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Invertebrate distribution on a macroalgae/macrophyte mixed mat in flowing water

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With 6 figures and 3 tables

Abstract: In flowing waters, aquatic fauna is typically concentrated in the benthos, wood or other fixed substrates. Aquatic plants and filamentous algae may also offer refugia for invertebrates within the water column, due to flow attenuation, relatively stable substrate and provision of food. We quantified invertebrate abundance, size distribution and species composition along linear, flow-oriented gradients of mixed *Cladophora* sp. and *Elodea canadensis* mats in Crow Creek, northern Montana (USA). Mats were divided into four sections (0–20, 20–40, 40–60 and 60–80 cm, ordered basal to distal) using a customized sampler. Mat biomass, invertebrate richness and abundance were significantly higher in the 20–40 cm section, driven primarily by *Cladophora* biomass. Meanwhile, *Elodea* biomass was correlated with invertebrate richness in the 60–80 cm section. Most taxa, however, were not individually related to *Cladophora* or *Elodea* biomass, except for a positive relationship between *Elodea* biomass and the amphipod *Hyalella azteca* in the 0–20 cm section, and with cladocerans and copepods (meiofauna) in the 60–80 cm section. Biomass size spectra showed no difference among mat segments, but were prominently skewed towards smaller size classes (meiofauna), demonstrating that mats allow the presence of the meiofauna well into the water column of flowing waters. Stream epiphytic invertebrate communities may exhibit complex patterns in abundance and composition, potentially following a neutral model of colonization, movement, and loss of individuals along a linear flow-oriented substrate, but with strong interacting effects of substrate biomass, possible interspecific interactions, or distinct microhabitat preferences.

Key words: macrophyte biomass, meiofauna, neutral model, size distribution, *Cladophora*, *Elodea.*

Introduction

Benthic algae dominate primary production in small streams and are the food source for many stream macroinvertebrates (Brown et al. 2008). Benthic algae and attached biofilm enhance benthic structure (Dodds & Biggs 2002, Battin et al. 2003) and the resultant habitat heterogeneity contributes to riverine taxonomic richness (Ward 1998). Considered to be among the most abundant stream algae (Whitton 1970), *Cladophora* is one of the most important contributors to heterogeneity in streams (Dudley et al. 1986), and has been a significant subject of study (McCormick & Stevenson 1991, Dodds 1991a, b, Dodds & Gudder 1992, Biggs 1996, Shannon et al. 1994, Lamberti 1996, Stevenson 1997, Kemp & Dodds 2001). *Cladophora* mats are very dynamic environments capable of interacting with animal communities in many ways (Dudley et al. 1986, Dodds 1991b, Shannon et al. 1994), producing a stable yet mobile and changing substrate in running waters, lowering water velocity inside and around the mats, and providing spatial structure (Dud-

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ley et al. 1986). Interaction between *Cladophora* and aquatic vascular macrophytes has received occasional mention in the literature, being documented as an epiphyte on *Potamogeton pectinatus,* and a potential competitor with *Eleodea* and *Phragmites* (Whitton 1970, Dodds & Gudder 1992). Although these interactions are less well studied, the heterogeneity afforded by *Cladophora* may be augmented when combined with macrophytes, the resulting habitat of mixed mat communities potentially extending well into the water column of rivers and streams.

Common inhabitants documented from *Cladophora* mats include insects, amphipods, isopods, and water mites (Stevenson 1997). Meiofauna (Arthropods that pass a 0.5 mm mesh size) are also expected to occur within the heterogeneous substratum of *Cladophora* (Dudley et al. 1986, Dodds & Gudder 1992). Meiofauna are increasingly recognized as an important component of hyporheic or epibenthic environments (Robertson et al. 2000), however, they remain poorly studied from algal mats or macrophyte communities in fluvial systems. While the water column of lower order streams is less suitable for smaller planktonic organisms due to short water residence times, the key factors influencing meiofaunal abundance in streams, lower water velocities (e.g., boundary layer effects) and relatively stable substratum (Silver et al. 2002) are expected within algal mats and macrophytes. Mats may therefore contribute to the maintenance of meiofauna populations in rivers, among the various habitat patches that allow the persistence of riverine plankton populations (Thorp et al. 2006). The specific function of fluvial mats may vary depending on context, as temporary refugia, stable source populations, or metapopulations (*sensu* Bohonak & Jenkins 2003 for aquatic ecosystems). Organisms inhabiting these mats may in turn may be linked to conspecifics occupying other mats, flow-through lakes, backwaters, temporarily inundated zones, epibenthic, hyporheic or other suitable habitats, at the scale of reaches (e.g., Robertson et al. 1995) to riverscapes (Thorp et al. 2004).

We studied the arthropod community living inside and along what appeared to be relatively stable associations of *Cladophora* mats complexed with the macrophyte *Elodea canadensis* (mixed mats), in order to: (1) validate the potential for a significant meiofaunal community therein; (2) document the spatial patterns of invertebrate richness, abundance and size structure; and (3) determine the potential drivers of any small scale variability. We expected that the more flow sensitive meiofauna (in an inclusive sense, i.e. zooplankton that would have difficulty swimming against moderate currents, or positively thigmotactic organisms) would persist within the boundary layer of the mixed macrophyte mats, in a fluvial habitat where normally only fast-water macro-invertebrate species would be expected to occur. We expected that spatial patterns in metazoan abundance and diversity would be driven

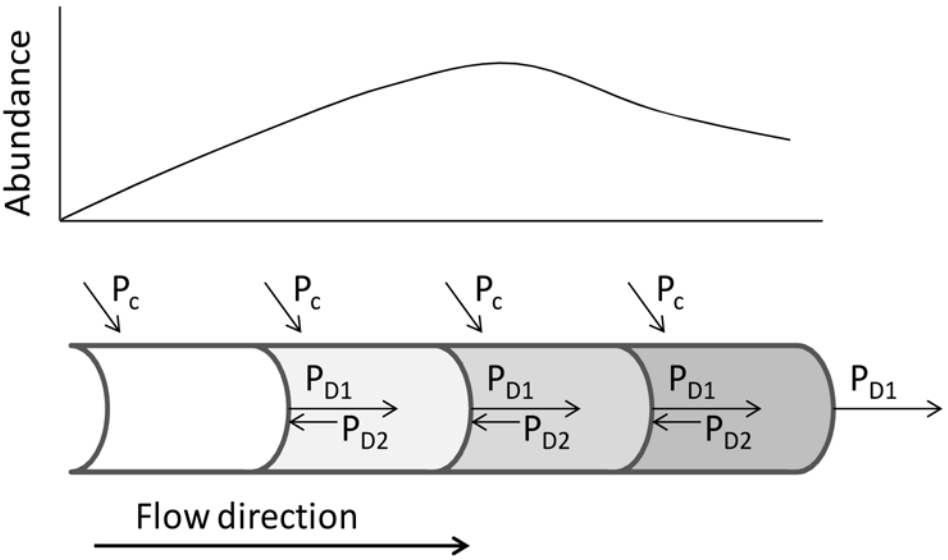

Fig. 1. Neutral model for colonization and passive dispersal along 4 sections of a macrophyte in flowing water. The probability of colonization from the water column or adjacent mats (Pc) is assumed to be equal for all sections. The probability of downstream dispersal (Pd1) and upstream dispersal (Pd2) are assumed to be unequal due to the increased energy required for swimming upstream. The downstream segment does not receive upstream dispersal and can only lose organisms to the water column. The model predicts peak abundance in the middle sections, assuming no interspecies interactions and no dependence on plant biomass.

by corresponding gradients in primary producer biomass (*Cladophora*, *Elodea*, or an interaction between the two). Spatial patterns of mixed mat invertebrates might also result from the differential probabilities of colonization, movement, and loss of individuals along a linear flow-oriented substrate, depending on metazoan size and adaptations (i.e., meiofauna vs. macroinvertebrates). The latter effects form the basis for a neutral model (*sensu* Gotelli & McGill 2006): colonization and dispersal dynamics predict peak abundance in middle sections of flowing-water mat communities (Fig. 1), assuming no interspecies interactions or dependence on plant biomass. Finally, size distribution might shift to larger species along the flow gradient, assuming growth of individuals along this gradient (a micro-succession gradient, or chronosequence).

The presence of significant meiofauna populations in algal mats and macrophyte beds may have important trophic implications: the small size classes and corresponding high turnover rate would result in enhanced water column secondary production, which otherwise may be negligible in small mountain streams. The fine scale distribution of epiphytic organisms in mixed mat communities may also provide insight towards appropriate sampling methods for zooplankton in small order rivers (Sluss et al. 2011).

Study site

A first order branch of North Crow creek was sampled, southwest of Ronan, Lake County, Montana, USA (lat 47° 30′ N, long 114° 04′ W). The study site is a medium gradient reach originating in the Mission Mountains, situated in the inter-montane valley, with open riparian zone and minimal agricultural activity in the 19.6 km^2 watershed. Water temperature was 10 ± 2 °C throughout the study, water depth ranged from 0.66 m to 0.62 m and discharge $0.4\,\text{m}^3\,\text{s}^{-1}$ to $0.24\,\text{m}^3\,\text{s}^{-1}$ during the study period (August and September 2002 respectively, U.S. Geological Survey, station 12375900). Water chemistry data was not available for the study period; however streams originating in the cordillera in this region are typically oligotrophic where agricultural impacts are minimal. Pure *Cladophora* sp. mats were rare in this stream, and Cladophora occurred in association with the macrophyte *Elodea canadensis*. The mixed mat assemblages covered a high percentage of the hard substratum (nearly 100 % in the reach). Water velocity close to the plants (SonTek/YSI Flow Tracker ADV, acoustic Doppler velocimeter, held 10 cm from mats) was characterized by stable nearly laminar flow, with a mean of 8.4 cm/s, and was not significantly different among plants ($p > 0.05$).

Fig. 2. Sampling device for mixed-mat floating macrophyte community, showing typical sample material.

Material and methods

A closed chamber algal sampler was designed to sample mixed mats oriented horizontally and parallel to the current, without interfering with flow patterns and thereby avoiding loss of fauna (Fig. 2). The sampler consists of a transparent acrylic tube 1 m long and 20 cm diameter, initially open at both ends, which was positioned downstream of the selected mat, and gently moved upstream to enclose the entire length of mats. The sampler was then capped at both ends, and four circular acrylic blades were inserted into slots at 20 cm intervals along the sampling tube, dividing the mat into as many as five equal 20 cm sections (6.28 liters each, only four sections were sampled due to limitations in mat length). Mats were selected based on the following criteria: (1) each mat was identifiable as a distinct unit; (2) *Cladophora* was the dominant algae within the mat; (3) total mat length was at least 60 cm. Sampling events (t_1, t_2, t_3) were spaced 15 days apart in August and September 2002, and three individual macrophyte/algal mats were sampled along a 50 m stream reach during each event. A total of 9 mats and 32 sections were collected (for four stations only three sections could be collected due to shorter mat lengths).

Invertebrates were removed from the algae or algae/macrophyte sections, identified and counted at 25×magnification. Head capsules of dominant taxa (insects, Cladocera and *Hyalella azteca*) were measured with an ocular micrometer and classed in eight groups ranging from 0.1 mm to 0.7 mm. *Cladophora* filaments were carefully removed from *E. canadensis* for separate biomass determination. Biomass density (macrophyte or algal biomass per volume sampled) was determined from ash-free dry mass (AFDM) and 2 dm^{-3} sample volume using standard methods. Biomass was used to indicate total amount of habitat available for arthropods. Reference material for identified specimens was deposited in the Flathead Lake Biological Station (University of Montana) collection.

Data analysis

A multivariate analysis was performed to determine the contribution of each taxon to the different sections. We used Reciprocal Average or Correspondence Analysis using PC-ORD software (McCune & Mefford 1997), non-hierarchical classification method, with down weighting for rare species. All other statistical analyses were performed using SPSS software. The influence of plant biomasses on ordination was tested using Pearson correlation. Abundance data were transformed as log (x + 1) and richness data were transformed as square root of y + 0.5 and analyzed using linear regression analysis (Zar 1984). Head size distributions of neighboring sections were compared using Wilcoxon signed ranks test (Zar 1984). Size spectra were analyzed from log base 2 transformed abundance and size (modified from Akoumianaki et al. 2006, based on head capsule length as described above).

Results

Elodea biomass was significantly lower than *Cladophora* biomass in the middle sections 20–40 cm section (paired sample t-test: t = 3.646, $p < 0.007$) and insignificant in the 40–60 cm section (mean 19.97 g m^{-3}, t = 2.68, $p < 0.028$). Biomass was not significantly different between the two taxain sections 0–20 cm and 60–80 cm (Fig. 3a). Differences in whole mat biomass between *Cladophora* and *Elodea* (pooled across segments) were most pronounced in sampling period t_1 (paired samples t-test: t = 2.785, $p = 0.019$, n = 11) and t_2 (t = 2.622, $p = 0.024$, n = 12), but were not significantly different in t_3.

A total of 10,242 invertebrates were collected and 30 taxa were identified (Table 3). Invertebrate abundance ranged between 30 and 2105 individuals per sample. The chironomid family Orthocladinae dominated with 4990 individuals, occurring in 100 % of the samples. *Hydroptila* sp. and other chironomids (except Pentaneurinii) were also among the most abundant invertebrates collected (> 500 individuals each). Less frequent species (< 5 individuals total) included occasional biting midge *Bezzia* sp. and water mite *Feltria* sp. Invertebrate abundance in 0–20 cm and 20–40 cm was significantly correlated with *Cladophora* biomass, while the 20–40 cm section was the only one where invertebrate abundance was correlated with *Elodea* biomass (Table 1). Overall invertebrate abundance based on sample volume was significantly

Table 1. Regression analyses of invertebrate richness and abundance per segment as a function of respective *Cladophora* or *Elodea* biomass (*$p < 0.05$, **$p < 0.005$).

Seg.	y	*Cladophora*			*Elodea*		
		R^2	F	*p*	R^2	F	*p*
0–20 cm	Rich	0.701	16.384	0.005 **	0.037	0.037	0.62
	Abun	0.692	15.726	0.005 **	0.128	1.02	0.345
20–40 cm	Rich	0.515	7.42	0.03 *	0.244	2.58	0.177
	Abun	0.593	10.198	0.015 *	0.426	6.94	0.034 *
40–60 cm	Rich	0.281	2.73	0.142	0.140	1.142	0.321
	Abun	0.227	2.056	0.195	0.024	0.173	0.69
60–80 cm	Rich	0.067	0.357	0.576	0.726	13.24	0.015 *
	Abun	0.065	0.348	0.581	0.464	4.336	0.092

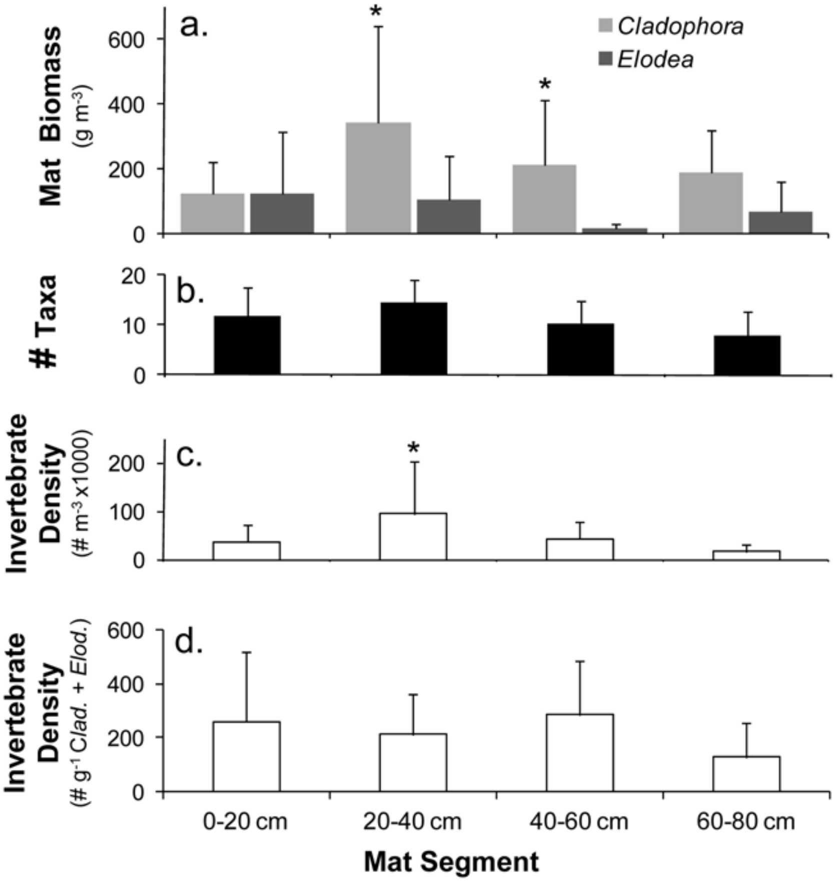

Fig. 3. Spatial distribution of mixed mat and associated invertebrate fauna averaged across the three sample dates: **(a)** mean (± s.d.) biomass of *Elodea* and *Cladophora* for each sample section (* significant within-segment difference in biomass between *Cladophora* and *Elodea, p* <0.05); **(b)** invertebrate taxonomic richness totaled over the three sample intervals; **(c)** mean (± s.d.) invertebrate density (* significant difference among segments, $p<0.05$); **(d)** mean (± s.d.) invertebrate density normalized for total plant biomass.

Table 2. Regression analyses results for richness of invertebrate taxa in relation to mat biomass (g AFDM m^{-3}*Cladophora, Elodea, Cladophora* + *Elodea*) in each period (t_i) (*$p<0.05$, **$p<0.005$).

time	*Cladophora*			*Elodea*			*Cladophora* + *Elodea*		
	R^2	F	*p*	R^2	F	*p*	R^2	F	*p*
t_1	0.631	15.402	0.003 **	0.146	1.542	0.246	0.599	15.965	0.003 **
t_2	0.373	5.937	0.035 *	0.027	0.275	0.611	0.279	3.865	0.078
t_3	0.145	1.528	0.248	0.306	3.967	0.078	0.309	4.028	0.076

higher in the 20–40 cm segment (t = 2.827, $p=0.02$, n = 9, Fig. 3c), while invertebrate abundance normalized for combined mixed mat biomass showed no trend along the horizontal length of the mat (Fig 3 d). General invertebrate abundance was significantly correlated with mixed-mat biomass (r = 0.793, $p=0.01$, n = 9, Fig. 4), the correlation was stronger with total *Cladophora* + *Elodea* (R^2 = 0.571) than with *Cladophora* biomass (R^2 = 0.493).

Total mean arthropod richness was 11.32 (SD = 5.32, n = 32), and was significantly and positively related to overall *Cladophora* biomass (F = 16.326, $p<0.05$). *Cladophora* biomass had the strongest positive correlation with invertebrate richness in sections 0–20 cm and 20–40 cm (Table 1). There was no relationship between overall invertebrate richness and *Elodea* biomass (F = 0.237, $p=0.989$), and among sections only 60–80 cm showed a positive relationship to *Elodea* biomass (Table 1). Among mat sections only 20–40 cm showed a significant relationship between invertebrate richness and *Cladophora* + *Elodea* biomass (r^2 = 0.505, $p=0.032$, n = 9, Fig. 3b), being significantly higher in 20–40 cm than 40–60 cm sections (t = 2.588, $p<0.03$, n = 9). Sampling over time showed that invertebrate richness followed *Cladophora* biomass in t_1 and t_2, and *Cladophora* + *Elodea* biomass in t_1 only (Table 2). In general invertebrate richness decreased when *Elodea* biomass became an important

Table 3. List of invertebrate taxa and corresponding multivariate analysis code.

Class	Order	Family	Genus/Tribe	CA code	Total abundance
Insecta	Plecoptera	Nemouridae	*Prostoia* sp.	Pros	$< 1\%$
	Ephemeroptera	Baetidae	*Baetis* sp.	Bae	271
			Procloeon sp.	Pro	$< 1\%$
		Leptophlebiidae	*Neochoroterpes* sp.	Neo	$< 1\%$
		Ephemerellidae	*Attenella* sp.	Att	$< 1\%$
	Trichoptera	Hydroptilidae	*Hydroptila* sp.	Hyd	619
		Limnephilidae	*Lepisostoma* sp.	Lep	260
	Diptera	Simuliidae	*Simulium* sp.	Sim	113
		Ceratopogonidae	*Bezzia* sp.	Bezz	$< 0.05\%$
		Chironomidae	Orthocladiinae	Ort	4990
			Prodiamesiinae	Prod	1587
			Tanytarsinii A	TaA	640
			Tanytarsinii B	TaB	775
			Pentaneurini	Pen	239
	Coleoptera	Haliplidae	*Brychius* sp.	Bry	205
			Haliplus sp.	Hal	$< 1\%$
		Dytiscidae	*Dytiscus* sp.	Dyt	$< 1\%$
		Elmidae	*Rhyzelmis* sp.	Rhy	$< 1\%$
Crustacea	Amphipoda	Hyalellidae	*Hyalella* sp.	Hyal	127
	Cladocera	Chydoridae	*Alona* sp.	Al	107
			Chydorus sp.	Chy	$< 1\%$
			Camptocercus sp.	Cam	$< 1\%$
	Harpacticoida	Canthocamptidae	*Canthocampthus* sp.	Can	$< 1\%$
	Cyclopoida	Cyclopidae	*Paracyclops* sp.	Par	$< 1\%$
Acari	Hydrachnidia	Hygrobatidae	*Hygrobates* sp.	Hyg	118
		Torrenticolidae	*Testudacarus* sp.	Tes	$< 1\%$
		Sperchontidae	*Sperchon* sp.	Sper	$< 1\%$
			Sperchonopsis sp.	Spe	$< 1\%$
		Feltridae	*Feltria* sp.	Fel	$< 0.05\%$
		Lebertiidae	*Lebertia* sp.	Leb	$< 1\%$

fraction of mat biomass (mean paired difference $t_3 = 98.01$, $SD = 215.51$, $n = 11$).

Multivariate analysis did not clearly indicate differences in invertebrate composition among sections ($\lambda_1 = 0.11$ and $\lambda_2 = 0.07$). However, some taxa showed a strong affiliation with specific sections: e.g. *Testudacarus* sp. in the 0–20 cm section, *Sperchon* sp. and the occasional *Feltria* sp. and *Bezzia* sp. in 20–40 cm section, and *Lepisostoma* sp. in the 40–60 cm section (Fig. 5). Removing infrequent taxa from the analysis did not significantly alter the results from that of the initial analysis. The 60–80 cm section showed a strong affiliation based on community composition to the20–40 cm section. There was a significant relation between axis I and *Elodea* biomass (Pearson Correlation: $r = -0.987$, $p = 0.022$), but there was no significant relationship between *Elodea* and axis II ($r = 0.125$, $p = 0.438$). Neither axis showed a significant response to *Cladophora* or *Cladophora* + *Elodea* biomass($p > 0.05$).

ANOVA regression analysis of different groups revealed a positive relation between *Hyalella azteca* and *Elodea* on 0–20 cm section ($r^2 = 0.527$, $F = 7.79$, $p = 0.027$). *Hydroptila* sp. was positively related to *Cladophora* biomass ($p = 0.027$) and *Elodea* biomass ($p = 0.001$) on 60–80 cm section. Almost all crustacean meiofauna were significantly correlated ($p < 0.05$) with *Elodea* biomass on the 60–80 cm section. The harpacticoid copepod *Canthocamptus* sp. was significantly related to *Elodea* biomass on 0–20 cm section ($p = 0.004$), but it was absent from the 60–80 cm section.

Invertebrate head capsule lengths were significantly different between adjacent sections ($p < 0.05$ Wilcoxon signed rank test for paired data). Invertebrate size spectra for all segments showed significant negative trends (negative slope indicating that the smallest sizes were most frequent, Fig. 6, ANCOVA, $R^2 = 0.914$, $\beta = -0.841 \pm 0.061$, $p < 0.000$), with a higher intercept for the 20–40 cm section (driven by differ-

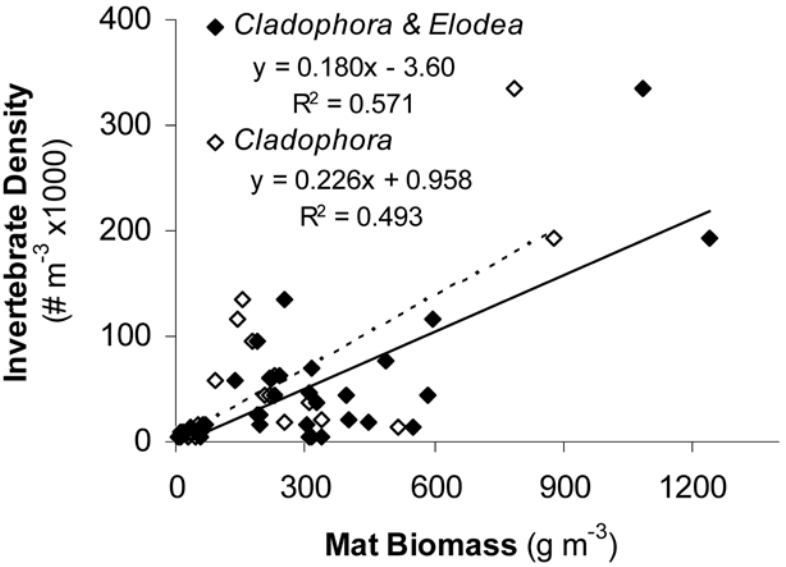

Fig. 4. Relationship between invertebrate density and mixed mat biomass or *Cladophora* biomass.

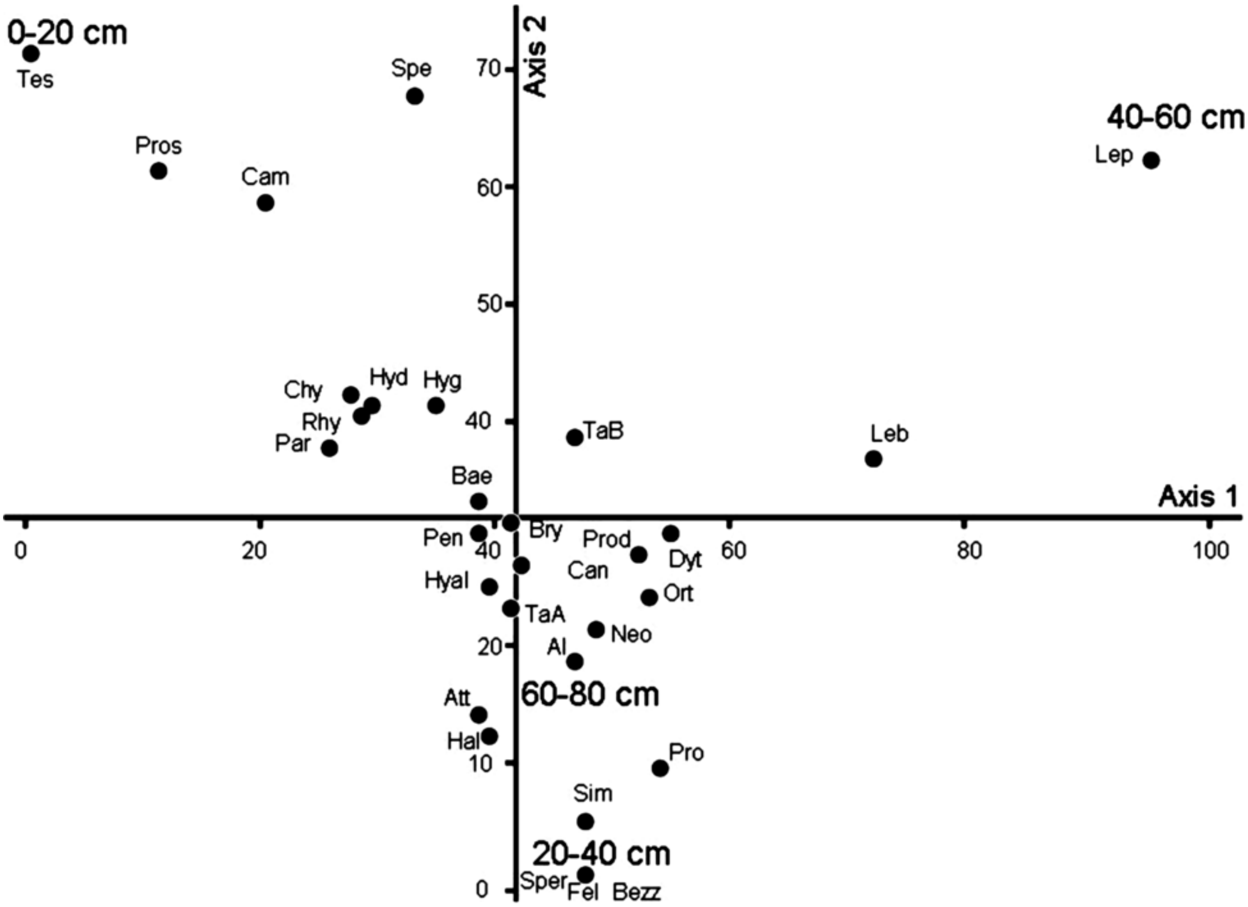

Fig. 5. DCA biplot for invertebrates and corresponding mixed mat segments. Species codes are listed in Table 3.

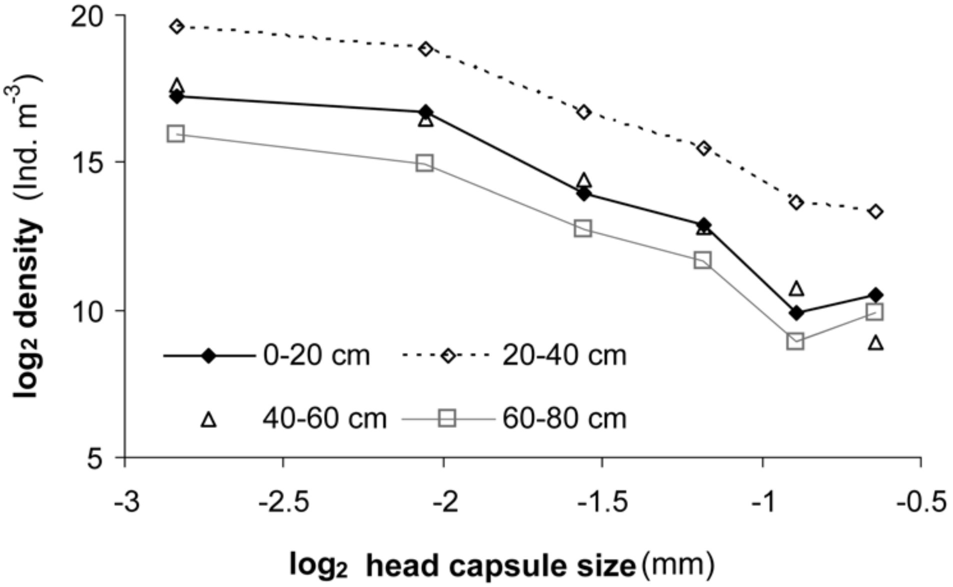

Fig. 6. Invertebrate size spectra (based on head capsule length) for respective mat segments, pooled over the three sample periods. Note the higher representation of smaller size classes, however body size distribution (slopes of regression lines) is not significantly different among segments.

ences in overall invertebrate abundance). Regression slopes were not different among mat sections, indicating that the distribution of size classes was the same for all mat segments.

Discussion

Meiofauna may provide a significant contribution to the stream benthic invertebrate community (Shiozawa 1991) and the water column of larger rivers (Sluss et al. 2011). Here we demonstrate that in lower order streams a significant meiofaunal community may extend into the water column, facilitated by the presence of macrophytes, algae or mixed mats. Unlike previous studies on epiphytic stream invertebrates, we did not use meshes to concentrate samples in the field. Therefore our samples included small invertebrates and smaller size classes that are probably underestimated in other studies (Dudley et al. 1986, Rundle & Hildrew 1990, Hakenkamp et al. 2002). Meiofauna such as cladocerans, copepods and water mites were strongly represented, and could be regarded as the dominant organisms; among our samples only the Ephemeroptera, Plecoptera, Trichoptera (which were less frequent) and Amphipoda are considered macroinvertebrates (> 0.5 mm body size).

Significant differences in biomass among the two primary producer taxa, and significant spatial variation within taxa was observed. Invertebrate populations also showed significant spatial patterns. In general, primary producer biomass together with invertebrate density and invertebrate richness peaked in the middle sections. However, beyond this generalization, finer scale or species specific patterns are more complex. At the scale of whole mats, invertebrate richness and abundance corresponded with *Cladophora* biomass (Figs 3, 4), but this overall pattern was driven mainly by stronger relationships in the middle sections of the mats, co-varying with significantly lower *Elodea* biomass. During the course of the study, the effect of *Cladophora* on invertebrate dynamics was strongest in the first sampling period t_1, when the only two pure *Cladophora* mats were collected. *Elodea* was more sparsely (i.e. intermittently) distributed, suggesting that *Cladophora* was the dominant substrate-forming mat species. This was followed by purely mixed mats in t_2, where biomass of *Elodea* was not linked to overall patterns of invertebrate biomass or richness (except for isolated effects on abundance in 20–40 cm segment and richness in 60–80 cm segment). In fact, invertebrate richness decreased with an increase in *Elodea* biomass, contrary to observations by Suren (1991) and Dodds & Biggs (2002) that suggested that macrophytes potentially increase reach-scale biodiversity through increasing habitat heterogeneity. The effect of macrophytes may in fact be indirect, offering structure for epiphytic algae or mixed macrophyte/algal mats.

Specifically in the case of *Elodea*, a negative relationship with invertebrate dynamics may be expected due to chemical defenses and toxicity of this macrophyte species (Newman 1991), but impossible to determine directly based on this study.

The differential probabilities of colonization, movement, and loss of individuals along a linear flow-oriented substrate (neutral model, Fig. 1) may be a factor in forcing invertebrate patterns (Fig. 3c). However abundance normalized for plant biomass eliminated any trend (Fig. 3d). Species richness follows the same pattern of peak abundance in middle sections, but this may be an indirect effect due to rare species sampling effect (Connor & McCoy 1979). Confounding physical factors may also modify the neutral effect. Experimental work by Sand-Jensen & Mebus (1996) showed that velocity reduction within *E. canadensis* reached a maximum effect in the interior the mats, between one and two-thirds of the distance from upstream to downstream end of the mats. Although flow attenuation in mixed mats is not known, in general the highest flow attenuation of *Elodea* corresponds with the 20–40 cm and 40–60 cm sections, and may offer another mechanism for peak invertebrate abundance for these sections.

Analysis at the scale of individual taxa provides evidence that substrate patchiness and more complex community dynamics may have a strong modifying effect on any neutral patterns or direct effects of primary producer biomass. In spite of the short gradient considered, we observed a very patchy distribution for some taxa (*Testudacarus* sp., *Sperchon* sp., Limnephilidae, *Simulium* sp.), conforming with observations by Young (1969). Among the insects, only *Hydroptila* sp. was correlated with mat biomass. Ordination on axis I corresponded with *Elodea* biomass wherever low eigenvalues resulted; hence the distribution of water mites suggests active avoidance of *Elodea* plants, while the amphipod *Hyalella azteca* and the harpacticoid *Canthocamptus* sp. preferred the 0–20 cm section. These patterns were especially evident for the 0–20 cm section, with relatively higher *Elodea* biomass, stronger stem and larger leaves. Hence, *Hyalella* may be responding to the substratum structure rather than to mat biomass (Hansen et al. 2011). Crustacean meiofauna responded positively to the *Elodea* biomass. In spite of low correlation between *Elodea* biomass to invertebrate community dynamics across individual plants, it may be an important factor for certain species distributions within mixed mats.

Distribution of cladocerans such as *Camptocercus* sp., *Alona* sp., *Chydorus* sp. and also the copepod *Paracyclops* sp. corresponded with relatively higher *Elodea* biomass at the distant 60–80 cm section, but not in the first section. These organisms are swimmers in lentic systems, but may persist in mixed mats in flowing waters because of relative flow attenuation (Dodds & Biggs 2002). However the 60–80 cm segment was the most exposed section in the mats, and may not necessarily correspond with peak flow attenuation (Sand-Jensen & Mebus 1996), suggesting that factors other than physical structure or overall plant biomass influence these observed distributions.

With respect to alternative explanations for plant-invertebrate patterns in the mixed mat communities, direct consumption of either *Elodea* or *Cladophora* biomass is unlikely. Koslucher & Minshall (1973) reported *H. azteca* as an occasional *Cladophora* consumer (< 20 %) in a desert stream of an Idaho-Utah valley. Epiphytic algal production may be significant and also specific to host taxa, which might translate into finer scale patterns in herbivore distribution. Shamsudin & Sleigh (1995) report epiphytic algae from *Cladophora*, particularly diatoms and lesser numbers of cyanophytes, however epiphytes were significantly less frequent on *Cladophora* than for the macrophyte *Ranunculus* in the same system. Not much is known about *Elodea* epiphytes, possibly the more rigid *Elodea* leaves produces a similarly more developed film of microscopic plants, animals and organic debris than *Cladophora*. Shannon et al. (1994) found a positive correlation between amphipod *Gammarus lacustris* and the epiphytic diatom assemblage on *Cladophora glomerata* in the laboratory, but this association was weak in the field. Soszka (1975) affirms that macrophytes provide a more significant role as substratum for periphyton, detritus trap or refugium, than as a direct food base for invertebrate herbivores. In his review of submersed macrophyte fauna, Newman (1991) found low number of vascular plant feeders compared to algae and detritus feeders, and suggested that more work on food preferences among epiphytic invertebrates is essential.

Conclusions

A significant meiofaunal community may extend into the water column in lower order streams, facilitated by the presence of macrophytes, algae or mixed mats. Choice of sampling methods (processing whole sample volumes instead of using mesh to concentrate samples in the field) played a key role in arriving at this conclusion, small invertebrates and smaller size classes are probably underestimated in other studies of epiphytic fauna. Significant differences in biomass and significant spatial variation was observed for the two primary producer taxa and invertebrate populations. In general, primary producer biomass, invertebrate density and invertebrate richness peaked in the middle sections. However, beyond this generalization, finer scale or species specific patterns are more complex. Various lines of evidence indicate mixed mat biomass and corresponding structure may be the potential drivers of these patterns, while neutral mechanisms are probably a lesser factor. However other more complex interactions such as herbivory and *Elodea* toxicity may also be inferred, but require more specific testing.

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