COOPERATIVE RESEARCH CENTRE FOR **CATCHMENT HYDROLOGY**

# THE RESPONSE OF AQUATIC MACROPHYTES TO RIPARIAN SHADING IN A STREAM REHABILITATION SITE

**TECHNICAL REPORT**
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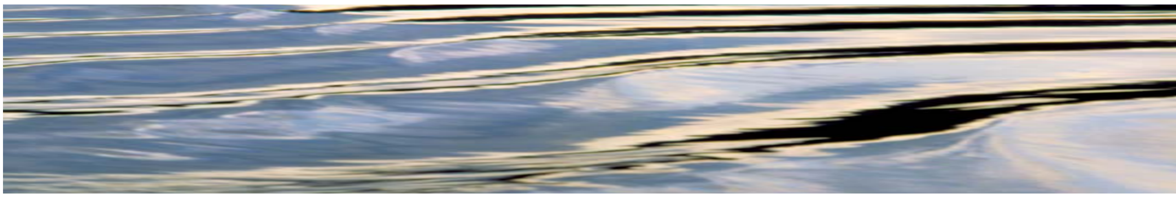
April 2005

**Stephen Mackay / Nick Marsh**



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Bibliography

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# The Response of Aquatic Macrophytes to Riparian Shading in a Stream Rehabilitation Site

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## Preface

Despite the considerable Government and private resources invested in the rehabilitation of damaged environments, little is known about the success of such projects. The Cooperative Research Centre (CRC) for Catchment Hydrology conducted a project (2000-2003) in collaboration with the CRC for Freshwater Ecology and the Moreton Bay and Catchments Healthy Waterways Partnership to assess the impact of stream rehabilitation on a few key elements of stream health.

The project aimed to quantify the affect of a commonly adopted stream rehabilitation strategy on a small stream in southeast Queensland. The stream rehabilitation strategy was to exclude stock by fencing the stream, provide off-stream stock watering and to revegetate the riparian zone using endemic native species for a 1.5 $km^2$ catchment (Echidna Creek) near Nambour in southeast Queensland. Four key elements were monitored through the life of the project:

1. Suspended sediment load;
2. Channel morphology;
3. Water temperature;
4. Aquatic macrophyte growth.

The results of the response of aquatic macrophyte growth to revegetation are presented in this report. The other key research areas are presented in separate CRC for Catchment Hydrology technical reports.

Mike Stewardson
Program Leader – River Restoration
CRC for Catchment Hydrology

## Acknowledgments

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## Executive Summary

Control of nuisance aquatic macrophyte growth by riparian shading is often a goal of riparian rehabilitation. Artificial shading can substantially reduce aquatic macrophyte biomass but few data are available to show that revegetation of previously forested streams can reduce aquatic macrophyte abundance or restore macrophyte assemblages to a pre-disturbance state. This report presents the results of a two-year monitoring program in which the effects of shading by riparian revegetation on the growth of aquatic macrophytes was investigated. The study was conducted in a 500 m reach of Echidna Creek, a tributary of the South Maroochy River, southeast Queensland. The goal of the riparian rehabilitation program for Echidna Creek was to achieve canopy closure (>75% shading) throughout the rehabilitation reach within two years of revegetation.

The growth of five macrophyte taxa dominant in the rehabilitation reach was monitored on 50 permanent transects from March 2002 – March 2004. These taxa were curly leaf pondweed (*Potamogeton crispus* L.), swamp lily (*Ottelia ovalifolia* (R.Br.) Rich), river clubrush (*Schoenoplectus validus* (Vahl) A. Löve and D. Löve), typha (*Typha* spp.) and the exotic watercress (*Rorippa nasturtium-aquaticum* (L.) Hayek). We hypothesised that riparian shading would have varying impacts upon these species depending upon growth form and light requirements for growth. We also hypothesised that hydraulic conditions would influence the growth of these species, in accordance with conceptual models of macrophyte growth in streams.

Canopy closure was not achieved within the monitoring period. Mean riparian canopy cover of the study reach increased from 52% to 71% over the two-year monitoring period. Riparian canopy cover varied considerably throughout the study reach due to the presence of remnant riparian vegetation, variations in the growth rate of tubestock, and death of some tubestock from frosts.

Logistic regression models indicated that spatial variations in the distribution of the five dominant macrophyte taxa throughout the rehabilitation reach were most strongly related to riparian canopy cover. The effect of riparian canopy cover was greatest upon *R. nasturtium-aquaticum*, followed by *S. validus* and *P. crispus*, generally supporting our conceptual model. The spatial distribution of taxa throughout the study reach was not correlated with hydraulic disturbance parameters, although *Typha* spp. occurred more frequently on fine substrates. Multiple linear regression (MLR) and simultaneous autoregressive (SAR) models describing relationships between species abundances and environmental variables were generally poor fits to the data. These models showed that spatial variations in species abundances were more strongly related to riparian canopy cover than hydraulic parameters.

Temporal variations in species abundances were related to riparian canopy cover and days since bankfull discharge. The relative contribution of hydraulic disturbance to temporal variations in species abundances varied according to growth form. Days since bankfull discharge explained 24% of the temporal variation in *S. validus* abundance but explained greater than 50% of the temporal variation in *P. crispus*, *Typha* spp. and *R. nasturtium-aquaticum* abundances, as determined from univariate regression curves. From these regression models it was estimated that riparian canopy cover greater than 70% would be required to eliminate *S. validus*, *Typha* spp. and *R. nasturtium-aquaticum* whereas riparian canopy cover greater than 80% would be required to eliminate *P. crispus*. These are probably underestimates since all taxa were recorded on transects where riparian canopy cover exceeded 80%.

The results of the monitoring program indicate that riparian canopy cover will reduce the distribution and abundance of *P. crispus*, *O. ovalifolia*, *S. validus*, *Typha* spp. and *R. nasturtium-aquaticum* in the study reach. The extent to which riparian canopy cover can reduce the distribution and abundance of the dominant taxa in the rehabilitation reach is species-specific and dependent upon the hydrology of Echidna Creek. We predict that riparian revegetation will not completely eliminate the five dominant taxa from the rehabilitation reach.

An important potential issue associated with riparian revegetation in this system, especially if nutrients

remain relatively high, is invasion of the rehabilitated system by shade-tolerant exotic taxa such as dense waterweed (*Egeria densa* Planchon), umbrella sedge (*Cyperus involucratus* Rottb.), crofton weed (*Ageratina adenophora* (Spring.) R.M. King and H. Rob.) and the ornamentals *Commelina* spp. and *Tradescantia* spp. Invasion of rehabilitated sites by introduced, shade-tolerant taxa does not appear to be widely considered in planning rehabilitation projects.

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# 1. Introduction

Light is one of the principal abiotic factors limiting the growth of aquatic vascular macrophytes in streams (Spence, 1975; Canfield and Hoyer, 1988; Sand-Jensen *et al.*, 1989; Biggs, 1996). In forested headwater streams light is limited by riparian shading, and vascular aquatic macrophytes (particularly submerged species) are generally absent from these systems (e.g. Westlake and Dawson, 1976; Vannote *et al.*, 1980; Sheath *et al.*, 1986; Howard-Williams *et al.*, 1987; Everitt and Burkholder, 1991). The loss of riparian vegetation from forested streams has been widely associated with the establishment of exotic macrophyte species, increased vascular macrophyte biomass and encroachment of emergent semi-aquatic vegetation into stream channels (Howard-Williams *et al.*, 1987; Bunn *et al.*, 1998; Wilcock *et al.*, 2002). Shading through re-establishment of riparian vegetation is considered an effective means of controlling the growth of nuisance aquatic macrophytes (Dawson and Kern-Hansen, 1979; Bunn *et al.*, 1998). Shade cloth is effective in reducing macrophyte biomass (see below) but riparian revegetation is considered a more practical and longer-term solution than shade cloth, in addition to other ecological benefits it provides (e.g. Vannote *et al.*, 1980; Jorgensen *et al.*, 2000; Harrison and Harris, 2002; England and Rosemund, 2004). There are, however, very few studies to show that increased stream shading by riparian revegetation can control nuisance macrophyte growth or restore macrophyte assemblages to a "pre-disturbance" state (but see Fletcher *et al.*, 2000; Parkyn *et al.*, 2003).

## 1.1. Responses of Aquatic Macrophytes to Artificial and Riparian Shading

Artificial shading has proved effective in reducing macrophyte biomass. Dawson and Kern-Hansen (1979) compared the biomass of three macrophyte species (*Ranunculus peltatus* Schrank, *Elodea canadensis* Michx. and *Potamogeton crispus* L.) in unshaded, naturally shaded and artificially shaded stream sections. Artificial shade was provided by netting suspended over the entire wetted stream width, reducing light reaching the stream surface by 10–65%. The authors did not report in detail the results of the artificial shading treatments but noted that macrophyte biomass in artificially shaded stream sections was inversely proportional to the light available at the stream surface. For shaded sites, plots of biomass versus irradiance (at stream surface, expressed as proportion of irradiance at open and unshaded sites) showed that *P. crispus* could maintain small populations in shaded areas where surface irradiance was less than 30% of unshaded areas. Macrophytes in shaded areas were also found to produce fewer stems than macrophytes in "less shaded" areas. Reducing light to approximately 50% of open areas was expected to halve the macrophyte standing crop, with reductions in light to well below half that of open areas "leading to the disappearance of aquatic plants" (Dawson and Kern-Hansen, 1979).

Dawson and Hallows (1983) used shade material suspended above and below the water surface to control the growth of aquatic rooted macrophytes. The shade material reduced light availability by approximately 70%. Substantial reductions in biomass (typically 60–80% when compared to adjacent open stream sections) were recorded for both submerged and emergent macrophytes. The reductions in biomass achieved varied between species, partly due to some species having "food reserves" in rhizomes. Submerged shade cloth was especially effective in reducing macrophyte biomass because detritus accumulated on the shade cloth, increasing its shading capacity.

Jorga *et al.* (1982) investigated relationships between macrophyte biomass and light in order to control "mass development" of macrophytes, defined as biomass levels exceeding 250 grams of dry weight per square metre (gDWm-2). Jorga *et al.* (1982) produced a table of predicted biomass ranges for different irradiance values measured at a stream depth of 0.35 m (typical depth for sites in the region studied by the authors), defined as L35. L35 values in the range of 15–40% of full sunlight were predicted to allow mass development of macrophytes (i.e. dry weight > 250 gDWm-2). Substantial reductions in dry weight were recorded at L35 below 15% full sunlight, such that at L35 values corresponding to less than 1% full sunlight dry weight biomass was less than 5 gDWm-2.

Bunn *et al.* (1998) examined the effectiveness of shade cloth to control the growth of the exotic para grass, *Brachiaria mutica* (Forssk.) Stapf, in Bamboo Creek, an Australian tropical lowland stream. The catchment and riparian zone of Bamboo Creek have been extensively cleared for sugar cane cultivation and *B. mutica* has established nuisance populations in the creek. Two shade cloth treatments (50% and 90% light reduction) were applied for three months at five sites in Bamboo Creek. After the treatment period, significant reductions in biomass were recorded compared to the control (0% shade). The greatest reduction in biomass occurred in the 90% shade treatment: biomass in this treatment was 22% of the control. Bunn *et al.* (1998) concluded that riparian revegetation would be an effective means of controlling macrophytes in disturbed streams.

Wilcock *et al.* (2002) examined the effects of suppression of macrophyte growth by artificial shade on nutrient retention in New Zealand streams. Unshaded stream sections were dominated by the emergent exotic *Persicaria hydropiper* (L.) Spach (water pepper) whereas shaded stream sections (light reduction approximately 90%) were characterised by *P. hydropiper, Nitella hookeri* A. Braun (native) and *Potamogeton ochreatus* Raoul (native). Substantial reductions in biomass were achieved by the application of shade cloth. The mean biomass of shaded reaches (quantified on two occasions) was 190 $gDWm^{-2}$ and 380 $gDWm^{-2}$, whereas comparative biomass in unshaded reaches was 1080 $gDWm^{-2}$ and 1270 $gDWm^{-2}$ respectively (Wilcock *et al.*, 2002).

Several key points can be drawn from the artificial shading experiments described above. The extent of the reduction in biomass that can be achieved is dependent upon the morphology and physiology of the macrophyte species present. In some studies (e.g. Dawson and Kern-Hansen, 1979; Bunn *et al.*, 1998) macrophytes were not totally eliminated from artificially shaded areas despite substantial reductions (70–90%) in light availability. It is not clear from these experiments whether macrophytes would have been eliminated from the study sites if shading experiments were allowed to continue indefinitely. However, reductions in light availability of approximately 40–60% can be expected to significantly reduce macrophyte biomass. Similar estimates of the riparian canopy cover required to control nuisance macrophyte or algal growth have been calculated by Bunn *et al.* (1999) for the Mary River (southeast Queensland) and by Canfield and Hoyer (1988) for Florida streams.

It is unknown whether restoration of a degraded riparian zone through revegetation is as effective as artificial shade in controlling the growth of nuisance aquatic macrophytes. The effectiveness of riparian shading is dependent upon vegetation type, stream width, channel aspect or orientation and channel morphology (Dawson and Kern-Hansen, 1979), whereas the application of shade cloth is not as restricted by these factors. For example, Parkyn *et al.* (2003) compared physicochemical and biological characteristics of riparian buffer strips with adjacent unbuffered (unfenced, grazed) control reaches in nine New Zealand streams. Macrophyte cover was estimated within a 1-m belt transect at each site. Macrophyte cover was found to be significantly lower for buffer strips at three sites, where stream width was less than 6 m. Fletcher *et al.* (2000) demonstrated the importance of riparian species composition on light availability and the structure of aquatic macrophyte assemblages. Fletcher *et al.* (2000) examined the responses of aquatic vegetation to riparian rehabilitation in two third-order streams previously subjected to thermal discharges from power stations. The recovery time of the two impacted streams prior to sampling was 10 and 7 years respectively. Macrophyte assemblages in the impacted streams were compared with assemblages in two reference streams. Total macrophyte cover was negatively correlated with riparian canopy cover. Riparian canopies dominated by hardwoods had greater canopy cover and very low macrophyte cover whereas the highest macrophyte cover was associated with open riparian zones dominated by herbaceous vegetation, with intermediate macrophyte cover associated with riparian zones dominated by willows. Relationships between riparian canopy cover and the cover of emergent, floating and submerged macrophytes varied. Floating macrophyte cover had the strongest relationship with riparian canopy cover, followed by emergent vegetation cover, with submerged vegetation cover showing the weakest relationship. Since submerged macrophytes could grow further into the stream channel than emergent or floating species they

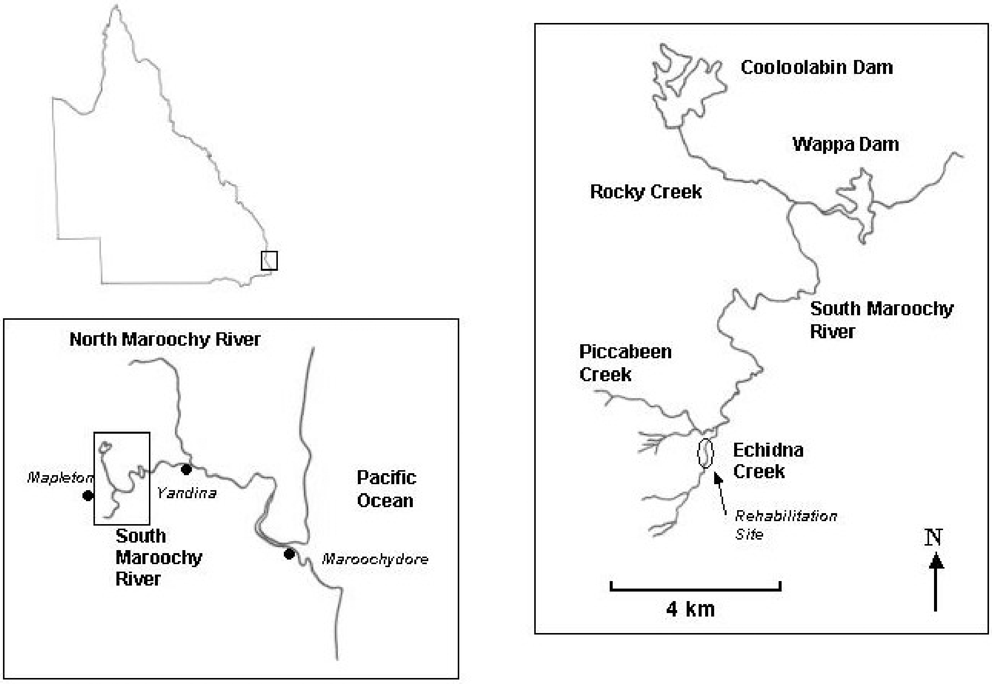

Figure 1. Location of Echidna Creek and the Riparian Rehabilitation Site.

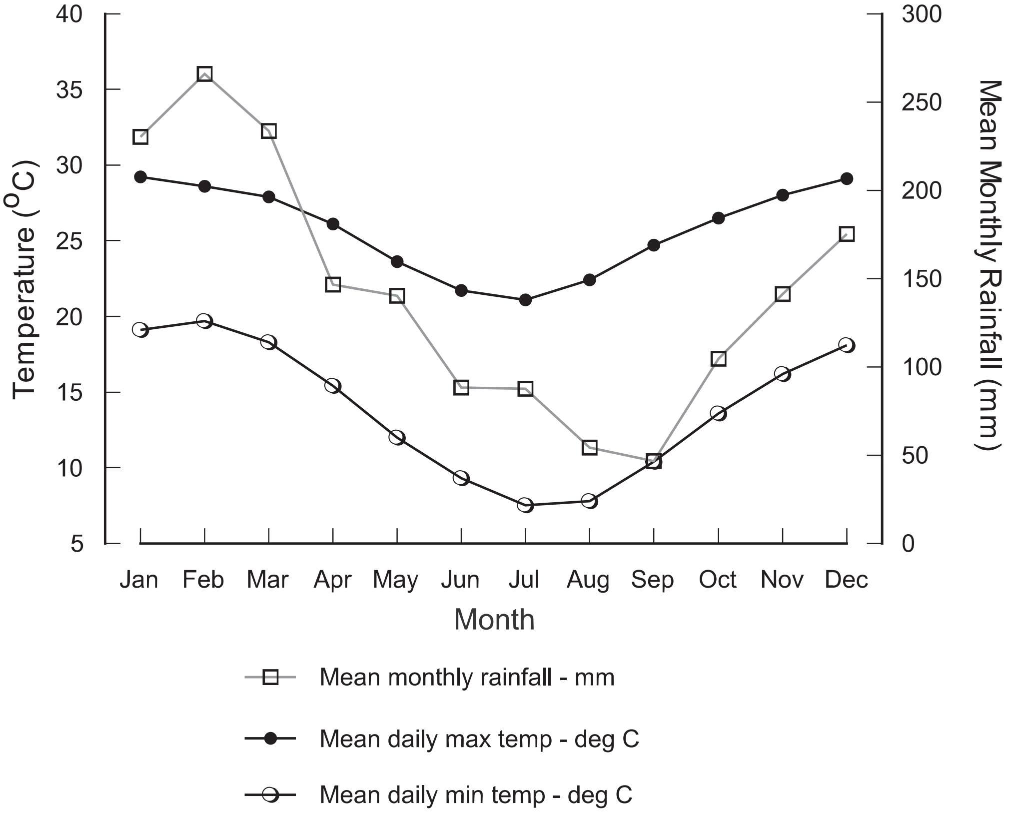

Figure 2. Climate Data for Nambour Department of Primary Industries Weather Station (No. 040282), the Closest Station to Echidna Creek (Bureau of Meteorology, http://www.bom.gov.au).

could better escape the effects of riparian shading (Fletcher *et al.* 2000).

## 1.2. Riparian Revegetation of Echidna Creek, Southeast Queensland

Echidna Creek (total catchment area 2 km$^2$) is a second order tributary of the South Maroochy River, southeast Queensland (Figure 1). Echidna Creek originates from the Kureelpa Plateau (altitude 400 m) at the foot of the Blackall Ranges and descends approximately 160 m to the confluence with the South Maroochy River. Mean monthly rainfall varies seasonally, peaking in February (mean monthly average 250 mm) and decreasing to a spring minimum of approximately 50 mm (Figure 2). Annual rainfall typically exceeds 1500 mm (Butcher *et al.*, 1976). Air temperatures also follow distinct seasonal patterns with January–February maxima and July minima (Figure 2). Although the region experiences a subtropical climate, frosts may occur. The occurrence of frosts is highly dependent upon local topography, with valleys in hilly areas particularly susceptible to frosts from June to August (Butcher *et al.*, 1976).

The vegetation of the Echidna Creek Catchment and adjacent foothills has been extensively cleared but previously consisted of open forest (blue gum, brush box, pink bloodwood, grey ironbark and grey gum), rainforest and wet sclerophyll forest (Butcher *et al.*, 1976). The riparian vegetation of small streams such as Echidna Creek draining the foothills of the Blackall Range consisted of rainforest dominated by bunya pine (*Araucaria bidwillii* Hook) (Butcher *et al.*, 1976). These streams would have been highly shaded. Remnant riparian vegetation along Echidna Creek includes bunya pine and sandpaper figs (*Ficus coronata* Spin) with lomandra (*Lomandra* spp.) occurring as a groundcover species on stream margins.

Conductivity, pH and nutrient concentrations for Echidna Creek exceed ANZECC and ARMCANZ (2000) trigger values for upland rivers (>150 m altitude) (Table 1). Total nitrogen (TN) and total phosphorus (TP) concentrations are approximately double ANZECC and ARMCANZ trigger values for these parameters (although ammonium and turbidity are below trigger values). Water quality data for Piccabeen Creek, a forested catchment 2.5 km northwest of Echidna Creek and indicative of reference condition for Echidna Creek, are also presented in Table 1. The water quality of Piccabeen Creek generally conforms to ANZECC and ARMCANZ guidelines for upland rivers (Table 1). With the exception of oxides of nitrogen (NOx), nutrient concentrations for Piccabeen Creek are well below trigger values.

Two farm dams are located on the headwaters of Echidna Creek. These dams account for approximately two-thirds of the discharge through the rehabilitation reach. Simultaneous gauging of an unnamed tributary (which contributes approximately one-third of the discharge through the rehabilitation reach) and the

Table 1. Water Quality Data for Echidna Creek and Piccabeen Creek.

| Water Quality Parameters | Echidna Creek (Rehabilitation Site) | Piccabeen Creek (Forested) | Trigger Values |
|---|---|---|---|
| **Conductivity ($\mu$S cm$^{-1}$)** | **850** | **130** | **30–350** |
| **pH** | **8.80** | **7.15** | **6.5–7.5** |
| **Turbidity (NTU)** | **3** | **3** | **2–25** |
| **Alkalinity (as $CaCO_3$)** | **380** | **21.5** | **-** |
| **Bicarbonate, $HCO_3$ (mgL$^{-1}$)** | **430** | **26.5** | **-** |
| **Ammonium, $NH_4$ (mgL$^{-1}$)** | **0.012** | **0.005** | **0.013** |
| **Oxides of Nitrogen, NOx (mgL$^{-1}$)** | **0.022** | **0.034** | **0.015** |
| **Filterable Reactive Phosphorus, FRP (mgL$^{-1}$)** | **0.021** | **0.003** | **0.015** |
| **Total Nitrogen, TN (mgL$^{-1}$)** | **0.460** | **0.110** | **0.250** |
| **Total Phosphorus, TP (mgL$^{-1}$)** | **0.048** | **0.012** | **0.020** |

The Piccabeen Creek Catchment is adjacent to the Echidna Creek Catchment and the primary land use is State Forest. Water quality data from Smith et al. (2001). Trigger values are from ANZECC and ARMCANZ (2000) water quality guidelines for "slightly disturbed ecosystems".

main channel in the 2002 wet season showed that the dams had no discernible effect on the shape of flood hydrographs (N. Marsh unpublished data).

From February to May 2001 a riparian rehabilitation plan was implemented for a 5 ha site within the Echidna Creek Catchment. The rehabilitation plan included fencing to prevent stock access and an intensive revegetation scheme along approximately 1400 m of stream channel (Anon., 2000). Tubestock (native climax and understorey species) was planted at 2 m intervals within the rehabilitation site to establish a 10 m wide riparian zone. The goal of the rehabilitation program was to achieve >75% riparian canopy cover throughout the reach. It was anticipated that 75% canopy cover for the rehabilitation reach could be achieved within two years depending on weather conditions (Anon., 2000). Although control of aquatic vegetation was not specifically stated as an objective of the Echidna Creek rehabilitation plan (Anon., 2000), the project offered an opportunity to monitor the effectiveness of riparian revegetation in controlling nuisance aquatic macrophyte growth.

### 1.2.1 Aquatic Macrophytes of Echidna Creek

Site reconnaissance indicated that extensive macrophyte beds occurred in open (unshaded) areas of Echidna Creek whereas highly shaded areas of Echidna Creek with remnant riparian vegetation were devoid of macrophytes or supported only very low macrophyte biomass. Five macrophyte taxa dominated the study reach in terms of distribution and abundance. These species were *Potamogeton crispus* L., *Ottelia ovalifolia* (R.Br.) Rich., *Schoenoplectus validus* (Vahl) A. Löve and D. Löve, *Typha* spp. and *Rorippa nasturtium-aquaticum* (L.) Hayek. With the exception of the latter these species are native. The morphological attributes of the five species are summarised in Table 2. *Potamogeton crispus*, *Typha* spp. and *R. nasturtium-aquaticum* have wide geographical distributions (Catling and Dobson, 1985; Bolduan *et al.*, 1994; Preston and Croft, 1997). *Potamogeton crispus* is a habitat generalist, occurring in slow to fast-flowing waters at a variety of depths (Preston and Croft, 1997). It is generally associated with eutrophic waters but occurs over a wide range of nutrient concentrations (Preston and Croft, 1997). Spence and Maberly (1985) classified *P. crispus* as a species preferring high alkalinity (>60 mgL$^{-1}$ as $CaCO_3$).

*Typha* spp. are robust emergent species that can form dense monospecific stands (Aston, 1977). The two species occurring in Queensland (*T. domingensis* Pers. and *T. orientalis* C. Presl) are difficult to distinguish in the field (Stephens and Dowling, 2002) and for the purposes of this report we assume that both species are present. *Typha* spp. are especially common in disturbed areas with little riparian shading, e.g. urban creeks and drainage ditches. *Typha* spp. occur in still

Table 2. Morphological Attributes of the Five Dominant Macrophyte Taxa Occurring in the Echidna Creek Study Reach.

| Taxon | Common Name | Maximum Stem Length | Habit | Leaf Morphology |
|---|---|---|---|---|
| *P. crispus* | Curly leaf pondweed | 3 m | Submerged | Linear, elliptic, up to 7 cm long. |
| *O. ovalifolia* | Swamp lily | 1 m | Submerged or floating (attached) | Submerged leaves lanceolate (strap-like), floating leaves oval or elliptic, leaf blade up to 16 cm long. |
| *Typha spp.* | Bulrush; cumbungi; *typha* | 3 m | Emergent | Linear, up to 1 m long. |
| *S. validus* | River clubrush | 3 m | Emergent | Reduced; sheathing bracts or very short blades |
| *R. nasturtium-aquaticum* | Watercress | 2.5 m | Emergent, occasionally submerged | Leaves pinnate (composed of "leaflets"); up to 12 cm long. Leaflets elliptic. |

From Aston (1977); Stanley and Ross (1983, 1989); Sainty and Jacobs (1994).

waters up to 2 m deep where water levels are relatively stable (Sainty and Jacobs, 1981; Blanch *et al.*, 1999, 2000). The growth of *Typha* spp. is generally considered to be enhanced under conditions of high nutrient availability (Goes, 2002), especially phosphorus (Miao *et al.*, 2000; Lorenzen *et al.*, 2001). *Schoenoplectus validus* can be found in similar conditions in southeast Queensland streams. The growth of *S. validus* can be prolific in unshaded areas but this species does occur in shaded environments (S. Mackay unpublished). Like *Typha* spp. it can form dense monospecific stands and is associated with stable water levels (Blanch *et al.*, 1999, 2000).

*Rorippa nasturtium-aquaticum* is a low-growing emergent species often found in still or slow-flowing shallow waters but capable of growing completely submerged (Michaelis, 1976). Watercress thrives in nutrient-rich water (Sainty and Jacobs, 1994) and its presence is thought to be indicative of groundwater inputs (Robach *et al.*, 1997). Stems are hollow and decumbent (i.e. creeping with ascending tips). Although stem lengths may reach 2.5 m, stands of this species are typically less than a metre high (Aston, 1977; Sainty and Jacobs, 1981).

There is little ecological information available for *O. ovalifolia*. Although widespread in southeast Queensland it seldom occurs in large or extensive stands but can occur in shaded habitats (Mackay *pers. obs*.). Young plants have submerged, lanceolate leaves and older plants have floating, elliptic leaves. Floating leaves may infer some advantages for photosynthesis (c.f. submerged leaves) as floating leaves can utilise atmospheric carbon dioxide (e.g. Frost-Christensen and Sand-Jensen, 1995) and are not limited by the relatively low diffusion rates of $CO_2$ in water (Spence and Maberly, 1985).

## 1.3. Predicted Responses of Aquatic Macrophytes to Riparian Shading in Echidna Creek

Aquatic macrophyte growth in streams is influenced by the availability of resources (light and nutrients) for growth and spatial and temporal variations in hydraulic habitat that cause biomass loss (Biggs, 1996; Riis and Biggs, 2001). This is represented diagrammatically as a conceptual model in Figure 3. The extent to which grazing by herbivores (a potential disturbance source) can reduce macrophyte biomass is a contentious issue (e.g. Lodge, 1991; Lodge *et al.*, 1998). For the purposes of this investigation grazing by herbivores is considered to cause insignificant reductions in macrophyte biomass in Echidna Creek. We use the conceptual model to predict macrophyte assemblage structure in Echidna Creek following riparian canopy closure.

Within the habitat template defined by the conceptual model (Figure 3) we hypothesise that the reference condition for Echidna Creek would have been low (growth-limiting) light availability with periodic hydraulic disturbance from floods and spates. Vascular macrophytes are expected to be absent under these conditions. The loss of riparian canopy cover from Echidna Creek has allowed extensive aquatic macrophyte beds to establish. If light availability and hydraulic disturbance are the major abiotic factors

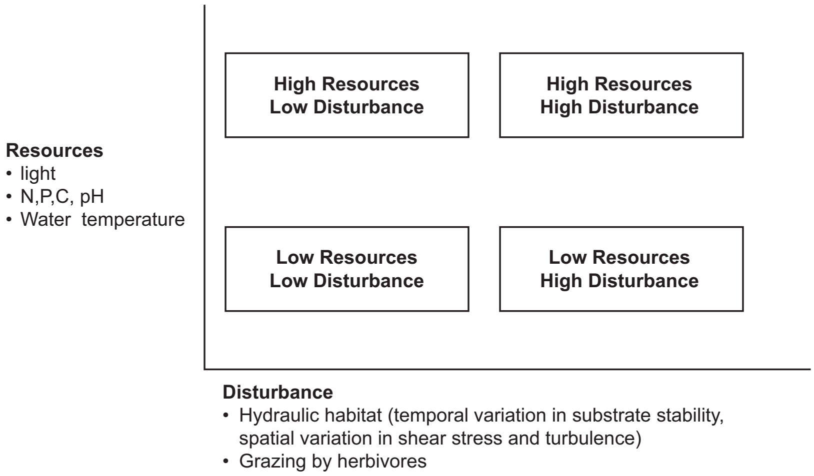

Figure 3. The Conceptual model of Biggs (1996) and Riis and Biggs (2001). pH and water temperature are included for their effects upon nutrient availability, nutrient uptake and metabolic rates.

controlling growth of aquatic macrophytes in Echidna Creek, restoration of the riparian canopy is hypothesised to restore Echidna Creek to a pre-disturbance state, with elimination of vascular macrophytes following canopy closure. It is assumed that the hydraulic regime of Echidna Creek has not changed substantially despite the presence of dams in the headwaters.

The five dominant macrophyte taxa occurring in Echidna Creek can be placed within the conceptual model based on relative light requirements for growth and relative tolerance to hydraulic disturbance, i.e. floods and spates. The composition of the aquatic macrophyte flora of Echidna Creek following canopy closure can then be predicted. We attempted to use photosynthetic characteristics of the five dominant taxa as indicators of light requirements for growth and tolerance to low light conditions (Table 3). However, there are inherent difficulties in comparing photosynthesis data between species and from different studies, as photosynthesis is dependent upon light, temperature, the availability of carbon and degree of acclimation prior to measurement and experimentation (Kirk, 1994). In addition, units for key descriptors of photosynthetic capacity reported in the literature vary, making direct comparisons difficult. *P.crispus* and *Typha* spp. were the only taxa for which extensive photosynthesis data could be compiled (Table 3).

*Potamogeton crispus* is tolerant of very low light intensity (Bolduan *et al.*, 1994; Table 3) and capable of winter growth in temperate regions (Kunii, 1989), even under ice (Nichols and Shaw, 1986). Pearsall (1920), cited by Nichols and Shaw (1986), considered *P. crispus* to be a member of a deep water (lentic) community that typically developed in light intensities of less than 15% full sunlight. Light compensation points (LCP, the point at which photosynthesis balances respiration) reported for *P. crispus* are substantially lower than LCPs reported for *Typha domingensis* (Table 3). LCP values were not available for *S. validus*, *O. ovalifolia* or *R. nasturtium-aquaticum* but a value similar to that for *T. domingensis* has been reported for *Schoenoplectus hallii* (A. Gray) S.G. Smith (Table 3). In general, submerged macrophytes such as *P. crispus* are considered to be shade plants (White *et al.*, 1996) and have relatively low light compensation points (Salisbury and Ross, 1985). Shade plants have the following general traits (Salisbury and Ross, 1985):

1. Photosynthetic rates in full sunlight may be lower than for species typical of open unshaded areas;
2. Photosynthetic pathways are light saturated at relatively low light levels;
3. Rates of photosynthesis at low light levels are higher than for other species.

Photosyntheticrates, $P$ and $P_{\max}$, values reported in Table 3 for *P. crispus* are not directly comparable with values reported for other taxa due to differences in units of measurement. However, as a shade plant we place *P. crispus* low on the light (resource) axis relative to the other taxa. *Typha* spp. and *S. validus* are placed higher on the light (resource) axis relative to *R. nasturtium-aquaticum* and *O. ovalifolia* since *Typha* spp. and *S. validus* are commonly associated with open unshaded environments. Extensive shading can limit the growth of *R. nasturtium-aquaticum*. Dawson (1978) noted that in a shaded section of stream where incident light was reduced by 80% the biomass of watercress was reduced to 150–260 gm$^{-2}$ (from >350 gm$^{-2}$ in open areas, presumably as dry weight biomass). Dawson and Hallows (1983) recorded an 80% reduction in watercress biomass when incident light was reduced by approximately 70% with shade cloth. However, shading does not prevent the growth of watercress; this species occurs in shaded habitats in southeast Queensland streams (S. Mackay unpublished; see also Kaskey and Tindall, 1979). Romanowski (1998) also notes the occurrence of *R. nasturtium-aquaticum* along cool and shaded streams. Note that the reduced watercress biomass recorded by Dawson (1978) (i.e. 150–260 gm$^{-2}$) in shaded areas can be considered a substantial biomass.

The placement of *O. ovalifolia* on the resource axis is complicated by the fact that submerged leaves may have different photosynthetic properties compared to floating leaves (e.g. Cenzato and Ganf, 2001). Since *O. ovalifolia* has been observed more frequently in Echidna Creek with floating leaves than submerged leaves, the placement of *O. ovalifolia* within the conceptual model is based on plants with floating leaves. Plants with floating leaves have been observed in shaded reaches of southeast Queensland streams

Table 3. Photosynthetic Properties of *Potamogeton crispus*, *Typha* spp., *Schoenoplectus hallii* and *Rorippa nasturtium-aquaticum.*

| Taxon | Temp (ºC) | Light | Light Compensation Point | α | Photosynthetic Rate (*P*) | Light Saturated Photosynthetic Rate ($P_{max}$) | References |
|---|---|---|---|---|---|---|---|
| *P. crispus* | | | 9 $\mu Em^{-2}s^{-1}$ | | | | Van 1976, in Ganf *et al.* (1977) |
| | | | 2 $\mu Em^{-2}$ | | | | Bolduan *et al.* (1994) |
| | | | 10 lux (approx. 4.8 $\mu Em^{-2}s^{-1}$) | | | | Bolduan *et al.* (1994) |
| | 15ºC | 250 µmol $m^{-2}$ $s^{-1}$ (PAR) | | | 247 µmol $O_2$ $g^{-1}$ $h^{-1}$ (measured at water velocity of 1 cm $s^{-1}$) | | Madsen *et al.* (1993) |
| | 20ºC | 560 µmol $m^{-2}$ $s^{-1}$ (PAR) | | 0.56 µmol $mol^{-1}$ $CO_2$ m3 $s^{-1}$ $DM^{-1}$ at pH 5.5 | | • 0.80 mmol $O_2$ g $DW^{-1}$ $h^{-1}$, pH 5.5<br>• 0.77 mmol $O_2$ g $DW^{-1}$ $h^{-1}$, pH 8.8 | Allen and Spence (1981) |
| | 15ºC | 450 µmol photons $m^{-2}$ $s^{-1}$ | | 2.58 µmol $mol^{-1}$ $CO_2$ m3 $s^{-1}$ $DM^{-1}$ at pH 5.5 | | | Maberly and Madsen (1998) |
| | 15ºC | 40 µmol $m^{-2}$ $s^{-1}$ | | | | 351 µmol $O_2$ $g^{-1}$ $DWh^{-1}$ | Maberly and Madsen (2002)[1] |
| | 15ºC | 120 µmol $m^{-2}$ $s^{-1}$ | | | | 411 µmol $O_2$ $g^{-1}$ $DWh^{-1}$ | Maberly and Madsen (2002) [1] |
| | 15ºC | 350 µmol $m^{-2}$ $s^{-1}$ | | | | 598 µmol $O_2$ $g^{-1}$ $DWh^{-1}$ | Maberly and Madsen (2002) [1] |
| | 15ºC | 470 µmol $m^{-2}$ $s^{-1}$ (PAR) | | | • 17.1 $mgO_2$ $(gDW)^{-1}h^{-1}$, ambient $[CO_2]$;<br>• 36.0 $mgO_2$ $(gDW)^{-1}h^{-1}$ at elevated $[CO_2]$ (approx. 0.8 mM). | | Sand-Jensen *et al.* (1992) [2] |
| | 12ºC | 400 µmol photons $m^{-2}$ $s^{-1}$ | | | • 563 µmol $O_2$ $g^{-1}$ $DWh^{-1}$ at $[CO_2]$ 20 µM<br>• 632 µmol $O_2$ $g^{-1}$ $DWh^{-1}$ at $[CO_2]$ 40 µM<br>• 813 µmol $O_2$ $g^{-1}$ $DWh^{-1}$ at $[CO_2]$ 280 µM | | Sand-Jensen and Frost-Christensen (1998) |
| *Typha domingensis* | 26ºC | 1200 µmol $m^{-2}$ $s^{-1}$ PAR | 25 µmol $m^{-2}$ $s^{-1}$ | | | >1100 µmol $m^{-2}$ $s^{-1}$ | Pezeshki *et al.* (1996) |
| | 30ºC | Ambient (2000 µmol $m^{-2}$ $s^{-1}$) | | | | 17.0 µmol $CO_2$ $m^{-1}s^{-1}$ | Miao *et al.* (2000) |
| | 30ºC | Ambient (2000 µmol $m^{-2}$ $s^{-1}$) | | | | 19.9 µmol $CO_2$ $m^{-1}s^{-1}$ | Miao *et al.* (2000) |
| | 30ºC | Ambient (2000 µmol $m^{-2}$ $s^{-1}$) | | | | 45.1 µmol $CO_2$ $m^{-1}s^{-1}$ | Miao *et al.* (2000) |
| | 18.5–30ºC | Ambient | | 0.042 mol $mol^{-1}$ | 17.8 µmol $m^{-2}$ $s^{-1}$ | | Jones (1988) |
| | 23–30ºC | 2000 µmol $m^{-2}$ $s^{-1}$ | | | | 15 µmol $CO_2$ $m^{-2}$ $s^{-1}$ | Mendelssohn *et al.* (2001) |
| *Typha latifolia* | 28.4ºC (average) | 3431 µmol $m^{-2}$ $s^{-1}$ (PAR) | | | 5.2–10.3 $mg_2 CO_2$ $h^{-1}$ $cm^{-}$ | | Crowe *et al.* (2001) |
| *Schoenoplectus hallii* | 25ºC | 700 µmol photons $m^{-2}$ $s^{-1}$ PPF | 24 µmol photons $m^{-2}s^{-1}$ | | | 13.3 µmol $CO_2$ $m^{-1}s^{-1}$ | Smith and Houpis (2004) |
| *Rorippa nasturtium-aquaticum* | 15ºC | 350 µmol photons $m^{-2}$ $s^{-1}$ PAR | | | • 8.08 µmol $O_2$ $m^{-2}$ $s^{-1}$ (aerial leaves), $[CO_2]$ 15 µM<br>• 5.77 µmol $O_2$ $m^{-2}$ $s^{-1}$ (aquatic leaves), $[CO_2]$ 100 µM | | Sand-Jensen and Frost-Christensen (1999) |

[1] Alkalinity 0.5 equivalents $m^{-3}$ and $[CO_2]$ 250 mmol $m^{-3}$.

[2] Dissolved inorganic carbon 2.2 $mEqL^{-1}$.

**Definition of Terms Used in Table 3 (from Kirk, 1994; Nilsen and Orcutt, 1996).**

**PAR:** Photosynthetically Active Radiation, wavelengths between 400 and 700 nm that are involved directly in photosynthesis.

**Light Compensation Point:** the irradiance value at which photosynthesis balances respiration.

$\alpha$**:** rate of photosynthesis per unit biomass per unit of incident irradiance. A measure of the efficiency in which plant biomass utilises light. Also called quantum yield.

**Photosynthetic Rate (*P*):** rate of photosynthesis, expressed per unit of biomass, volume of water or surface area of substrate.

**Light Saturated Photosynthetic Rate ($P_{max}$):** The point where the rate of photosynthesis ceases to increase with increasing light (irradiance). Also referred to as photosynthetic capacity.

such as Eudlo Creek (Maroochy Catchment) and Burnett Creek (Logan Catchment) (Mackay *pers. obs.*). *Rorippa nasturtium-aquaticum* and *O. ovalifolia* are placed lower on the resource axis relative to *Typha* spp. and *S. validus* due to their occurrence in shaded stream reaches.

The five dominant macrophyte taxa are predicted to vary in their response to hydraulic disturbance due to differences in morphology. *Potamogeton crispus* is placed on the high extreme of the hydraulic disturbance axis as it occurs in slow to fast-flowing water (Bilby, 1977; Stanley and Ross, 1989; Champion and Tanner, 2000; Mackay *et al.*, 2003) and is therefore assumed to tolerate relatively high hydraulic stress. Following the strategy classification scheme of Grime (1977), *P. crispus* is often classified as a competitive-ruderal, ruderal or disturbance tolerator (e.g. Rørslett, 1989; Murphy *et al.*, 1990; Riis and Biggs, 2001). Traits possessed by such species include vegetative (clonal) reproduction, rapid growth, ability to utilise bicarbonate for photosynthesis and ability to form canopies (Rørslett, 1989). Additional traits possessed by this species indicative of tolerance to hydraulic stress include flexible stems and leaves that reduce frontal area exposed to flow, thereby reducing drag (e.g. Sand-Jensen, 2003). Flexible stems can also minimise drag through alignment parallel to the direction of flow and bending and forming a shielding canopy close to the substrate where free-stream water velocities are lower, thereby exposing only the upper surfaces to higher velocities (Sand-Jensen, 2003).

*Rorippa nasturtium-aquaticum* and *O. ovalifolia* are placed lower on the hydraulic disturbance axis relative to *P. crispus*. *Rorippa nasturtium-aquaticum* has weak, hollow stems and would not be expected to have high resistance to hydraulic disturbance. *Rorippa nasturtium-aquaticum* does have an advantage over *O. ovalifolia* in being able to colonise rapidly from vegetative fragments and hence may display rapid recovery from biomass loss. Grime *et al.* (1988), cited in Preston and Croft (1997), state that “detached stem pieces have a remarkable ability to root and form new plants”. Henry and Amoros (1996) have also noted the importance of downstream propagule drift as a means of colonisation for this species. Unusually for aquatic plants, the genus *Ottelia* appears to have poor vegetative dispersal capabilities (Cook and Urmi-Konig, 1984) and may rely on regeneration from seed banks.

*Typha* spp. and *S. validus* are placed in an intermediate position on the hydraulic disturbance axis. Both species are generally associated with stable water levels but do have means of recovery from disturbance. The linear leaves of *Typha* spp. would be expected to reduce drag (e.g. Willby *et al.*, 2000) but longer leaves would experience higher drag than shorter leaves (e.g. Sand-Jensen, 2003). Bornette *et al.*, (1994) noted that *Typha latifolia* (L.) was intolerant of flood scouring. However, the rhizome provides a means of recovery from biomass loss or death of aboveground biomass, and in some species of *Typha* detached pieces of rhizome can float and establish new colonies (Preston and Croft, 1997).

There is scant information on hydraulic tolerances of *S. validus*. Like *Typha* spp. the rhizomatous growth form of *S. validus* may allow rapid recovery from hydraulic disturbance in the event that aboveground biomass is lost and also serves to anchor the plant in the substrate. Emergent plants such as *Typha* spp. and *S. validus* can tolerate some bending in currents (e.g.

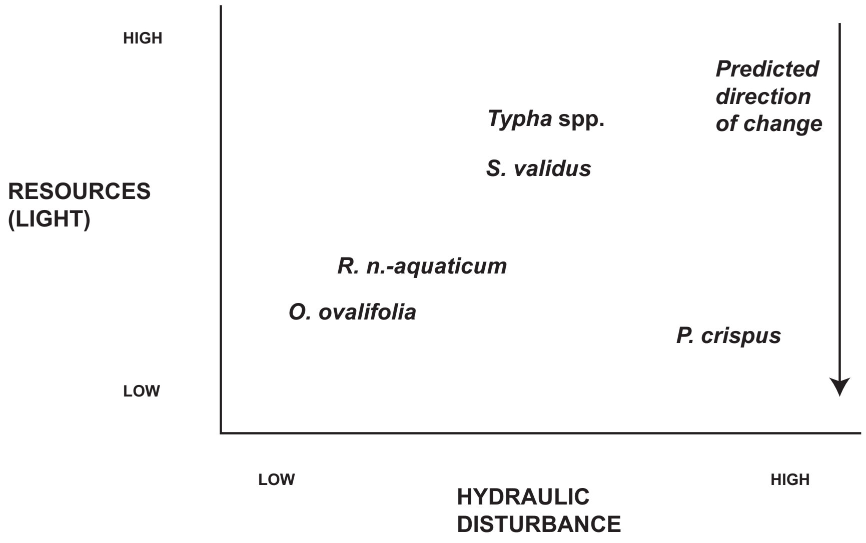

Figure 4. Predicted Occurrence of the Five Dominant Macrophyte Taxa within the Conceptual Model and Predicted Direction of Change in Assemblage Composition with Increasing Riparian Canopy Cover.

Sirjola, 1969). Groeneveld and French (1995) examined the tolerance of *Scirpus acutus* (tule) to hydrodynamic drag. Tule and *S. validus* have similar growth forms, i.e. the stem is a tapering cylinder with leaves reduced to scales. The internal structure of the tule stem provides both stem flexibility and resistance to bending deformation (Groeneveld and French, 1995). *Schoenoplectus validus* will tolerate flowing water; it has established populations in shallow water of moderate water velocity (approximately 0.30–0.50 $ms^{-1}$) downstream of Wivenhoe Dam on the Brisbane River (Mackay unpublished) indicating that this species also has some degree of stem flexibility. *Schoenoplectus validus* is therefore placed higher on the disturbance axis than *Typha* spp.

We therefore predict that Echidna Creek will change from a system dominated by robust emergent species (*Typha* spp., *S. validus*) to one dominated by submerged or low-growing emergent species (Figure 4).

## 1.4. Aims

This investigation has two objectives:

1. Assess the contribution of riparian shading and hydraulic conditions to spatial and temporal variations in the distribution and abundance of aquatic macrophytes in Echidna Creek; and
2. Compare macrophyte assemblage structure following canopy closure (riparian canopy cover at 75% or greater) with predictions from the conceptual model.

We focused our monitoring program on the five dominant taxa in the rehabilitation reach. We hypothesise from the conceptual model (Figure 4) that riparian revegetation and reduced light availability will favour the growth of *P. crispus*, *O. ovalifolia* and, to a lesser extent, *R. nasturtium-aquaticum* (shade tolerant) over the growth of *S. validus* and *Typha* spp., typically associated with unshaded habitats.

# 2. Materials and Methods

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## 2.1. Transect Establishment and Monitoring

In March 2002 fifty randomly-spaced permanent transects were established within a 500 m reach of the Echidna Creek rehabilitation site (Appendix 1). Each transect was marked by steel pegs and orientated perpendicular to the direction of streamflow. Depending on stream width either one or three quadrats (area 0.11 $m^2$) were located on each transect. Quadrats were distributed evenly across each transect. The location of each quadrat was fixed on the first survey.

## 2.2. Macrophyte Sampling

For each quadrat the cover of each of the five dominant taxa (i.e. *P. crispus*, *O. ovalifolia*, *S. validus*, *Typha* spp. and *R. nasturtium-aquaticum*) was recorded as <1%, 1%, 5%, and thereafter to the nearest 10%. From survey three onwards cover for each species was also estimated within a belt transect extending 50 cm each side of the transect line (total belt transect width 1 m). In addition to cover estimates, several morphological attributes were recorded for each species as indirect measures of abundance (Table 4). With the exception of *R. nasturtium-aquaticum* the length of all stems in each quadrat was measured to the nearest centimetre with a ruler. For *R. nasturtium-aquaticum* we measured the length of the longest stem and estimated the total number of stems in the quadrat. Measuring individual stems for this species was difficult as they naturally entangle and tended to break when teased apart.

## 2.3. Environmental Parameters

A series of environmental variables were quantified to characterise riparian canopy cover and hydraulic conditions within the study reach (Table 5). Riparian canopy cover at each transect was estimated using a spherical densiometer (Lemmon, 1956). Riparian canopy cover was measured at the centre quadrat on each transect. A single measure was considered representative of the entire transect because of the narrow channel widths (Appendix 1). The depth of each quadrat was determined to the nearest centimetre with a ruler, and the dominant substratum particle (as clay, silt, sand, cobble, rock, small boulder, boulder, bedrock) was also determined for each quadrat. Transect orientation (relative to magnetic north) was measured with a compass while facing upstream.

The wetted width, bankfull width and bankfull depth of each transect were determined from cross-sectional surveys with a staff and dumpy level. These parameters were used in a one-dimensional hydraulic model (HECRAS) to calculate shear stress, depth-averaged velocity and Froude Number at bankfull and low flow conditions for each transect. Stream discharge was determined from a gauge at the downstream end of the study reach. From discharge data, time since last bankfull discharge (DAYBFULL) and the number of freshes (DAYFRESH, defined as an instantaneous discharge exceeding 5 $Lsec^{-1}$) in the 28 days prior to each survey were calculated. These variables represent measures of hydraulic disturbance. Environmental parameters and their scale of measurement are summarised in Table 5.

Table 4. Summary of Attributes Recorded for Macrophytes.

| **Parameters** | ***P. crispus*** | ***O. ovalifolia*** | ***Typha* spp.** | ***S. validus*** | ***R. nasturtium-aquaticum*** |
|---|---|---|---|---|---|
| Quadrat Cover (%) | X | X | X | X | X |
| Belt Transect Cover (%) | X | X | X | X | X |
| Stem Length or Height[1] | X | X | X | X | |
| Total number of Stems | X | X | X | X | X |
| Number of Leaves | | | X | | |
| Length of Longest Stem | | | | | X |

[1] All stems present in each quadrat.

Table 5. Environmental Parameters Recorded and Scale of Measurement. Substrate Categories: Clay, Silt, Sand, Cobble, Rock, Small Boulder, Boulder, Bedrock.

| | | Scale of Measurement | | |
|---|---|---|---|---|
| **Variable** | **Description** | **Quadrat** | **Transect** | **Reach** |
| DEP | Depth (m) | X | | |
| SUB | Dominant substratum type | X | | |
| RIPCOVER | Riparian canopy cover (%) | | X | |
| ORIENT | Orientation (aspect) of transect (º) | | X | |
| BANKDEP | Bankfull depth (m) | | X | |
| BANKWID | Bankfull width (m) | | X | |
| WETWIDTH | Wetted width (m) | | X | |
| FROUDMAX | Maximum Froude No. in period 28 days prior to sampling (dimensionless) | | X | |
| SHEARMAX | Maximum shear stress in period 28 days prior to sampling ($Nm^{-2}$) | | X | |
| VELMAX | Maximum water velocity in period 28 days prior to sampling ($ms^{-1}$) | | X | |
| DAYBFULL | Days since last bankfull discharge | | | X |
| DAYFRESH | Instantaneous discharge > 5 $Lsec^{-1}$ | | | X |

## 2.4. Statistical Analysis

Unless otherwise specified, analyses presented in this report are based on the mean number of stems per transect for each species.

Regression models were developed to investigate the relative contribution of riparian canopy cover and hydraulic parameters to the growth of aquatic macrophytes in Echidna Creek and make preliminary predictions of assemblage composition when riparian canopy cover reaches 75%, the target of the rehabilitation plan (Anon., 2000). Logistic regression models were used to investigate relationships between the distribution of individual species and environmental variables; multiple linear regression (MLR) and simultaneous autoregressive (SAR) models were used to examine relationships between species abundance (as mean stem counts) and environmental variables.

Prior to regression analysis correlations between environmental (predictor) variables were examined using Spearman's non-parametric correlation coefficients. Highly intercorrelated environmental variables were removed to reduce collinearity (Tabachnick and Fidell, 1989; Graham, 2003) and the remaining variables were standardised (zero mean and unit variance). Response variables (i.e. stem counts for each species) were square-root transformed (Zar 1996). For both logistic and MLR models all environmental predictors were directly entered into the models. Constants were included for all models.

Autocorrelation within the dataset was also investigated. Autocorrelation is the lack of independence between observations, i.e. the value of an observation at a particular locality can be predicted from neighbouring localities (Legendre, 1993). Autocorrelation results in inflated Type I error and violates the assumption of independence of observations for classical methods of statistical analysis such as regression (Legendre and Trousellier, 1988). We tested for spatial and temporal autocorrelation in response (stem counts) and predictor (environmental) variables using Moran's *I* (Legendre and Fortin, 1989). Moran's *I* is calculated from the formula

$$I = \frac{n}{\sum_{i=1}^{n}\sum_{j=1}^{n} w_{ij}} \frac{\sum_{i=1}^{n}\sum_{j=1}^{n} w_{ij}(x_i - \bar{x})(x_j - \bar{x})}{\sum_{i=1}^{n}(x_i - \bar{x})^2}$$

where:

$w_{ij}$ are weights and $n$ is the number of lags, i.e. distance or time classes. Moran's $I$ ranges between +1 and -1, with positive values indicating positive autocorrelation (samples more similar than predicted from chance), negative values indicating negative autocorrelation (i.e. less similar than predicted by chance) and zero values indicating randomness (Legendre and Fortin, 1989). Values of Moran's $I$ can be plotted against lag to produce a correlogram. Before examining significance values for individual Moran's $I$ coefficients a global significance test for the correlogram is performed by examining significance values for individual Moran's $I$ coefficients with Bonferroni-corrected significance values i.e. $\frac{\alpha}{\text{lags}}$ (Legendre and Fortin, 1989). The number of lags can affect resolution of the correlogram. More classes provide better resolution and the power of the test is increased when there are greater numbers of distance pairs in each distance class. Sturge's rule was used to determine the appropriate number of lag classes, using the formula:

$$\text{Number of Classes} = 1 + 3.3\log_{10}(m),$$

where:

$m$ is the number of values in the matrix (i.e. upper or lower triangular matrix: each pair is only counted once) (Legendre and Legendre, 1998). Moran's $I$ was calculated using the SPDEP package in R (R Development Core Team, 2004), with a binary weighting scheme.

SAR models were used to investigate relationships between species abundances and environmental variables in the presence of spatial autocorrelation. Autoregressive (AR) models differ from linear regression models in having an additional term that accounts for autocorrelation i.e. patterns in species abundance that are not predicted by environmental variables but are related to species abundances in neighbouring locations (Keitt *et al.*, 2002). SAR models were developed using the procedure of Lichstein *et al.* (2002) and the SPDEP package in R (R Development Core Team, 2004). Following Lichstein *et al.* (2002), broadscale spatial patterns in species abundance data were examined to determine whether there was any broadscale spatially-structured variation in species abundance data not explained by environmental variables. Broadscale spatial pattern was modelled by trend surface analysis (Lichstein *et al.*, 2002) and all significant terms from the trend surface analysis were included in MLR and SAR models for each species. Spatial autocorrelation in the residuals of the MLR models was examined using Moran's $I$ as described above.

# 3. Results

## 3.1. Riparian Canopy Cover and Hydrology

A total of 11 surveys were conducted between the 11th March 2002 and 18th March 2004. Over this period mean riparian canopy cover of the study reach (i.e. mean of all transects per survey) increased from 52% to 71% and variability in mean riparian canopy cover (measured as standard deviation) decreased by 8% (Table 6), indicating a more uniform riparian canopy cover throughout the rehabilitation reach. Increases in the mean riparian canopy cover of the rehabilitation reach had been relatively small until Spring 2003 (Table 6).

The magnitude of change in riparian canopy cover varied considerably between transects (Figure 5; Appendix 1). Transects with initially high riparian canopy cover (>70%) showed little temporal variation in riparian canopy cover, even where death of trees and saplings occurred. Transects with low initial riparian canopy cover displayed considerable temporal variation in canopy cover (Figure 5). Temporal variation in canopy cover on initially unshaded transects was due to death of trees from frosts and flooding, and self-shading from *Typha* spp. and *S. validus*. These species were able to influence spherical densiometer readings when taller than 1.5 m. For example, the largest nett increase in riparian canopy cover (72%, transect 254 m, Appendix 1) was due to shading by *Typha* spp. and *S. validus*. Nett decreases in riparian canopy cover exceeding 10% were recorded for only three transects (Appendix 1).

The first 10 months of the study period were characterised by low stream discharge and relatively benign hydraulic conditions for aquatic macrophyte growth (Figure 6). More pronounced flooding occurred during the summer of 2002–2003 and intensive flooding occurred during the summer of 2003–2004 due to thunderstorm activity. The final four months of the study were therefore characterised by relatively high temporal variability in hydraulic conditions (Figure 6).

## 3.2. Spatial and Temporal Variations in Macrophyte Distribution and Abundance

The distribution and abundance of the five dominant macrophyte taxa varied considerably throughout the study period. From the initial survey in March 2002 the number of vegetated transects (i.e. transects with at least one of the dominant taxa present) increased through winter–late spring 2002 to a maximum of 82%, then decreased until September 2003 (Figure 7). The number of vegetated transects increased in November 2003 by approximately 10% but decreased again to 50% during the summer of 2003–2004 (Figure 7). The increase in the number of transects colonised during autumn–late spring of 2002, a period of generally low discharge in south-east Queensland,

Table 6. Sampling Dates and Mean Riparian Canopy Cover Recorded for each Survey ($n$=50 for each survey).

| Date | Mean Riparian Cover (%) | Standard Deviation (%) | Range (Min-Max) |
|---|---|---|---|
| 11/03/2002 | 52 | 34 | 0–99 |
| 5/04/2002 | 51 | 33 | 1–99 |
| 19/06/2002 | 51 | 33 | 1–100 |
| 12/07/2002 | 51 | 34 | 2–100 |
| 13/09/2002 | 52 | 32 | 1–99 |
| 4/11/2002 | 58 | 28 | 5–99 |
| 12/02/2003 | 55 | 35 | 0–100 |
| 4/04/2003 | 55 | 33 | 4–100 |
| 3/09/2003 | 57 | 30 | 5–100 |
| 4/11/2003 | 62 | 27 | 8–99 |
| 18/03/2004 | 71 | 26 | 12–100 |

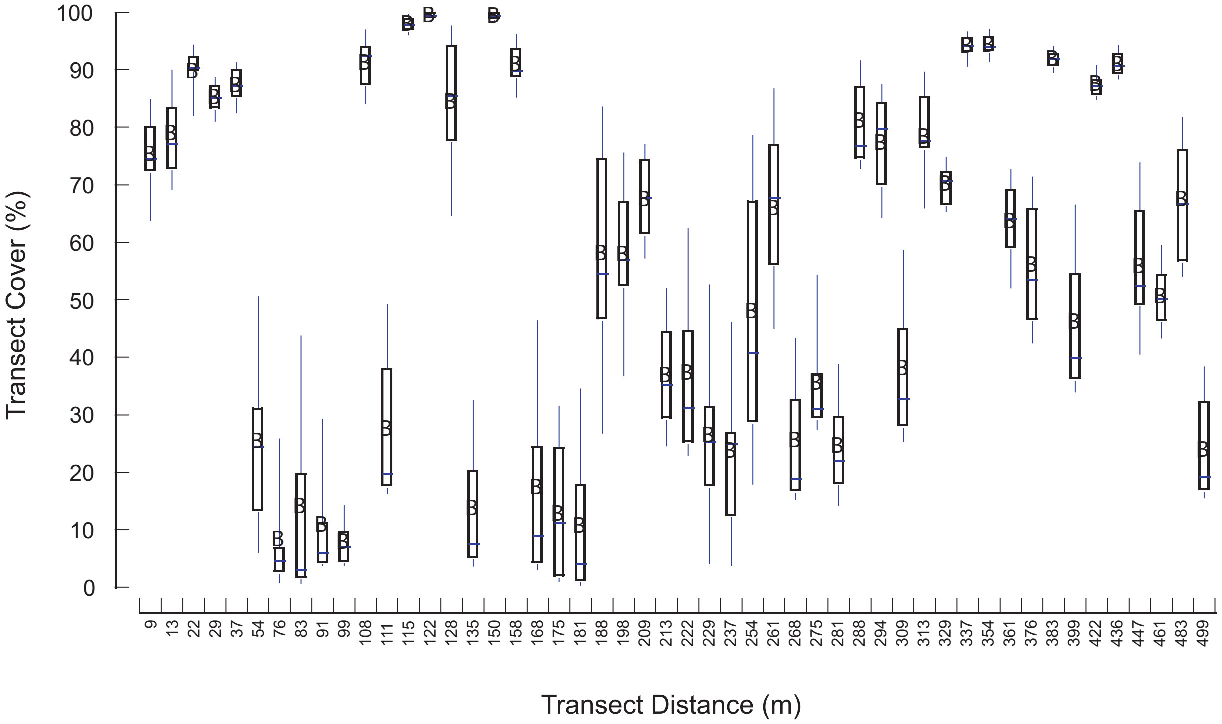

Figure 5. Box and Whisker Plot of Riparian Canopy Cover Recorded for Each Transect over Eleven Surveys Conducted from March 2002 to March 2004.

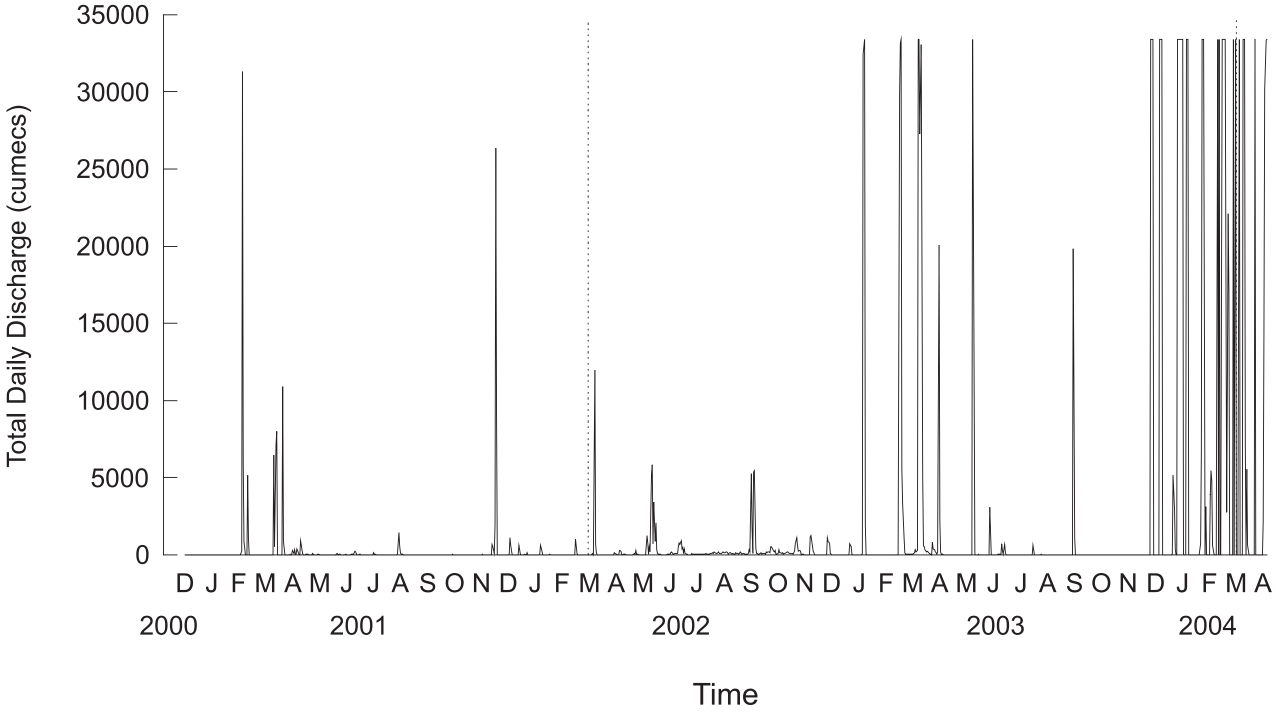

Figure 6. Hydrology of Echidna Creek. Dashed Lines Show the Study Period (March 2003–March 2004).

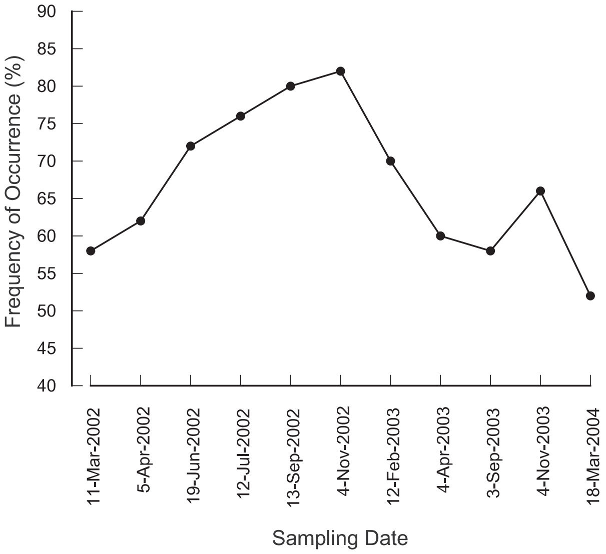

Figure 7. The Frequency of Occurrence of the Five Dominant Macrophyte Taxa on Transects on Each of the Eleven Echidna Creek Surveys (*n* = 50 per survey date).

Table 7. Spearman Rank Correlation Coefficients for Relationships between Proportion of Transects Colonised by the Dominant Macrophyte Taxa, Riparian Canopy Cover and Days since Bankfull Discharge (n = 11). Significance 0.05<P<0.01.

| **Parameter** | **No. Transects Colonised** | **Mean Riparian Canopy Cover** | **Days Since Bankfull Discharge** |
|---|---|---|---|
| **No. transects colonised** | **1** | **-** | **-** |
| **Mean riparian canopy cover** | **-0.329** | **1** | **-** |
| **Days Since Bankfull Discharge** | **0.721*** | **-0.427** | **1** |

suggests that macrophytes became established during this period despite lower water temperatures, and were scoured during higher flow periods in late spring–summer of 2002–2003 and 2003–2004 (e.g. Figure 6). The number of transects colonised on each occasion was significantly correlated with days since bankfull discharge but was not correlated with riparian canopy cover (Table 7).

The emergent taxa (*S. validus*, *Typha* spp. and *R. nasturtium-aquaticum*) were the most widely distributed species throughout the study reach (Figure 8). These species were generally recorded on at least 30% of transects during each survey. *Schoenoplectus validus* and *Typha* spp. showed relatively little temporal variation in the proportion of transects colonised although *Typha* spp. showed peaks in transect cover in late spring of 2002 and 2003 (Figure 8). In contrast, *P. crispus* and *R. nasturtium-aquaticum* displayed greater temporal variation in the number of transects colonised (Figure 8). Like *Typha* spp., the frequency of occurrence of *R. nasturtium-aquaticum* peaked in late spring each year. From 2003 *P. crispus* declined considerably in distribution throughout the study reach and was not recorded on any transect in the latest survey (March 2004). *Rorippa nasturtium-aquaticum* was also not recorded during this survey. This survey followed a period of relatively harsh hydraulic conditions (see Figure 6). *O. ovalifolia* was rare in the reach, occurring at fewer than 10% of transects during each survey.

All species except *O. ovalifolia* were recorded from transects with riparian canopy cover >75% (Table 8). *Potamogeton crispus* occurred on relatively few transects where riparian canopy cover was less than 40% but occurred on a greater proportion of transects (and in greater abundances) where riparian canopy cover exceeded 40% (Table 8). This may be due to competition for space from *Typha* spp. and *S. validus*,

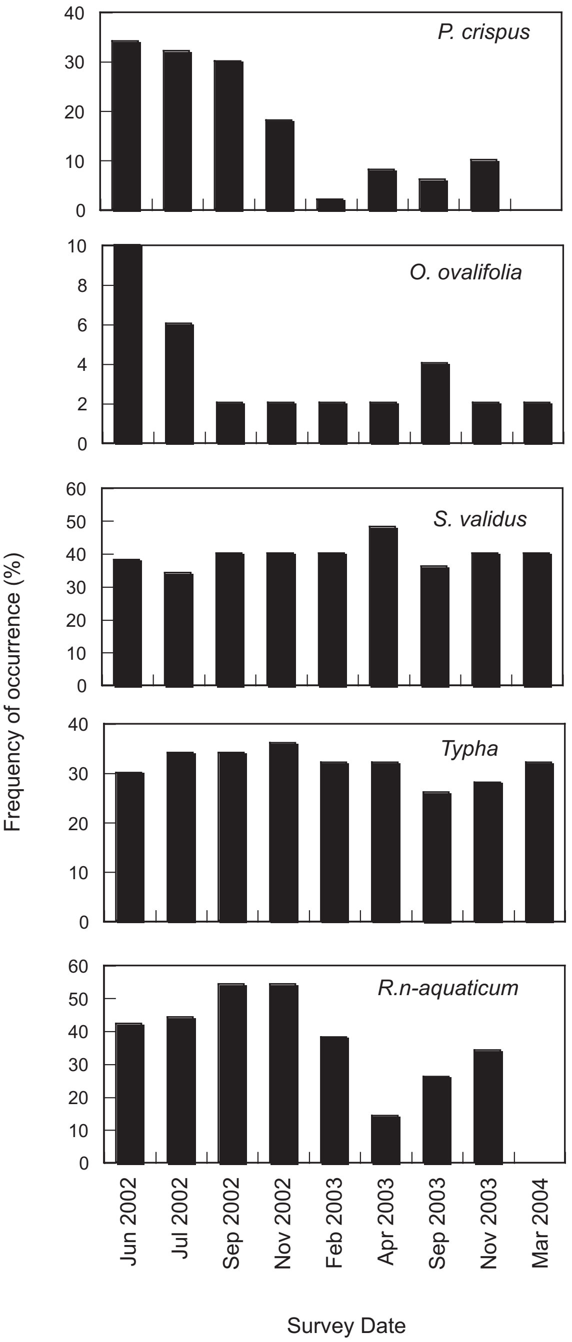

Figure 8. Frequency of Occurrence of the Five Dominant Macrophyte Taxa on Transects on Each of the Eleven Survey Dates.

which occurred more frequently where riparian canopy cover was less than 40% (Table 8). *Rorippa nasturtium-aquaticum* also occurred more frequently where riparian canopy cover was less than 40%. This suggests that *P. crispus*, *R. nasturtium-aquaticum*, *S. validus* and, to a lesser extent, *Typha* spp., could maintain populations in Echidna Creek even if riparian canopy cover throughout the reach was at least 75%.

The five dominant macrophyte taxa were not recorded on transects 22, 108, 115, 122, 150, 288, 337 and 354 on any of the eleven surveys. To compare the environmental characteristics of transects that did not support macrophytes (non-vegetated) with those that did (vegetated), environmental data were ordinated using semi-strong hybrid multidimensional scaling (SSHMDS; Belbin, 1995). Environmental data for each transect were averaged over the eleven surveys and range standardised to account for different scales of measurement. From the range standardised dataset a transect x transect association matrix was generated using the Euclidean distance measure. 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. 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 and 1000 randomisations (Belbin, 1995).

The eight non-vegetated transects did not differ appreciably from vegetated transects in terms of environmental conditions but non-vegetated transects were positioned on the negative extremity of axis 1 and the positive extremity of axis 2 (Figure 9). Non-vegetated transects tended to have higher RIPCOVER, higher SHEARMAX, lower VELMAX and coarser substrates than vegetated transects (Figure 9). The structure of the riparian canopy may be important; transects 108, 115, 122 and 150 had a dense riparian canopy of low-growing sandpaper figs that were more efficient in shading than taller bunya pines and other riparian species. It is also possible that high riparian canopy cover, combined with high shear stress, may limit the distribution of aquatic macrophytes within the study reach (e.g. Biggs, 1996).

The abundance of the dominant macrophyte taxa in relation to riparian canopy cover and maximum shear stress is shown in Figure 10. Relatively high abundances of *P. crispus* occurred over a wide range of riparian canopy cover and maximum shear stress values greater than 200 $Nm^{-2}$. In comparison,

Table 8. Frequency of Occurrence and Abundance (as Mean Stem Counts) of the Five Dominant Macrophyte Taxa on Transects, arranged by Riparian Canopy Cover Categories (*n*=550).

| | | **Riparian Canopy Cover (%)** | | |
|---|---|---|---|---|
| **Taxon** | **Parameter** | **<40% (*n* = 207)** | **40-75% (*n* = 148)** | **>75% (*n* = 195)** |
| *P. crispus* | Frequency of occurrence | 1.0 | 14.9 | 13.3 |
| | Mean no. stems | 0.01 | 0.42 | 0.42 |
| *O. ovalifolia* | Frequency of occurrence | 2.6 | 4.1 | 0 |
| | Mean no. stems | 0.02 | 0.06 | 0 |
| *S. validus* | Frequency of occurrence | 30.8 | 18.9 | 9.2 |
| | Mean no. stems | 1.97 | 1.39 | 0.21 |
| *Typha* spp. | Frequency of occurrence | 42.1 | 21.6 | 4.8 |
| | Mean no. stems | 0.89 | 0.26 | 0.04 |
| *R. n.-aquaticum* | Frequency of occurrence | 39.0 | 23.0 | 10.6 |
| | Mean no. stems | 3.54 | 1.86 | 0.77 |

Riparian canopy cover categories based on key values cited in the literature for controlling aquatic macrophyte growth (Dawson and Kern-Hansen, 1979; Jorga *et al.*, 1982; Bunn *et al.*, 1999) and the target canopy cover for Echidna Creek (Anon., 2000).

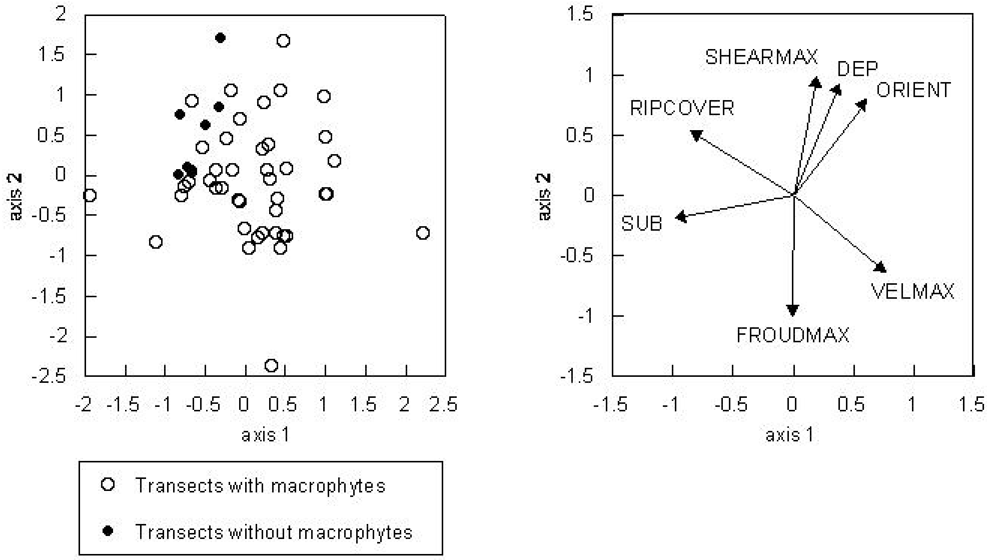

Figure 9. SSHMDS Ordination of Transect Habitat Data (stress = 0.146, two dimensions, interval regression). (a) Distribution of transects in ordination space. (b) Significant environmental variables correlated with the ordination space ($P<0.05$). See Table 5 for variable acronyms.

maximum abundances of the remaining species tended to occur below a maximum shear stress of 150 $Nm^{-2}$ and riparian canopy cover below 60% (Figure 10). *Rorippa nasturtium-aquaticum* was more abundant below 150 $Nm^{-2}$ but was also abundant over a wide range of riparian canopy cover values (Figure 10). All species were recorded on transects where riparian canopy cover exceeded 75% (Figure 10). With the exception of *P. crispus* all species generally occurred at maximum shear stress values below 100 $Nm^{-2}$, thus supporting the placement of *P. crispus* on the positive extreme of the hydraulic axis of the conceptual model (see Figure 4).

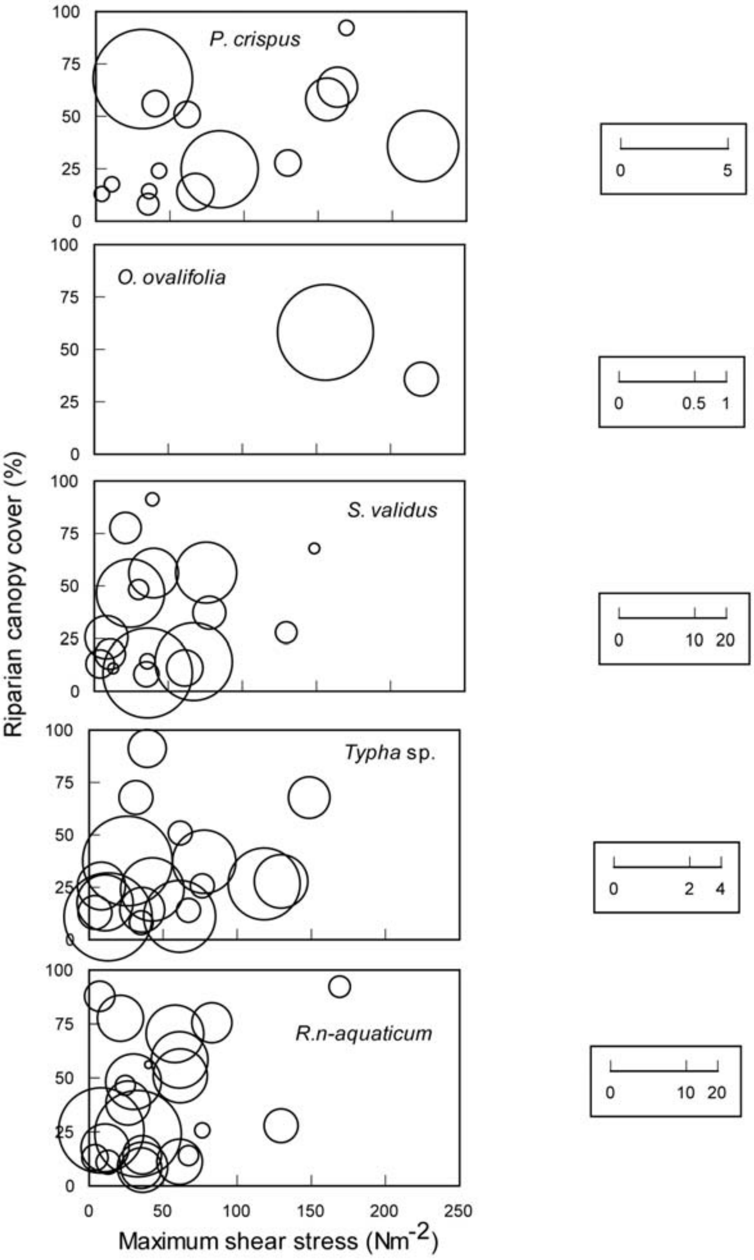

Figure 10. Bubble Plots of Mean Number of Stems per Transect Versus Riparian Canopy Cover and Maximum Shear Stress.

## 3.3. Regression Models

### 3.3.1 Autocorrelation

Correlograms assessing spatial and temporal autocorrelation in the dataset are presented in Appendices 2–5. Although the shape of a correlogram is indicative of underlying spatial or temporal patterns (Sokal and Oden, 1978a,b; Anselin, 1996) we have not provided an in-depth interpretation of correlogram shape as our intention was only to assess the extent of autocorrelation in the dataset.

### 3.3.2 Spatial Autocorrelation

Determination of the number of lag (distance) classes using Sturge's rule (Legendre and Legendre, 1998) produced 11 classes with relatively few distance pairs in the 11th lag class. Since the last distance class contained fewer than 1% of the total records it was considered unreliable (Legendre and Fortin, 1989) and was not interpreted.

There was little significant spatial autocorrelation in the dataset (Appendices 2–3). Riparian cover, transect orientation and substrate composition were the only environmental variables to display significant positive autocorrelation (Appendix 2). Positive autocorrelation for riparian canopy cover within the first lag (1–45 m) is not surprising when considered in relation to Figure 5. Adjacent transects tend to have similar riparian canopy cover (e.g. compare transects 9–37; 54–99; 168–181; 213–237). Positive autocorrelation in transect orientation may reflect the sinuousity of the stream channel and the distances at which changes in channel direction occur. Similarly, positive autocorrelation in substrate composition at the first lag indicates similarity in substrate composition over short distances. This may also reflect the distances between hydraulic units (i.e. riffles and pools).

*Typha* spp. was the only taxon to show significant positive autocorrelation in mean stem counts (Appendix 3). Although the coefficient for *P. crispus* at the 5th lag (distance class 181–225 m) was significant ($P<0.05$) the overall correlogram was not significant at the Bonferroni-adjusted significance level. Positive spatial autocorrelation at the first lag for *Typha* spp. may reflect its ability to colonise laterally into adjacent habitats through rhizome extension (e.g. Miao *et al.*, 2000). The correlogram for *O. ovalifolia* (a straight line with zero intercept) suggests randomness in the abundance of this species; correlograms for *S. validus* and *R. nasturtium-aquaticum*, with alternating peaks, indicate patchiness in species abundance (Legendre and Fortin, 1989).

### 3.3.3 Temporal Autocorrelation

Determination of the number of lag (time) classes using Sturge's rule (Legendre and Legendre, 1998) produced 7 lag classes. Significant temporal autocorrelation was present in only one environmental variable (DAYBFULL, see Appendix 4) and significant temporal autocorrelation was not present in the biotic variables (Appendix 5). Correlograms for SHEARMAX and VELMAX were very similar as these variables are highly intercorrelated (see Table 9). Correlograms for *P. crispus* and *S. validus* both showed spikes at 371.5 days (time class 319–424 days) which may indicate an annual population cycle. Correlograms for *Typha* spp. and *R. nasturtium-aquaticum* both displayed increasing negative autocorrelation with increasing time.

### 3.3.4 Regression Models

Spearman correlation coefficients indicated little correlation amongst environmental variables (Table 9). VELMAX was significantly correlated with SUB, DEP, FROUDMAX and SHEARMAX and therefore was not included in regression models. There was little significant correlation between mean stem counts for individual species. However, *P. crispus* was significantly correlated with *O. ovalifolia* stem counts, whereas *S. validus* stem counts were significantly correlated with *Typha* spp. and *R. nasturtium-aquaticum* stem counts (Table 9), suggesting some degree of association between these species. Mean stem counts for each species were correlated with different environmental variables (Table 9). *Typha* spp. and *S. validus*, both robust emergent species, were both negatively correlated with RIPCOVER and SUB, indicating greater abundances of these species were associated with unshaded areas with fine substrates. *Potamogeton crispus* and *R. nasturtium-aquaticum* stems counts were also negatively

Table 9. Spearman Rank Correlation Coefficients for Biotic (stem counts) and Abiotic (environmental) Variables.

| | PCRISP | OTTELIA | SCHOENO | TYPHA | CRESS | RIPCOVER | ORIENT | SUB | DEP | FROUDMAX | SHEARMAX | VELMAX |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **PCRISP** | 1.000 | | | | | | | | | | | |
| **OTTELIA** | 0.384** | 1.000 | | | | | | | | | | |
| **SCHOENO** | | | 1.000 | | | | | | | | | |
| **TYPHA** | | | 0.370** | 1.000 | | | | | | | | |
| **RORIPPA** | | | 0.404** | | 1.000 | | | | | | | |
| **RIPCOVER** | -0.381** | | -0.546** | -0.587** | -0.496** | 1.000 | | | | | | |
| **ORIENT** | | | | | | | 1.000 | | | | | |
| **SUB** | -0.335* | | -0.310* | -0.701** | | 0.506** | | 1.000 | | | | |
| **DEP** | 0.284* | 0.298* | | | -0.609** | | 0.321* | | 1.000 | | | |
| **FROUDMAX** | | | | | | | | 0.367** | -0.408** | 1.000 | | |
| **SHEARMAX** | | 0.318* | | | -0.367** | | | | | -0.440** | 1.000 | |
| **VELMAX** | | | | | | | | 0.328* | -0.363** | 0.892** | -0.387* | 1.000 |

Biotic and abiotic variables summarised across all surveys for each transect ($n = 50$). Significance levels * $0.05>P>0.01$; ** $P<0.01$.

Table 10. Parameter Estimates (± standard error) for Logistic Regression Models Predicting the Occurrence of Macrophyte Taxa from Standardised Environmental Variables (zero mean and unit variance).

| Parameter | *P. crispus* | *S. validus* | *Typha* spp. | *R. n-aquaticum* |
|---|---|---|---|---|
| RIPCOVER | -0.92±0.38* | -1.47±0.49** | | -2.59±1.03* |
| ORIENT | | | | 2.68±1.16* |
| DEP | | | | -2.30±1.07* |
| SUB | | | -5.38±2.57* | |
| Constant | | -0.84±0.41* | -1.98±0.87* | 4.82±2.08* |
| Nagelkerke $R^2$ | 0.266 | 0.478 | 0.655 | 0.724 |
| Absence correctly predicted (%) | 77.8 | 87.5 | 90.6 | 84.6 |
| Presence correctly predicted (%) | 69.6 | 55.6 | 83.3 | 97.3 |
| Overall | 74.0 | 76.0 | 88.0 | 94.0 |

Only significant parameters shown. Significance *$0.05>P>0.01$ **$0.01>P>0.001$ *** $P<0.001$. See Table 5 for a description of environmental parameters.

Table 11. Parameter Estimates for Multiple Linear Regression Models of Stem Counts (mean per transect) for Individual Macrophyte Species.

| Parameter | *P. crispus* | *S. validus* | *Typha* spp. | *R. n-aquaticum* |
|---|---|---|---|---|
| RIPCOVER | -0.295* | -0.454** | -0.314* | -0.337** |
| ORIENT | | | -0.306* | |
| DEP | 0.347* | | | -0.358** |
| SUB | | | -0.286* | |
| FROUDMAX | | | | 0.259* |
| SHEARMAX | | | | |
| $x$ | | | | |
| $x^2$ | | | -0.425* | |
| $x^3$ | | | | |
| Intercept | *** | *** | *** | *** |
| Durbin-Watson | 1.946 | 1.831 | 1.743 | 1.888 |
| ANOVA | 2.942* | 2.994* | 3.152** | 6.355*** |
| Adjusted $R^2$ | 0.192 | 0.196 | 0.283 | 0.396 |

Only significant variables shown. All environmental variables standardised (zero mean and unit variance) prior to analysis. Significance *$0.05>P>0.01$ **$0.01>P>0.001$ *** $P<0.001$. $x$, $x^2$ and $x^3$ are significant parameters from the trend surface regression describing broadscale spatial structure. See Table 5 for a description of environmental parameters.

correlated with RIPCOVER. *Potamogeton crispus* and *O. ovalifolia* were positively correlated with DEP. SHEARMAX was positively correlated with *O. ovalifolia* abundance and negatively correlated with *R. nasturtium-aquaticum* abundance (Table 9).

Preliminary regression models included data from all transects and surveys (i.e. $n = 550$). However, the large number of zero values within the dataset resulted in poor regression models with low $R^2$ and poor distribution of residuals. We therefore summarised data for each transect across all surveys (i.e. $n = 50$) and used this smaller dataset to construct regression models. Regression models were not developed for *O. ovalifolia* due to the low number of records for this species.

Logistic regression models showed that the distribution of *P. crispus*, *S. validus*, *Typha* spp. and *R. nasturtium-aquaticum* was associated with different environmental variables (Table 10). The distribution of *P. crispus*, *S. validus* and *R. nasturtium-aquaticum* was negatively associated with riparian canopy cover. Standardised regression coefficients indicated that the effect of riparian canopy cover was greatest upon *R. nasturtium-aquaticum*, followed by *S. validus* and *P. crispus*, generally supporting the conceptual model (Figure 4). The spatial distribution of taxa throughout the study reach was not correlated with hydraulic (disturbance) parameters, although *Typha* spp. occurred more frequently on fine substrates (Table 10). The presence and absence of all species could be correctly predicted with success rates of between 55.6 and 97.3% (Table 10). Overall success rates ranged from 74.0% for *P. crispus* to 94% for *R. nasturtium-aquaticum* (Table 10).

In comparison to logistic models, multiple linear regression (MLR) models were generally poor predictors of mean stem counts for each species (Table 11). MLR models for *P. crispus*, *S. validus* and *Typha* spp. explained approximately 20% of the variation in mean stem counts, with 40% of the variation in mean stem counts for *R. nasturtium-aquaticum* explained by the environmental variables. Mean stem counts were negatively correlated with RIPCOVER for all species. Standardised regression coefficients showed that riparian canopy cover had the greatest effect on *S. validus* abundance and the least effect on *P. crispus* abundance (Table 11). Like logistic models, hydraulic variables were poor predictors of assemblage attributes. Mean stem counts for *R. nasturtium-aquaticum* were positively correlated with FROUDMAX and negatively correlated with DEP, indicating that higher abundances of *R. nasturtium-aquaticum* occur in shallow areas.

Residuals from the MLR models (Figure 11) indicated heteroscedascity (i.e. errors in prediction are not equal) which can weaken regression models (Tabachnik and Fidell 1989). Similar patterns were observed in the residuals for all models. These patterns do not appear to be caused by autocorrelation as Moran's *I* for residuals from individual species models showed very little autocorrelation to be present (Figure 11). Autocorrelation within the residuals for *S. validus* and *Typha* spp. indicated that SAR models were appropriate for these species. SAR models were also produced for *P. crispus* and *R. nasturtium-aquaticum* for comparison with MLR regression models. For *S. validus* and *R. nasturtium-aquaticum* Aikike's Information Criterion (AIC) for the full model exceeded the AIC value for the null model, indicating poor model fits. Thus the model fit for *P. crispus* was poor. Removing variables from the models provided only slight improvements in model fits, as determined by AIC and Wald statistics (Table 12).

Differences between MLR and simultaneous autoregressive (SAR) models were evident for *Typha* spp. (compare Tables 11 and 12). RIPCOVER was the only significant parameter for the *Typha* spp. MLR model but RIPCOVER, ORIENT, SUB and $x^2$ (a significant term from the trend surface analysis) were significant terms in the *Typha* spp. SAR model. The MLR and SAR models for *S. validus* produced similar parameter estimates, although the SAR model for *S. validus* must be interpreted with caution (Table 12). MLR and SAR models for *P. crispus* and *R. nasturtium-aquaticum* produced similar parameter estimates but SAR models for *P. crispus* also included SHEARMAX and terms from the trend surface regression, indicating broadscale spatial pattern (Table 12).

To examine the relative contribution of riparian canopy cover and hydraulic disturbance to temporal trends in species abundance we used univariate curve fitting procedures to fit curves to scatterplots of (a) species abundance versus riparian canopy cover and (b) species abundance versus DAYBFULL (as an indicator of hydraulic disturbance) (Figure 12). CurveExpert 1.3 was used to fit a variety of curves to each scatterplot. Biologically meaningful curves were selected in each case. Thus the curve fits presented in Figure 12 and Table 14 may not have necessarily explained the most variation in species abundance but were the most biologically interpretable.

The relative variation explained by riparian canopy cover and days since bankfull discharge varied between species (Table 13). RIPCOVER explained very little temporal variation in *P. crispus* abundance (8% versus 60% for DAYBFULL). DAYBFULL also explained more of the variance in *R. nasturtium-aquaticum* abundance than RIPCOVER. RIPCOVER and DAYBFULL explained equal proportions of the variance in *S. validus* abundance but RIPCOVER explained a greater proportion of the variation in *Typha* spp. abundance than DAYBFULL. Greater abundances of all species occurred as the number of days since bankfull discharge increased, especially where days since bankfull discharge exceeded 400 days (Figure 12).

Curve fits for RIPCOVER (Table 13) were used to determine the riparian canopy cover where the abundance of each species would be zero. From these models it was estimated that riparian canopy cover greater than 70% would be required to eliminate *S. validus*, *Typha* spp. and *R. nasturtium-aquaticum* whereas riparian canopy cover greater than 80% would be required to eliminate *P. crispus*.

Table 12. Parameter Estimates (± standard error) for Simultaneous Autoregressive (SAR) Models Describing Relationships between Stem Counts for Individual Species and Standardised Environmental Variables.

| **Parameters** | ***P.crispus*** | ***S. validus*** | ***Typha* spp.** | ***R. n-aquaticum*** |
|---|---|---|---|---|
| **RIPCOVER** | **-0.32 ± 0.10**** | **-0.47 ± 0.12***** | **-0.14 ± 0.07*** | **-0.39 ± 0.11***** |
| **ORIENT** | ▨ | | | ▨ |
| **DEP** | **0.32± 0.11**** | ▨ | | **-0.32 ± 0.11**** |
| **SUB** | ▨ | ▨ | | |
| **FROUDMAX** | ▨ | | | **0.26 ± 0.10**** |
| **SHEARMAX** | **0.24 ± 0.10**** | | ▨ | ▨ |
| $x$ | **0.39 ± 0.01**** | ▨ | ▨ | ▨ |
| $x^2$ | **0.32 ± 0.10**** | | | **0.31 ± 0.01*** |
| $x^3$ | ▨ | ▨ | ▨ | ▨ |
| **CONSTANT** | **0.59 ± 0.21**** | | **0.31 ± 0.13*** | **0.75 ± 0.21**** |
| **Rho** | **-0.625** | **0.282** | **0.337** | **-0.316** |
| **Wald** | **4.280*** | **1.898** | **3.017** | **1.527** |
| **AIC** | **113.05** | **136.56** | **77.88** | **122.71** |
| **AIC (LM)** | **114.75** | **136.08** | **78.85** | **121.83** |
| **LM test for residual correlation** | **0.414** | **3.917*** | **0.404** | **0.183** |

Significance * $0.05>P>0.01$; **$0.01>P>0.001$; *** $P<0.001$. Shaded boxes indicate variables excluded from final model. $x$, $x^2$ and $x^3$ are significant parameters from the trend surface regression describing broadscale spatial structure. See Table 5 for a description of environmental parameters. The Wald statistic is a test of the hypothesis that there is no relationship between predictor and response variables, i.e. $\beta = 0$ (Quinn and Keough, 2002).

Table 13. Univariate Regression Curve Fits for Stem Counts Versus Riparian Canopy Cover and DAYBFULL.

| **Taxon** | **Predictor** | **Equation** | **Canopy Cover Where Abundance = 0** |
|---|---|---|---|
| ***P. crispus*** | **RIPCOVER** | $Y = 0.734 - 0.0084x$; ($R^2 = 0.08$) | **87%** |
| | **DAYBFULL** | $Y = 0.086 + 0.0005x$; ($R^2 = 0.60$) | |
| ***S. validus*** | **RIPCOVER** | $Y = -23.38 + 0.827x - 0.0069x^2$; ($R^2 = 0.26$) | **74%** |
| | **DAYBFULL** | $Y = 0.818 + 0.0010x$; ($R^2 = 0.24$) | |
| ***Typha* spp.** | **RIPCOVER** | $Y = 1.852 - 0.026x$; ($R^2=0.67$) | **71%** |
| | **DAYBFULL** | $Y = 0.216 + 0.00055x$; ($R^2=0.53$) | |
| ***R. n-aquaticum*** | **RIPCOVER** | $Y = 9.205 - 0.1280x$; ($R^2=0.39$) | **72%** |
| | **DAYBFULL** | $Y = 0.8716 + 0.00354x$;($R^2=0.53$) | |

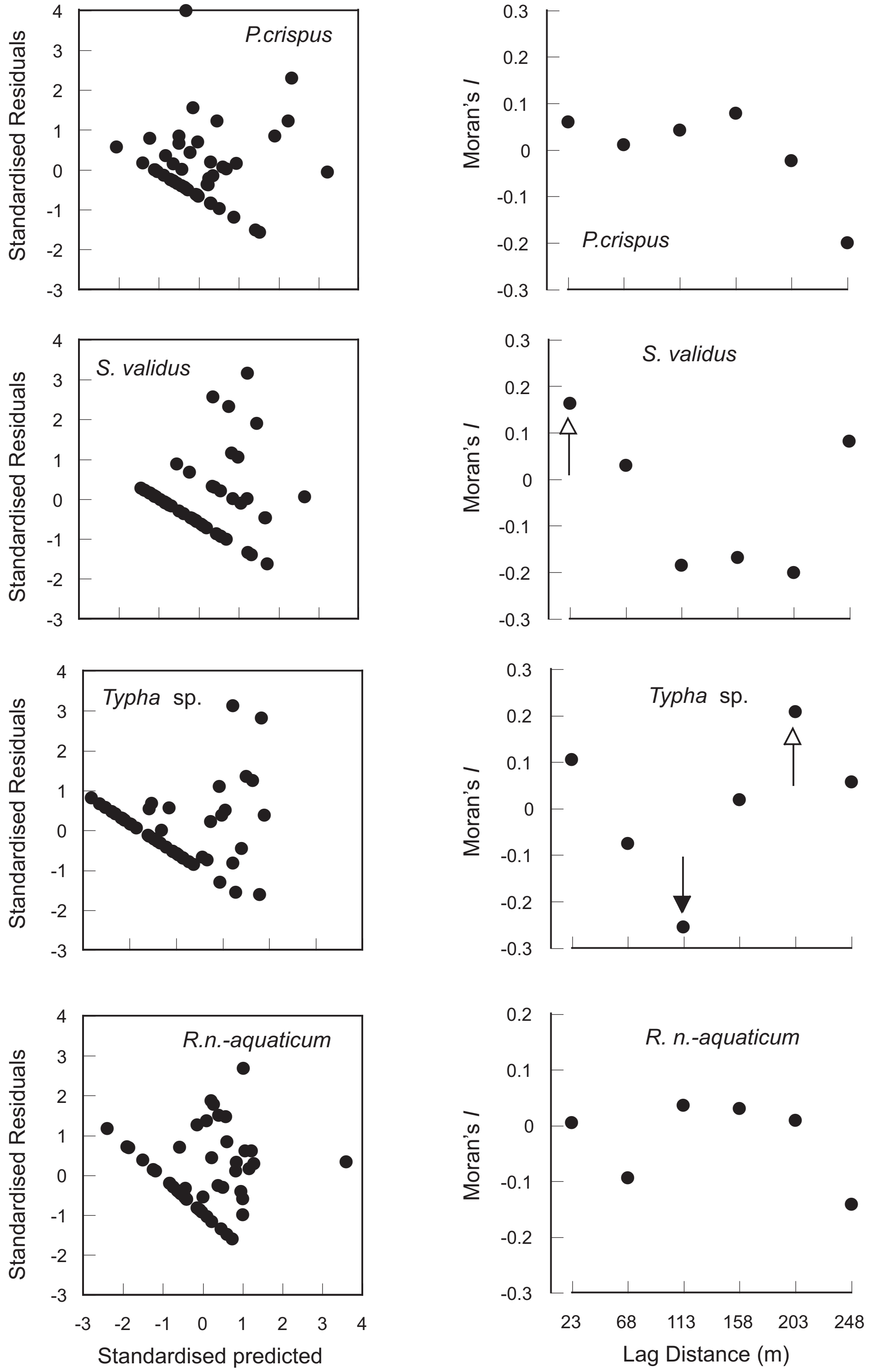

Figure 11. Residuals from Multiple Regression Models and Moran's *I* Correlograms for Autocorrelation within Model Residuals. Arrows indicate significant positive autocorrelation (open arrow) and significant negative autocorrelation (filled arrow).

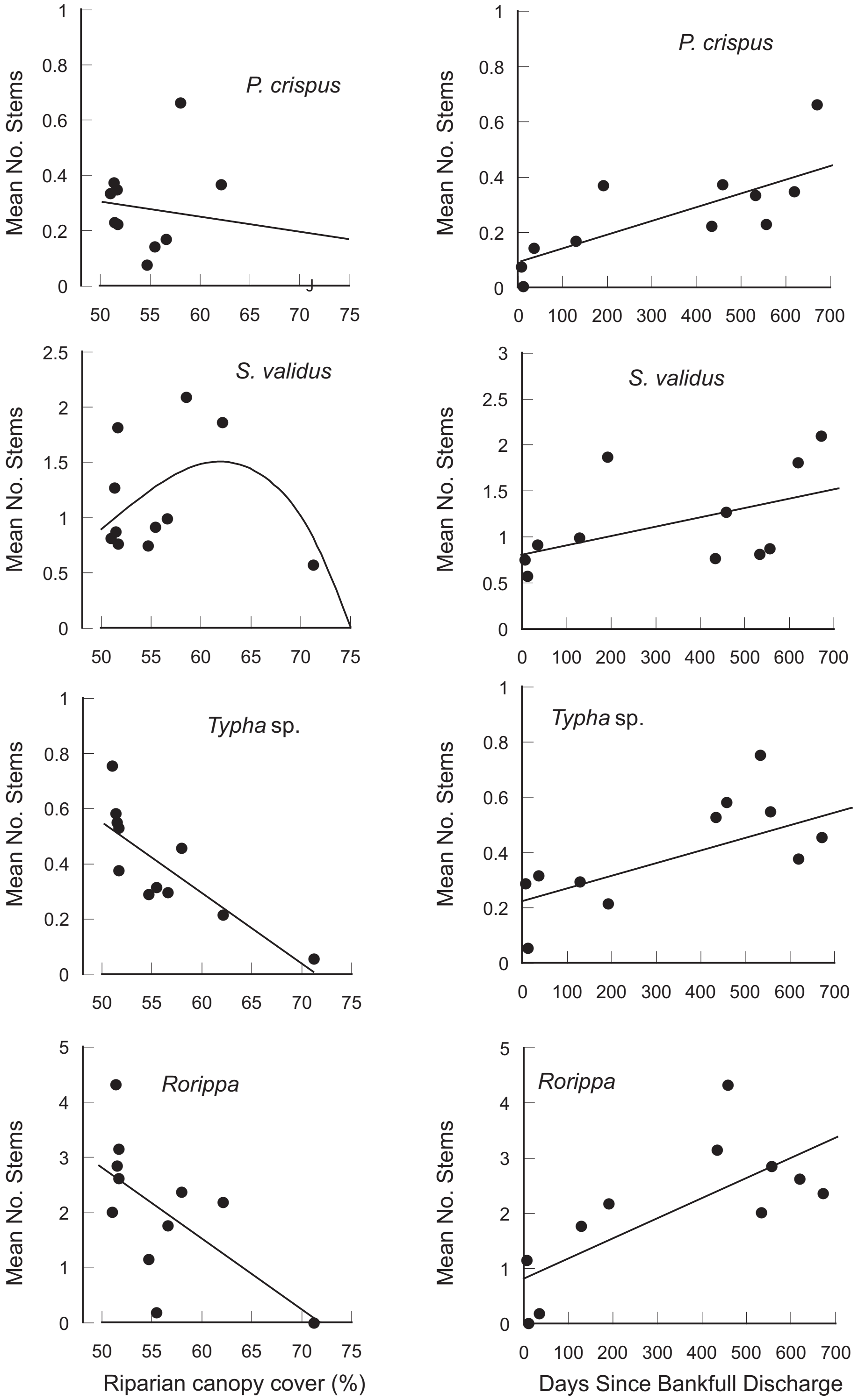

Figure 12. Univariate Curve Fits for Mean Number of Stems per Survey Versus Riparian Canopy Cover and Days since Bankfull Discharge.

## 4. Discussion

Riparian canopy closure within the entire rehabilitation reach (i.e. canopy cover of >75%) was not achieved within the desired time frame (Anon., 2000) and therefore the results of the aquatic macrophyte monitoring program have not been as dramatic as anticipated. An additional season of growth may be required before substantial increases in the minimum riparian canopy cover are achieved (see Table 6). Nonetheless the results of the monitoring program to date have provided insights as to the relative contribution of riparian shading and hydraulic habitat to the growth of aquatic macrophytes in a disturbed headwater stream, and permit tentative predictions of species distribution and abundances following canopy closure to be made. We hypothesised from our conceptual model (Figure 4) that riparian canopy cover and hydraulic conditions would be the primary abiotic determinants of macrophyte assemblage structure in Echidna Creek and that the different macrophyte growth forms would respond in different ways to riparian shading. The results of the monitoring program have to some extent validated these hypotheses.

Spatial and temporal variations in macrophyte distribution and abundance were controlled by different abiotic factors for each species. The spatial distribution of the dominant macrophyte species throughout the rehabilitation reach was most strongly related to riparian canopy cover. The strength of this relationship varied according to growth form. The magnitude of standardised regression coefficients from logistic regression models indicated that riparian canopy cover most strongly influenced the distribution of *R. nasturtium-aquaticum*, followed by *S. validus* and *P. crispus*. The conceptual model predicted that the distribution of *P. crispus* would be the least influenced by riparian canopy cover and *Typha* spp. and *S. validus* the most strongly influenced. The distribution of *Typha* spp. was not related to riparian canopy cover but was strongly related to substrate composition. Within the rehabilitation reach *Typha* spp. often occurs on clay or silt substrates possibly due to the ease with which rhizome extension can occur. Catchment management practices that reduce silt deposition in streams may therefore have more impact on the distribution of *Typha* spp. than increased riparian shading.

The factors controlling spatial variations in species abundances were more difficult to determine due to the poor MLR and SAR model fits. The environmental variables measured during this investigation could not adequately explain spatial variation in the species abundances although these parameters (light, discharge, substrate composition, depth) are often correlated with the distribution and abundance of aquatic macrophytes in streams (Canfield and Hoyer, 1988; Carr *et al.*, 1997; Mackay *et al.*, 2003). Similarities between the significant parameters selected for both logistic and MLR models suggest that similar processes are controlling both the distribution and abundance of macrophytes within the rehabilitation reach. Both logistic and MLR models indicated that the effect of riparian canopy cover was greater on emergent vegetation than submerged vegetation, in line with predictions from the conceptual model (Figure 4).

MLR and SAR models implicated broad and fine-scale spatial structure as potential influences on the abundance of aquatic macrophytes within the study reach. Potential sources of finescale and broadscale spatial structure include colonisation dynamics (local scale dispersal via rhizomes and larger scale dispersal by fragments or seeds), competition (space, light, nutrients) and occurrence of habitat units suitable for colonisation. With the exception of *O. ovalifolia* the common macrophyte species occurring in Echidna Creek can spread vegetatively via stolons (runners) or rhizomes (root-like stems). Aquatic macrophytes are considered to have excellent dispersal capabilities and rhizomes are an effective means of colonisation and vegetative reproduction. For example, Miao *et al.*, (2000) report that rhizome expansion by a single *typha* plant covered approximately 1 $m^2$ in seven months. The small proportion of variance explained by the regression models also suggests that stochastic processes such as chance colonisation events may be involved.

Hydraulic parameters explained little of the spatial variation in species distribution and abundance. Watercress abundance was positively correlated with

FROUDMAX but this may simply indicate a preference for shallow habitats (Froude number is a function of depth). This species often occurs in shallow habitats in Echidna Creek (Mackay unpublished). Temporal variations in species abundances were more closely related to hydraulic habitat than riparian canopy cover but this relationship also varied with growth form. Days since bankfull discharge explained 60%, 53% and 53% of the temporal variation in stems counts for *P. crispus*, *Typha* spp. and *R. nasturtium-aquaticum* respectively. Thus growth rates for these species were largely dependent upon periods of low hydraulic disturbance for colonisation and establishment.

Days since bankfull discharge only explained 24% of the temporal variation in stem counts for *S. validus*. This may indicate slow recovery from hydraulic disturbance, requirements for growth were not being met, or may have resulted from biotic interactions with other species. Spearman correlation coefficients (Table 9) indicated that *S. validus* stem counts were positively correlated with *Typha* spp. and *R. nasturtium-aquaticum* stem counts. Thus above-ground biomass accrual for *S. validus* does not appear to be influenced by competition from *Typha* spp. Slow recovery from hydraulic disturbance may be the result of rhizome uprooting. Published rooting depths for *S. validus* range from <10 cm to 76 cm (see Tanner, 1996) but rooting depths for *S. validus* in Echidna Creek have not been determined.

Four of the five dominant macrophyte taxa could clearly maintain populations in highly shaded sections of the rehabilitation reach. Insufficient data were available to assess the capacity of the fifth species, *O. ovalifolia*, to maintain populations in Echidna Creek when riparian canopy cover reaches 75%. Estimates of riparian canopy cover required to eliminate the remaining four taxa were 71% for *Typha* spp., 72% for *R. nasturtium-aquaticum*, 74% for *S. validus* and 87% for *P. crispus* (see Table 13). These values are underestimates for *Typha* spp., *S. validus* and *R. nasturtium-aquaticum* but the value of 87% for *P. crispus* may be a realistic estimate (see Table 8; Figure 10). A number of factors may influence the impact of riparian shading upon aquatic macrophytes and the capacity of riparian shading to eliminate macrophytes. The degree of shading provided by riparian vegetation is a function of vegetation type, stream width, channel aspect or orientation and channel morphology (Dawson and Kern-Hansen, 1979). Although ordination of habitat data did not clearly show that transects not colonised by aquatic macrophytes differed markedly in riparian canopy cover from other transects our observations of the reach indicate that the structure of the riparian canopy cover may be a critical factor. Three transects in particular (115, 122 and 150) have a structurally low riparian canopy consisting of sandpaper figs. A riparian canopy dominated by sandpaper figs visibly reduces incident light more efficiently than riparian canopies dominated by bunya pines and other taller trees. Aquatic macrophytes are also capable of physiological and morphological adjustment to improve light absorption properties and maximise photosynthesis in low light environments. These include altering leaf thickness and pigmentation densities (Maberly and Madsen, 2002; Enriquez and Sand-Jensen, 2003), leaf morphology (Spence, 1975) and allocation of a greater proportion of available biomass to photosynthetic structures (e.g. Cenzato and Ganf, 2001).

The results of the monitoring program indicate that riparian canopy cover will reduce the distribution and abundance of *P. crispus*, *O. ovalifolia*, *S. validus*, *Typha* spp. and *R. nasturtium-aquaticum* in the study reach. The extent to which riparian canopy cover can reduce the distribution and abundance of the target species in the rehabilitation reach is species-specific and also dependent upon the hydrology of Echidna Creek. Riparian shading will not completely eliminate the five target species from the rehabilitation reach. Restoration of the riparian canopy may not have substantial impacts upon water quality of the study reach and therefore nutrient availability (as carbon, nitrogen and phosphorus) may remain high. Elevated nutrient levels may ameliorate some of the effects of low light availability (e.g. Schmitt and Adams, 1981; Lippert *et al.*, 2001). Water quality data (Table 1) show that carbon availability in Echidna Creek is substantially greater than would be expected under reference or pre-disturbance conditions. The results of the monitoring program to date suggest that while riparian revegetation will reduce the distribution and abundance of vascular macrophytes in the rehabilitation reach, a pre-disturbance state will not be achieved without improvements in water quality.

A potential outcome of riparian revegetation in this system, especially if nutrient availability remains relatively high, is invasion of the rehabilitated system by shade-tolerant exotic taxa. In southeast Queensland potential shade-tolerant invaders include dense waterweed (*Egeria densa* Planchon), umbrella sedge (*Cyperus involucratus* Rottb.), crofton weed (*Ageratina adenophora* (Spring.) R.M. King and H. Rob.) and the ornamentals *Commelina* spp. and *Tradescantia* spp. (already present in the reach). *Egeria densa* can establish extensive populations in highly shaded habitats and is widespread within southeast Queensland (Mackay unpublished). Small populations of crofton weed occur in shaded areas of Echidna Creek. Invasion of rehabilitated sites by introduced, shade-tolerant taxa does not appear to be widely considered in planning rehabilitation projects.

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# Appendix 1

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Geomorphological Attributes and Riparian Canopy Values of Transects Established in Echidna Creek.

| | | | Riparian Canopy Cover | | |
|---|---|---|---|---|---|
| Transect Distance (m) | Orientation (°) | Bankfull Width (m) | Initial (%) | Final (%) | Change (%) |
| 9 | 189 | 3.3 | 80 | 90 | 10 |
| 13 | 180 | 2.9 | 72 | 94 | 21 |
| 22 | 184 | 2.7 | 93 | 96 | 3 |
| 29 | 159 | 3.8 | 83 | 90 | 7 |
| 37 | 149 | 3.6 | 88 | 91 | 3 |
| 54 | 169 | 6.3 | 5 | 32 | 27 |
| 76 | 199 | 4.3 | 1 | 42 | 41 |
| 83 | 179 | 2.2 | 3 | 62 | 59 |
| 91 | 189 | 6.8 | 5 | 42 | 37 |
| 99 | 169 | 5.8 | 10 | 20 | 10 |
| 108 | 180 | 2.8 | 93 | 98 | 5 |
| 111 | 199 | 3.3 | 19 | 58 | 39 |
| 115 | 230 | 3.7 | 99 | 98 | -1 |
| 122 | 264 | 3.5 | 99 | 100 | 1 |
| 128 | 280 | 2.8 | 74 | 99 | 22 |
| 135 | 314 | 8.3 | 8 | 22 | 14 |
| 150 | 339 | 4.3 | 99 | 100 | 1 |
| 158 | 319 | 6.3 | 90 | 97 | 7 |
| 168 | 299 | 5.2 | 4 | 60 | 56 |
| 175 | 289 | 5.1 | 0 | 31 | 31 |
| 181 | 289 | 3.1 | 0 | 41 | 41 |
| 188 | 304 | 4.4 | 48 | 89 | 41 |
| 198 | 249 | 4.1 | 54 | 83 | 29 |
| 209 | 259 | 3.4 | 61 | 79 | 17 |
| 213 | 239 | 5.3 | 22 | 51 | 29 |
| 222 | 159 | 3.4 | 29 | 71 | 42 |
| 229 | 159 | 4.3 | 29 | 19 | -10 |
| 237 | 159 | 3.7 | 23 | 12 | -11 |
| 254 | 199 | 4.6 | 20 | 92 | 72 |
| 261 | 229 | 3.4 | 42 | 84 | 42 |
| 268 | 239 | 3.7 | 19 | 54 | 35 |
| 275 | 249 | 5.1 | 38 | 53 | 15 |
| 281 | 289 | 4.3 | 22 | 47 | 25 |
| 288 | 220 | 4.0 | 75 | 97 | 22 |
| 294 | 229 | 4.0 | 90 | 84 | -6 |
| 309 | 294 | 5.7 | 26 | 59 | 33 |
| 313 | 319 | 9.2 | 87 | 88 | 1 |
| 329 | 189 | 3.9 | 67 | 78 | 11 |
| 337 | 180 | 5.1 | 95 | 98 | 3 |
| 354 | 200 | 4.3 | 96 | 97 | 1 |
| 361 | 219 | 9.2 | 69 | 77 | 8 |
| 376 | 284 | 9.7 | 51 | 78 | 27 |
| 383 | 259 | 11.6 | 91 | 95 | 4 |
| 399 | 269 | 5.5 | 33 | 78 | 45 |
| 422 | 259 | 5.5 | 87 | 93 | 6 |
| 436 | 190 | 4.1 | 89 | 94 | 5 |
| 447 | 184 | 5.3 | 52 | 81 | 29 |
| 461 | 184 | 5.0 | 44 | 60 | 16 |
| 483 | 179 | 4.9 | 81 | 65 | -16 |
| 499 | 149 | 5.5 | 20 | 42 | 22 |

# Appendix 2

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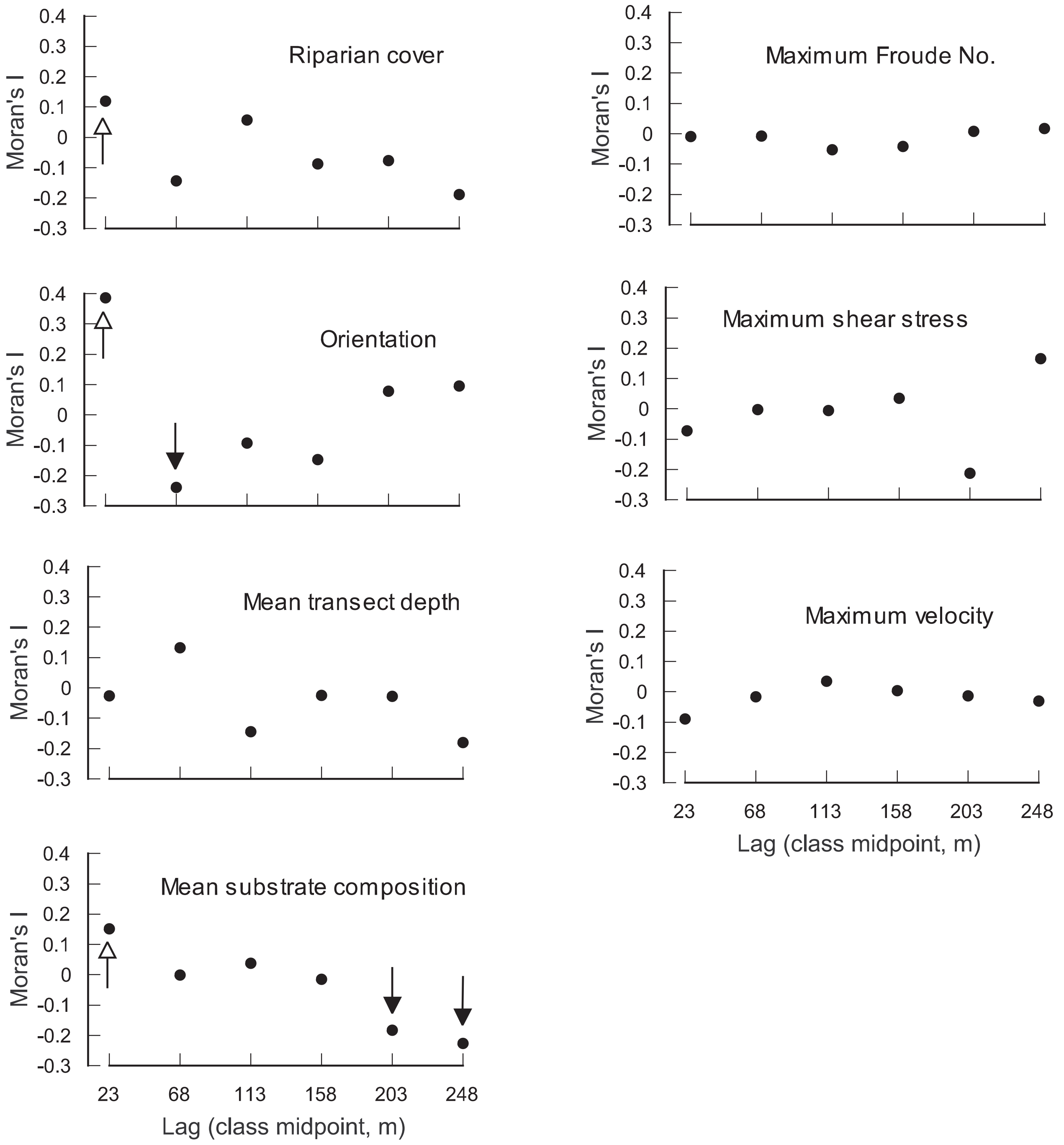
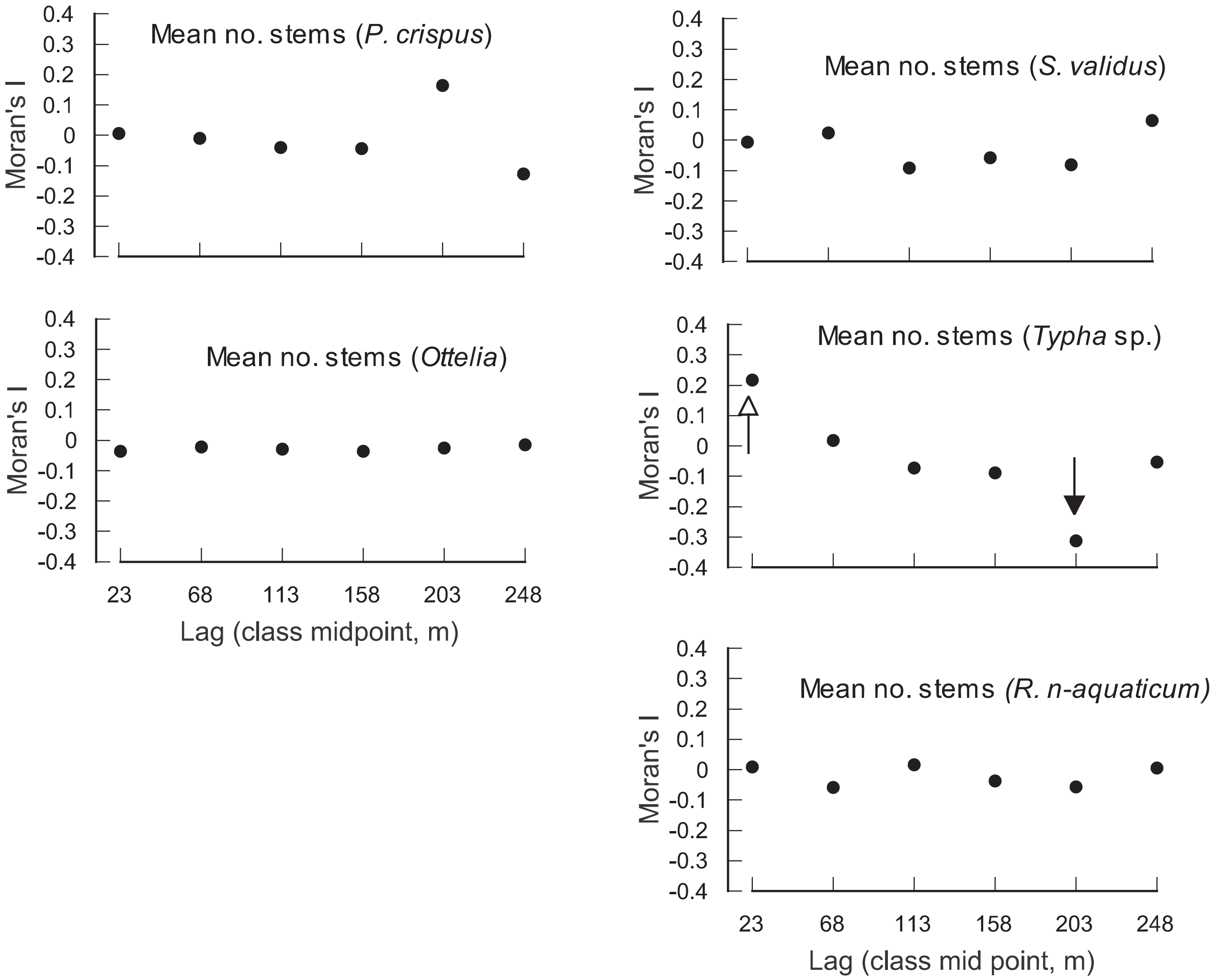
Moran's Correlograms for Spatial Autocorrelation in Environmental Variables. Significant correlations indicated with arrows (positive autocorrelation = open arrows, negative autocorrelation = filled arrows). Bonferroni adjusted significance level $\alpha/11 = 0.0045$.



# Appendix 3

Moran's Correlograms for Spatial Autocorrelation in Biotic Variables. Significant correlations indicated with arrows (positive autocorrelation = open arrows, negative autocorrelation = filled arrows). Bonferroni adjusted significance level $\alpha/11 = 0.0045$.



# Appendix 4

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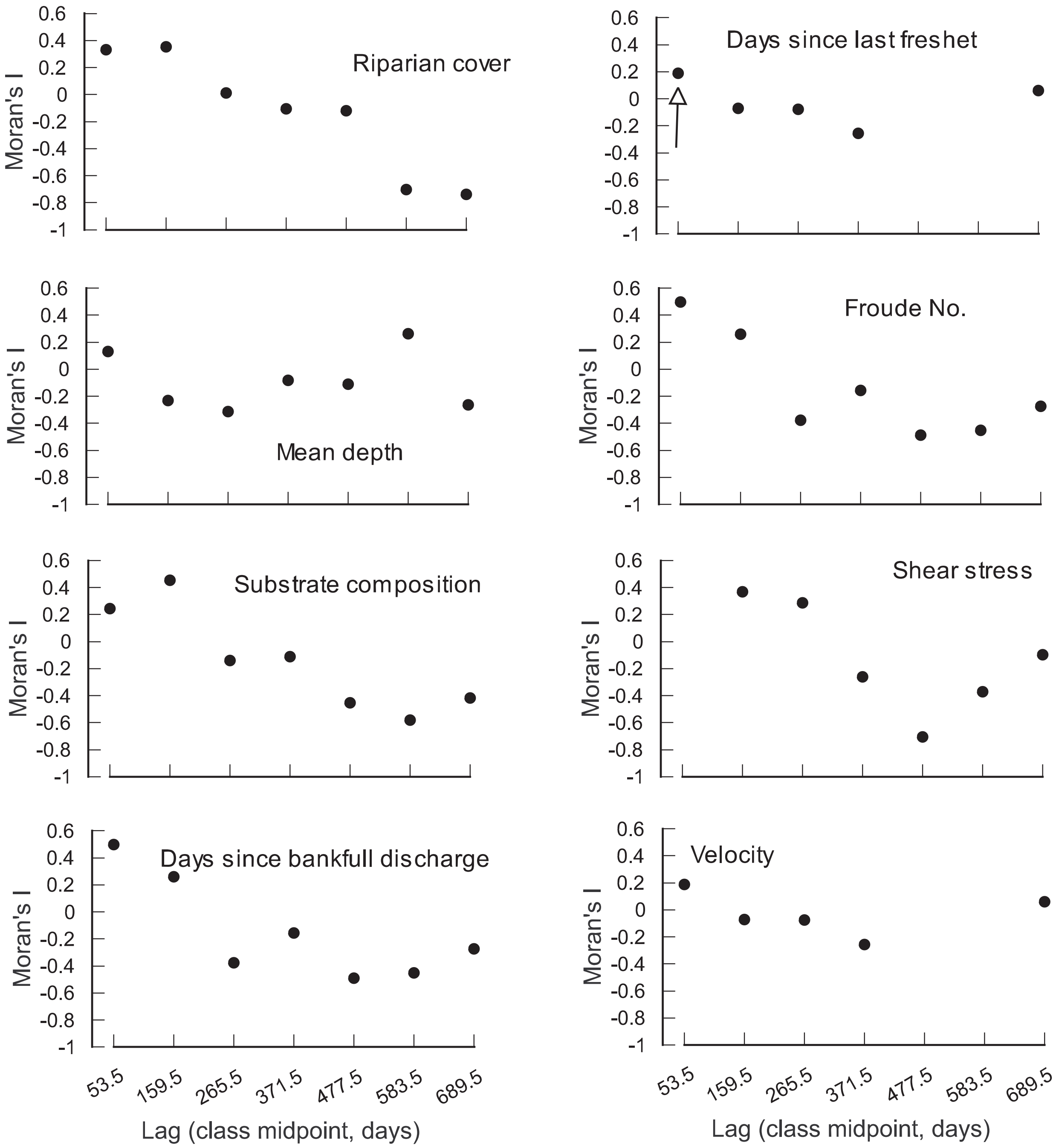
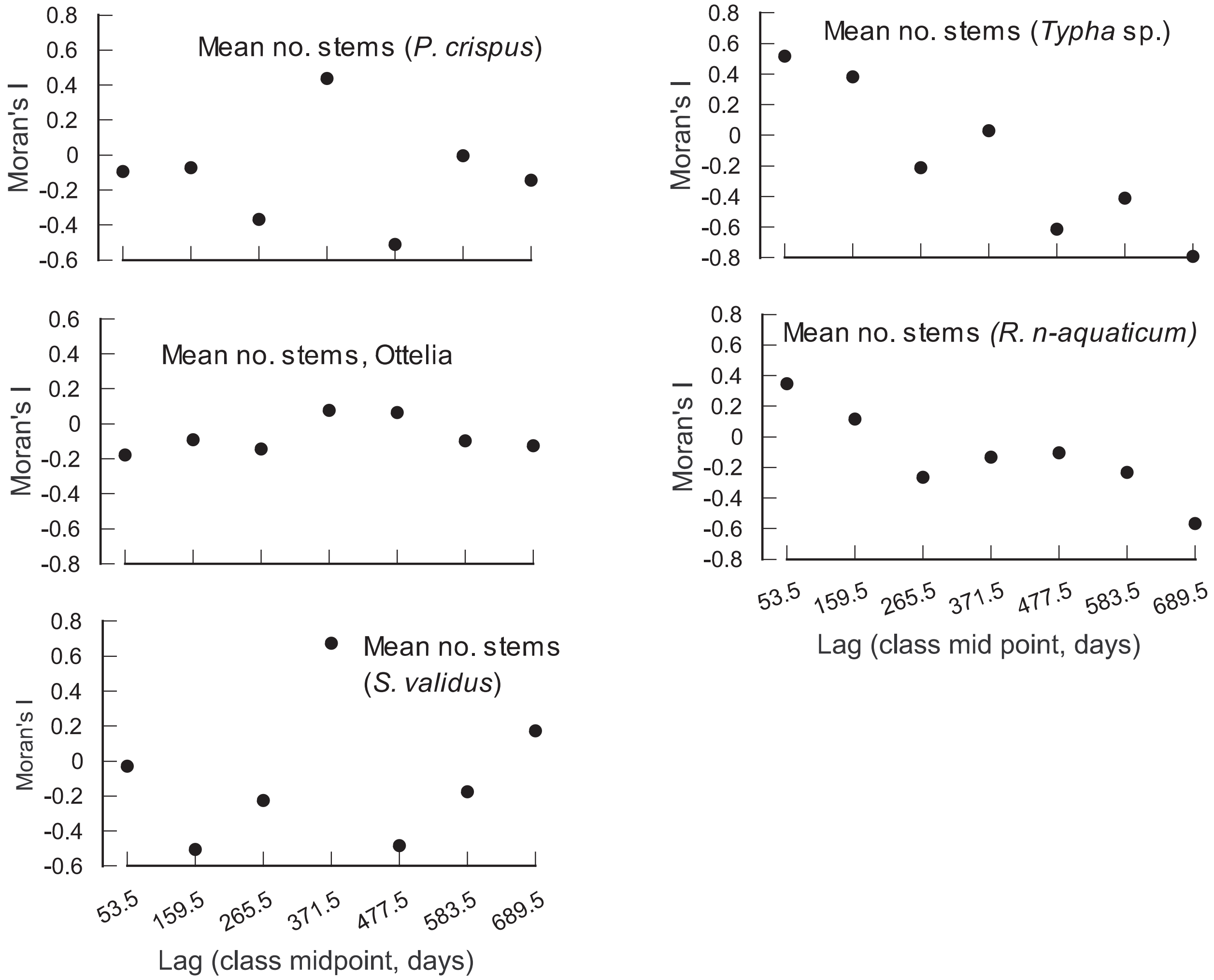
Moran's correlograms for temporal autocorrelation in environmental variables. Significant correlations indicated with arrows (positive autocorrelation = open arrows, negative autocorrelation = filled arrows). Bonferroni adjusted significance level $\alpha/7 = 0.0071$.



# Appendix 5

Moran’s correlograms for temporal autocorrelation in biotic variables. Significant correlations indicated with arrows (positive autocorrelation = open arrows, negative autocorrelation = filled arrows). Bonferroni adjusted significance level $\alpha/7 = 0.0071$.



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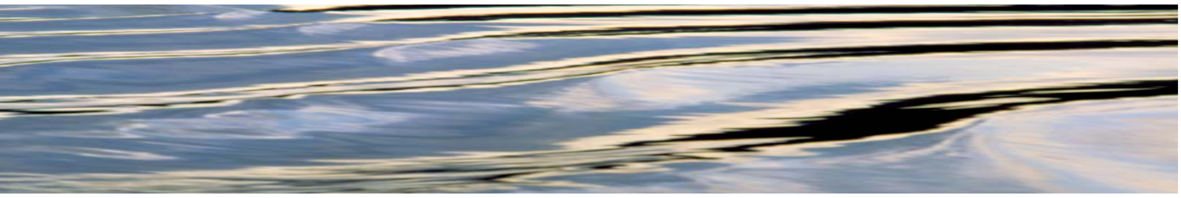

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