

Habitat structural complexity mediates food web dynamics in a freshwater macrophyte community

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Abstract A considerable amount of research has investigated the influence of habitat structure on predator success, yet few studies have explored the implications for community structure and food-web dynamics. The relative importance of macrophyte structure and fish predation on the composition of the macroinvertebrate and periphyton communities in a lowland river was investigated using a multifactorial caging experiment. We hypothesised that: (1) fish predators are less effective in a more structurally complex macrophyte analogue; (2) strong direct and indirect effects of fish predators (e.g. trophic cascades) are less likely to occur in a structurally complex habitat; and (3) the strength of these patterns is influenced by the composition of the prevailing community assemblage. We measured the abundance and composition of the macroinvertebrate and periphyton communities associated with three different-shaped macrophyte analogues, under different fish predator treatments and at different times. Macrophyte analogue architecture had strong, consistent effects on both the macroinvertebrate and periphyton communities; both were most abundant

and diverse on the most structurally complex plant analogue. In contrast, the fish predators affected only a subset of the macroinvertebrate community and there was a suggestion of minor indirect effects on periphyton community composition. Contrary to expectations, the fish predators had their strongest effects in the most structurally complex macrophyte analogue. We conclude that in this system, macrophyte shape strongly regulates the associated freshwater assemblage, resulting in a diverse community structure less likely to exhibit strong effects of fish predation.

Keywords Fish predation · Macroinvertebrates · Periphyton · Macrophyte structure · Trophic interactions

Introduction

In vegetated aquatic systems, habitat structure is often provided by macrophytes, and their importance as a habitat is demonstrated by a far greater abundance of macroinvertebrates than in unvegetated areas (Heck and Crowder 1991). The abundance and richness of the macroinvertebrate community appears to be proportional to the density, or biomass, of freshwater macrophytes (Crowder and Cooper 1982; Stoner and Lewis 1985). However, this relationship is less clear when referring to the type or shape of structure rather than the density of structural elements, because different macrophyte species tend to support different epiphytic communities (Rooke 1986; Chilton 1990; Humphries 1996). The shape of a particular habitat is not necessarily directly related to the density of habitat, and although some researchers have distinguished between shape and

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density as separate components of structural complexity (Stoner and Lewis 1985; McCoy and Bell 1991), they have rarely been treated as such in ecological studies.

Fish predators have often been shown to be less effective foragers in more complex habitats (Gotceitas and Colgan 1989; Nelson and Bonsdorff 1990; Swisher et al. 1998), and it has been hypothesised that more complex structures provide more refuge from predation (Heck and Crowder 1991). However, these studies have only tested the presence and absence of habitat structure, or the density of structural elements, on predator success. Very few studies have assessed the shape of the structure, and while there is some suggestion macrophyte shape can also affect predator success (Leber 1985; Persson and Eklöv 1995), these conclusions have been confounded by a failure to distinguish the shape from the density of the structure. Laboratory experiments have shown that the foraging success of a fish predator can be mediated by macrophyte shape, but be unaffected by macrophyte density, illustrating the potentially different roles these components of habitat structure may play in trophic interactions (Warfe and Barmuta 2004).

Fish predators can have substantial impacts on their prey communities, the most striking of which are trophic cascades where a predator can have indirect effects cascading down the trophic levels of a community to influence the biomass of the primary resource (Carpenter et al. 1987; Pace et al. 1999). Yet these cascades have generally been observed in systems with relatively little, or uniform, habitat structure (Polis et al. 2000) and, despite the large body of work investigating the effects of habitat structure on predator-prey interactions, few studies have looked at the implications for community structure and food-web dynamics (Diehl and Kornijów 1998). If habitat structure can influence the strength of direct and indirect predator effects, then it might influence how strongly a community is regulated by predation, and thus the importance of predation might depend on the habitat in which it occurs (Power 1992). While significant variation in fish impacts has been found between vegetated and unvegetated areas in aquatic systems (Crowder and Cooper 1982), there is currently no published field research comparing predator impacts on community structure in different morphological types of vegetation.

The direct and indirect effects of predation are also likely to depend on the composition of the prey community (and the interactions therein) prevailing at the time or season of observation, therefore the strength of these effects may differ between seasons. Initial differences in community composition can influence community succession and determine the outcomes of

disturbance (de Szalay and Resh 1996), intraguild predation (Price and Morin 2004), and competitive interactions (Underwood and Anderson 1994; Nandakumar 1996) on the resulting assemblages.

This experiment was motivated by observations of macrophyte beds in the Macquarie River, a slow-flowing, lowland river in Tasmania, Australia. These beds are structurally diverse and have abundant macroinvertebrate and periphyton communities, which vary in composition between seasons (Warfe 2003). They also support large populations of the southern pygmy perch, *Nannoperca australis*, which eat the macrophyte-associated macroinvertebrate fauna (Humphries 1995). We conducted a multifactorial cage experiment to investigate the influence of macrophyte structure on the direct and indirect effects of this fish predator on the macrophyte-associated macroinvertebrate and periphyton communities. We hypothesised that: (1) fish predators are less effective in a more structurally complex macrophyte; and (2) strong direct and indirect effects of fish predators (e.g. trophic cascades) are more prevalent in simple habitats and less likely to occur in structurally complex habitats. We also hypothesised that (3) effects of fish predators vary depending on the seasonal composition of the community.

Methods

Study site

The experiment was conducted in the macrophyte beds of the Macquarie River, Tasmania (147°28'E, 41°57'S), a slow-flowing sinuous river which drains an area of 3,765 km² over its 155-km length and has an average daily discharge of 1.5–20 m³s⁻¹; most of its flow occurring between winter and mid-spring (Humphries 1996). The riparian vegetation is sparse and comprised of woolly tea-tree (*Lepstospermum lanigerum*), native grasses, remnants of dry sclerophyll woodland and some introduced crack willow (*Salix fragilis*). However, the native aquatic vegetation is abundant and diverse, comprising up to 30 macrophyte species but dominated by *Myriophyllum* spp., *Vallisneria gigantea*, *Scirpus fluitans*, *Juncus* spp., *Eleocharis sphacelata* and *Triglochin procera* (Humphries 1996; D.M. Warfe, unpublished data).

Experimental design

The cage experiment was a partially nested design, where the main factors of macrophyte analogue (three levels) and predator treatment (four levels) were fully

crossed and replicated at six sites. Site was used as a blocking factor and nested in time-of-start (two levels), and each unique treatment combination was sampled on two fixed dates (two levels).

Floating cages were constructed of black plastic oyster mesh (mesh size 6 mm to allow macroinvertebrate movement, Nylex, Melbourne, Vic., Australia), 500 mm long \times 500 mm wide \times 300 mm high. Each was attached to a square upper frame (500 mm \times 500 mm) of sealed polyvinylchloride piping (75 mm diameter), which acted as the float. Each cage had removable panels (300 mm \times 240 mm) on two opposing sides to allow colonisation by periphyton and macroinvertebrates.

Macrophyte shape comprised three levels of structural complexity: low, medium and high. Artificial analogues of three macrophyte species, varying in shape and common to the Macquarie River (Humphries 1996), were constructed (Fig. 1). Their structure was quantifiable using a range of different indices and corresponded to our intuitive classification of their relative complexity (Warfe and Barmuta, in review). A previous laboratory experiment showed macrophyte shape, but not density, affected the foraging success of pygmy perch (Warfe and Barmuta 2004), so the macrophyte analogue densities used in this experiment were based on median field densities found in surveys of natural macrophyte beds in the Macquarie River. Green electrical conduit (7 mm diameter) represented the cylindrical reed-like shape of *E. sphacelata*, the plant with the most simple structure, and 280 mm lengths were attached to the cage floors at a density of 220 stems/cage (880 stems/m²). Green plastic packing strap (12 mm wide) represented the long flat leaves of the water ribbon, *T. procera*, the macrophyte of intermediate structural complexity. Each “plant” consisted of 18 lengths of packing strap (three of each length 100, 130, 170, 200, 260 and 280 mm, with the longer ones towards the centre) and was attached to the cage floors at a density of 25 plants/cage (100 plants/m²). Plastic “fox-tail” aquarium plants (Tetra Secondnature, Blacksburg, Va., USA) represented the macrophyte with the most complex structure, *Myriophyllum variifolium*. Each comprised four stems of whorled leaves with a high degree of leaf dissectedness, and they were attached to the cage floors at a density of 45 plants/cage (180 plants/m²). The macrophyte analogues are hereafter referred to by their generic names.

The predator treatment factor had four levels: control, predator access, predator enclosure and predator enclosure cages. The control cage lacked sides or the PVC frame and consisted of the cage floors, with analogues, weighted to 300 mm depth. The predator access cage had the two panels removed to allow fish predators



Fig. 1 The macrophyte analogues constructed for the experiment (on the left) and their natural counterparts (on the right). The analogues were constructed to represent species of differing structural complexity, from the top: *Myriophyllum variifolium* (the most complex), *Triglochin procera* (of intermediate complexity) and *Eleocharis sphacelata* (the most simple). Each analogue is 280 mm height

free access, and the predator enclosure cage had the panels replaced after colonisation with three pygmy perch (30–60 mm length) enclosed within it. The pygmy perch were matched by size across enclosures to establish a similar size distribution of fish predators in each cage, and the density was representative of low field density estimates (Humphries 1995). The predator enclosure treatment was a closed cage with no fish.

One complete set of the 12 treatment combinations (i.e. three levels of macrophyte shape \times four levels of predator treatment) was placed in macrophyte beds at each of six sites in the river; “sites” are thus treated as random “blocks”. These sites were spread over 1.5 km of river length, and each was separated by at least 200 m, in areas of negligible flows ($<0.02 \text{ m}^3\text{s}^{-1}$; D.M.

Warfe, unpublished data) with extensive macrophyte growth (often extending to the centre of the main channel). The cages were placed in macrophyte beds at least 2 m apart, and anchored to the riverbank.

The predator treatments were applied at two starting times, summer and winter, to control for the timing of treatment application as the algal and invertebrate communities appeared to differ seasonally (Warfe 2003). This design resembles the “staircase design” recommended by Walters et al. (1988) to avoid confounding treatment effects with any peculiarities that may have prevailed at the time the treatment was applied, e.g. any seasonal variation in community composition. Three blocks commenced in mid-summer and ran for 8 months, and three in mid-winter, running concurrently for the remaining 2 months. These treatment levels were referred to as S1...S8, and W1 or W2, where the letter denotes the time-of-start and the number denotes the month of sampling after initiation. Given the staggered time-of-start design, the three summer-start blocks were sampled over the first 3 months [S1 (7 February 2000), S2 (6 March 2000) and S3 (3 April 2000)], and again at 7 and 8 months (S7 and S8), on 24 July and 21 August 2000, respectively. The winter-start blocks were sampled at 1 and 2 months after their initiation (W1 and W2), concurrently with S7 and S8, on 25 July and 22 August 2000, respectively. All cages and plants were allowed colonisation by periphyton and macroinvertebrates for 10 weeks prior to the application of the predator treatments, and the cage walls were scrubbed monthly to prevent periphyton accumulating on the mesh (cage controls also received simulated scrubbing disturbance).

Plant analogues were randomly sampled by removal with a 250- μ m mesh net, and replaced with a new plant which was eliminated from future sampling. For the purposes of sampling, four stems of the low complexity macrophyte analogue, *Eleocharis*, were considered an “individual” plant to roughly equate (by overall canopy volume in the water column) to a single tufted *Triglochin* analogue and a single four-stemmed *Myriophyllum* analogue. All samples and attached periphyton and macroinvertebrates were preserved with 5% formalin. The plant analogues were cleaned of periphyton and macroinvertebrates over a 250- μ m sieve; the macroinvertebrates were identified to the lowest possible taxonomic level and the periphyton samples were frozen for further analysis.

Macroinvertebrate methods

Seventy-seven macroinvertebrate taxa were identified and the total abundance, taxon richness and commu-

nity composition of the macroinvertebrate assemblage were analysed. The experimental design did not allow us to determine initial invertebrate densities, nor immigration and emigration rates, so we focussed on relative differences in invertebrate parameters between treatments. We also grouped taxa on the basis of trophic status and their vulnerability to pygmy perch predation (cf. Rader 1997). Invertebrate predators formed one group; over 92% of this group consisted of the coenagrionid damselfly, *Ischnura heterosticta tasmanica*. Other odonates (*Austrogomphus guerini*, *Austroaeshna* sp., *Aeshna* sp. and *Austrolestes analis*), naucorid hemipterans (*Naucoris congrex*) and dytiscid adults (*Antiporus* sp.) comprised the remainder.

The second group, “vulnerable invertebrate grazers”, comprised a subset of all non-predatory invertebrates. This subset was formed by firstly classifying all taxa according to their relative vulnerability to pygmy perch predation using four traits: abundance, body size, mobility/exposure and presence in pygmy perch guts. These traits were adapted from Rader’s (1997) scheme for classifying invertebrate vulnerability to visually-feeding salmonids. “Abundance” denoted the average total abundance of each taxon collected over the duration of the experiment; we assumed a more abundant taxon would be more likely to be preyed upon by a generalist fish predator such as pygmy perch (Humphries 1995). “Body size” was split into two categories, body length <5 and \geq 5 mm, and taxa were scored according to the largest size observed during the experiment, as larger invertebrates have been shown to be targeted by fish predators (Diehl 1992). “Mobility/exposure” distinguished between taxa that tended to be relatively immobile and hidden within periphyton, versus those taxa which tended to be active swimmers and thus more exposed to visually-feeding pygmy perch. Active macroinvertebrates have also shown to be preferentially targeted by fish predators (Crowder and Cooper 1982) and taxa were scored for this trait based on field and laboratory observations and the published literature (Gooderham and Tsyrlin 2002). The fourth trait quantified the frequency of occurrence of the taxon in the gut contents of pygmy perch using Humphries’ (1995) analysis of the gut contents of 365 pygmy perch from the Macquarie River over 1 year. For each trait, low scores indicated low vulnerability and high scores indicated high vulnerability to predation. Scores for each trait were added for each taxon to give an overall taxon score, the taxon scores were ranked and three taxa (ostracods, the amphipod *Austrochiltonia australis*, and the mayfly *Atalophlebia australis*) clearly ranked higher than all other taxa and formed the group “vulnerable invertebrate grazers”.

Periphyton methods

The periphyton community composition was analysed by a method adapted from O'Connor (1993), which estimates the relative proportions of dominant items in the periphyton. Green algae, blue-green algae and detritus comprised the majority of the periphyton; fungal hyphae and red algae contributed less than 1% of the total proportions and were excluded from the analyses. An estimate of periphyton biomass was obtained from the ash-free dry weight (AFDW) of each sample. The samples were dried to constant weight at 50°C for 48 h, and then ashed in a muffle furnace at 500°C for 2 h.

Data analyses

To reiterate, the staggered start of the experiment was designed to test the hypothesis that effects of macrophyte shape and fish predation depend on the community composition prevailing at the time of treatment application. Only analyses of the final two sampling events, the concurrent summer-start and winter-start blocks (S7/W1 and S8/W2), are presented here. Thus the overall design was a split-plot or partially nested design (sensu Quinn and Keough 2002) where sites acted as random blocks, with three sites nested within each of the two levels of time-of-start. Within each block, cages acted as plots and each cage was randomly allocated to a unique combination of macrophyte (three levels) crossed with predator treatment (four levels). Each cage was then sampled on two fixed dates (sampling event: two levels).

Our expectation was that differences in the main effects between start-times would indicate that the prevailing assemblages differed between seasons, and would lead to different macrophyte or predator effects. Analyses comparing treatments of the same “age” (S1/W1 and S2/W2; D.M. Warfe, unpublished data), and looking at changes over time (S1...S8; Warfe 2003), showed very similar patterns of macrophyte shape and predator treatment effects and are not presented in detail here as they are being prepared for another paper.

Distance-based permutational multivariate analysis of variance (DB-PERMANOVA; Anderson 2001; McArdle and Anderson 2001) was used to analyse the effects of macrophyte shape, predator treatment, time-of-start and sampling event on the macroinvertebrate assemblage, where all 77 taxa comprised the multiple response variables. Site nested within time-of-start was used as the blocking factor. The multivariate data were fourth-root transformed prior to computing Bray–Curtis dissimilarities, and pre-planned contrasts were conducted for significant main effects and interactions.

These multivariate analyses were conducted using XMATRIX (Anderson 2003) to design the matrices corresponding to the relevant factor and interaction terms, and DISTLM Version 5 (Anderson 2004) was used to test the multivariate data against these effects. Indicator Value analysis (Dufrêne and Legendre 1997) was conducted to determine which taxa characterised the differences between treatment assemblages. IndVal Version 2 (Dufrêne and Legendre 1997) was used for this analysis, and 4,999 randomisations were used for each permutation test.

Univariate general linear models were used to test the effects of macrophyte shape, pygmy perch predation and time-of-start on the univariate macroinvertebrate variables specified earlier (total macroinvertebrate abundance, macroinvertebrate taxon richness, invertebrate predators and vulnerable invertebrate grazers). Sampling event (S7/W1 or S8/W2) was included as a repeated measure. Periphyton biomass was also analysed using these general linear models, although the accidental loss of samples from W1 necessitated the exclusion of these data, hence only data from the final sampling event (S8/W2) were analysed. The univariate data were log-transformed where necessary to meet assumptions of normality, and pre-planned comparisons were conducted on the main effects of macrophyte shape (*Eleocharis* vs *Triglochin* and *Triglochin* vs *Myriophyllum*) and predator treatment where they were significant. Planned comparisons between predator treatment levels were conducted between control versus access cages, to test for the presence of the cage, between access versus enclosure cages, to test for the enclosure of pygmy perch, and between enclosure versus enclosure cages to test for the presence of pygmy perch. Effect sizes were indicated by presenting the percentage difference between means. These univariate tests were conducted using the statistical software R (R Development Core Team 2005).

The effects of macrophyte shape, pygmy perch predation, time-of-start and sampling event on periphyton composition were assessed using parametric MANOVA. The multiple response variables were green algae, blue-green algae and detritus, which comprised over 99% of the periphyton, varied proportionally with one another, and met the assumptions of MANOVA. The proportions of these three variables usually summed to 1 for nearly all replicates, so we followed the standard practice of omitting one variable when conducting the MANOVA (Harris 1975). Pillai's Trace was used to determine significance, and pre-planned contrasts were conducted to interpret significant effects and interactions using SYSTAT Version 9 (Wilkinson 1999).

Results

Macroinvertebrate community composition

Distance-based permutational multivariate analysis of variance showed the main effect of predator treatment was significant (Table 1), with the pre-planned contrasts suggesting a cage effect between the uncaged controls and the access cages ($P=0.006$), but no defensible differences between the access cages and the cages enclosing pygmy perch ($P=0.157$) nor between the enclosure cages and the exclosure cages ($P=0.118$). Indicator Value analysis showed the assemblages in the access cages were characterised by copepods, ostracods and *Paratya australiensis* (indicator values of 77.7, 63.9 and 19.4%, respectively, all $P<0.05$), suggesting the cage walls may have provided extra habitat for these epifaunal taxa.

The highly significant effect of macrophyte analogue interacted strongly with time-of-start and less strongly with sampling event (Table 1). The pre-planned contrasts showed that the macrophyte analogues maintained different invertebrate assemblages in both the summer- and winter-start treatments, although the difference between *Triglochin* and *Myriophyllum* was less marked in summer-start ($P=0.023$) than in winter-start cages ($P=0.002$). Similarly, the macrophyte analogues supported different communities on both sampling events, but the difference between *Triglochin* and *Myriophyllum*

was slightly smaller on the second S8/W2 sampling event ($P=0.004$) than on the first ($P=0.0006$). There was also a strong interaction between time-of-start and sampling event (Table 1), although on both sampling events, the summer- and winter-start treatments remained significantly different from each other.

Indicator Value analysis was conducted on the macrophyte analogues within each level of time-of-start, but the statistically significant taxa involved were the same as those identified by the main effect of macrophyte analogue alone. The *Myriophyllum* analogues supported an invertebrate assemblage characterised by 28 taxa at $P<0.01$, whereas *Triglochin* was significantly characterised by only one taxon, the freshwater limpet *Ferrissia tasmanica*, and *Eleocharis* analogues had no taxa significantly characterising its assemblages (Table 2). On *Myriophyllum*, the highest indicator values belonged to the amphipod *A. australis* at 78%, Chironominae at 67.1% and the coenagrionid damselfly *I. H. tasmanica* at 63.4%. IndVal also showed the summer-start macroinvertebrate community had 13 significant indicator taxa at $P<0.05$ and was predominantly characterised by chironomid larvae (specifically Chironominae at 52.7%, tanytarsiini at 49% and orthocladiinae at 46.7%) and copepods at 49%. The winter-start community had only two significant indicator taxa at $P<0.05$, which were daphniids at 47.3% and chydorids at 44.3%.

Total macroinvertebrate abundance

The total abundance of macroinvertebrates was greatest on the *Myriophyllum* analogue, the most structurally complex plant shape, and least on *Eleocharis*, the most simple shape (Table 3, Fig. 2a). A significant effect of predator treatment on total macroinvertebrate abundance was due to a greater abundance of macroinvertebrates in the predator access cages than in the cage controls (Table 3, Fig. 2b). Again, this may be due to cage effects as total abundance did not significantly differ between pygmy perch enclosures and exclosures. There was also a significant effect of sampling event (Table 3), with 42.6% more macroinvertebrates at S8/W2 than S7/W1 regardless of time-of-start.

Taxon richness

Taxon richness was strongly affected by macrophyte shape and showed some effect of sampling event, but was unaffected by predator treatment. There were significantly more taxa on *Myriophyllum* analogues than *Triglochin* (by 18.7%; Table 3), and significantly more taxa on *Triglochin* than *Eleocharis* (by 44.9%; Table 3). There was a weak effect of sampling event,

Table 1 Distance-based permutational multivariate analysis of variance of effects of *ToS* time-of-start, *Mphyte* macrophyte analogue, *Pred* predator treatment and *Sevent* sampling event on the 77 macroinvertebrate taxa sampled at S7/W1 and S8/W2

Effect	<i>df</i>	Pseudo- <i>F</i>	Monte Carlo <i>P</i>
Between sites			
ToS	1,4	6.985	<0.001
Within sites			
Mphyte	2,8	15.824	<0.001
ToS × Mphyte	2,8	2.963	0.006
Pred	3,12	2.148	0.020
ToS × Pred	3,12	1.370	0.176
Mphyte × Pred	6,24	1.116	0.323
ToS × Mphyte × Pred	6,24	1.328	0.132
Within sampling events			
Sevent	1,4	12.076	<0.001
Tos × Sevent	1,4	4.690	0.004
Mphyte × Sevent	2,8	2.071	0.041
ToS × Mphyte × Sevent	2,8	1.472	0.167
Pred × Sevent	3,12	1.253	0.236
ToS × Pred × Sevent	3,12	1.264	0.241
Mphyte × Pred × Sevent	6,24	1.503	0.056
ToS × Mphyte × Pred × Sevent	6,24	0.827	0.733

Treatment combinations were replicated three times and data were fourth-root transformed prior to calculating Bray–Curtis dissimilarities. $P<0.05$ are in bold for significant interactions, or where the main effects only are significant

Table 2 Selected macroinvertebrate taxa characterising the macroinvertebrate community on each macrophyte analogue, with their respective indicator values (%) as calculated by IndVal Version 2 (Dufrene and Legendre 1997)

<i>Eleocharis</i>		<i>Triglochin</i>		<i>Myriophyllum</i>	
Taxon	IV	Taxon	IV	Taxon	IV
<i>Gyraulus tasmanicus</i> (Planorbidae)	0.69	<i>Ferrissia tasmanica</i> (Ancyliidae)	9.38	<i>Physastra gibbosa</i> (Planorbidae)	46.63
<i>Triplectides</i> sp. (Leptoceridae)	2.08	<i>Leptocerus</i> sp. 2 (Leptoceridae)	5.61	<i>Notalina</i> sp. (Leptoceridae)	60.95
<i>Austrolestes</i> sp. (Lestidae)	1.04	<i>Oecetis</i> sp. (Leptoceridae)	2.08	<i>Helyethira</i> sp. (Hydroptilidae)	54.92
<i>Helochaeres australis</i> (Hydrophilidae)	2.08	<i>Orthotrichia</i> sp. (Hydroptilidae)	4.17	<i>Ecnomus</i> sp. (Ecnomidae)	31.03
Unidentified Hydrophilidae sp.	2.08	<i>Diaprepocoris</i> sp. (Corixidae)	2.08	<i>Atalophlebia australis</i> (Leptophlebiidae)	43.13
Pezidae (Hydracarina)	4.17	Arrenuridae (Hydracarina)	2.08	<i>Ischnura heterosticta tasmanica</i> (Coeanagronidae)	63.44
		Glossiphonidae (Hirudinea)	4.17	Chironomini (Chironomidae: Chironominae)	67.09
				<i>Austrochilontia australis</i> (Ceinidae)	78.00
				Ostracoda	60.69
				Naididae (Oligochaeta)	65.90

Indicator values in bold are significant at $P < 0.05$. *Myriophyllum* analogues supported 28 significant indicator taxa, compared to one significant indicator taxon on *Triglochin*, and none on *Eleocharis*

with slightly more taxa sampled at the final S8/W2 sampling event (Table 3). Predator treatment had no effect on taxon richness ($F_{3,12} = 0.69$, $P = 0.570$).

Invertebrate predators

Invertebrate predators occurred at low abundances, averaging $< 1\%$ and never contributing more than 6% to the total macroinvertebrate abundance. There were significantly more invertebrate predators on *Myriophyllum* analogues than *Triglochin* analogues (Table 3), and there were no significant effects of pygmy perch predation ($F_{3,12} = 1.41$, $P = 0.290$).

Vulnerable invertebrate grazers

Vulnerable invertebrate grazers (ostracods, the amphipod *A. australis* and the mayfly *A. australis*) averaged 5.4% of the total invertebrate abundance, but contributed up to 32% in some treatment combinations. Macrophyte shape and predator treatment interacted to significantly affect their abundance (Table 3). Pre-planned contrasts showed that there were significantly more vulnerable invertebrates in the predator enclosure cages than in the cages where pygmy perch were enclosed, but that this effect was only apparent on the *Myriophyllum* analogues; there was no such increase on the *Triglochin* analogues (Table 3, Fig. 3). There were no significant differences in vulnerable grazers in any of the other predator treatments, nor between *Eleocharis* and *Triglochin* analogues (Table 3). There was no significant effect of either time-of-start

(Table 3) or sampling event ($F_{1,4} = 2.89$, $P = 0.160$) on the abundance of vulnerable invertebrate grazers.

Periphyton composition

The periphyton composition was strongly affected by the time-of-start factor, as there were hardly any blue-green algae, and correspondingly more green algae and detritus, in the winter-start blocks than the summer-start blocks (Fig. 4). This resulted in the time-of-start factor significantly interacting with macrophyte shape ($F_{4,16} = 5.469$, $P = 0.006$). Pre-planned contrasts showed there was less green algae on *Eleocharis* than *Triglochin* analogues in the summer-start blocks ($t = 6.777$, $P = 0.023$), and the smaller proportion of blue-green algae in the winter-start blocks led to this effect being reversed in the winter-start blocks; *Eleocharis* supported more green algae than *Triglochin* ($t = 20.056$, $P = 0.001$; Fig. 4a).

There was the suggestion of an interaction between time-of-start and predator treatment ($F_{6,16} = 2.326$, $P = 0.065$), and pre-planned contrasts showed there was more blue-green algae (and less detritus) in the pygmy perch enclosures compared the enclosures (Fig. 4b). However, this was apparent only in the summer-start blocks and was not significant ($t = 3.548$, $P < 0.065$; all other contrasts, $P > 0.11$).

Periphyton biomass

Periphyton biomass was only analysed at the final S8/W2 sampling event and was greatest on *Myriophyllum*, the most structurally complex plant analogue,

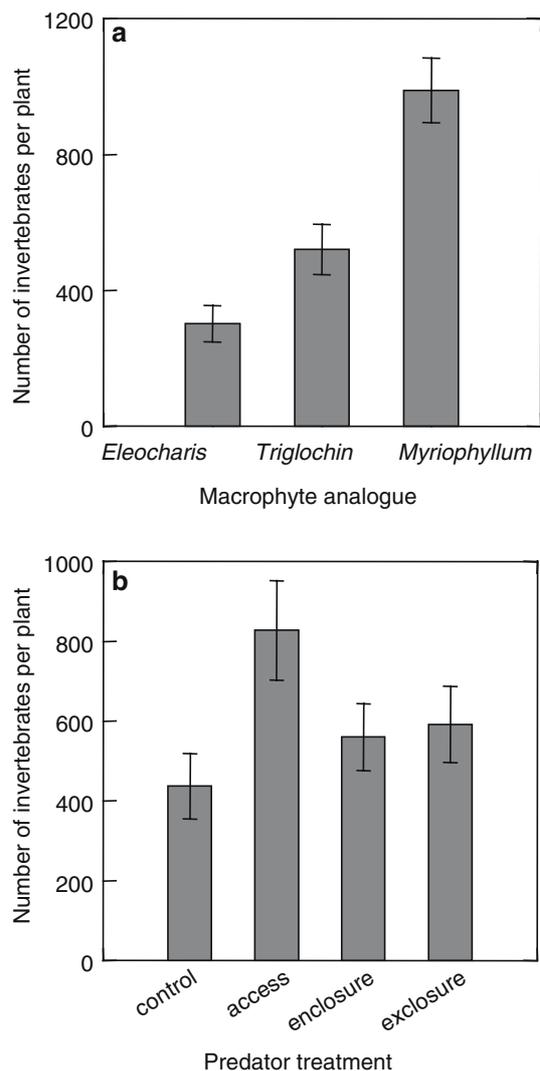


Fig. 2 The total abundance of macroinvertebrates on (a) each macrophyte analogue, and (b) in each predator treatment. Pre-planned contrasts showed there were significant differences between each macrophyte analogue, and between the control and access cages only. Error bars are one standard error about the mean

regardless of time-of-start ($F_{2,8}=8.663$, $P<0.01$). There was 62% more periphyton on *Myriophyllum* than on *Triglochin* analogues ($t=3.126$, $P<0.02$), and 8% more periphyton on *Triglochin* than on *Eleocharis* analogues ($t=0.674$, $P=0.519$). The access cages had 29% more periphyton than any other predator treatment cages, suggesting a potential cage effect, but this was not significant ($F_{3,12}=3.322$, $P>0.056$).

Discussion

This experiment tested the relative influence of both habitat structure and fish predation on macroinvertebrate and periphyton community structure. Our

expectations that pygmy perch effects would be greatest in the structurally simple habitat (*Eleocharis*) and smallest in the most structurally complex habitat (*Myriophyllum*) were not supported. Habitat structure, as represented by macrophyte analogue shape, was consistently a much stronger force shaping these communities than the effects of predation by pygmy perch.

Habitat structure

Different communities on different macrophyte species have often been attributed to habitat structure—a more structurally complex habitat will support a more diverse and abundant community by providing (1) more surface for food collection and attachment, and (2) more interstitial space that acts as a refuge from predation (Heck and Crowder 1991; McCoy and Bell 1991; Crowder et al. 1998; Diehl and Kornijów 1998). Our results certainly support the first hypothesis. Of all three macrophyte analogues, *Myriophyllum*, the most structurally complex, supported the greatest abundance and diversity of macroinvertebrates, as well as the greatest periphyton biomass. The implicit assumption in these hypotheses is that a more complex structure will have a greater surface area. Although it has proved difficult to disentangle the separate elements of surface area and plant architecture, macroinvertebrates can be more abundant where there is more surface area (Dvořák and Best 1982), and can respond to surface area over any architectural features of the habitat (Stoner and Lewis 1985). However, surface area alone is an insufficient explanation of the patterns found in this experiment. While there was an obvious difference in morphology between the macrophytes, individual plant analogues of medium (*Triglochin*) and high (*Myriophyllum*) structural complexity had similar surface areas (820 and 860 cm², respectively; Warfe and Barmuta, in review), yet there was a consistently higher periphyton biomass and macroinvertebrate abundance and diversity on *Myriophyllum*. Some studies have held surface area constant and shown that macroinvertebrate abundance (Jeffries 1993) and diversity (Parker et al. 2001) are greater on more structurally complex macrophytes and seaweeds, suggesting the shape of the habitat rather than surface area per se can be responsible for macroinvertebrate abundance and diversity and periphyton biomass.

The leaves on *Myriophyllum* face inwards towards the main stem, thereby exposing only half the total surface area, whereas the *Eleocharis* and *Triglochin* analogues have almost their entire surface area exposed and accessible to pygmy perch, providing little refuge from predation (Warfe and Barmuta 2004). On the *Myriophyllum* analogues, pygmy perch cannot get through the

Table 3 Results summary of univariate tests by general linear models

Effect	<i>df</i>	MS	<i>F</i> -value	P
Total macroinvertebrate abundance				
Between sites				
ToS	1,4	36.60	14.40	0.019
Within sites				
Mphyte	2,8	37.20	35.90	<0.001
<i>Eleo</i> versus <i>Trig</i>	–	–	3.26	0.011
<i>Trig</i> versus <i>Myrio</i>	–	–	2.69	0.028
ToS × Mphyte	2,8	0.10	0.14	0.872
Pred	3,12	2.37	3.75	0.041
Con versus Acc	–	–	2.56	0.025
Acc versus Pen	–	–	1.53	0.152
Pen versus Pex	–	–	0.73	0.478
Tos × Pred	3,12	0.21	0.33	0.802
Mphyte × Pred	6,24	0.23	0.38	0.890
ToS × Mphyte × Pred	6,24	0.24	0.39	0.880
Within sampling events				
Sevent	1,1	32.30	13.48	0.021
ToS × Sevent	1,1	13.50	5.63	0.077
Taxon richness				
Between sites				
ToS	1,4	1,284.00	30.8	0.005
Within sites				
Mphyte	2,8	1,181.00	55.19	<0.001
<i>Eleo</i> versus <i>Trig</i>	–	–	4.77	0.001
<i>Trig</i> versus <i>Myrio</i>	–	–	2.75	0.025
ToS × Mphyte	2,8	5.00	0.22	0.810
Within sampling events				
Sevent	1,1	191.40	8.33	0.045
ToS × Sevent	1,1	117.40	5.11	0.087
Invertebrate predators				
Between sites				
ToS	1,4	217.60	5.48	0.080
Within sites				
Mphyte	2,8	319.00	8.60	0.010
<i>Eleo</i> versus <i>Trig</i>	–	–	0.43	0.681
<i>Trig</i> versus <i>Myrio</i>	–	–	4.08	0.004
ToS × Mphyte	2,8	154.00	4.16	0.058
Vulnerable invertebrate grazers				
Between sites				
ToS	1,4	14,082.00	1.61	0.270
Within sites				
Mphyte	2,8	36,201.00	7.81	0.013
ToS × Mphyte	2,8	3,866.00	0.83	0.469
Pred	3,12	4,165.00	5.82	0.011
Tos × Pred	3,12	1,438.00	2.01	0.166
Mphyte × Pred	6,24	2,762.00	5.08	0.002
(Con versus Acc) × (<i>Eleo</i> versus <i>Trig</i>)	–	–	1.66	0.109
(Con versus Acc) × (<i>Trig</i> versus <i>Myrio</i>)	–	–	1.45	0.159
(Acc versus Pen) × (<i>Eleo</i> versus <i>Trig</i>)	–	–	1.73	0.096
(Acc versus Pen) × (<i>Trig</i> versus <i>Myrio</i>)	–	–	0.84	0.409
(Pen versus Pex) × (<i>Eleo</i> versus <i>Trig</i>)	–	–	0.93	0.362
(Pen versus Pex) × (<i>Trig</i> versus <i>Myrio</i>)	–	–	5.12	<0.001
ToS × Mphyte × Pred	6,24	1,151.00	2.12	0.089

The main effects tested were *Mphyte* macrophyte analogue, *Pred* predator treatment, *ToS* time-of-start and *Sevent* sampling event. The dependent variables were total invertebrate abundance, taxon richness, invertebrate predators and vulnerable invertebrate grazers. Only the significant results ($P < 0.05$) and pre-planned comparisons are presented. *Eleo*, *Trig* and *Myrio* represent the macrophyte analogues *Eleocharis*, *Triglochin* and *Myriophyllum*, respectively. Con, Acc, Pen and Pex represent the predator treatments as follows: cage control, access cages, cages with pygmy perch enclosed and cages with pygmy perch excluded. Each treatment combination was replicated three times, and data were log-transformed where necessary to meet assumptions of normality. $P < 0.05$ are in bold for significant interactions, or for main effects (and planned contrasts) only, where they are significant

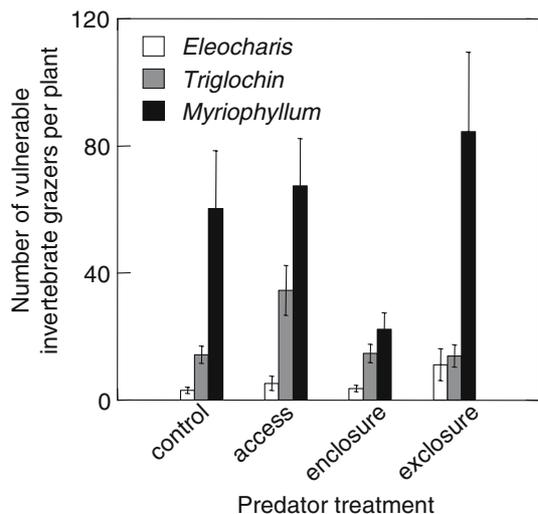


Fig. 3 The abundance of vulnerable invertebrate grazers on the *Eleocharis*, *Triglochin* and *Myriophyllum* analogues in each predator treatment. Pre-planned contrasts showed there was a significant difference in the number of vulnerable grazers between the enclosure and exclosure cages, but only on the *Myriophyllum* analogue. Error bars are one standard error about the mean

gaps between the dissected leaves to access the inside, thus the structure of *Myriophyllum* affords the greatest amount of surface area on which macroinvertebrates are safe from pygmy perch predation. Similarly, this orientation of *Myriophyllum* leaves may reduce local water velocities, as it has been shown to do for the highly-dissected leaf structure of *Ranunculus aquatilis* (Gregg and Rose 1982), providing more protection against physical disturbance and therefore, more periphyton growth. The shape of the habitat and the associated refuge space may be more important for macroinvertebrate and periphyton distributions than the absolute surface area (Warfe and Barmuta, in review).

Fish predation and habitat structure

Pygmy perch did not influence the overall macroinvertebrate assemblage, only a subset of the community: the vulnerable invertebrate grazers. Contrary to our expectations, however, pygmy perch had their greatest impact in the most structurally complex plant analogue, *Myriophyllum*. There were significantly fewer vulnerable invertebrate grazers on *Myriophyllum* when pygmy perch were enclosed rather than excluded, than on *Eleocharis* or *Triglochin* analogues. We hypothesise this unexpected result is caused by changes in both prey behaviour and predator behaviour as a direct result of the more complex structure of *Myriophyllum*.

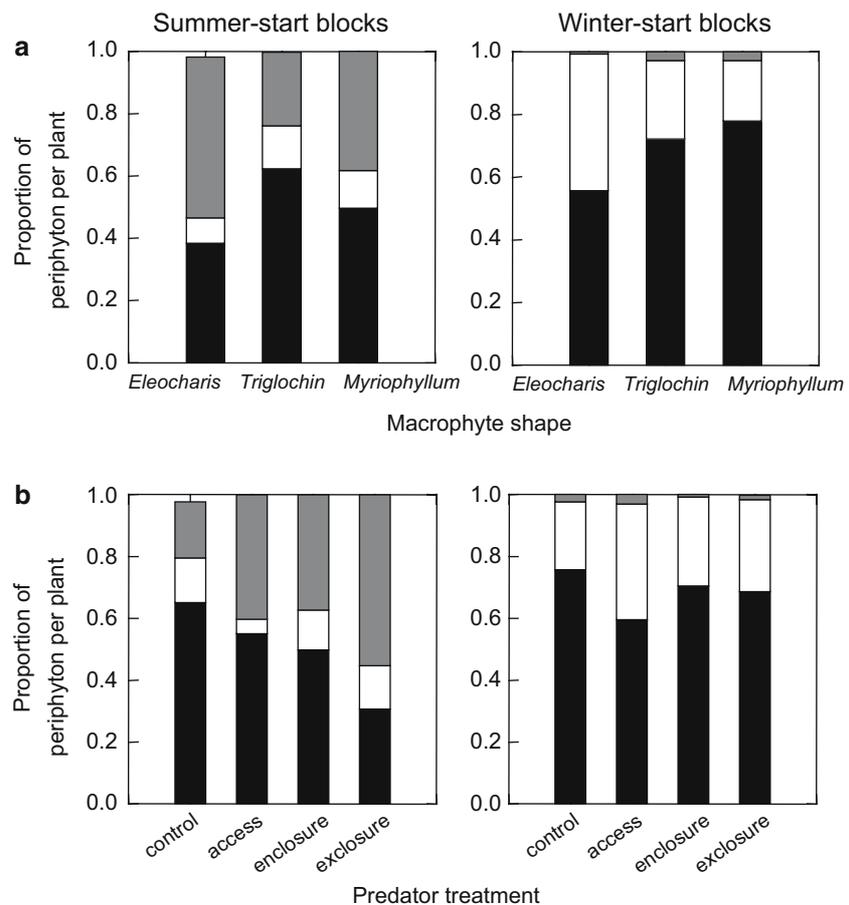
Vulnerable invertebrate grazers may alter their behaviour in *Myriophyllum* as a result of (1) interactions

with other members of the community and/or (2) an inability to detect the presence of predators, such that they increase their exposure and thereby their risk of predation in this particular plant analogue. The *Myriophyllum* analogues supported a greater abundance and diversity of animals, particularly invertebrate predators, which may have increased the number of potential predator-prey and/or competitive interactions. In the same manner that the escape response of mayflies to dragonfly predators increased their risk of predation by bluegill sunfish (Swisher et al. 1998), the escape response of vulnerable grazers to damselfly predators may have increased their exposure to, and their risk of predation from, pygmy perch. Similarly, competitive interactions can lead to the competitive loser suffering a greater risk of predation from fish predators (Coen et al. 1981).

Alternatively, vulnerable invertebrate grazers may have been unable to “perceive” the risk of predation in *Myriophyllum* compared to the other plant analogues and, therefore, increased their activity in this plant analogue. Mayfly larvae and ostracods have been shown to assess their risk of predation by fish and alter their behaviour accordingly (McIntosh and Townsend 1996; Uiblein et al. 1996). These studies imply that prey must be able to perceive the presence of a predator in order to exhibit changes in behaviour. If a highly-dissected leaf structure can dampen local current velocities (Gregg and Rose 1982), then it may also dampen the hydrodynamic cues of predators so their macroinvertebrate prey are unable to detect their presence and alter their behaviour, and reduce their exposure, accordingly (Dodson et al. 1994).

Fish predators can also change their behaviour depending on their habitat structure and have been shown to switch their foraging strategies with increasing vegetation density from searching to ambush (Savino and Stein 1982) or from ambush to searching, the latter possibly depending on their own risk of predation from higher-order predators (James and Heck 1994; Warfe and Barmuta 2004). Consequently, our unexpected result of pygmy perch having their strongest effects in the most structurally complex macrophyte may be due to an increased encounter rate between pygmy perch and their vulnerable prey. We hypothesise that this increased encounter rate arises from two mechanisms: that pygmy perch use a searching foraging strategy (and increase their mobility) in *Myriophyllum*, and that vulnerable invertebrate grazers are more exposed in *Myriophyllum*, whether through interactions with other invertebrates or an inability to perceive the risk of predation. But despite the greater effects of pygmy perch in *Myriophyllum*, these effects did not cascade down to the periphyton.

Fig. 4 The proportions of detritus (*closed bars*), green algae (*open bars*) and blue-green algae (*hatched bars*) comprising the periphyton on (a) each macrophyte analogue, and (b) in each predator treatment. The proportions of each periphyton component are presented separately for the summer- and winter-start cages due to a significant interaction between these main effects and time-of-start



Pygmy perch had no indirect effects on periphyton biomass, which contrasts with observations of strong indirect effects of fish predators on periphyton biomass in other studies (Power 1990; Martin et al. 1992). Pygmy perch only had an impact on a subset of the entire grazing community, whereas the patterns in the periphyton biomass probably reflected pressure from all grazers, many of which were not affected by pygmy perch predation.

However, the periphyton composition differed slightly with predator treatment; there was a trend towards less detritus and more blue-green algae in the cages without pygmy perch. These cages also supported greater numbers of vulnerable invertebrate grazers, but on *Myriophyllum* only. An increase in blue-green algae with greater densities of algal grazers appears to be relatively common and is explained by competitive interactions between green and blue-green algae (Power 1992; Rosemond 1996; Polis et al. 2000). While there was no corresponding decrease in the proportion of green algae in the predator exclusions, there was proportionally less detritus. If the green algae were resistant to herbivory, the vulnerable invertebrate grazers may have been consuming detritus instead, releasing space for the increased growth of blue-green

algae. It is possible that while the abundance of vulnerable grazers on the *Triglochin* and *Eleocharis* analogues may not have altered with predator treatment, they may have changed their behaviour and consumed more detritus on these analogues as well, which would explain why this pattern in the periphyton composition did not differ between the plant analogues. As tempting as this explanation may be, we have no strong data to support it and consider these indirect effects were very weak, only appearing in the summer-start cages after 6 months. This may reflect the low power for each time-of-start in this experiment. As it stands, we found no evidence of clear indirect effects of pygmy perch, nor any conclusive evidence of a trophic cascade, and we suggest this is a result of the strong influence of macrophyte structure on the macroinvertebrate and periphyton communities.

Timing of experimental initiation

Seasonal differences in community structure are often considered to be obvious, yet are rarely taken into account in the design of field experiments investigating community dynamics, despite having been shown to influence various community parameters (Underwood

and Anderson 1994; Nandakumar 1996; Price and Morin 2004). Our experimental design was used to distinguish the response of the community composition at the time of treatment application from the treatment response itself (Hurlbert 1984; Walters et al. 1988). Macroinvertebrate assemblages were predominantly characterised by insect taxa in the summer-start blocks and micro-crustacea in the winter-start blocks, and all macroinvertebrate groups were more abundant in the summer-start blocks. Furthermore, the proportion of blue-green algae was remarkably lower in the winter-start blocks than the summer-start blocks, changing the composition of the overall periphyton community. What distinguishes our results here is that even though there was an effect of time-of-start on periphyton and macroinvertebrate assemblage composition, suggesting seasonal effects on successional processes, this did not influence the major patterns observed in this experiment. Macrophyte shape strongly influenced the macroinvertebrate and periphyton communities, regardless of assemblage composition at the time of treatment application.

The comparison between S1 and S2 with W1 and W2 was not presented here as it showed very similar results; that macrophyte shape strongly dictated the composition of macroinvertebrate assemblages, and despite differences in the seasonal assemblages, there were no effects of pygmy perch predation (D.M. Warfe, unpublished data). For example, while there were considerably more taxa present in the summer blocks (S1 and S2; $F_{1,4}=98.1$, $P<0.001$), this did not significantly interact with the greater number of taxa found on *Myriophyllum* analogues ($F_{2,8}=44.7$, $P<0.001$), nor with the lack of a predator treatment effect ($F_{3,12}=0.78$, $P=0.53$). The S1/W1 and S2/W2 comparison could be considered a “true” test of time-of-start, whereas the comparison we presented here, the summer-start (S7 and S8) and winter-start (W1 and W2) blocks, was confounded by treatment “age”: the summer-start blocks were not only initiated in a different prevailing community, but also ran for 6 months longer than the winter-start blocks. The advantage of such a comparison is that we were able to identify predator effects in the S7 and S8 blocks, the only blocks to show such effects. This suggests that regardless of differences in initial assemblage composition, pygmy perch had very minor effects in this system, which were only observable after 6 months.

Conclusions

Implicit in the concept of trophic cascades is the phenomenon of “runaway consumption” (sensu Strong 1992) in that trophic cascades rely on strong interac-

tions for their presence (Pace et al. 1999; Polis et al. 2000). Strong (1992) and Polis (1999) have suggested that consumers generally do not have strong impacts, and trophic cascades are possibly less likely under conditions of high-diversity or extensive omnivory (Pace et al. 1999). The macrophytes in the Macquarie River support both these conditions. Macroinvertebrates were very abundant and diverse, particularly on the *Myriophyllum* analogue, which has measurably more space and surface rugosity (Warfe and Barmuta, in review) and is therefore more likely to support a more diverse range of microhabitats for macroinvertebrates. High-diversity communities are able to channel the effects of trophic interactions down many different pathways, and are therefore more able to buffer and absorb these effects than simple, low-diversity communities (Strong 1992; Polis et al. 2000). Pygmy perch consume prey on the basis of their abundance, mobility and exposure, and body size rather than their trophic status, and are thus omnivorous like some other fish predators (Humphries 1995; Warfe 2003). Omnivory, by its very nature, does not encourage clear separation between trophic levels and some research indicates that it is common in a range of food webs and can actually help stabilise webs that have a loose structure without sharply defined and delineated trophic levels (McCann et al. 1998). The high-diversity nature of our macrophyte-associated community probably contributes to the omnivorous habit of pygmy perch in this system.

Macrophyte structure strongly affected the structure of both the macroinvertebrate and periphyton communities, primarily through its effects of shape, and less so through its mediating effects on pygmy perch predation. When investigating the role of trophic interactions such as predation in regulating community structure, it is important to consider the habitat in which they are occurring, as this may prove to be a stronger regulating influence.

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