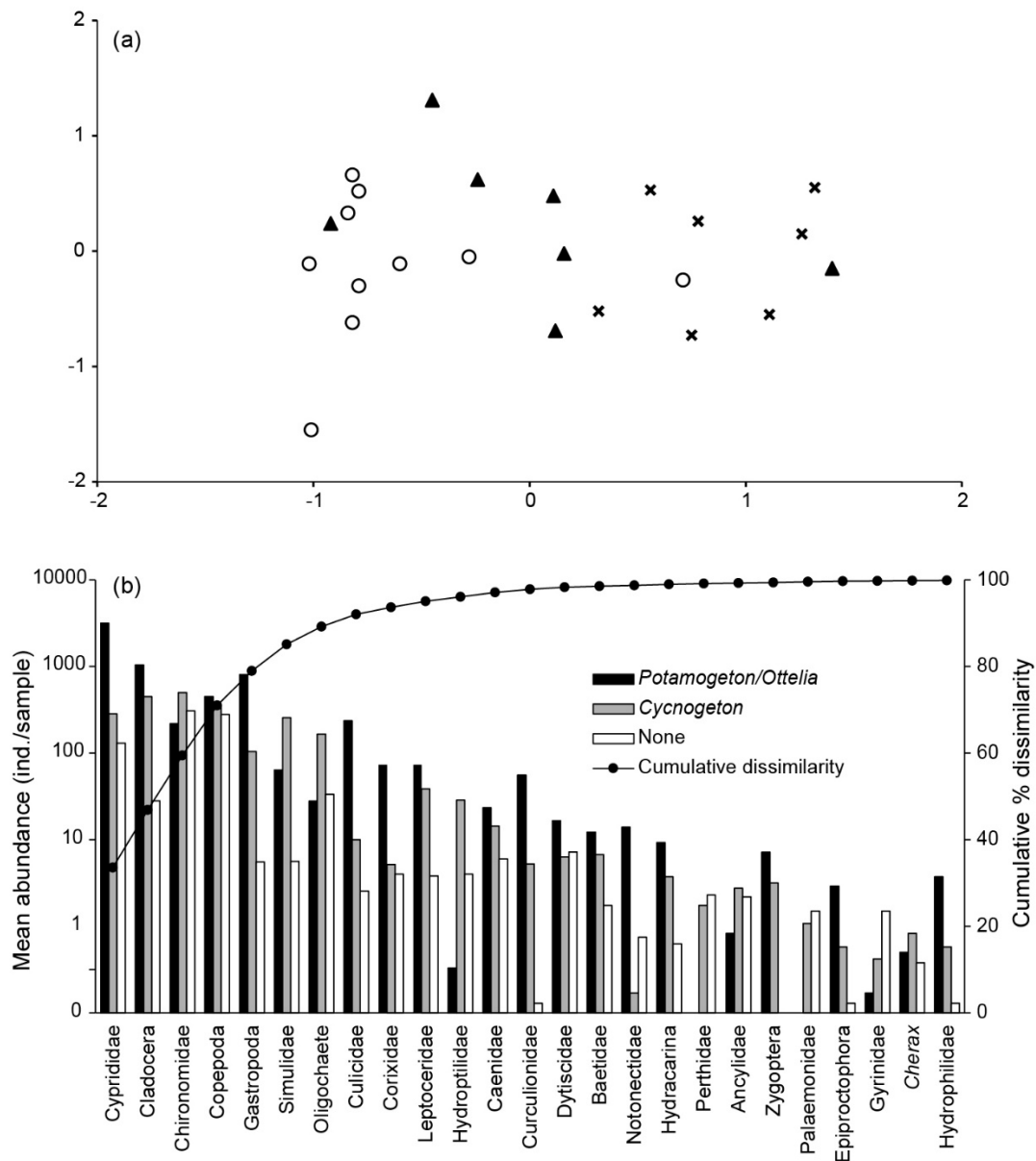
Figure 3.8. Comparison of macroinvertebrate community composition for macrophyte assemblages using MDS ordination of invertebrate abundance data (a) (2D stress = 0.14); comparison of taxon abundance within each assemblage (b: bars); and cumulative contribution to dissimilarity between presence and absence of macrophytes (b: line). Data points in (a) indicate macrophyte assemblage groups: *Cycnogeton* (triangles), *Potamogeton/Ottelia* (crosses) and no macrophytes (open circles).

Discussion

Native macrophyte occurrence

Native submerged macrophytes were relatively common in these seasonally-flowing streams but species richness was low, a maximum of three per reach, consistent with reach-scale macrophyte richness in eastern Australian streams (Quinn et al. 2011). Two distinct macrophyte assemblages were observed: *Cycnogeton* spp.; and *O. ovalifolia* co-occurring with *Potamogeton* spp. (*P. ochreatus* and/or *P. drummondii*). While both assemblages were associated with poor riparian condition, they had contrasting associations with shade (discussed further below).

The association of macrophyte absence with low total discharge and short hydroperiod suggests larger streams with a longer growing season were more favourable for development of macrophyte beds. This influence of flow contrasts with larger perennial systems, where flood disturbance and velocity are primary limiting factors for macrophyte distribution (Riis and Biggs 2003; Franklin et al. 2008). Physical limitation of plant growth by current is unlikely in these streams; instead, lower flow rates and shorter hydroperiods are more likely to influence macrophyte distribution (Figure 3.1). Hydrology within the study area has changed dramatically over the last five decades, with reduced streamflow and hydroperiod as a consequence of both catchment-scale land use (drainage, impoundment and abstraction) and declining regional rainfall; and reach-scale base flow velocity was generally low. While low flows can enhance macrophyte growth due to physical stability (Suren and Riis 2010) and both assemblages can clearly persist under seasonally dry conditions, shorter periods of flow may be detrimental because plants must complete their life cycle within the flow period to grow successfully the following year (Warwick and Brock 2003).

Substrate type is important in terms of recruitment and anchorage of macrophytes (Bornette and Puijalon 2011), with loose stones providing poor substrate (Butcher 1933). Not surprisingly, macrophyte absence was associated with pebble substrate in these reaches, and plants were not found in reaches without fine substrate. Runoff from cleared lands and erosion of unstable banks has resulted in substantial mobilisation of sediment in these river catchments. Depositional forces often dominate in streams with low gradient (Bornette et al. 2008), as found on the Swan Coastal Plain, and extensive sediment deposition along stream beds was common. This accumulation of finer-textured sediment provides new areas of suitable substratum for colonisation (Figure 3.1; Gurnell et al. 2006; Suren and Riis 2010).

Larger macrophyte stands occurred in reaches with sediment deposition, indicating colonisation of deposited sediment (Lind et al. 2009) and sediment accumulation within plant stands is also likely (Figure 3.1; Gurnell et al. 2006).

Stock access appeared to preclude macrophyte growth, although presence and absence of macrophytes were equally likely in reaches with no stock access. Livestock impede macrophyte growth by grazing, and trampling during the dry season can prevent re-establishment during the following flow period (Pettit et al. 2012). Cattle access can increase nutrient and chlorophyll a concentrations and decrease light penetration (Pettit et al. 2012) which, together with indirect effects of reduced riparian cover and reduced bank stability, may have variable effects on macrophyte growth (Figure 3.1).

Elevated nutrient concentrations were correlated with poor riparian condition, as would be expected in this agricultural landscape. Although elevated stream nutrient levels in agricultural regions may enhance macrophyte growth (Chambers 1987; Mebane et al. 2014), there was no association between macrophytes and nutrients in this study. The few other Australian studies have also not found strong correlations between nutrient status and macrophyte distribution (Chessman and Royal 2010; Mackay et al. 2010), and increased water column nutrients may have little positive effect on macrophytes in rivers and streams (Madsen and Cedergreen 2002, Hilton et al. 2006).

Although clearly part of lotic ecosystems, with flow providing an important dispersal pathway (Nilsson et al. 2010), the growth of submerged macrophytes in these streams occurs during seasonal conditions of low- to no-flow, which at times more closely resemble lentic environments. However, the focus of macrophyte research in lentic and lotic systems has differed markedly. In rivers, much work examines macrophyte interactions with the abiotic conditions of flow, substrate, light and nutrients (e.g. Sand-Jensen 1998; Barrat-Segretain 1996; Clark 2002; Gurnell et al. 2006; Franklin et al. 2008) and the variable response of different growth forms (e.g. Chambers and Klaff 1987; Rea and Ganf 1994; Blanch et al. 1998; Deegan et al. 2012). In shallow lentic systems, research has focussed on interactions of macrophytes with chemical processes (e.g. Wigand et al. 1997; Barko and James 1998) and trophic relationships (e.g. Timms and Moss 1984; Jeppesen et al. 1999; Norlin et al. 2005), and the implications for lake restoration (e.g. Moss 1990; van Donk and van de Bund 2002; Sondergaard et al. 2007). Historically, these streams would have experienced greater flow volumes and velocities, and in some cases perennial flows; have been less dominated by fine

substratum; and been heavily shaded, even in the lower reaches. However, rainfall decline, altered hydrology and extensive clearing has changed the character of these streams, so they are less limited by flow disturbance, substratum characteristics and riparian shading. Rather, as seen in seasonal wetlands, macrophytes in these streams are limited to environments with sufficient hydroperiod to complete their life cycle and grow successfully the following year (Warwick and Brock 2003). Furthermore, as in shallow lakes, these data suggest that macrophytes influence trophic relationships by increasing grazer numbers and overall invertebrate richness and abundance. Under some circumstances then, as in shallow lakes, it may be appropriate to consider macrophytes in restoration of seasonally-flowing lowland streams (discussed further below).

Macrophyte assemblage response to riparian condition

While both macrophyte assemblages were associated with poor riparian condition, high light availability appeared to be important for the *Potamogeton/Ottelia* assemblage, while *Cycnogeton* spp. were associated with cooler, shaded reaches. The occurrence of distinct macrophyte assemblages commonly arises from differing autecology among species leading to different patterns of competitive advantage at particular locations (Barrat-Segretain 1996). Our observations suggest these species' differing responses to shade may explain their different distribution pattern in degraded streams. The *Potamogeton/Ottelia* assemblage, which was associated with poorly-shaded reaches, has potential for wider distribution in the Geographe Bay catchment where riparian vegetation is commonly degraded. This positive response is less likely for *Cycnogeton* spp, which was associated with shadier reaches.

Growth of *Cycnogeton* spp. in shaded sites reflects their ability to reallocate resources from tubers to support rapid elongation of shoots to maximise exposure to light (Middelboe and Markager 1997). Their association with shade may also relate to a lower risk of seasonal desiccation in shaded reaches, where moist microclimates would extend the growing season of *Cycnogeton* spp., providing more favourable conditions for both vegetative growth and regrowth from perennial tubers, and increasing success of sexual reproduction (Rea and Ganf 1994). The presence of *Cycnogeton* spp. in shade in both good and poor condition reaches may indicate that these are remnant populations persisting despite changes to riparian condition and hydrology. The association with degraded riparian zones may simply reflect the predominance of reaches in this condition in the Geographe Bay catchment.

Restriction of the *Potamogeton/Ottelia* assemblage to degraded sites with little shade suggests dependence on high light availability. This is consistent with other Australian studies in which low riparian canopy cover has been associated with *P. ochreatus*, the ecologically similar *Potamogeton perfoliatus* and the floating-leaved *Potamogeton tricarinatus* (Mackay et al. 2003; Chessman and Royal 2010). In lentic systems, where light is limited primarily by water transparency, these species tolerate turbid conditions by canopy formation near the surface (*P. ochreatus*) and development of floating leaves (*P. drummondii* and *O. ovalifolia*) (Chambers 1987). However these adaptations are not advantageous where light at the water surface is limited by shade. This assemblage is also able to tolerate greater exposure to desiccation in unshaded reaches, because both *Potamogeton* and *Ottelia* produce drought-tolerant propagules (Wiegleb and Brux 1991; Jiang and Kadono 2001), enabling re-establishment from a seed bank following seasonal drying. These species occur commonly in lentic systems and are not well adapted to high flow velocity (being comparatively broad-leaved). They are likely to thrive in well-lit, low-flow conditions where sediment deposition is occurring, and may thus represent a colonising assemblage in these degraded streams. Yet despite a positive association with stream degradation, excessive growth of this plant assemblage was not observed. Excessive growth is perhaps prevented by seasonal drying (Deegan et al. 2012), which restricts dispersal and vegetative growth required for widespread colonisation (Barrat-Segretain 1996). In addition, self-regulation of patch size may result from the diversion of flow around plant stands, created by resistance within the stands that in turn creates adjacent areas of high velocity and coarser, less stable substrate that are unsuitable for macrophyte colonisation (Sand-Jensen and Mebus 1996; Garcia et al. 2012).

Macroinvertebrates

This study found higher macroinvertebrate abundance in reaches with macrophytes compared to those without. Higher family richness in reaches with macrophytes appeared due to the capacity of plant stands to support more individuals, although the families present in plant stands also showed functional responses to plant presence (e.g. families that graze epiphytic algae) and several taxa were only found among macrophytes. Submerged macrophytes are often found to support substantially higher abundance and diversity of aquatic invertebrates in streams and rivers, and this is generally attributed to provision of habitat, food resources and refuge from predation (Heck and Crowder, 1991; Humphries et al, 1996; Lind et al. 2006; Shupryt and Stelzer 2009). In this study, higher abundance of grazers, responding to the increased productivity of epiphytic algae in macrophyte sites, accounted for most of the

difference in abundance. Many other groups also had greater abundance in reaches with macrophytes and several were absent from reaches without macrophytes, including some that depend on plants for aspects of their life history (e.g. damselfly nymphs hatching from endophytic eggs). Because plants in this study did not grow in dense beds, the potential negative impacts of dense growth on macroinvertebrates (Suren and Riis 2010; Stiers et al. 2011) did not occur, so native submerged macrophyte presence in degraded reaches supported abundant and taxa-rich invertebrate communities.

While total abundance did not differ significantly, the more structurally complex *Potamogeton/Ottelia* assemblage supported greater abundance of grazers (Cyprididae, Cladocera, Curculionidae and Gastropoda) and shredders (Leptoceridae), although some taxa were more associated with *Cycnogeton* spp. Greater complexity offers protection from flow and supports periphyton growth, providing large amounts of food for grazing organisms (Warfe and Barmuta, 2006), particularly in the unshaded conditions associated with this assemblage. Greater abundance of primary consumers in turn support larger numbers of predators (Humphries et al, 1996), and reaches with *Potamogeton/Ottelia* also had more Corixidae, Notonectidae, Leptoceridae and Odonata than those with *Cycnogeton* or without macrophytes. In contrast the strap-like leaves of *Cycnogeton* have less effect on local flow conditions (Sand-Jensen, 1998) and thus supported suspension-feeders that rely on flow (Hershkovitz and Gasith 2013; Bell et al. 2013), taxa which graze on flat surfaces such as limpets and hydroptilid caddisflies, and crustaceans that require flow for oxygen supply but also use macrophytes as a refuge from predation (Hacker and Steneck 1990). Also, because *Cycnogeton* was found in shaded reaches it may provide moist refuge habitat during the dry season, necessary for amphipods and palaemonid shrimp that have no desiccation-resistant life stages (Robson et al. 2011). Greater structural complexity is often related to higher diversity (Warfe et al. 2008; Bell et al. 2013), but the results obtained here showed no difference in family richness between the two plant assemblages. While this relationship is not always clear (Humphries et al. 1996; McAbendroth et al, 2005), the family level identification used in the present study may have been too coarse a resolution to show differences related to structural complexity. Alternatively, the river reaches studied here may have been sufficiently degraded to lose more sensitive families, limiting the capacity for macroinvertebrate richness to respond to habitat complexity (Lake et al. 2007).

Although the presence of submerged macrophytes supported macroinvertebrates in these reaches, abundance and richness metrics do not incorporate taxa sensitivity (Palmer et al.

2014). The communities present may be characterised by tolerant, opportunistic species with generalist diets which are able to thrive in degraded reaches where alternative resources are available. The use of family-level or higher classifications does not enable us to determine whether sensitive taxa were present. The loss of riparian vegetation and associated habitat and resources no doubt has negative consequences for stream biota (Allan 2004), and a shift to an invertebrate community supported by macrophytes may be indicative of altered ecosystem process and poor stream health (Bunn et al. 1999). However, in these degraded streams, the resulting invertebrate community may nonetheless provide a food source for vertebrate predators which are also of high conservation value, particularly the highly endemic, and often threatened, native fish fauna of south-west Australia (Morgan et al. 2011).

Management implications

Although recolonisation of macrophytes is a common goal of restoration in Europe (Lorenz et al. 2012), they are rarely considered in this context in Australian streams. This study indicates the potential for positive growth response of some submerged native macrophyte species to stream degradation in seasonally-flowing streams, and demonstrates that these plant assemblages can support a more abundant and diverse aquatic fauna in reaches where riparian vegetation is degraded or absent. Colonisation of degraded reaches by native macrophytes may compensate for loss of natural submerged habitat (*sensu* Lind et al. 2009) when riparian inputs decline as a result of vegetation clearing. While aquatic plants may be perceived as potentially invasive, this seems unlikely when restoring native species in seasonally-flowing systems, even under nutrient enriched conditions. In contrast, assimilation of nutrients from diffuse sources and stabilisation of bed sediments are potential benefits of submerged macrophyte restoration in streams (Clarke 2002). Colonisation of fine substrates by submerged macrophytes would be valuable in stabilising sediment deposits and preventing downstream transport to receiving waters (Lind et al. 2009). In degraded systems, provision of ecosystem functions by macrophytes where they naturally occur, have managed to colonise, or potentially could be planted, warrants consideration.

While large scale management intervention is necessary to improve hydrologic connectivity and water quality, and rehabilitation of riparian zones is an essential component of stream channel restoration (Palmer et al. 2014), submerged macrophytes could be considered as part of in-channel habitat enhancement. The two assemblages found in this study have different responses to light and flow, showing a variation in traits that provides options for restoration of diverse reach conditions. Their rapid seasonal growth has potential for improved

biodiversity outcomes over short time periods (months), while other management actions are implemented (e.g. riparian revegetation), or could be valuable in areas where opportunities for riparian restoration are limited.

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