Freshwater Biology (2000) **43**, 591–604

Do submerged aquatic plants influence periphyton community composition for the benefit of invertebrate mutualists?

J. IWAN JONES*, BRIAN MOSS, JOHN W. EATON AND JOHNSTONE O. YOUNG
School of Biological Sciences, Derby Building, University of Liverpool, PO Box 147, Liverpool, L69 3BX, UK

SUMMARY

1. It has been suggested that submerged aquatic plants can influence the periphyton which grows on their surfaces, making it nutritionally beneficial to snails. In return, preferential feeding by snails clears the plants from a potential competitor, with both plants and grazers gaining from this mutualistic relationship.
2. A highly replicated experiment was conducted, in which the nature of the plant (isoetid and elodeid types compared with similar shaped inert substrata), the nutrient availability (10–200 $\mu g\ L^{-1}$ P, 0.2–4 $mg\ L^{-1}$ N) and the influence of periphyton grazers, *Physa fontinalis*, were controlled. The plants were cleaned of periphyton before use and an algal inoculum added to all treatments. At the end of the growth period, quantitative measures of the periphyton community composition were made and related to the treatments using both ordination and analysis of variance.
3. Grazing had the largest influence on community composition and algal numbers. A community of unicellular and adpressed filamentous forms developed in the presence of snails, and of erect filamentous forms in their absence. Three algal species, *Cocconeis placentula*, *Chamaesiphon incrustans* and *Aphanochaete repens*, increased in real numbers in the presence of snails, probably as a result of reduced competition whilst being able to withstand grazing.
4. The second largest effect was the influence of host plant. However, differences between the two artificial plants were as great as between the real plants and their artificial counterparts, indicating that physical structure was as important as any active contribution by the plants. Nutrients had a small but significant effect on community composition, but not all species responded in the same way to nutrient enrichment.
5. Although submerged aquatic plants exert an influence over the community composition of the periphyton which develops on their surfaces, it is unlikely that they manipulate it to make it more attractive to grazers such as snails.

Keywords: algae, *Elodea nuttallii*, *Littorella uniflora*, macrophyte, mutualism, *Physa fontinalis*, plant architecture, snail

Introduction

It seems inevitable that the submerged parts of aquatic plants become coated with a layer of periphyton; however, there is controversy over the extent to which the host plant can influence this community of algae. It has variously been suggested that the plants are simply inert platforms (Shelford, 1918), hosts which mildly affect the behaviour of the periphyton (Cattaneo & Kalff, 1979; Carignan & Kalff, 1982) or part of an interacting system in which the

*Correspondence and present address: J. I. Jones, School of Biological Sciences, Queen Mary & Westfield College, University of London, London E1 4NS, U.K. E-mail: J.I.Jones@qmw.ac.uk

plants exert considerable influence (Allen, 1971; Wetzel, 1983). Hence, the extent to which the communities growing on artificial plants reflect those on real plants has been strenuously debated (Cattaneo & Kalff, 1979; Cattaneo & Kalff, 1981; Gough & Gough, 1981).

Evidence that plants release nutrients (McRoy & Goering, 1974; Carignan & Kalff, 1982; Burkholder & Wetzel, 1989), and possibly carbohydrates (Pip & Stewart, 1976), which are subsequently taken up by periphyton would imply a high degree of interaction. Furthermore, biologically active chemicals which influence algal growth have been isolated from plant tissues (Anthoni *et al*., 1980; Planas *et al*., 1981; Wium-Andersen *et al*., 1982, 1983, 1987; Elankovich & Wooten, 1989; Pip & Philipp, 1990; Pip, 1992; Gross & Sütfeld, 1994; Gross, Meyer & Schilling, 1996), and allelopathy has been suggested as another mechanism by which the plants may control their periphyton. A number of attempts have been made to relate the specific composition of the algal periphyton community to different aquatic plant hosts in the same lake (Gough & Woelkerling, 1976; Cattaneo & Kalff, 1978; Eminson & Moss, 1980; Carignan & Kalff, 1982; Blindow, 1987; Cattaneo *et al*., 1998). However, such correlations could merely reflect different microhabitat conditions in which the hosts were growing rather than giving evidence of causal manipulation of the periphyton community by the plant. A specific relationship between periphyton and host plant appears most evident in conditions of low nutrient availability (Eminson & Moss, 1980) and breakdown in eutrophic waters, where the distinction between periphyton and phytoplankton community composition is also severely eroded (Moss, 1981). This might suggest that it is the plant, in providing nutrients or other benefits, rather than the plant's microhabitat, which is behind the specificity. It also opens up the possibility that certain configurations of the periphyton community are less disadvantageous to the host plant than others and that the plant might manipulate the community composition to its own advantage.

Therefore, a mutualistic relationship has been suggested between submerged aquatic plants and invertebrates which graze periphyton, particularly snails (Hutchinson, 1975; Thomas, 1990). If the host plant can encourage algae which are highly edible and nutritious rather than non-ingestible or indigestible, then invertebrate grazers could be encouraged to graze these algae preferentially and keep periphyton biomass low. The plants benefit from a reduced periphyton load, whilst in return for preferential grazing, the snails gain nutritionally. Given the apparent advantages to either partner, the potential for co-evolution is strong (Thomas, 1990).

Experimental manipulation indicates an apparent inability of the host plant to control broad features of the nutritional composition of its periphyton, or of the plant to provide benefits to a snail grazer not provided by artificial and inert replicas of itself (Jones *et al*., 1999). Hence, it would seem that evidence for the mutualistic interaction proposed by Thomas (1990) and hinted at by the possibilities of selective grazing and allelopathy might be sought in the specific composition of the periphyton community. A controlled experiment where the separate effects of plant species, nutrients and grazing could be isolated is described in the present paper. It represents a considerable advance on the field-based correlational studies which have hitherto been the sole approaches to this issue.

Methods

Two species of plant were used, *Elodea nuttallii* (Planch.) St John and *Littorella uniflora* (L.) Asch., and compared with artificial plants of similar architecture, but which are not physiologically active. Both plant species used in the present study exhibit reduced growth and survival under conditions of enhanced periphyton (Sand-Jensen & Søndergaard, 1981; Birch, 1990; Jones *et al*., 1999). The two plants display contrasting characteristics of growth rate, leaf texture and exchange between the leaf and the surrounding water. The snail species used, *Physa fontinalis* (L.), is associated with a wide variety of plants including the two species used in the present study (Boycott, 1936; McMillan, 1946; J. I. Jones, 1999, personal observations).

Sixteen plants of one treatment type were placed in buckets containing a 5-cm depth of natural sediment and 8 L of water, either in the presence or absence of snails, and at one of three weekly additions of nutrients:

1 10 $\mu g\ L^{-1}$ P as NaH_2PO_4 and 0.2 $mg\ L^{-1}$ N as NH_4NO_3;

2 50 $\mu g\ L^{-1}$ P as NaH_2PO_4 and 1 $mg\ L^{-1}$ N as NH_4NO_3; and

3 200 μg L^{-1} P as NaH_2PO_4 and 4 mg L^{-1} N as NH_4NO_3.

Hereafter, these are referred to as nutrients 1, 2 and 3. To ensure that diatoms had a supply of silicate, 2 mg L^{-1} Si as $Na_2SiO_3.5H_2O$ was added weekly to all the buckets. These nutrient levels approximately correspond to those found under nutrient poor to very nutrient rich conditions (Moss, 1998).

The sediment was taken from the Leeds and Liverpool Canal, UK (53° 30′ N, 2° 57′ W), frozen to –24 °C to kill any invertebrates, sieved (0.5-mm mesh) and mixed to ensure uniformity. The water was obtained from a borehole, then diluted with deionized water to reduce the nutrient content to 0.2 mg L^{-1} dissolved inorganic nitrogen, < 0.1 μg L^{-1} total phosphorus and 1 mmol L^{-1} dissolved inorganic carbon (for water chemistry methods, see Mackereth, Heron & Talling, 1989). No particulates were detectable in the borehole water. Polyethylene aquarium plants were adapted to form individual shoots of equal size. *Elodea nuttallii* plants, obtained from the Leeds and Liverpool Canal (53° 29′ N, 2° 56′ W), were cut to 10 cm, and *L. uniflora*, obtained from Llyn Tegid, North Wales, UK (52° 54′ N, 3° 35′ W), were trimmed to three leaves before use.

To ensure the real and artificial plants were in a similar condition at the start of the experiment, the plant material was vigorously shaken in water until the surfaces were free from algae. A 25-mL aliquot of a mixed algal inoculum, obtained from a collection of several plant species from various waterbodies over a wide range of nutrient conditions by shaking, was then added to each treatment.

In spring 1994, adult snails were collected from the Shropshire Union Canal, UK (53° 14′ N, 2° 54′ W) and cultured in the laboratory (Standen, 1951) until the animals reproduced. Using the same technique, these offspring were reared in the laboratory to provide a standard population of individuals from which 20 individuals were added to each of the appropriate buckets.

All 24 treatments, replicated four times in four randomized blocks, were then incubated for 8 weeks (from July to September 1994) at 20 °C, illuminated by 150 μmol m^{-2} s^{-1} photosynthetically active radiation on a 16 h:8 h light:dark cycle. The blocks were arranged on either side of two controlled temperature growth rooms. Each bucket was continually aerated and any losses to evaporation replaced with deionized water.

Harvesting

Every 2 weeks during the growth period, the periphyton biomass on one randomly selected plant from each bucket was measured to determine the grazing rate of the snails (see Jones *et al*., 1999).

At the end of the 8-week growth period, the buckets were harvested block-wise, one block per day. All the periphyton was removed from each of the remaining 13 plants by 1 min of vigorous shaking in 400 mL of tap water (as demonstrated by Zimba & Hopson, 1997). This was confirmed by visual inspection, and even very firmly attached algal species (e.g. *Aphanochaete repens*, *Cocconeis placentula*, basal cells of *Stigeoclonium, Oedogonium* and *Coleochaete*) were regularly found in the samples. The plant was removed from the washings and real plants dried to constant weight. A 50-mL aliquot of the resultant algal suspension was preserved with Lugol's iodine for counting, and the remainder used for analysis of algal biomass and nutritional quality (Jones *et al*., 1999).

All measurements were expressed per unit surface area of the host plant, since it is this parameter which is presented to the algae and grazing invertebrates, and by doing so, measurements taken from the four plant types could be directly compared. The dimensions of the leaves and stem of the artificial plants were determined, and the area calculated. The area of the real plants was calculated from their dry mass, using linear equations determined at the start of the experiment (after Sher-Kaul *et al*., 1995).

Counting was carried out block-wise, using inverted microscopes, by three observers, who counted to pre-agreed standards of effort and taxonomy. Taxonomy was determined according to Prescott (1951) and Ettl *et al*. (1986–1991). Counts were expressed per unit surface area of plant or replica, and analysed by canonical correspondence analysis (CCA) using canoco (ter Braak, 1987). The effect of block was found to be highly significant, possibly through variation among the counters, but mainly through block effects which were apparent throughout the data set (see Jones *et al*., 1999). Such block effects may have been attributable to slight differences in light availability. Therefore, the effects of block were removed ('partialled out') from the final ordination. To remove excess sample influence and normalize abundances (of colonial algae in particular), the data were transformed using *ln* (1 + x). Monte-Carlo tests

Table 1 Taxa recorded in an experiment to investigate the effects of substratum, nutrients and snail grazing on the composition of periphyton communities, and the abbreviations (codes) used for these in Fig. 1. The abbreviations in parentheses are: (D) diatom; (BG) blue-green alga; (G) green alga; (E) euglenophyte; (Ch) chrysophyte; (Cp) cryptophyte; and (X) xanthophycean. The identifications followed Prescott (1951) and Ettl *et al*. (1986–1991), in which authorities for specific nomenclature are given

Code	Taxa	Code	Taxa	Code	Taxa
Achs	*Achnanthes* sp. (D)	Achc	*Achnanthes lanceolata* (D)	AcHz	*Actinastrum hantzscii* var. *fluviatile* (G)
Acnn	*Achnanthes linearis* (D)	Amph	*Amphora ovalis* (D)	Anal	*Anabaena* large (BG)
Anas	*Anabaena* small (BG)	Aphc	*Aphanocapsa* sp. (BG)	Aphr	*Aphanochaete repens* (G)
Apt1	*Aphanothece* sp. 1 (BG)	Apt2	*Aphanothece* sp. 2 (BG)	Astf	*Asterionella formosa* (D)
bgfl	Blue green filament (BG)	Carf	*Characium falcatum* (G)	Carg	*Characium gracilis* (G)
Caro	*Characium obtusum* (G)	Chae	*Chaetophora* sp. (G)	Chat	*Chaetophora attenuata* (G)
Chlg	*Chlorogonium* sp. (G)	Chsp	*Chamaesiphon* (BG)	Clad	*Cladophora* sp. (G)
Clah	*Cladophora* huge (G)	Clam	*Chlamydomonas* (G)	Cllv	*Chlorella vulgaris* (G)
Clol	*Closterium* large (G)	Clos	*Closterium* small (G)	clum	Clumped green (G)
Cocc	*Cocconeis placentula* (D)	Coel	*Coelastrum microporum* (G)	Cosg	*Cosmarium globosum* (G)
Cos1	*Cosmarium* large (G)	Cos2	*Cosmarium* small (G)	Croo	*Chroococcus minor* (BG)
Cryp	*Cryptomonas ovata* (Cp)	Cycl	*Cyclotella* sp. (D)	Cygm	*Cylindrocapsa geminella* (G)
Cymb	*Cymbella ventricosa* (D)	Cymv	*Cymbella naviculiformis* (D)	dias	Diatom sp. (D)
Diat	*Diatoma* sp. (D)	Dino	*Dinobryon sertularia* (Ch)	Epit	*Epithemia* sp. (D)
Eugl	*Euglena gracilis* (E)	Euno	*Eunotia pectinalis* (D)	Frcp	*Fragilaria capucina* (D)
Frcr	*Fragilaria crotonensis* (D)	Frpn	*Fragilaria pinnata* (D)	Geml	*Geminella ellipsoidea* (G)
Goms	*Gomphosphaeria aponina* (BG)	Gleo	*Gloeotrichia* sp. (BG)	Gmol	*Gomphonema olivaceum* (D)
Gmpv	*Gomphonema parvulum* var. *micropus* (D)	grfl	Green filament (G)	Haem	*Haematococcus lacustris* (G)
Melo	*Melosira varians* (D)	Meri	*Merismopaedia* sp. (BG)	Mgt1	*Mougeotopsis* sp. 1 (G)
Mgt2	*Mougeotopsis* sp. 2 (G)	Micp	*Microspora pachyderma* (G)	Mono	*Monoraphidium falcatus* (G)
Mugm	*Mougeotia* medium (G)	Mugn	*Mougeotia* narrow (G)	Mugw	*Mougeotia* wide (G)
Neph	*Nephrocytium limneticum* (G)	Nvbc	*Navicula bacillaris* (D)	Nvcc	*Navicula cincta* (D)
Nvcy	*Navicula cryptocephala* (D)	Nvrd	*Navicula radiosa* (D)	Nvry	*Navicula rhyncocephala* (D)
Nvs1	*Navicula* sp. 1 (D)	Nvs2	*Navicula* sp. 2 (D)	Nzac	*Nitzscia acicularis* (D)
Nzam	*Nitzschia amphibia* (D)	Nzat	*Nitzscia acuta* (D)	Nzln	*Nitzschia linearis* (D)
Nzpl	*Nitzschia palea* (D)	Nzrc	*Nitzschia recta* (D)	Nzsg	*Nitzschia sigmoidea* (D)
Nzsm	*Nitzschia sigma* (D)	Nzth	*Nitzschia thermalis* (D)	Oed1	*Oedogonium* sp. 1 (G)
Oed2	*Oedogonium* sp. 2 (G)	Oed3	*Oedogonium* sp. 3 (G)	Oed4	*Oedogonium* sp. 4 (G)
Oocy	*Oocystis* sp. (G)	Osac	*Oscillatoria acutissima* (BG)	Osc1	*Oscillatoria* sp. (BG)
Oslm	*Oscillatoria limosa* (BG)	Osub	*Oscillatoria subbrevis* (BG)	Palm	*Palmella mucosa* (G)
Pedb	*Pediastrum boryanum* (G)	Pedt	*Pediastrum tetras* (G)	Phor	*Phormidium* small (BG)
Pinn	*Pinnularia hemiptera* (G)	prok	Prokaryote filament (BG)	Rhoi	*Rhoicosphenia curvata* (D)
Rhop	*Rhopalodia gibba* (D)	Scdb	*Scenedesmus bijuga* (G)	Scdi	*Scenedesmus dimorphus* (G)
Scdq	*Scenedesmus quadricauda* var. *longispina* (G)	Spir	*Spirulina subsalsa* (BG)	Spgy	*Spirogyra* sp. (G)
Stg1	*Stigeoclonium* sp. (G)	Stig	*Stigeoclonium tenue* (G)	Stsb	*Stigeoclonium subsecundum* (G)
Suri	*Surirella linearis* var. *helvetica* (D)	Syns	*Synedra* small sp. (D)	Synu	*Synedra ulna* (D)
Tetr	*Tetraëdron caudatum* (G)	Trib	*Tribonema* sp. (X)	Uxsb	*Ulothrix subconstricta* (G)
Uxtr	*Ulothrix tenerrima* (G)				

of 999 runs constrained within the four blocks were used to test the significance of the treatments and the significance of the whole ordination. Discriminant analysis was also undertaken using canoco. Forward selection using Monte-Carlo tests of 999 runs constrained within the four blocks was used to test the significance of the algal species in explaining the difference between the plant types at different nutrient additions. Algal species were only included in the model if $P < 0.05$. The responses of individual algal species were also analysed by an analysis of variance (ANOVA) using a mixed model and nested design, and corrected for any missing values (SAS, 1989)

Results

One hundred and twenty-one taxa were agreed to have been distinguishable by the counters. It was decided to use in the CCA only those species which were found in more than 0.5% of the 1168 samples. The final list of 112 taxa (Table 1) included 18 Cyanophycota (blue-green algae), 49 Chlorophycota (green algae), one Xanthophyceae, one Chrysophyceae, one Euglenophycota, one Cryptophyceae and 41 Bacillariophyceae (diatoms). The 'Discussion' will centre on the blue-green algae, green algae and diatoms. The commoner life-forms (Table 2) were: non-motile unicellular diatoms, with *Cocconeis*, *Achnanthes*, *Gomphonema*, *Rhopalodia*, *Epithemia* and *Synedra* prominent; motile pennate diatoms (*Navicula* and *Nitzschia*); non-motile colonial green algae (*Aphanochaete*, *Scenedesmus*, *Pediastrum* and *Monoraphidium*); and filamentous diatoms (*Fragilaria* and *Melosira*) green (*Stigeoclonium*, *Ulothrix*, *Mougeotia* and *Oedogonium*) and blue-green (*Anabaena* and *Oscillatoria*) algae.

The results of the CCA indicate that presence or absence of snails was the strongest influence on community composition, followed by the distinction between different plant types (Fig. 1). The largest difference along this second, vertical axis was that between real *Littorella* and artificial *Elodea*, but there was almost as much difference between the two artificial plants as between the real plants and their artificial counterparts. The effect of increasing nutrients was also aligned along the second axis with increased nutrient addition producing a community more akin to those on artificial plants. Out of all the treatments, nutrients had the least effect on community composition. Many periphyton taxa were clustered around the origin of the diagram, indicating minimal specificity to treatment. Monte-Carlo tests showed significant effects of all experimental treatments. Out of these, snail presence or absence explained the greatest proportion (12%) of the total variance, with all other variables explaining a further 8% (Table 3). The majority of the variance in the data was attributable to differences between blocks.

Figure 1 indicates an association of erect, filamentous forms (*Ulothrix*, *Mougeotia*, *Oedogonium* and *Fragilaria*) in the absence of snails, and a flora of unicellular (*Synedra*, *Chamaesiphon*, *Cocconeis*, *Eunotia* and *Gomphonema*) and adpressed filamentous (*Stigeoclonium*, *Aphanochaete* and *Chaetophora*) forms in their presence. The clustering of the centroids for plant species close to the origin of the diagram suggests much less specificity for the nature or species of plant, and none was obvious during the experiment.

To determine if the differences between the periphyton community growing on different plant species were more apparent at low nutrient availability, discriminant analysis was undertaken using only the data from the ungrazed treatments (nutrients had little effect on overall algal abundance in the grazed treatments). If this was true, the communities growing on different plant types should converge with increasing nutrients. No such relationship was found (Fig. 2). Artificial *Elodea* became more distinct with increasing nutrients. At nutrient addition 2, real *Littorella* was less distinct than at nutrient addition 1, but at nutrient addition 3, it was very distinct from all the other types. Real *Elodea* and artificial *Littorella* were very similar, and showed little change in community composition with increasing nutrient addition. Overall, the communities did not converge with increasing nutrients (Fig. 2).

The position of a taxon on Fig. 1 gives only the degree of faithfulness of a species to a treatment, but does not illustrate the numerical response of the species. Comparison of means among treatments gives additional information. The response of the algal community as a whole (as areal chlorophyll) to the treatments showed an overriding influence of grazing by snails (Fig. 3). In the absence of snails, there was a marked influence of plant type; most chlorophyll was found on artificial *Elodea* and least on real *Elodea*, whilst the opposite was found between real and artificial *Littorella* (Fig. 3). There were

Table 2 Number of taxa (used in the ordination analysis and listed in Table 1) classified by life-form among periphyton algae recorded in an experiment to investigate the effects of substratum, nutrients and snail grazing on the composition of periphyton communities

Life-form	Diatoms	Green algae	Blue-green algae	Others
Non-motile unicells	16	4	1	1
Flagellated unicells	0	3	0	2
Motile unicells, but non-flagellate	20	5	0	0
Non-motile colonies	1	14	6	0
Flagellated colonies	0	0	0	1
Filaments	4	23	11	0

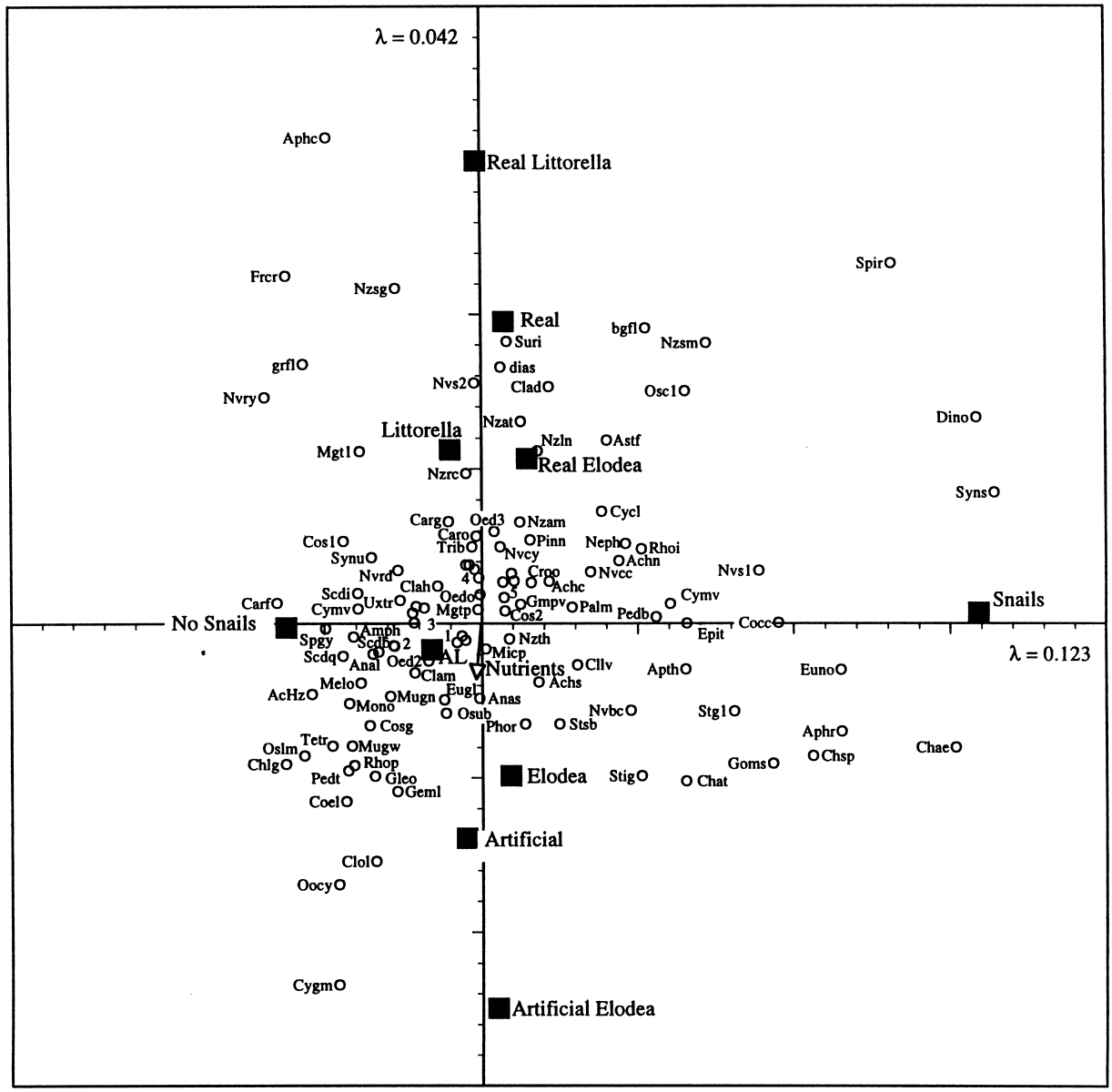

Fig. 1 Ordination diagram obtained through canonical correspondence analysis of the distributions of periphyton taxa in an experiment to investigate the effects of substratum, nutrients and snail grazing on the composition of periphyton communities. The solid squares represent the centroids of the treatments used: the presence and absence of snails; the effect of plant species; real versus artificial plants; and real and artificial plants combined for each plant species (AL, artificial *Littorella*). The arrow indicates the effect of increasing nutrient additions. The open circles indicate the optima of individual taxa. Only taxa found in more than 0.5% of the samples were used; abbreviations are shown in Table 1. Where taxa are so close for individual labelling to be confusing, the clusters are numbered: (1) Haem, prok, Meri; (2) Frpn, Mugm; (3) Frcp, Clos, Uxsb, clum; (4) Cryp, diat, Nzpl, Oed2; and (5) Apt2, Gmol, Nzac, Osac. The diagram accounts for 5.0% and 80.5% of the taxon and taxon-environment variance. The first four eigenvalues are 0.123, 0.042, 0.017 and 0.012. The sum of all unconstrained eigenvalues is 3.280, after fitting covariables.

significant differences between the two artificial plants, as well as between the two real plants. The response of the different algal taxa to the treatments is not so clear cut. Figure 4 shows the effects of treatments on taxa selected because these were particularly abundant or are of frequent occurrence in natural periphyton communities. Table 4 shows which treatments and their interactions had a sig-

nificant effect on the abundance of these taxa.

Figure 4a shows data for four filamentous taxa which were generally placed close to the centroid for absence of snails in Fig. 1. These taxa show consistently lower abundance in the presence of snails compared with the absence of snails, as do several other filamentous taxa (Table 4). Most also show significant effects of nutrients, but there is no consistent pattern of increase or decrease. *Gloeotrichia* increased with nutrients (Fig. 4a), particularly on the ungrazed artificial plants (constitution*snail*nutritent addition in Table 4). *Fragilaria* increased with nutrients on artificial *Elodea* (Fig. 4a), but decreased on artificial *Littorella* (species*constitution*nutrient addition in Table 4). *Oedogonium* species 1 decreased with nutrients (Fig. 4a). The main effects of species or constitution (artificial versus real plants) and their interaction (species*constitution) were significant for several species (Table 4). *Microspora pachyderma*, *Gloeotrichia* and *Mougeotia* showed a consistently greater abundance on artificial plants than on real plants, and *Fragilaria* showed this in most cases (Fig. 4a, see also significant effects on Table 4). *Ulothrix* showed significant effects of constitution, but the trend was reversed with different nutrient treatments (constitution*nutrient addition). In general, *Mougeotia* and *Oedogonium* were more abundant on *Littorella* than on *Elodea*. Thus, the occurrence of these filamentous species appears to be influenced by all factors in a complex way, varying among taxa, but overall grazing reduced the abundance of these species (Fig. 4a, Table 4).

Representative responses to the treatments of short, single-celled algae are shown in Fig. 4b, including the largely non-motile diatoms *Cocconeis* and *Gomphonema*, the motile diatom *Nitzschia*, and the firmly attached blue-green alga, *Chamaesiphon*. *Cocconeis* and *Chamaesiphon* showed absolute increases in the presence of snails. Only the latter showed a significant main effect of nutrients, although there were some interaction effects (Table 4). All but *Chamaesiphon* showed main effects of host plant species, with *Cocconeis* more abundant on *Elodea* than on *Littorella*. In contrast, *Gomphonema* and *Nitszchia* were more abundant on *Littorella*. The lesser importance of nutrients, the contrast between the firmly attached *Coccconeis* and *Chamaesiphon* and the motile diatom taxa, and the absolute increases in *Cocconeis* and *Chamaesiphon* suggest important influences of grazing vulnerability and intraspecific competition in this group.

The encrusting filamentous group is represented by *Aphanochaete repens* and *Stigeoclonium* spp. (Fig. 4c). All treatments had main effects on absolute abundance, except for snail presence in the case of *Stigeoclonium*, where there were several interaction effects involving snails instead (Table 4). As upright branches were lost to snails, numbers may have been compensated by encrusting cells of the same species. The effect of nutrients was more prominent in this group of algae than in other cases, and the general effect of snails was to increase the absolute abundances of these forms. Abundances were also greater on artificial than on real substrata and on *Elodea* rather than *Littorella*.

Table 3 Summary of the results of Monte-Carlo tests conducted on the canonical correspondence analysis for the ordination of samples of periphyton removed from different plants, and determined as the number of cells per unit area in an experiment to investigate the effects of substratum, nutrients and snail grazing on the composition of periphyton communities. The results from forward selection of the cumulative effects of treatments are shown. The effects of experimental design (block and counter error) were removed from the ordination as covariables

Variable	*F*-ratio	*P*-value	Cumulative variance explained
Snails/no snails	44.78	0.01	0.12
Real/artificial/ real *Littorella*/ artificial *Elodea*	12.35	0.01	0.15
Elodea/*Littorella*	9.06	0.01	0.19
Nutrients	4.51	0.01	0.20
Overall test trace (0.2)	15.36	0.01	–

Discussion

The complex experimental design used in the present study has strength in its ability to illustrate the many connections between factors, but the large number of factors can confound the issue and divert attention from important effects. The main question asked in the present investigation was whether different plants specifically affect the periphyton growing on their surfaces to the benefit of grazers, and therefore, keep their surfaces as clear of competitive periphyton as possible. In terms of the nutritional quality of the periphyton, this proved not to be the case (Jones *et al.*,

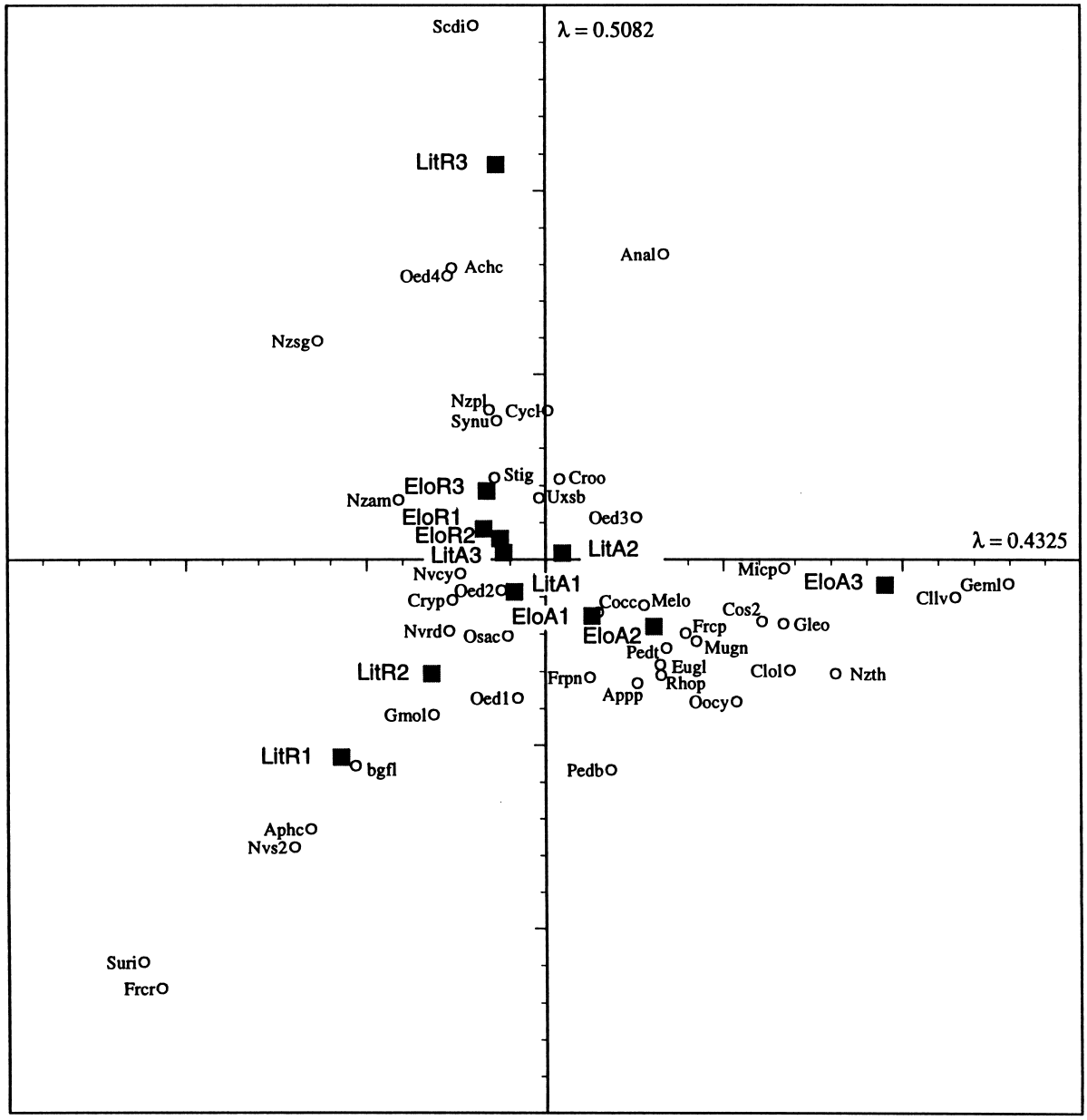

Fig. 2 Discriminant analysis biplot showing the distributions of periphyton taxa which were significant ($P < 0.05$) at separating the different plant types used (EloR, real *Elodea*; EloR, artificial *Elodea*; LitR, real *Littorella*; LitA, artificial *Littorella*) at three nutrient additions (i.e. 1, 2 or 3, as given in text) in the absence of snails. The solid squares represent the centroids of the treatments. The open circles indicate the optima of individual taxa. Only taxa found in more than 0.5% of the samples were used; abbreviations are shown in Table 1. The influence of the algal taxa was determined by forward selection, using Monte-Carlo tests of 999 runs constrained within the four blocks. The first four eigenvalues are 0.508, 0.433, 0.358 and 0.346.

1999), nor were snail grazers mutualistically supported by real plants through increased growth and reproduction (Jones *et al.*, 1999).

In the aspect of the experiment considered in the present paper, the determination of periphyton community composition, these previous conclusions were supported. Although there was some specificity in the determination of community composition by the different species of plant used, the presence or absence of grazers was far more important, explaining

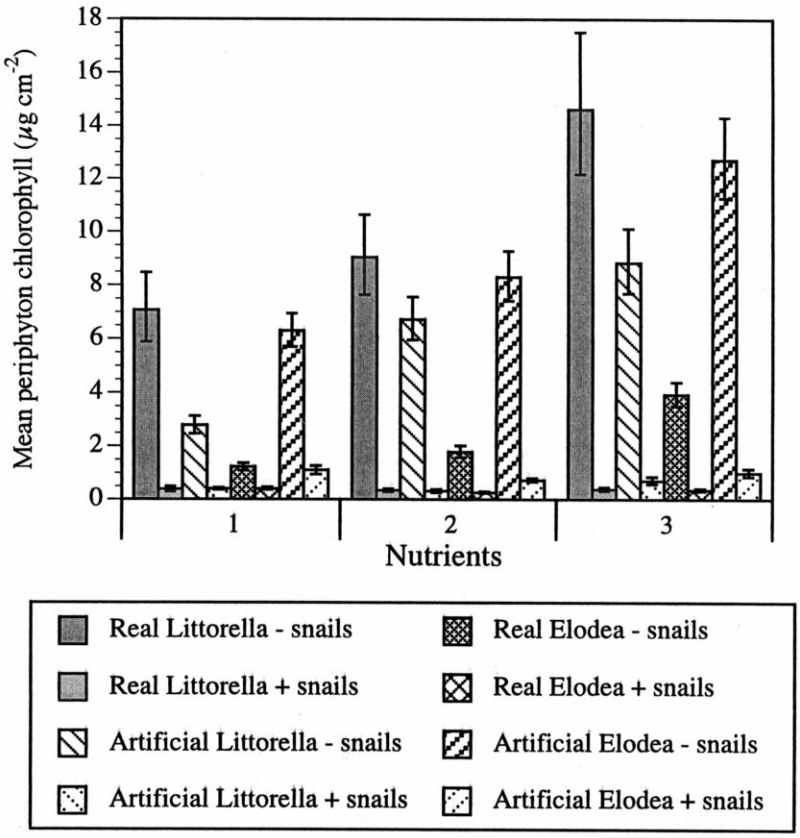

Fig. 3 Effect of plant species, plant constitution, snails and nutrient addition (given in text) on mean periphyton chlorophyll per unit area of plant surface (± SE, $35 \leqslant n \leqslant 52$) (redrawn from Jones *et al.*, 1999).

12% of the variance in community composition. The nature of the substratum explained an additional 7% and the nutrient addition a further 1%. A significant difference was found between all the plant types used. However, the difference between the two artificial plants, which differed only in their shape, was almost as large as that between the real plants and their artificial counterparts, indicating that the physical structure of the host plant was as important as any active contribution by the plants. Such an effect of plant architecture on algal communities has been suggested (Lalonde & Downing, 1991; Cattaneo *et al.*, 1998), but only shown as separate from taxonomic and areal differences for invertebrate communities (Jeffries, 1993).

There was some evidence of an increase in certain species as a result of the presence of snails (i.e. *Cocconeis placentula*, *Chamaesiphon* and *Aphanochaete repens*; see Fig. 4), but most species declined in the presence of grazers (Figs 1 & 4). It is likely that species which fared better in the presence of snails than in their absence did so because of reduced competition (for light and nutrients) from taller growing algae, whilst being able to withstand (or avoid) the grazing action of the snails. As with larger plants, these may fall into two categories, grazing-resistant and grazing-tolerant forms. Given that the latter both increase in number whilst providing the snails with food, there is the potential for a mutualistic relationship to evolve between these taxa and snails (Thomas, 1990; Underwood & Thomas, 1990). However, proving increased fitness of individuals (Stenseth, 1983) and differentiating this from the unevolved lateral food-web effect of apparent mutualism ('the enemy of my enemy is my friend') is difficult.

The present experiment shows grazing to be pre-eminent in determining periphyton community composition, allowing a three-dimensional growth of loosely associated green algal and other filaments to persist in its absence, and leaving (and to a certain extent promoting) a close cover of adpressed filaments and diatoms in its presence (Fig. 1). Such effects have been shown elsewhere (Cuker, 1983; Brönmark, 1989; Swamikannu & Hoagland, 1989; Jones, Moss & Young, 1997), especially in studies of the epilithic cover in streams (Lamberti & Resh, 1983;

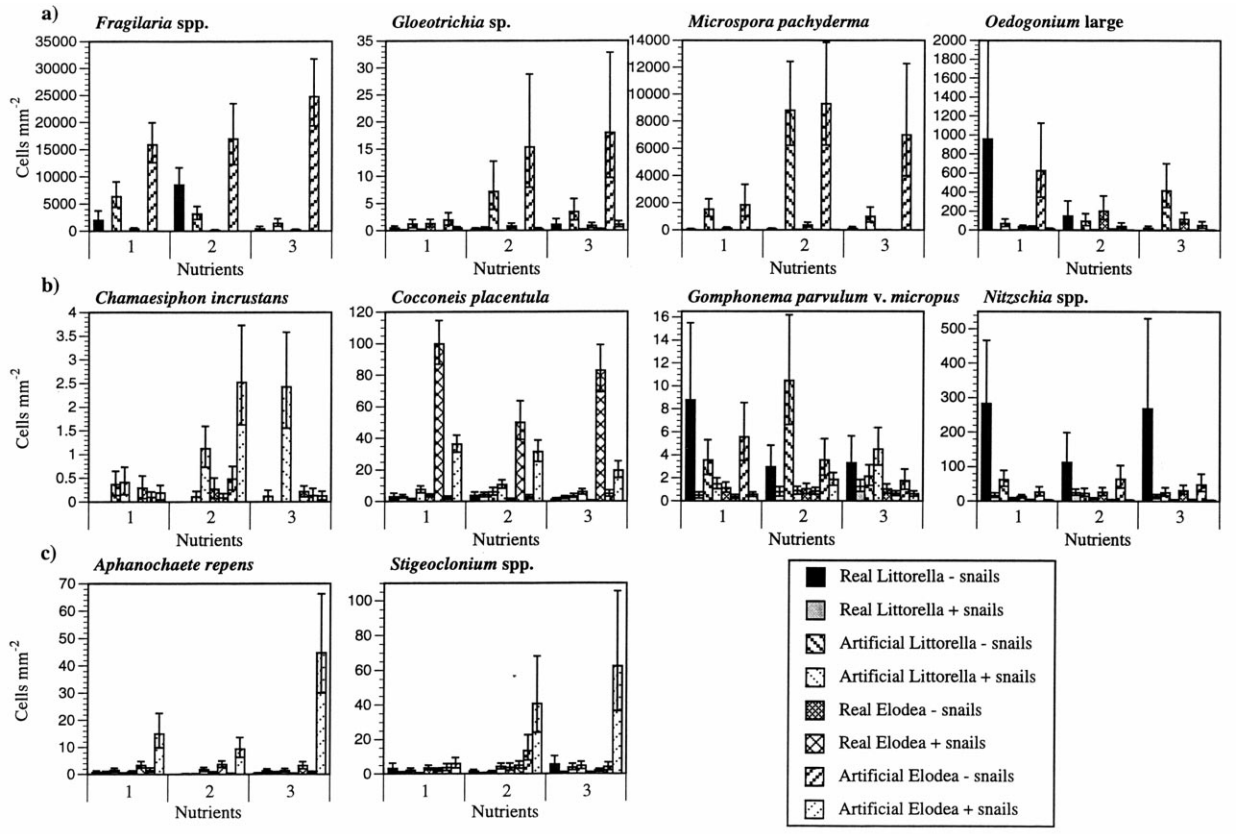

Fig. 4 Effect of plant species, plant constitution, snails and nutrient addition (given in text) on the mean abundance per unit area of plant surface of some (a) filamentous (*Fragilaria*, *Gloeotrichia*, *Microspora pachyderma* and *Oedogonium*), (b) short or adpressed (*Chamaesiphon incrustans*, *Cocconeis placentula*, *Gomphonema parvulum* var *micropus* and *Nitzschia*) and (c) encrusting (*Aphanochaete repens* and *Stigeoclonium*) periphytic algae (± SE, $35 \leqslant n \leqslant 52$).

Jacoby, 1987; Feminella, Power & Resh, 1989; Feminella & Hawkins, 1995). After grazing the nature of the substratum is important (Fig. 1). In this experiment, the relative fertility had a minor effect on the periphyton community composition (although a substantial effect on the total biomass produced; Fig. 3). This is surprising considering the major influence of key nutrients in determining the nature of phytoplankton communities, although the lowest addition used here did not represent severely nutrient-deficient conditions.

There has been considerable controversy about the factors which determine periphyton community composition (Gough & Woelkerling, 1976; Cattaneo & Kalff, 1979; Cattaneo & Kalff, 1981; Gough & Gough, 1981; Aloi, 1990; Cattaneo & Amireault, 1992). There has been no resolution of the issue largely because different investigations have used varying stringency for the demonstration of specificity (Gough & Woelkerling, 1976; Cattaneo, 1978; Baker & Orr, 1986; Blindow, 1987; Aloi, 1990; Cattaneo & Amireault, 1992). Furthermore, most investigations have been in the field and did not control the initial status of the periphyton community, and could not control the effect of plant location. Thus, demonstrations of specificity of algae to substrata could simply be demonstrations of the differential effects of age in the compared species (Delbecque, 1983; Patterson & Wright, 1986), of different opportunities for colonization (Cattaneo, 1978; Delbecque, 1983; Kairesalo, 1983) or of different physico-chemical differences at adjacent locations (Kairesalo & Koskimies, 1987; O'Neil-Morin & Kimbal, 1983; Cattaneo *et al*., 1998; Romo & Galanti, 1998).

These features were all controlled in this experiment. Little specificity was found, and perhaps even

Table 4 Statistical significance of treatment effects and their interactions following an analysis of variance on numbers of prominent filamentous, adpressed or encrusting algal taxa per square millimetre of plant surface in an experiment to investigate the effects of substratum, nutrients and snail grazing on the composition of periphyton communities

Algal taxa	Block	Spp	Const	Spp Const	Snails	Spp Snails	Const Snails	Spp Const Snails	Nuts	Spp Nuts	Const Nuts	Spp Const Nuts	Snails Nuts	Spp Snails Nuts	Const Snails nuts	Spp Const Snails nuts	Rep (Nested)
Filamentous																	
Anabaena spp.	***		**		***				***	***	***	***	***	***	***	***	
Fragilaria spp.	***		***	***	***		***	***	***	**		**		*	*		
Gloeotrichia sp.	***	***	***	*	***		***		**		**		**		***		
Microspora pachyderma	***		***		***	*	***		***			**				***	
Mougeotia spp.	***	***	***	***	***	***	***		***			*	***	*			
Oedogonium sp. 1	***	**		**	***	**		*	*	**	***	***		**		***	
Oedogonium other spp.	***	*		**	***	***		***			*		*			***	
Ulothrix spp.	***		*	***	***			**	***		***	***	**	**	***	**	
Adpressed																	
Achnanthes spp	***	***		**	**					**		*			*		
Chamaesiphon incrustans	***		***	*	***		***		**	**	*	**	*	**	***	*	
Cocconeis placentula	***	***		**	***	***		***		*							
Gomphonema parvulum	***	***	***		***			**					**	*		**	
Navicula spp.	***	**	**	***	***			***		***				*		***	
Nitzschia spp.	***	***	***	***	***			***		***				***			
Encrusting																	
Aphanochaete repens	***	***	***	**	***	***	***	***	*			**	***				
Stigeoclonium spp.	***	***	***	***		***	***		**	***	***		*	*	*		

Block = effect of experimental block design; Spp = species (*Elodea* or *Littorella*); Const = constitution (real or artificial); Snails = snails present or absent; Nuts = nutrient addition (low, medium or high); Rep = the difference between individual plants within each bucket, nested within the other treatments.

*$P = 0.05$.

**$P = 0.01$.

***$P = 0.001$.

more important, the effects of substrate, grazing and nutrient addition failed to explain 80% of the variance in the community composition. It seems that either environmental differences or chance are by far the most important determinants of periphyton community composition.

Of course, it is not permissible to state that powerful plant-associated mechanisms may not determine periphyton communities elsewhere. It could be argued that the conditions of the present experiment were simply not appropriate. Specificity may be best shown at very low nutrient concentrations where nutrient leakage from the plant may have an overriding effect in an impoverished external medium (Eminson & Moss, 1980; Burkholder & Wetzel, 1989). The communities produced here might be artefacts of the laboratory, and it could be argued that specificity is only demonstrated between evolved genotypes in the same lake or by other plant species with different properties. However, the species used in the present study differed greatly in their biology, the texture of their surfaces and the habitats from which they were drawn. Nonetheless, these species behaved rather similarly to plastic replicas of themselves. The nutrient regimes given covered a wide range and a regime much less fertile than the lowest used would support a very sparse plant community in nature. Increased nutrient availability had little effect on algal community composition (Fig. 1), and did not lead to increasingly similar communities on the different plant types (Fig. 2) as would be expected if the plants were exerting a considerable influence (Eminson & Moss, 1980; Burkholder & Wetzel, 1989). Field investigations have been unable to demonstrate an alellopathic effect of macrophytes (Forsberg, Kleiven & Willen, 1990). Furthermore, the periphyton communities produced in the experiment were by no means unusual. There was a high diversity and the species and genera found have been repeatedly recorded as characteristic of periphyton in field-collected samples (Round, 1985). Indeed, these were all derived from a mixed sampling of natural periphyton.

The present authors believe this experiment to be the most thorough investigation yet into these phenomena and have reached the same general conclusion from several viewpoints. They conclude that: co-evolved mutualism between plants, periphyton and their grazers is unlikely in freshwater systems; that the nature of the plant and the nutrient status are of much less importance than grazing in determining the periphyton community; that the architecture of the plant is more important than whether or not it is living; and that chance, reflected in micro-environment and the multiple outcomes of competition between algal taxa, is by far the most powerful influence on community composition.

Acknowledgments

This work was funded by Natural Environment Research Council grant number GR39115, for which we are grateful. Thanks are also extended to the permanent and temporary technical staff of Liverpool University, and Luke Humphries and Gill Haynes in particular, for their invaluable assistance during the running and harvesting of this experiment.

References

Allen H.L. (1971) Primary productivity, chemo-organotrophy, and nutritional interactions of epiphytic algae and bacteria on macrophytes in the littoral of a lake. *Ecological Monographs*, **41**, 97–127.

Aloi J.E. (1990) A critical review of recent freshwater periphyton field methods. *Canadian Journal of Fisheries and Aquatic Sciences*, **47**, 656–670.

Anthoni U., Christophersen C., Madsen J.O., Wium-Andersen S. & Jacobsen N. (1980) Biologically active compounds from the green alga *Chara globularis*. *Phytochemistry*, **19**, 1228–1229.

Baker J.H. & Orr D.R. (1986) Distribution of epiphytic bacteria on freshwater plants. *Journal of Ecology*, **74**, 155–165.

Birch S.P. (1990) *An assessment of the interaction between* Elodea nuttallii *and its epiphyton.* Ph.D. Thesis, University of Liverpool, Liverpool.

Blindow I. (1987) The composition and density of epiphyton on several species of submerged macrophytes – the neutral substrate hypothesis tested. *Aquatic Botany*, **29**, 157–168.

Boycott A.E. (1936) The habitats of freshwater Mollusca in Britain. *Journal of Animal Ecology*, **5**, 116–186.

Brönmark C. (1989) Interactions between epiphytes, macrophytes and freshwater snails: a review. *Journal of Molluscan Studies*, **55**, 299–311.

Burkholder J.A.M. & Wetzel R.G. (1989) Epiphytic microalgae on natural substrata in a hardwater lake: seasonal dynamics of community structure biomass and ATP content. *Archiv für Hydrobiologie*, **83** (Suppl.), 1–56.

Carignan R. & Kalff J. (1982) Phosphorus release by submerged macrophytes: significance to epiphytes and phytoplankton. *Limnology and Oceanography*, **27**, 341–370.

Cattaneo A. (1978) The microdistribution of epiphytes on the leaves of natural and artificial macrophytes. *British Journal of Phycology*, **13**, 183–188.

Cattaneo A. & Kalff J. (1978) Seasonal changes in the epiphyte community of natural and artificial macrophytes in Lake Memphremagog (Que. & VT). *Hydrobiologia*, **60**, 135–144.

Cattaneo A. & Kalff J. (1979) Primary production of algae growing on natural and artificial aquatic plants: a study of interactions between epiphytes and their substrate. *Limnology and Oceanography*, **24**, 1031–1037.

Cattaneo A. & Kalff J. (1981) Reply to comment by Gough and Gough. *Limnology and Oceanography*, **26**, 988–989.

Cattaneo A. & Amireault M.C. (1992) How artificial are artificial substrata for periphyton? *Journal of the North American Benthological Society*, **11**, 244–256.

Cattaneo A., Galanti G., Gentinetta S. & Romo S. (1998) Epiphytic algae and macroinvertebrates on submerged and floating-leaved macrophytes in an Italian lake. *Freshwater Biology*, **36**, 725–740.

Cuker B.E. (1983) Grazing and nutrient interactions in controlling activity and composition of the epilithic algal community in an Arctic lake. *Limnology and Oceanography*, **28**, 133–141.

Delbecque E.J.P. (1983) A comparison of the periphyton of *Nuphar lutea* and *Nymphaea alba*. The distribution of diatoms on the underside of floating leaves. *Periphyton of Freshwater Ecosystems* (ed. R.G. Wetzel), pp. 41–47. Dr W. Junk Publishers, the Hague.

Elankovich S.D. & Wooten J.W. (1989) Allelopathic potential of sixteen aquatic and wetland plants. *Journal of Aquatic Plant Management*, **27**, 78–84.

Eminson D.F. & Moss B. (1980) The composition and ecology of periphyton communities in freshwaters. I. The influence of host type and external environment on community composition. *British Phycological Journal*, **15**, 429–446.

Ettl H., Gartner G., Gerloff J., Heynig H. & Mollenhauer D. (1986–1991) *Sußwasserflora von Mitteleuropa. Bacillariophyceae*, Tiel 1–4. Gustav Fischer-Verlag, Stutgart.

Feminella J.W. & Hawkins C.P. (1995) Interactions between stream herbivores and periphyton: a quantitative analysis of past experiments. *Journal of the North American Benthological Society*, **14**, 465–509.

Feminella J.W., Power M.E. & Resh V.H. (1989) Periphyton responses to invertebrate grazing and riparian canopy in three northern California coastal streams. *Freshwater Biology*, **24**, 445–457.

Forsberg C., Kleiven S. & Willen T. (1990) Absence of allelopathic effects of *Chara* on phytoplankton *in situ*. *Aquatic Botany*, **38**, 289–294.

Gough S.B. & Woelkerling W.J. (1976) Wisconsin desmids. II. Aufwuchs and plankton communities of selected softwater lakes, hardwater lakes and calcareous springs ponds. *Hydrobiologia*, **49**, 3–25.

Gough S.B. & Gough L.P. (1981) Comment on 'Primary production of algae growing on natural and artificial plants: a study of interactions between epiphytes and their substrate' (Cattaneo and Kalff). *Limnology and Oceanography*, **26**, 987–988.

Gross E.M., Meyer H. & Schilling G. (1996) Release and ecological impact of algicidal hydrolyzable polyphenols in *Myriophyllum spicatum*. *Phytochemistry*, **41**, 133–138.

Gross E.M. & Sütfeld R. (1994) Polyphenols with algicidal activity in the submersed macrophyte *Myriophyllum spicatum* L. *Acta Horticulturare*, **381**, 710–716.

Hutchinson G.E. (1975) *A Treatise on Limnology III. Limnological Botany.* John Wiley & Sons, Chichester.

Jacoby J.M. (1987) Alterations in periphyton characteristics due to grazing in a cascade foothill stream. *Freshwater Biology*, **18**, 495–508.

Jeffries M. (1993) Invertebrate colonisation of artificial pondweeds of differing fractal dimension. *Oikos*, **67**, 142–148.

Jones J.I., Moss B. & Young J.O. (1997) The interactions between periphyton, non-molluscan invertebrates, and fish in standing freshwaters. *The Structuring Role of Submerged Macrophytes in Lakes* (eds E. Jeppesen, Ma. Søndergaard, Mo. Søndergaard and K. Christophersen), pp. 69–90. Springer-Verlag, New York.

Jones J.I., Young J.O., Haynes G.M., Moss B., Eaton J.W. & Hardwick K.J. (1999) Do submerged aquatic plants influence their periphyton to enhance the growth and reproduction of invertebrate mutualists? *Oecologia*, **120**, 463–474.

Kairesalo T. (1983) Dynamics of epiphytic communities on *Equisetum fluviatile* L. Response to short-term variation in environmental conditions. *Periphyton of Freshwater Ecosystems* (ed. R.G. Wetzel), pp. 154–160. Dr W. Junk Publishers, the Hague.

Kairesalo T. & Koskimies I. (1987) Grazing by oligochaetes and snails on epiphytes. *Freshwater Biology*, **17**, 317–324.

Lalonde S. & Downing J.A. (1991) Epiphyton biomass is related to lake trophic status, depth, and macrophyte architecture. *Canadian Journal of Fisheries and Aquatic Sciences*, **48**, 2285–2291.

Lamberti G.A. & Resh V.H. (1983) Stream periphyton and insect herbivores: an experimental study of grazing by a caddisfly population. *Ecology*, **64**, 75–81.

Mackereth F.J.H., Heron J. & Talling J.F. (1989) *Water Analysis: Some Revised Methods for Limnologists.* Scientific Publication No. 36, Freshwater Biological Association, Kendal, U.K.

McMillan N.F. (1946) *Physa fontinalis* and *Bithynia tentaculata* in 'closed' ponds. *Journal of Conchology*, **22**, 214.

McRoy C.P. & Goering J.J. (1974) Nutrient transfer between the seagrass *Zostera marina* and its epiphytes. *Nature*, **248**, 172–173.

Moss B. (1981) The composition and ecology of periphyton communities in freshwaters. II. Inter-relationships between water chemistry, phytoplankton populations, and periphyton populations in a shallow lake and associated experimental reservoirs ('Lund Tubes'). *British Phycological Journal*, **16**, 59–76.

Moss B. (1998) *Ecology of Freshwaters. Man and Medium. Past to Future*, 3rd edn. Blackwell Science, Oxford.

O'Neil-Morin J.O. & Kimbal K.D. (1983) Relationship of macrophyte-mediated changes in the water column to periphyte composition and abundance. *Freshwater Biology*, **13**, 403–413.

Patterson D.M. & Wright S.J.Z. (1986) The epiphyllous algal colonization of *Elodea canadensis* Michx. community structure and development. *New Phytologist*, **103**, 809–819.

Pip E. (1992) Phenolic compounds in macrophytes from the Lower Nelson River system, Canada. *Aquatic Botany*, **42**, 273–279.

Pip E. & Stewart J.M. (1976) The dynamics of two aquatic plant–snail associations. *Canadian Journal of Zoology*, **54**, 1192–1205.

Pip E. & Philipp K. (1990) Seasonal changes in the chemical composition of *Ceratophyllum demersum* L. in a small pond. *Internationale Revue der Gesamten Hydrobiologie*, **75**, 71–78.

Planas D., Sarhan F., Dube L., Godmaire H. & Cadieux C. (1981) Ecological significance of phenolic compounds of *Myriophyllum spicatum*. *Verhandlungen der Internationale Vereinigung für Theoretische und Angewandte Limnologie*, **21**, 1492–1496.

Prescott G.W. (1951) *Algae of the Western Great Lakes Area.* Bulletin 31, Cranbrook Institute of Science, Detroit, MI.

Romo S. & Galanti G. (1998) Vertical and seasonal distribution of epiphytic algae on waterchestnut (*Trapa natans*). *Archiv für Hydrobiologie*, **141**, 483–504.

Round F.E. (1985) *The Ecology of Algae*. Cambridge University Press, Cambridge.

Sand-Jensen K. & Søndergaard M. (1981) Phytoplankton and epiphyte development and their shading effect on submerged macrophytes in lakes of different nutrient status. *Internationale Revue der Gesamten Hydrobiologie*, **66**, 529–552.

SAS Institute Inc. (SAS) (1989) *SAS/STAT.* SAS Institute, Inc., Cary, NC.

Shelford V.E. (1918) Conditions of existence. *Freshwater Biology* (eds H.B. Ward and G.C. Whipple), pp. 21–60. J. Wiley & Sons, New York, NY.

Sher-Kaul S., Oertli B., Castella E. & Lachavanne J.-B. (1995) Relationship between biomass and surface area of six submerged aquatic plant species. *Aquatic Botany*, **51**, 147–154.

Standen B.D. (1951) Some observations upon the maintenance of *Australorbis glabratus* in the laboratory. *Annals of Tropical Medicine and Parasitology*, **45**, 80.

Stenseth N.C. (1983) Grasses, grazers, mutualism and coevolution: a comment about handwaving in ecology. *Oikos*, **41**, 152–153.

Swamikannu X. & Hoagland K.D. (1989) Effects of snail grazing on the diversity and structure of a periphyton community in a eutrophic pond. *Canadian Journal of Fisheries and Aquatic Sciences*, **46**, 1698–1704.

ter Braak C.J.F. (1987) *Canoco – a FORTRAN program for Canonical Community Ordination by [Partial] [Detrended] [Canonical] Correspondence Analysis, Principal Components Analysis and Redundancy Analysis (Version 2.1).* Report LWA-88-02, Agricultural Mathematics Group, Wageningen.

Thomas J.D. (1990) Mutualistic interactions in freshwater modular systems with molluscan components. *Advances in Ecological Research*, **20**, 125–178.

Underwood G.J.C. & Thomas J.D. (1990) Grazing interactions between pulmonate snails and epiphytic algae and bacteria. *Freshwater Biology*, **23**, 505–521.

Wetzel R.G. (1983) Attached algal–substrata interactions: fact or myth, and when and how? *Periphyton of Freshwater Ecosystems* (ed. R.G. Wetzel), pp. 207–215. Dr W. Junk Publishers, the Hague.

Wium-Andersen S., Anthoni U., Christophersen C. & Houen G. (1982) Allelopathic affects on phytoplankton by substances isolated from aquatic macrophytes (Charales). *Oikos*, **39**, 187–190.

Wium-Andersen S., Anthoni U. & Houen G. (1983) Elemental sulphur, a possible allelopathic compound from *Ceratophyllum demersum*. *Phytochemistry*, **22**, 2613.

Wium-Andersen S., Jorgensen K.H., Christophersen C. & Anthoni U. (1987) Algal growth inhibitors in *Sium erectum* Huds. *Archiv für Hydrobiologie*, **111**, 317–320.

Zimba P.V. & Hopson M.S. (1997) Quantification of epiphyte removal efficiency from submersed aquatic plants. *Aquatic Botany*, **58**, 173–179.

(Manuscript accepted 4 September)