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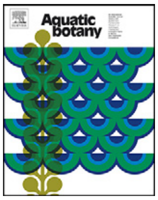

Macrophyte presence and growth form influence macroinvertebrate community structure

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ABSTRACT

Multivariate analysis demonstrated that macroinvertebrate assemblages of macrophyte-dominated sub-habitats within a small eutrophic pond differed markedly from those of *Bottom substrate* and *Open water* habitats. Certain habitats (e.g. *Nymphaea* and *Phragmites*) appeared to be quite similar in their macroinvertebrate communities, whereas others appeared to be very distinct in terms of the species composition (e.g. *Open water* habitat). Analysis of functional feeding groups also revealed differences between habitats in terms of the community structure. Again, the *Open water* habitat exhibiting the most marked difference. Macrophyte growth form does not cause significant differences in macroinvertebrate species richness and diversity but it has a significant effect on macroinvertebrate abundance. Habitats consisting of highly branched and dissected macrophyte growth forms provide more food resources and microhabitats supporting larger numbers of macroinvertebrates than macrophytes with firm undissected stalks and leaves. This study highlights the importance of maintaining the ecological quality of small freshwater habitats in order to promote macrophyte growth and thus maintain a high level of species richness within such ecosystems.

1. Introduction

The physical structure and architectural complexity of freshwater habitats determine the community that resides there (Rennie and Jackson, 2005). Macroinvertebrate distribution patterns in streams are typically dependent upon the particle size of the mineral component of the substrate (e.g. Tolkamp and Both, 1978; Khalaf and Tachet, 1980; Sheldon and Haick, 1981). Within still water bodies (e.g. lakes and ponds) it has been demonstrated that macroinvertebrate distribution, is predominantly determined by the vegetation type, and more importantly, by the architecture or growth form of the dominant macrophytes (e.g. Cyr and Downing, 1988; Duggan et al., 2001; Dvořak and Best, 1982; Karassowska and Mikulski, 1960; Korinkova, 1971; Rennie and Jackson, 2005; Scheffer et al., 1984; Taniguchi et al., 2003).

The importance of aquatic macrophytes as habitats in aquatic systems has been demonstrated by the abundant and diverse macroinvertebrate communities that they support (Warfe and Barmuta, 2004). Both macroinvertebrate diversity and abundance increase with increasing vegetation biomass and/or density (Warfe and Barmuta, 2004; and references therein). Macrophytes fill the water column in a characteristic way providing extensive substrate for periphyton, macroinvertebrates and developing eggs, as well as shelter against predation by larger animals such as fish. Furthermore, macrophytes influence the under water climate and chemistry via their uptake and release of chemical substances (e.g. nutrients, allelopathic substances) and influence bottom life via the input of macrophyte derived detritus (Van der Valk, 2006). Macrophytes therefore structure lentic communities (Den Hartog and van der Velde, 1988; Jeppesen et al., 1998). Macrophyte growth form, adding substrate and biomass with a particular architecture and structural complexity, has been referred as a driving factor behind macroinvertebrate community composition (Den Hartog and van der Velde, 1988; Jeffries, 1993; Van der Velde, 1980).

In this study the macroinvertebrate communities of several sub-habitats, represented by various macrophyte growth forms, within a single pond are described. Studying the influence of various growth forms of macrophytes within a single pond has the advantage that water chemistry and physical conditions are similar within the various types of sub-habitat and show comparable fluctuations, whilst macroinvertebrates represent one species pool and can easily select where to reside. Seasonal variation should

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normally be taken into consideration but can be ruled out here because all samples were obtained during the same period. In this way the direct influence of growth form on macroinvertebrate communities can be studied without large variation in other factors.

In this paper the macroinvertebrate species richness, diversity and abundance are described from seven different sub-habitats (five different macrophyte growth forms, bare bottom substrate and open water) within a freshwater pond. This study thus provides useful information pertaining to the ecological importance of macrophytes in small freshwater systems.

2. Materials and methods

2.1. Study area

This investigation was conducted in a small, eutrophic, still water pond in Fleetwood, NW England (Ordnance Survey Grid Reference: SD318449) (open water surface area approximately 700 m^2), with an average depth of <100 cm and a maximum depth of 140 cm. The bottom substrate is clay overlain with coarse gravel and fine organic silt.

Encroachment of vegetation is clearly evident from a large reed bed consisting predominantly of *Phragmites australis* interspersed with *Typha latifolia* and *Iris pseudacorus* at the southern end of the pond which is approximately the same size as the open pond itself. Almost the entire littoral zone is vegetated with five macrophyte species belonging to different growth forms predominating (Table 1).

2.2. Field collections

A standard pond-net (230 mm × 255 mm frame with 900 μm mesh) was used to collect 10 replicate macroinvertebrate samples from each of the seven main habitat types identified within the pond. Care was taken to avoid repeat sampling of the same area. Each sample was obtained using 1 m sweeps with the net being covered at the end of each sweep to prevent escape or contamination of the sample as the net was removed from the sampling point. This ensured that a standard volume of approximately 50 L was sampled each time. Samples taken from the bottom substrate were obtained by pushing the net rim approximately 2 cm into the substrate and then carrying out a 1 m sweep. For macrophyte habitats, samples were obtained from stands representing several growth forms as close to monospecific as possible. Care was taken to ensure that each net sweep was performed only in that specific habitat, i.e. when sampling weed beds care was taken not to touch, or disturb, the bottom sediment to avoid sampling invertebrate populations residing there. Similarly care was taken not to sample open water habitats above or surrounding weed beds to avoid sampling invertebrates in that region. All sampling was conducted within a 1 week period during July to avoid any potential differences associated with season. Whilst this study therefore pertains to only a limited time, this month is associated with high productivity for both macrophytes and macroinvertebrates thus main lines are likely to be observed.

Samples were immediately rinsed into 1 L plastic containers using de-ionised water and the net was thoroughly examined for any invertebrates still clinging to the net. Any macroinvertebrates found were gently removed using forceps or de-ionised water and added to the sample. Samples were later sorted in large white trays and all macro-invertebrates were removed from the sediment, water and/or vegetation, and preserved in 70% ethanol. Macroinvertebrates were identified to species level where possible.

2.3. Statistical methods

Berger-Parker Dominance Index (BPDI) was used as a simple measure of species diversity and is calculated as:

$$\text{BPDI score} = \text{Number of individuals of the most abundant species}/\text{Total number of Individuals of the sample}$$

BPDI scores closer to 0 indicate higher species diversity.

Data for macroinvertebrate abundance, species richness and species diversity for each habitat were tested for significant differences between habitats using a Kruskal–Wallis ANOVA followed by Dunns multiple comparisons post hoc test. Spearmans rank correlation coefficients were performed to test for linear relationships between these variables.

2.4. Multivariate analyses

A Canonical Correspondence Analysis (CCA), which is a direct gradient analysis, was performed on the log-transformed species data, using the CANOCO for Windows software package (version 4.5) (Ter Braak and Smilauer, 1998). A Detrended Correspondence Analysis (DCA) showed that the data had a long gradient length (4.1 for all data; 2.2 when open water data were excluded); therefore a unimodal ordination method was used. A CCA is a direct method, which means that in this case the species compositions can be directly explained by the environmental characteristics (habitat types).

To compare (dis)similarity of the communities between habitat types non-metric multi-dimensional scaling (nMDS) in combination with analyses of similarity (ANOSIM) were executed in Primer 5.2.9. Before analyses, all data were fourth-root transformed to minimise the effect of dominant species, and similarity analyses are based on the Bray–Curtis formula (Clarke and Gorley, 2001). An nMDS 2D representation was considered acceptable when the stress factor did not transgress 0.2. With ANOSIM, pair-wise comparisons of differences between habitat-types in the macrofauna communities were tested for taking a Bonferroni correction for multiple testing of the same kind, according to $P \leq 0.05/N$ (N = number of tests of the same kind) into account. One sample from the 'Open water' was excluded from the analyses as it contained no macrofauna.

3. Results

3.1. Growth forms

Seven key habitat types were identified (Table 1). These habitats can be further grouped into open water, bare bottom substrate, emergent helophyte (*P. australis*), nymphaeid (*Nymphaea alba*) and peplid (*Callitriche* sp.) both possessing floating leaves, and fully submerged elodeid (*Elodea canadensis*) and ceratophyllid (*Ceratophyllum demersum*) macrophytes.

The different habitat types represent a diverse range of habitats differing markedly in terms of their structural complexity. The *Open water* habitat is structurally non-complex due to the lack of vegetation or other three-dimensional components. The emergent (*Phragmites*) and floating leaved (*Nymphaea*) habitats exhibit some structural complexity with plant stalks running upwards through the water column to the waters surface. The three submerged (either partially or completely) habitat types containing macrophytes (*Elodea*, *Ceratophyllum* and *Callitriche*) are all complex in terms of their structural architecture due to the highly branched and dissected growth forms they exhibit. The non-vegetated bottom (*Bottom substrate*) habitat is unique in that it is complex in

Table 1
Description of the seven habitat types sampled in Rossall pond including depth range at which the habitat types were found and/or sampled. Growth forms of macrophytes according to the classification by Den Hartog and van der Velde (1988).

Habitat	Description	Complexity	Depth range (cm) sampled
Open water	Open water with no macrophytes present.	Highly simple	50–120
Bottom substrate	Bottom sediment consisting mainly of fine gravel and silt. No macrophytes present.	Complex	30–100
Elodeid	Predominantly *Elodea canadensis*. Submerged rhizophyte with upright shoots and with small but broad oval leaves typically in whorls of 4 at each node. No floating leaves.	Moderately complex	40–100
Ceratophyllid	Predominantly *Ceratophyllum demersum*. Submerged rhizophyte or pleustophyte with whorls of 5–12 leaves at each node. Leaves typically forked once or twice. No floating leaves.	Highly complex	40–100
Peplid	Predominantly *Callitriche* sp. Caulescent rhizophyte with branched structure with elliptical floating leaves in a rosette and linear submerged leaves.	Moderately complex	40–60
Nymphaeid	Predominantly *Nymphaea alba*. Large floating shield-shaped leaves attached to long simple submerged stalks.	Simple	70–120
Helophyte	Predominantly *Phragmites australis* although frequently interspersed with individuals of *Typha latifolia* and *Iris pseudacorus*. Plants rooting in the bottom, with basal parts continuously submerged running vertically through the water column; leaves and inflorescences far above the water surface.	Simple	30–50

terms of its structure (many and varied microhabitats) but does not project into the water column and contains no large, living, structural components.

3.2. Species richness, diversity and abundance

In total 39 different taxa were identified from 2707 individuals collected from seven different sub-habitats. The most abundant taxa overall were the water hog louse, *Asellus aquaticus* and the triclad flatworm, *Dugesia lugubris*, with 773 and 887 individuals respectively, from 70 samples. Damselfly larvae (Zygoptera; *Enallagma cyathigerum* and *Ischnura elegans*) were also common in occurrence and were the second and third most abundant predatory species (*D. lugubris* being the most abundant). Table 2 shows the occurrence and total numbers of the different taxa recorded from each habitat type.

The species richness of each habitat increased with increasing number of samples taken (Fig. 1). However, in all cases, except the *Phragmites* habitat, this number levelled off after approximately six samples had been analysed (Fig. 1). With regard to the total species richness observed, the habitats displayed the following order: *Bottom substrate* ≥ *Phragmites* > *Nymphaea* > *Callitriche* ≥ *Elodea* > *Ceratophyllum* > *Open water*. The *Phragmites* and *Bottom substrate* habitats were the most species rich, each found to match the species richness of the aggregated samples (for the whole pond) by >60%. Both of these sites also contained the highest number of species unique to those habitats (three each, Table 3). The *Open water* habitat was the poorest in terms of species richness with only nine different taxa being recorded.

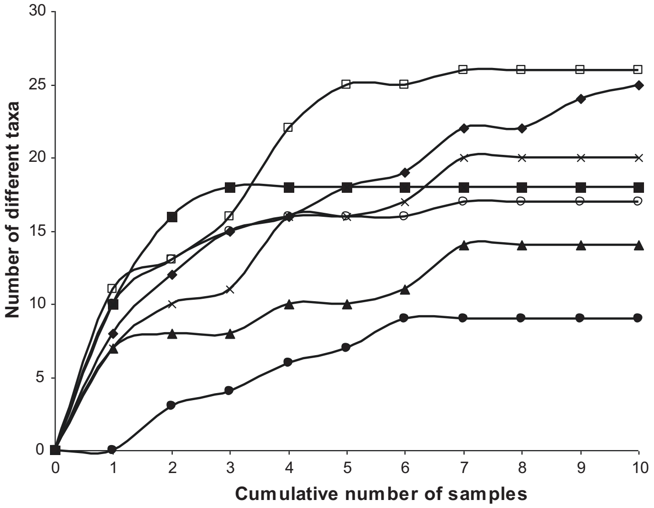

Fig. 1. Taxon accretion curves for all seven habitats. ○ = open water habitat; □ = bottom substrate habitat; ♦ = *Phragmites* habitat; × = *Nymphaea* habitat; ■ = *Callitriche* habitat; ● = *Elodea* habitat; ▲ = *Ceratophyllum* habitat.

Kruskall–Wallis test demonstrated significant differences in species richness between the different habitats ($P < 0.0001$; Table 3). Dunn's multiple comparison test revealed that vales for the *open water* habitat differed significantly from those of *Bottom substrate*, *Nymphaea*, *Callitriche* and *Elodea* habitats. With regard to the mean number of species observed, the habitats displayed the following, decreasing order: *Bottom substrate* > *Callitriche* > *Elodea* > *Nymphaea*, *Ceratophyllum*, *Phragmites* > *Open water*. Differences were also shown between habitats for species diversity (Kruskal–Wallis test – $P = 0.001$; Table 3) with Dunn's multiple comparison test demonstrating that these differences were only statistically significant between *Nymphaea* and *Elodea* habitats.

The total number of invertebrates collected from each habitat type showed a large range from just 19 individuals collected from *Open water* samples to 789 individuals collected from *Callitriche* samples. The total number of invertebrates collected were in decreasing order from *Ceratophyllum* > *Elodea* > *Bottom substrate* > *Callitriche* > *Phragmites* > *Nymphaea* > *Open water*. Significant differences in the mean invertebrate abundance per sample were observed between habitats (Kruskal–Wallis test – $P < 0.0001$; Table 3) with Dunn's multiple comparison test demonstrating that values for *Open water* habitat were significantly different from all other habitats apart from *Phragmites* and *Nymphaea* habitats. Significant differences were also observed between *Bottom substrate* and *Nymphaea*; *Phragmites* and *Elodea*; *Phragmites* and *Ceratophyllum*; *Nymphaea* and *Elodea*; and *Nymphaea* and *Ceratophyllum*. With regard to the mean number of individuals observed, the habitats displayed the

Table 2
Full species list including number of individuals sampled for each of the seven habitats in Rossall pond and functional feeding groups: D – detritivores; SGS – shredders, grazers and scrapers; F – filtrators; PrC – predatory carnivores; PaC – parasitic carnivores.

Habitat Taxa	Feeding group	*Phragmites australis*	*Nymphaea alba*	*Callitriche* sp.	*Ceratophylum demersum*	*Elodea canadensis*	*Substrate*	*Open water*
Insecta								
Diptera								
Chironomidae	D	2	14	10	21	10	32	
Ceratopogonidae	D	1						
Pedicia sp.	D	1						
Dixa sp.	F	1		1				
Eristalis sp.	D	2		7			5	2
Odonata								
Ischnura elegans	PrC	29	14	29	61	29	45	
Enallagma cyathigerum	PrC	12	31	23	3	15	10	1
Aeshna grandis	PrC						8	
Coleoptera								
Hygrotus inaequalis	PrC			3				
Hyphydrus ovatus	PrC		4				2	
Dryops sp.	PrC							1
Heteroptera								
Notonecta sp.	PrC	3		2		1	2	
Corixa punctata	D	37	4	19	9	13	67	2
Ephemeroptera								
Cloeon dipterum	SGS	1	3					
Trichoptera								
Arthripsodes aterrimus	SGS						2	
Lepidoptera								
Elophila nymphaeata	SGS		3					
Megaloptera								
Sialis lutaria	PrC			1	1		64	
Crustacea								
Eurycercus lamellatus	F	16		9	11	5	11	1
Simocephalus vetulus	F	2	2			2		
Asellus aquaticus	SGS	12	5	111	276	204	163	1
Argulus foliaceus	PaC	1	2				2	8
Cypris sp.	F	1		11			14	
Crangonyx pseudogracilis	SGS	2	4	8		7	1	
Mollusca								
Bivalvia								
Musculium lacustre	F	2						
Sphaerium corneum	F						61	
Pisidium sp.	F		1	1			1	
Gastropoda								
Physa fontinalis	SGS	5			10	1	7	2
Segmentina complanata	SGS	9	5	5		8	3	
Radix peregra/ovata	SGS	6	3		1	1		
Planorbis carinatus	SGS	7		10		7	4	
Planorbarius corneus	SGS				24	5		
Radix auricularia	SGS		8				5	
Hirudinea								
Helobdella stagnalis	PrC	1					2	
Hemiclepsis marginata	PaC				7			
Glossiphonia complanata	PrC		3		4			
Turbellaria								
Dugesia lugubris	PrC	8	16	71	357	425	9	1
Oligochaeta								
Tubifex sp.	D						5	
Arachnidae								
Argyroneta aquatica	PrC	2						
Hydracarina	PrC		3	5	10	10	5	

following, decreasing order: *Ceratophyllum* > *Elodea* > *Bottom substrate* > *Callitriche* > *Phragmites* > *Nymphaea* > *Open water*.

The habitats supporting the greatest number of macroinvertebrates were the *Ceratophyllum* and *Elodea* habitats. The combined abundance of these two habitats made up 56.9% of the abundance from the aggregated samples. In both cases, one taxon (*D. lugubris*) constituted approximately half of the habitats overall abundance. This indicates low evenness and this is reflected by their relatively poor scores for species diversity (Table 3). The *Phragmites* habitat had the BPDI score closest to 0 and therefore exhibited the highest species diversity out of the seven habitats sampled (Table 3). BPDI score was in decreasing order *Open water* > *Elodea* > *Ceratophyllum* > *Callitriche*, *Phragmites* > *Bottom substrate* > *Nymphae*a. Differences between habitats with regard to species diversity were only found to be significant between *Nymphaea* and *Elodea* habitats (Dunn's multiple comparison test: $P < 0.05$).

3.3. Multivariate analyses

For the Canonical Correspondence Analysis with all data included, the *Open water* habitat appeared to be completely different from the other habitats in terms of macroinvertebrate species present (see insert, Fig. 2). *Argulus foliaceus* (no. 21 in Fig. 2) was found more frequently in *Open water* than in any of the other habitats; *Dryops* sp. (no. 11 in Fig. 2) was observed only once. All the other taxa were observed in at least two habitats and/or in similar numbers. When the *Open water* data were excluded, the

Table 3
Macroinvertebrate species richness, abundance and BPDI (species diversity) values for the seven different habitats. Also shown is the proportion of the total pond species richness found in each of the habitats (% of total richness). % of total abundance = the proportion of the total number of macroinvertebrates sampled that were obtained from each habitat. The most abundant species for each habitat type are also given. Numbers in parentheses = 1 standard error.

	Phragmites	*Nymphaea*	*Callitriche*	*Ceratophyllum*	*Elodea*	*Substrate*	*Open water*
Richness	25	20	18	14	17	26	9
% of total richness	61	48.8	44	34.1	41.5	63.4	22
Number of unique taxa	3	1	1	1	0	3	1
Mean richness per sample (*n* = 10)	7 (2)	7.1 (2.2)	9 (2.3)	7.1 (1.7)	8.2 (1.8)	11.5 (3.3)	1.6 (1.2)
Abundance	167	127	326	789	753	530	19
% of total abundance	6.2	4.7	12	29.1	27.8	19.6	0.7
Most abundant taxa	*Corixa punctata*	*Enallagma cyathigerum*	*Asellus aquaticus*	*Dugesia lugubris*	*Dugesia lugubris*	*Asellus aquaticus*	*Argulus foliaceus*
Mean abundance per sample (*n* = 10)	16.7 (6.2)	32.6 (15.8)	78.9 (39.0)	12.7 (4.2)	53 (22.9)	1.9 (1.4)	75.3 (24.8)
Species diversity	0.22	0.24	0.34	0.45	0.56	0.31	0.42
Mean diversity per sample (*n* = 10)	0.38 (0.12)	0.34 (0.13)	0.4 (0.14)	0.51 (0.09)	0.36 (0.18)	0.67 (0.37)	0.56 (0.11)

distribution of the taxa in the other habitats is more distinct (Fig. 2). Eigenvalues for axes 1–4 are 0.295, 0.221, 0.160 and 0.101, respectively. The species – environment correlations are high, being 0.956 and 0.901 for the axes 1 and 2, respectively. The first ordination axis might be interpreted as the gradient from without vegetation to dense vegetation whereas the second axis might be related to the three-dimensional complexity of the vegetation structure in the water column. Therefore the *Nymphaea* and *Phragmites*

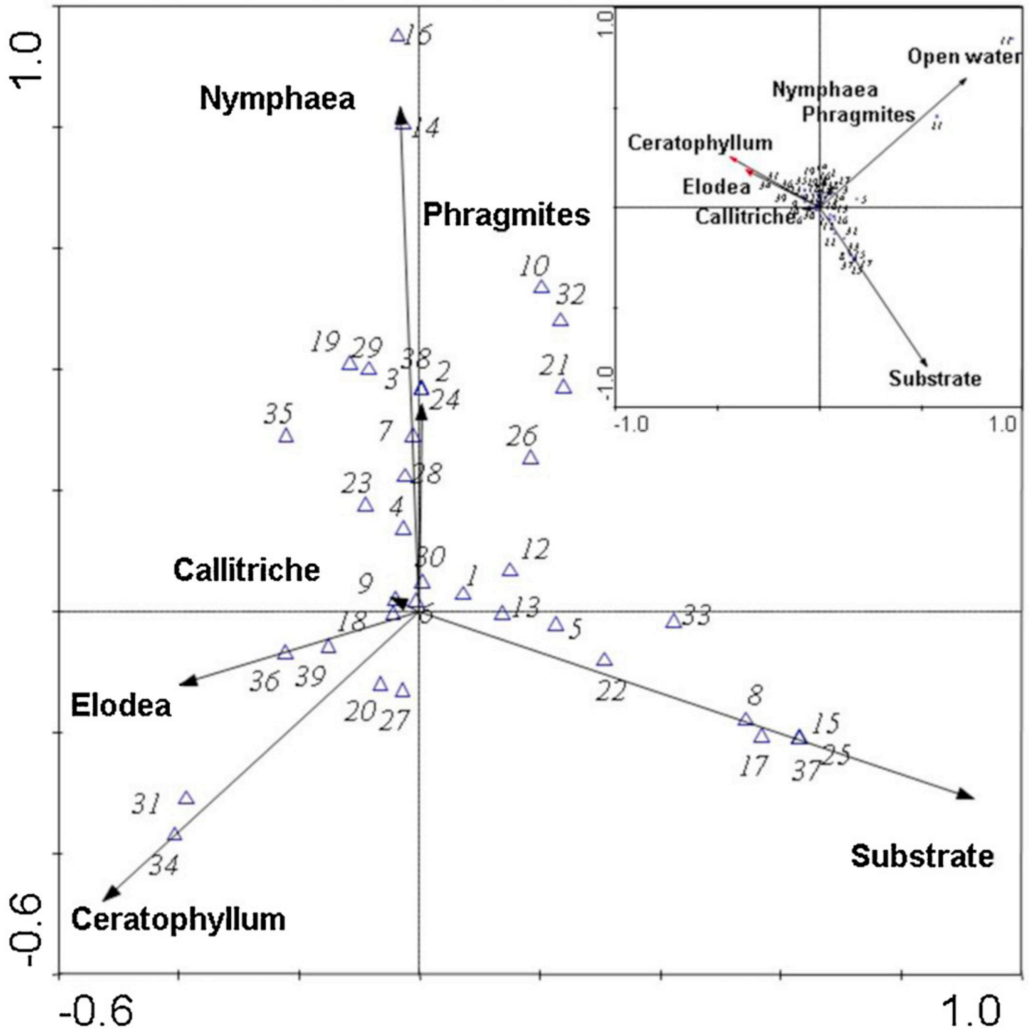

Fig. 2. CCA analysis without (a) and with (b) *Open water* habitat data. Chironomidae (1); Ceratopogonidae (2); *Pedicia* sp. (3); *Dixa* sp. (4); *Eristalis* sp. (5); *Ischnura elegans* (6); *Enallagma cyathigerum* (7); *Aeshna grandis* (8); *Hygrotus inaequalis* (9); *Hyphydrus ovatus* (10); *Dryops* sp. (11); *Notonecta* sp. (12); *Corixa puntata* (13); *Cloeon dipterum* (14); *Arthripsodes aterrimus* (15); *Elophila nymphaeata* (16); *Sialis lutaria* (17); *Eurycercus lamellatus* (18); *Simocephalus vetulus* (19); *Asellus aquaticus* (20); *Argulus foliaceus* (21); *Cypris* sp. (22); *Crangonyx pseudogracilis* (23); *Musculium lacustre* (24); *Sphaerium corneum* (25); *Pisidium* sp. (26); *Physa fontinalis* (27); *Segmentina complanata* (28); *Radix peregra* (29); *Planorbis carinatus* (30); *Planorbarius corneus* (31); *Radix auricularia* (32); *Helobdella stagnalis* (33); *Hemiclepsis marginata* (34); *Glossiphonia complanata* (35); *Dugesia lugubris* (36); *Tubifex* sp. (37); *Argyroneta aquatica* (38); Hydracarina (39). Insert = CCA analysis with *Open water* data included.

Table 4
Analyses of similarity (ANOSIM) test results (corresponding to the nMDS plot of Fig. 3) indicating significant differences between communities of the different habitat types. R-values for pair-wise comparisons varying between 0 and 1, indicating the degree of separation (from $R = 0$; communities completely overlap, to $R = 1$; communities are completely separated) are shown when differences are significant ($\alpha = 0.0024$ after Bonferroni correction; ns = not significant).

	Phragmites	*Nymphaea*	*Callitriche*	*Ceratophyllum*	*Elodea*	*Substrate*	*Open water*
Phragmites			Overall comparison of communities: $P = 0.001$, $R = 0.517$				
Nymphaea	0.410						
Callitriche	ns	0.485					
Ceratophyllum	0.565	0.776	0.684				
Elodea	0.432	0.592	0.315	ns			
Substrate	0.535	0.752	0.574	0.925	0.870		
Open water	0.466	0.567	0.566	0.571	0.577	0.539	

habitats appeared to have relatively similar species compositions. The three fully submerged, highly branched/dissected macrophyte sub-habitats also show a large degree of similarity in terms of their species composition. Few species are specifically related to *Callitriche*; these species can also be found in the other habitats in similar numbers.

These findings are confirmed by the results of the analyses of similarity (Table 4). As indicated by an overall R-value of 0.517 the communities of the different habitat types are clearly distinguishable, showing significant differences ($P = 0.001$). The nMDS plot of Fig. 3 indicates that there is some overlap in the species compositions but the samples for each of the habitat types cluster very well. Pair-wise comparisons (ANOSIM results Table 4) show that actually the communities of each of the habitat types significantly differ from each other habitat type, except for the mutual communities related to *Callitriche* and *Phragmites*, and the mutual communities of *Elodea* and *Ceratophyllum* habitat.

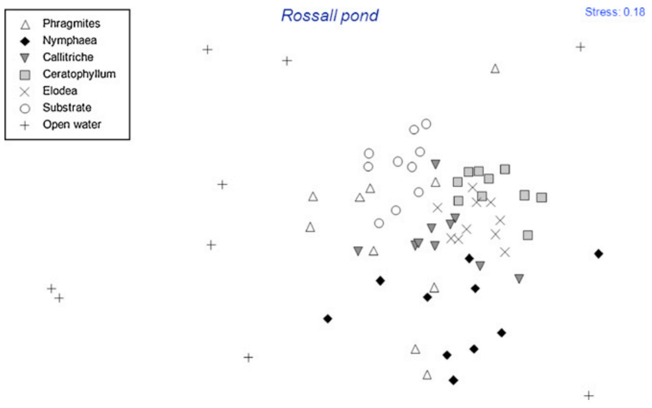

Fig. 3. Non-metric multi-dimensional scaling (nMDS) plot indicating the similarity of macrofauna communities per habitat type, showing the individual samples.

3.4. Functional feeding groups

Analysis of functional feeding groups showed that the overall abundance of predatory carnivores was higher than all other groups (Fig. 4). The group containing shredders, grazers and scrapers was the second largest of the five groups and the parasitic carnivores constituted only 1% of the pond community overall. This pattern is similar for macrophyte-dominated habitats (*Phragmites*, *Callitriche*, *Ceratophyllum*, *Nymphaea* and *Elodea* (Fig. 4)). The *Bottom substrate* and *Phragmites* habitat contained relatively most filter feeders and detritivores of all habitats studied. In the *Bottom substrate* habitat, predatory carnivores are only outnumbered by the group containing the shredders, grazers and scrapers. Only in the *Open water* habitat do predatory carnivores occur in fewer numbers than two of the other functional feeding groups. Parasitic carnivores were not found in large numbers although they did constitute the dominant (in terms of total number of individuals) functional feeding group in the *Open water* habitat.

4. Discussion

Zonation of aquatic macrophytes is typical in still-water-bodies and was also evident in the system studied here. This enabled

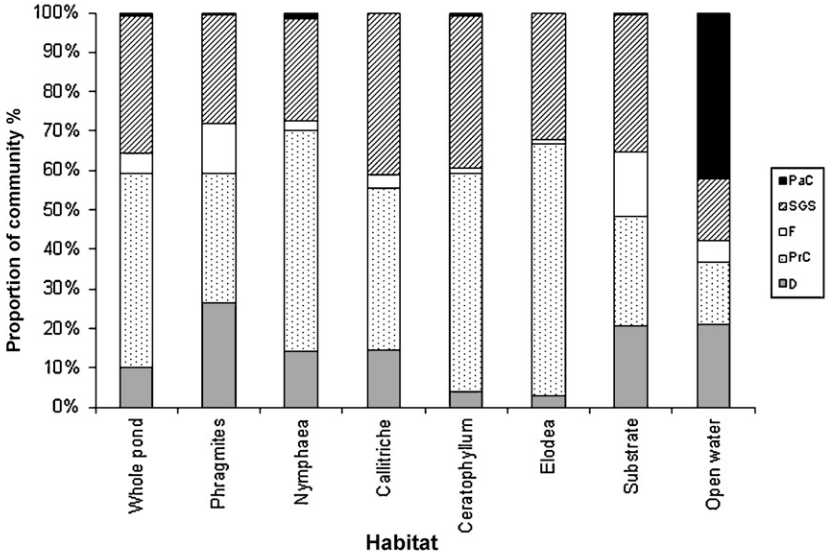

Fig. 4. Proportion of different macroinvertebrate feeding groups in Rossall pond showing proportions for seven different habitats also. D – detritivores; SGS – shredders, grazers and scrapers; F – filter feeders; PrC – predatory carnivores; PaC – parasitic carnivores.

sampling to be undertaken in relatively monotypic macrophyte stands. The rarefaction curves show that six samples are sufficient to estimate the species richness in each of the habitats (with the possible exception of the *Phragmites* habitat). A single operator collected and sorted all the samples thus reducing the margin for error that can occur when the same sampling technique is interpreted and employed by different researchers (Furse et al., 1981).

Structurally more complex habitats are generally assumed to be richer in the number of taxa residing there due to the greater range of microhabitats offering a greater range of niches. Krecker (1939) and Andrews and Hassler (1943) found that generally, the greater the leaf dissection of a submerged macrophyte, the larger and more varied was the animal population associated with it (Rosine, 1955). Furthermore, macrophyte species with a higher level of structural complexity (i.e. finely dissected leaf structure and intricate branching) seem to support a greater number of individual macroinvertebrates and a greater array of different taxa (Heck and Orth, 1980; Rooke, 1986). Jeffries (1993) predicted that the abundance of taxa and individuals should increase with increasing fractal complexity, which was demonstrated in experiments with artificial pondweeds of differing fractal dimension. Our data support the hypothesis that macrophytes with greater degrees of branching and leaf dissection support a greater number of macroinvertebrates but not necessarily a greater range of taxa.

In those habitats where relative abundance was highest (i.e. *Callitriche*, *Ceratophyllum*, *Elodea* and *Bottom substrate*), it was noted that one species typically dominated the samples. In particular *Asellus aquaticus* and *D. lugubris* occurred in high numbers in several habitats. *A. aquaticus* is known to be relatively non-specific, in terms of its diet, feeding on detritus, periphyton and even decaying macrophyte tissues (Soszka, 1975) or in the case of *Elodea* also young leaves (Marcus et al., 1978). *A. aquaticus* is not able to feed on living leaves of *Nymphaea*, because of high phenolic content but can feed on decaying leaves of that plant (Kok et al., 1992). *Elodea* contains low amounts of phenolic compounds (Smolders et al., 2000). *D. lugubris* is a predatory species but its prey are typically small, relatively numerous invertebrates associated with macrophyte surfaces. This species abundance was highest on the three fully submerged macrophyte species which also have the most branched and dissected growth forms and therefore can be considered the most complex. Their greater surface area provides a much larger colonisable surface for the prey items of *D. lugubris* in particular snails and *Asellus*.

Open water samples were significantly poorer than all other habitats in terms of the species richness, species diversity and invertebrate abundance. Few macroinvertebrates are specialist pelagic feeders. Many smaller invertebrate species (e.g. some cladocerans and copepod species) are able to filter feed in this habitat type however the large number of resident fish (*personal observations*) will undoubtedly impact heavily upon any invertebrates, both macro and smaller, residing in this sub-habitat. *Argulus foliaceus* is an intermittent crustacean ectoparasite on fish. It has been shown to employ two host-searching strategies, one in dark conditions and the other during light periods. During light periods this species employs a ‘sit-and-wait’ strategy, hovering in the water column waiting for a potential host fish to swim past so that it can ‘leap’ on to it (Mikheev et al., 2000). This behaviour offers a logical explanation for this species presence in *Open water* samples.

The SGS species were found in several habitats probably due to the generalist feeding strategies typical of these species. The CANOCO analysis shows that they typically reside in fully submerged macrophyte stands. These macrophyte species are highly dissected and branched in structure presenting a relatively high surface area for periphyton to colonise and also for detritus falling through the water column to settle upon thus providing a proportionately abundant food resource for generalist feeders such as *A. aquaticus*. In addition, high numbers of very small invertebrates such as rotifers, gastrotrichs, copepods, cladocerans and very young individuals of other common species (e.g. gastropods) as well as *Asellus* are likely to be found on these surfaces providing an abundant prey source for some of the generalist predators such as *D. lugubris* (Reynoldson and Young, 1963) and the zygopteran species.

The large numbers of predatory carnivores suggests that smaller prey organisms must also be present in relatively high numbers. However, large numbers of potential prey species were not generally observed apart from *A. aquaticus*. We speculate that these predatory species are predating upon smaller crustaceans such as cladocerans and copepods which were not recorded in this study probably due to the fact that most would pass through the mesh of the net used. It is also probable that these predatory species show a distinct lack of specificity with regard to what they would catch and eat.

In summary, the CCA analyses suggest that although seven habitat types were studied, they can be roughly grouped into four categories with the *Phragmites* (helophyte) and *Nymphaea* (nymphaeid) forming one group; *Callitriche* (peplid), *Ceratophyllum* (ceratophyllid) and *Elodea* (elodeid) forming a second group (although it should be stated that the *Callitriche* habitat is not as easily separated out as the others), the *Bottom substrate* forming a third group and finally the *Open water* habitat forming a very distinctive fourth group on its own. The nMDS results (Fig. 3) confirm the distinction of these community types although each vegetation type also clearly holds its own community. It is particularly the larger variation in community assemblage for a vegetation type like *Phragmites* or *Ceratophyllum* that leads to some overlap with the communities of other vegetation types, than that their communities would not have unique elements. The more gradient-like community change from *Ceratophyllum* via *Elodea* to *Callitriche* however emphasises that it is more the vegetation structure determining the macrofauna communities than that species are typically related to a certain plant species. Descriptions of macroinvertebrate communities from pond systems should take into account that communities vary considerably depending upon which habitat types are sampled and that different vegetation forms support different macroinvertebrate communities. Furthermore, the influence of other animals (e.g. fishes) may also influence macroinvertebrate community composition. Finally, this study highlights the importance different macrophyte growth forms with regard to biodiversity. Different macrophyte growth forms could thus play an important role in the stimulation of high biodiversity in constructed and semi-natural waterbodies (Vermonden et al., 2009, 2012).

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