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An experimental investigation of interactions in snail-macrophyte-epiphyte systems

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Summary. An experimental investigation under field conditions of enclosures containing freshwater pulmonate snails, the macrophyte *Ceratophyllum demersum* and epiphytes, produced evidence of beneficial interactions. *Ceratophyllum* growth, measured in terms of stem length, numbers of leaf-nodes and growing tips and leaf survival was significantly enhanced in the presence of snails. This effect was attributed to the increased availability of plant nutrients of snail origin, such as phosphates and ammonia, as well as to the snails' action as "cleaning symbionts" in reducing the density of bacterial and algal epiphyton potentially deleterious to macrophytes. Principal component analysis revealed both seasonal and treatment effects of snail grazing on algal epiphyton. Small adnate algal species (e.g. *Cocconeis placentula*) survived grazing and benefited from the removal of larger, competitor, species. Snail densities increased in all treatments, despite high (86%) juvenile mortality. It is concluded that freshwater pulmonate snails are strong interactors in lentic habitats, enhancing the growth of *Ceratophyllum* and producing characterisic epiphyte communities. This benefits not only the snails, but also the plants and epiphytes that are associated with them. Thus the interactions between these component parts of the community can be considered as mutualistic.

Key words: Freshwater snails – Macrophytes – Grazing – Epiphytes – Mutualism

Freshwater pulmonate snails are commonly found in association with macrophytic vegetation and their epiphyton (Thomas 1987; Thomas and Tait 1984; Lodge and Kelly 1985; Lodge 1985, 1986; Bronmark 1989). These macrophytes provide sites for snail oviposition, access to the air-water interface and shelter, and provide a surface for epiphyton development, which constitutes a major source of the food of freshwater snails (Thomas et al. 1985; Lodge 1986; Underwood and Thomas 1990).

It has been proposed that the close association of plants and snails in freshwater habitats since the Cretaceous (Thomas 1990) may have led to the development of mutually beneficial interactions (Thomas et al. 1985; Thomas 1987, 1990; Thomas et al. 1989). This hypothesis is supported by laboratory experiments which show that the presence of freshwater snails can increase macrophyte growth and leaf longevity (Rogers and Breen 1983; Bronmark 1985; Underwood 1991b). This effect appears to be due to both nutrient exchange and removal of epiphyton by feeding snails. (Underwood and Thomas 1990; Underwood and Baker 1991; Underwood 1991a, b).

This paper describes a field experiment which was designed to ascertain whether mutually beneficial interactions between freshwater snails, macrophytes and epiphyton occur under natural conditions. The experiment was carried out in enclosures situated in a calcium-rich eutrophic drainage dyke in the Lewes Brooks, Sussex, United Kingdom (Underwood and Thomas 1990), supporting large populations of freshwater pulmonate snails and abundant macrophytic vegetation.

Materials and methods

Experimental design

Cylindrical floating enclosures (30 cm diameter, 45 cm depth, mesh base, open top, 1 mm square plastic mesh) were attached to poles placed in a drainage dyke running north-south in March 1987.

Each enclosure was seeded with a similar healthy stem of *Ceratophyllum demersum* L. (a free floating plant), approximately 40 cm long, with 55 leaf nodes and seven growing tips, which had been cleaned of snails and their egg masses. Nylon twine was tied between leaf-nodes five and six on two growing shoots on each plant to measure the growth rate and age of leaves. The four treatments were as follows.

1. No snails added (control)
2. *Lymnaea peregra* (Mull.) present: six adult snails (length 12 mm ± 1 mm) added

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3. *Planorbis planorbis* L. present: eight adult snails (diameter 10 mm ± 2 mm) added
4. Assemblage of snail species present: six *L. peregra* (length 12 mm ± 1 mm), one *L. stagnalis* (L.) (length 25 mm), two *Physa fontinalis* (L.) (length 3 mm), eight *Planorbis planorbis* (width 10 mm ± 2 mm), two *P. contortus* (L.) (width 3 mm), one *P. vortex* (L.) (width 5 mm) and 11 *Bithynia tentaculata* (L.) (length 8 mm)

The initial experimental snail densities were based on values given by Aram (1970) as well as those obtained during more recent sampling (unpublished obs.).

Sampling

Numbers of snails, density of epiphytes, and growth of plants were monitored over a period of 116 days between 19 March and 13 July 1987. The length, number of leaf-nodes, and number of growing-tips of each *C. demersum* plant were recorded. This data was analysed using "repeated measures" analysis of variance with subsequent pairwise Tukey tests to determine the individual differences between samples (Zar 1984). Single leaves from the two nylon-marked leaf-nodes were removed, placed in Eosin yellowish (1 g l^{-1}) and stored at 4°C. The number and sizes of snails and the numbers of egg masses laid in each enclosure were recorded. Epiphytes on the *C. demersum* leaves were counted within three days of sampling after staining with phenolic aniline blue (Hossell and Baker 1979). Data from epiphyte counts were non-parametric, and were analysed using the Mann-Whitney *U*-test. The Shannon-Wiener diversity index, the mean number of taxa and the equitability of the communities were calculated from the epiphyte counts (Underwood and Thomas 1990). The species composition of the algal epiphyte communities were analysed using principal components analysis (Gauch 1984). After counting, leaf material was digested in chromic acid to obtain cleaned diatom frustules for identification.

Results

Growth of Ceratophyllum

Repeated measures analyses of variance on the plant growth data showed that there were significant treatment effects on the length (Fig. 1A, $F_{3,96} = 7.57$, $P < 0.001$), number of leaf-nodes (Fig. 1B, $F_{3,96} = 6.6$, $P < 0.001$) and the number of growing tips (Fig. 1C, $F_{3,96} = 13.54$, $P < 0.001$), with the plants in the Control treatment having the lowest length and numbers of leaf-nodes and growing tips. Subsequent Tukey tests showed that significant differences in the length, number of leaf-nodes and number of growing tips occurred between *C. demersum* grown in the presence of snails (treatments 1–3) and the control treatment (4) (indicated on Fig. 1A–C). There were no significant differences in the growth measurements of plants grown in the three treatments containing snails.

The percentage survival of the leaves growing on the original fifth leaf-node of the *C. demersum* plants is shown in Fig. 2. Analysis of these survivorship curves using Peto and Peto's log rank test (Pyke and Thompson 1986) showed that leaves of *C. demersum* grazed by snails survived significantly longer than comparable, ungrazed leaves on the control plants ($P < 0.05$, 0.05, and 0.01 for the *L. peregra, P. planorbis,* and mixed-snail treatments respectively).

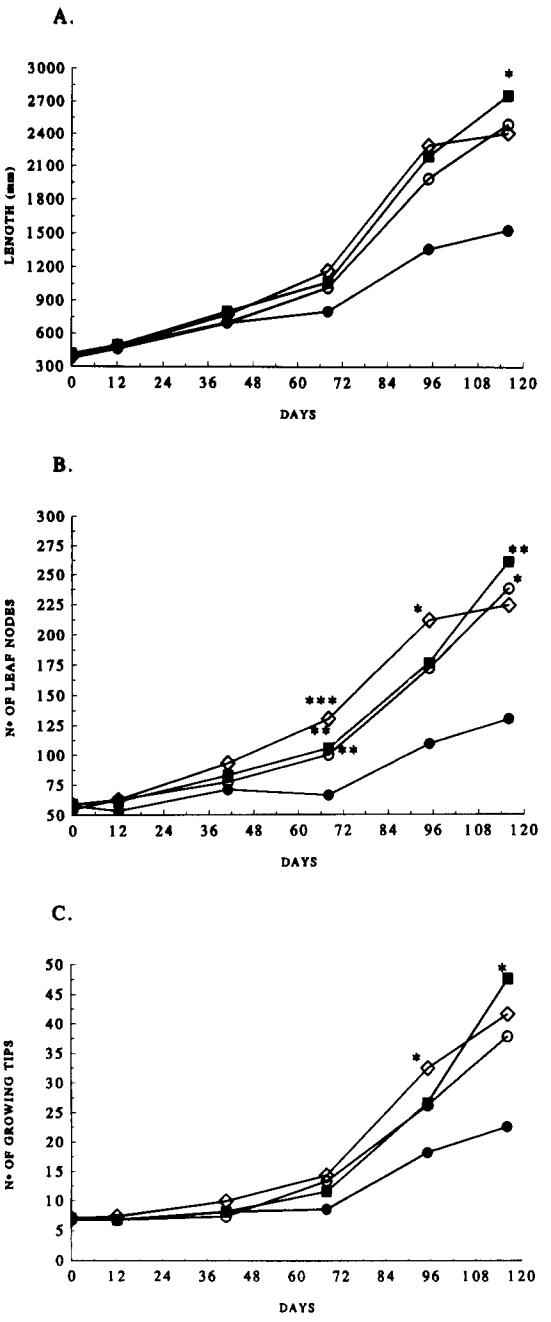

Fig. 1. **A** Length of *Ceratophyllum;* **B** number of leaf-nodes; **C** number of growing tips on *C. demersum* grown under four different treatments (each point mean of 5 plants). ● Control (no snails), ○ *L. peregra,* ■ *P. planorbis* and ◇ mixed-snail species treatments. *Asterisks* indicate significant differences between the controls and treatments containing snails (Tukey test, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$

Changes in bacterial and algal epiphyton density

The population densities of epiphytic organisms on the abaxial surface of *C. demersum* leaves are shown in Figs. 3A and 3B. Leaves growing on the original fifth leaf-node became senescent in the control treatments by day 95, and sampling of epiphytes was carried out on

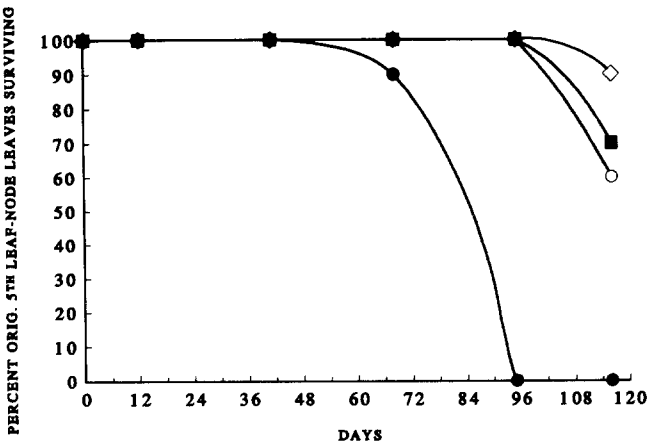

Fig. 2. Percent survival of original leaves under four different treatments (each point mean of 5 plants). ● Control (no snails), ○ *Lymnaea peregra*, ■ *Planorbis planorbis* and ◇ mixed snail species treatments

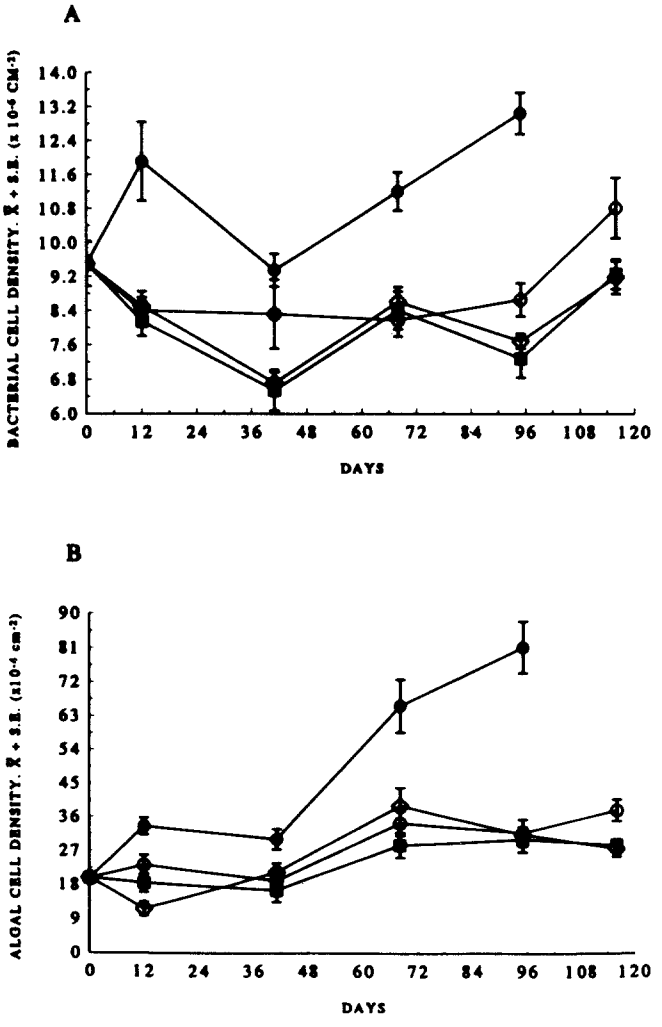

Fig. 3A, B. Changes in **A** bacterial and **B** algal density under four different grazing regimes (each point mean ± SE, $n = 5$). ● Control (no snails), ○ *L. peregra*, ■ *P. planorbis* and ◇ mixed snail species treatments

leaves from the original fourth leaf-node on all plants on day 95. No original control plant leaves survived until day 116.

Bacterial population densities on *C. demersum* leaves in the control were significantly higher than on leaves in the *L. peregra* treatment at days 12, 68, and 95 ($P < 0.01$, $P < 0.01$ and $P < 0.001$ respectively), in the *P. planorbis* treatment at day 12, 41, 68, ($P < 0.01$ in each case), and day 95 ($P < 0.001$), and in the mixed snail species treatment on days 12, 41, 68, and 95 (Mann-Whitney *U*-test, $P < 0.05$, $P < 0.001$, $P < 0.01$, $P < 0.001$ respectively) (Fig. 3a.) There were no significant differences in bacterial population density on the leaves of *C. demersum* between the three different snail treatments.

Epiphytic algal cell density in the control treatments increased with time and was significantly higher than the initial densities by day 68 (Fig. 3b, $P < 0.001$). Algal density on leaves in the snail treatments also showed a gradual increase with time, and were higher than the initial population densities by day 116 ($P < 0.01$, $P < 0.05$, and $P < 0.05$ for the *L. peregra, P. planorbis,* and mixed-snail treatments respectively). Algal population densities on leaves in the control treatments were significantly higher than in the *L. peregra* treatment [$P < 0.05$ (day 12) and $P < 0.01$ (days 41, 68, and 95)], *P. planorbis* treatment [$P < 0.01$ (day 12), $P < 0.05$ (day 41) and $P < 0.01$ (days 68 and 95)], and in the mixed-snail treatment ($P < 0.001$, $P < 0.05$, $P < 0.01$, and $P < 0.001$ for days 12, 41, 68, and 95 respectively).

Changes in epiphyton composition

The percentage composition (expressed as relative abundance) of epiphytic algal communities from day 0 to day 95 are shown in Fig. 4. The relative abundance (RA) of filamentous cyanobacteria (*Anabaena inaequalis* and *Lyngbya* sp.) in the control treatments increased by day 95. In the snail treatments the overall change in RA of filamentous cyanobacteria tended to be low, (with *Lyngbya* sp. RA increasing and *A. inaequalis* RA decreasing). The RA of coccoid green algae in epiphyton in the controls showed no trend with time, whereas in the three snail treatments they initially increased before declining. The RA of green algae with an adnate growth form (predominantly *Coleochaete scutata* Breb.), declined in all treatments.

Both the RA and cell densities of the diatom *Cocconeis placentula* Ehr. increased in the snail treatments, but did not increase in the controls. This resulted in larger *C. placentula* population densities in snail treatments than in the controls by the end of the experiment. *Achnanthes minutissima* Kutz. increased in all four treatments with there being were no significant differences in RA between treatments.

Principal component analysis of the epiphyton data showed two overlapping patterns. Principal components 1 and 2 (explaining 71.7% of the variation), grouped epiphyte assemblages by time (Fig. 5A), suggesting that temporal changes accounted for more of the variation in the data than treatment effects. The algal taxa which had

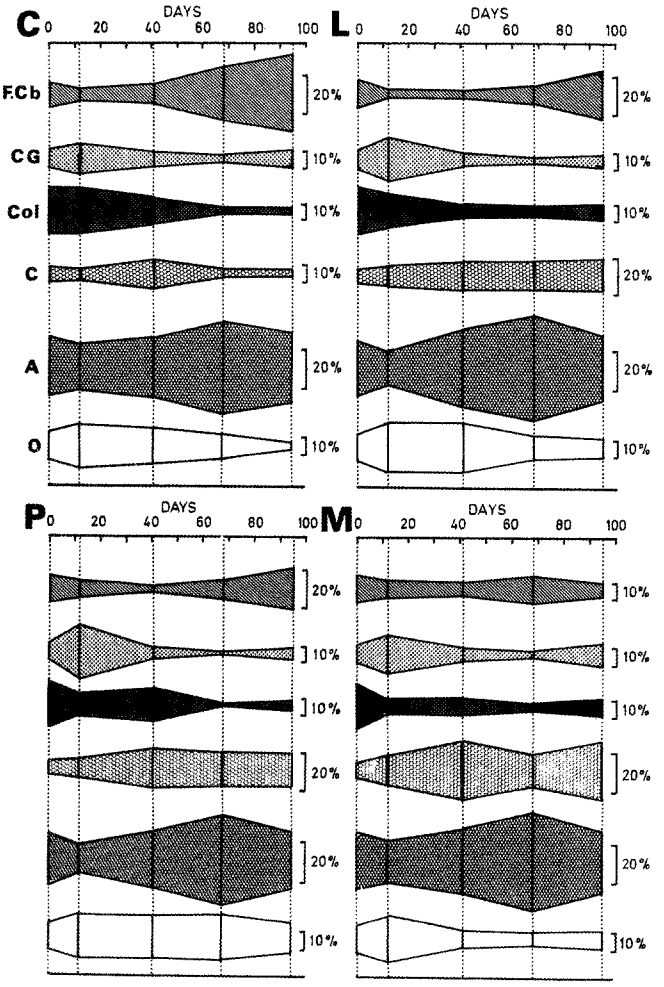

Fig. 4. Percentage relative abundance of epiphytic algal taxa in epiphyton growing on *C. demersum* under four different grazing regimes over 95 days. *C* = control treatment, *L* = *L. peregra*, *P* = *P. planorbis*, *M* = mixed species treatments. Species codes: *Fcb* = filamentous cyanobacteria, *CG* = coccal green algae, *Col* = *Coleochaete* spp., *C* = *Cocconeis placentula*, *A* = *Achnanthes minutissima*, *O* = other diatom species

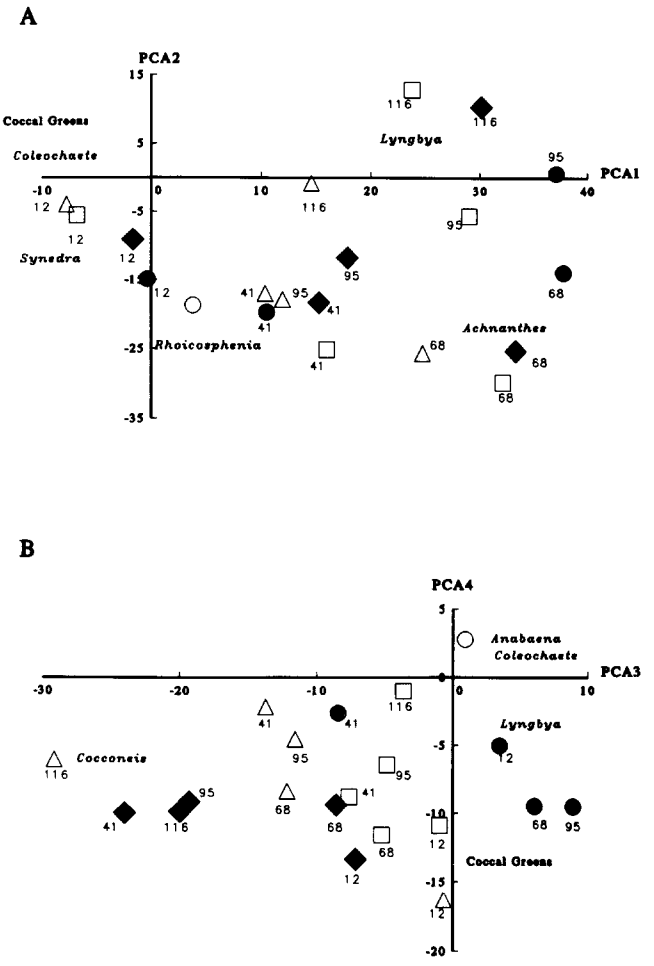

Fig. 5. **A** Principal component score-scatter diagrams for principal components 1 and 2. Each *point* represents a single epiphyte community, the *number* by each point is the sample time (days). ○ Initial epiphyton, ● control epiphyton, □ *L. peregra*-grazed epiphyton, △ *P. planorbis*-grazed epiphyton, ◆ epiphyton grazed by mixed-snail species. Areas of the plot strongly influenced by specific epiphyte taxa are indicated. **B** Principal component score scatter diagrams for components 3 and 4 (details as 5A)

the most influence on principal components 1 and 2 were coccal and adnate green algae, *A. minutissima* and *Lyngbya* sp. (Fig. 5A). Thus in all treatments the epiphyton was initially dominated by coccal green algae and *Coleochaete* spp., whereas towards the end of the experiment, it became dominated by *A. minutissima* and *Lyngbya* sp.

Principal components 3 and 4 explained a further 24.7% of the total variance in the assemblage composition data (Fig. 5B) and showed epiphyton assemblages grouped by treatment, with the control communities being influenced by *Lyngbya* and coccal green algae and the snail treatment assemblages being influenced by *Cocconeis*. Epiphyton in the *L. peregra* treatment was most similar to the control epiphyton, with the epiphyton communities in the *P. planorbis* and mixed-snail treatments occurring in the region greatly influenced by *Cocconeis-placentula*.

Epiphyton community indices

Epiphytic algal diversity (H') (Table 1) in the controls was higher than the epiphyton diversity (H') in the snail treatments ($F_{15,199} = 1.96$, $P < 0.05$). In the control treatments the diversity showed an initial increase, and then declined, whereas in all three snail treatments diversity declined over the course of the experiment. This pattern was also shown by the mean number of algal taxa (Table 2) ($F_{15,199} = 4.15$, $P < 0.001$). There were no significant trends in equitability of the algal communities with time (data not shown).

Snail population densities

The population densities of adult *Lymnaea peregra* in the *L. peregra* treatment enclosures fell to zero during the

Table 1. Shannon–Wiener diversity indices (H') for algal epiphytic communities growing under four different treatments over a period of 116 days in the Lewes Brooks

Date	Days	Treatment			
		Control	*Lymnaea*	*Planorbis*	Mixed
19.03.87	0	1.65 (0.17)	1.65 (0.17)	1.65 (0.17)	1.65 (0.17)
31.03.87	12	1.79 (0.20)	1.79 (0.13)	1.70 (0.31)	1.60 (0.29)
29.04.87	41	1.85 (0.38)	1.63 (0.45)	1.57 (0.30)	1.37 (0.38)
26.05.87	68	1.66 (0.41)	1.43 (0.25)	1.58 (0.19)	1.34 (0.35)
22.06.87	95	1.42 (0.22)	1.42 (0.25)	1.65 (0.22)	1.45 (0.44)
13.07.87	116	no data	1.59 (0.20)	1.38 (0.49)	1.51 (0.19)

Mean (standard deviation), $n = 10$

Table 2. Mean number of algal taxa in epiphyton growing under four different treatments over a period of 116 days in the Lewes Brooks

Date	Days	Treatment			
		Control	*Lymnaea*	*Planorbis*	Mixed
19.03.87	0	7.4 (0.97)	7.4 (0.97)	7.4 (0.97)	7.4 (0.97)
31.03.87	12	9.3 (1.16)	8.5 (1.43)	7.8 (1.55)	6.6 (1.90)
29.04.87	41	10.75 (2.25)	8.5 (2.37)	8.4 (2.37)	7.7 (2.41)
26.05.87	68	12.9 (2.58)	9.8 (2.3)	9.6 (1.5)	8.2 (1.99)
22.06.87	95	8.25 (1.67)	7.9 (2.38)	8.9 (1.66)	8.3 (2.5)
13.07.87	116	no data	7.0 (1.41)	7.43 (1.40)	6.56 (1.01)

Mean (standard deviation), $n = 10$

course of the experiment as a result of post-oviposition mortality (Fig. 6A). Oviposition occurred between late April and mid-June (days 12–68), and juvenile snails (approx. 2 mm long) were present by day 68. By day 95, juvenile (2–5 mm long) numbers had increased and at the end of the experiment only these juveniles (3–8 mm long) were present. Juvenile mortality was high; 82% of juveniles hatched between day 68 and day 95 died between days 95 and 116.

The population densities of *P. planorbis* in the *P. planorbis* treatment enclosures followed a similar pattern to that of *L. peregra* (Fig. 6B). Egg masses were not observed until day 41, with juveniles (2 mm shell diameter) present by day 68. Numbers of juveniles increased with time, with 86% of individuals hatched between days 68 and 95, dying between days 95 and 116. Surviving juveniles grew to 6 mm shell diameter by the end of the experiment. Some adult snails were still present in the enclosures at the end of the experiment.

In the mixed-snail treatments both *L. stagnalis* and *L. peregra* reproduced in the enclosures (Fig. 7A), with the adults suffering high mortalities during the latter period of the experiment. Eggs were present between days 12 and 95, but it was not possible to assign these to particular species. Juvenile *L. peregra* (2 mm long) were present by day 68, and these grew to about 5 mm long by the end of the experiment. Juvenile *L. stagnalis* were also present by day 68, and grew to about. 10 mm long by the end of the experiment. Juveniles of both species suffered high mortality rates. The numbers of adult *Bithynia tentaculata, Physa fontinalis, Planorbis contortus, P. vortex* and *P. planorbis* are shown in Fig. 7B. Only juvenile *P. planorbis* were found in the enclosures, the number of adults of the other species decreasing with time. Juvenile *P. planorbis* occurred in the enclosures by day 95 and the number of juveniles had increased by day 116.

The overall number of snails increased in all three treatments during the experiment ($P < 0.001$ in all three cases), with significantly more snails in the mixed-snail treatments than the two single-species treatments until day 41 ($P < 0.001$). However, there were no significant differences in the total number of snails present in any of the three treatments containing them by day 116.

Other invertebrates

A range of invertebrates normally encountered in the Lewes Brooks drainage ditches were present in all the enclosures (including the controls). These included larvae of *Centroptilum* sp. and *Caenis* sp. (Ephemeroptera), *Limnephilus* sp. and *Triaenodes* sp. (Trichoptera), chironomid larvae, oligochaete worms, leeches and flatworms. Qualitative observations suggested no apparent differences in the abundance of these taxa between treatments.

Discussion

Interactions between snails and Ceratophyllum

Ceratophyllum demersum grown in the presence of snails under field conditions was significantly longer and had more leaf-nodes and growing tips than when grown in the absence of snails. These results agree with laboratory studies involving *C. demersum* and snails (Bronmark 1985; Underwood 1991b), and with observations from estuarine (Hootsmans and Vermaat 1985; Howard and

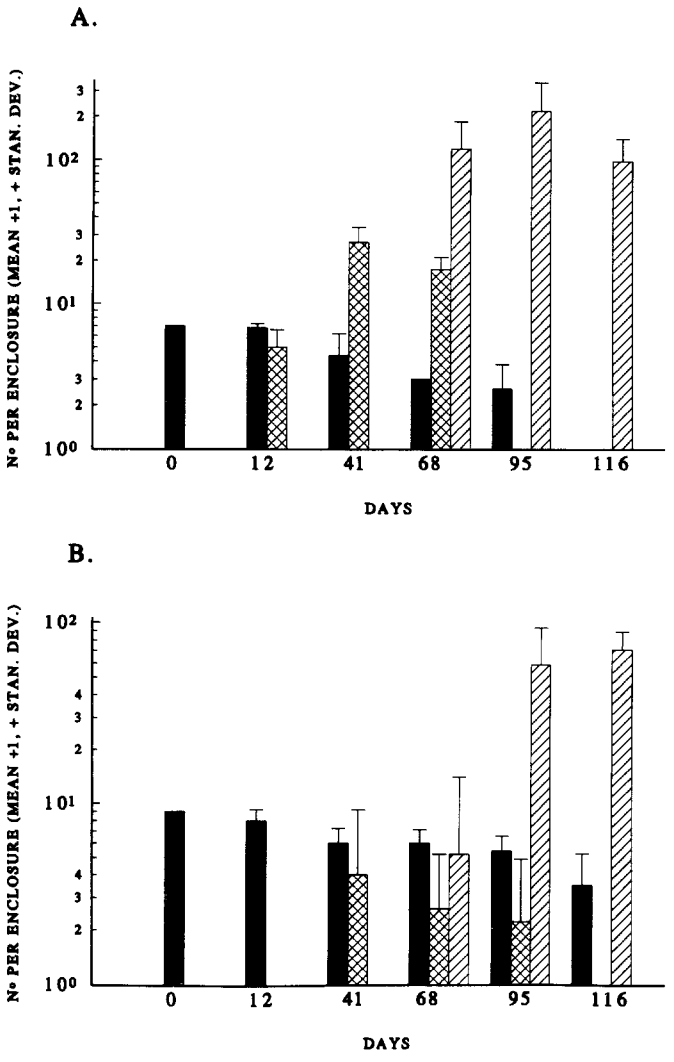

Fig. 6A, B. Mean numbers of adults, eggs and juvenile snails **A** in the *Lymnaea* treatment enclosures and **B** in the *Planorbis* treatment enclosures (mean + 1, + SE; note logarithmic Y axis) **A** ■ Adult *L. peregra,* ▩ Egg masses, ▨ Juvenile *L. peregra.* **B** ■ Adult *P. planorbis,* ▩ Egg masses, ▨ Juvenile *P. planorbis*

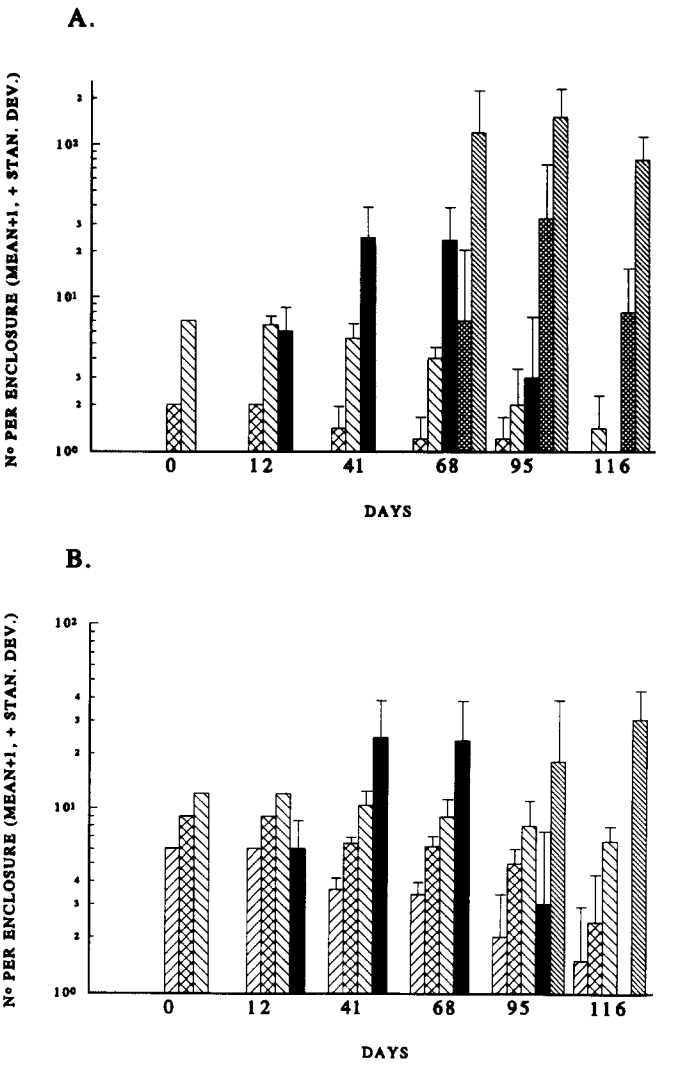

Fig. 7. A Population densities of lymnaeid snails in the mixed-snail treatment enclosures. (mean + 1, + SE; note logarithmic *Y* axis) ▩ Adult *Lymnaea,* ▧ Adult *L. peregra,* ■ Egg masses, ▩ Juvenile *L. stagnalis,* ▧ Juvenile *L. peregra.* **B** Population densities of planorbid, physid and prosobranch snails in the mixed-snail treatment enclosures. (mean + 1, + SE; note logarithmic *Y* axis). ▨ Adult *Planorbis vortex, P. contortus,* and *Physa fontinalis,* ▩ Adult *Bithynia tentaculata,* ▧ Adult *Planorbis planorbis,* ■ Egg masses, ▧ Juvenile *P. planorbis*

Short 1986) and marine habitats (Coen 1988). Freshwater pulmonate snails do not eat healthy *C. demersum* but remove epiphyton from its surface (Underwood and Thomas 1990). An outcome of this association is enhanced macrophyte growth. It has been shown in laboratory studies that growth enhancement may be partly caused by the recycling of nutrients present in material egested or excreted by the snails (Kairesalo and Koskimies 1987; Mat 1988; Underwood 1991 b). This recycling of nutrients is likely to be important to macrophytes during summer months when the combined effects of rapid plant growth and reduced water flow results in nutrient depletion (Subramaniam 1990). It is likely that non-rooting submersed plants such as *Ceratophyllum* will show a greater response to nutrients released by grazing invertebrates than rooted species of macrophyte. This hypothesis remains to be tested.

It has also been demonstrated that macrophyte growth can be enhanced due to the removal of potentially harmful populations of bacteria and competing epiphytic algae by grazing invertebrates (Rogers and Breen 1981, 1983; Bronmark 1985; Underwood and Thomas 1990; Underwood 1991a, 1991b; Underwood and Baker 1991). That *C. demersum* leaves in the treatments containing snails had significantly greater longevity than comparable leaves on control plants shows that this effect also occurs under field conditions.

Interactions between snails and bacterial and algal epiphyton

Because other invertebrates were present in the enclosures which were potential grazers of epiphyton, epiphyton in the control treatments can only be considered as ungrazed by snails, and not as totally ungrazed. The lower population densities of epiphytic algae and bacteria on *Ceratophyllum* leaves in the treatments with snails compared with controls without snails is in agreement with other studies on snail grazing (Kesler 1981; Cattaneo 1983; Cuker 1983a, b; Jacoby 1985; Cattaneo and Kalff 1986; Lamberti et al. 1987; Lowe and Hunter 1988; Fairchild et al. 1989; Underwood and Thomas 1990). Other invertebrate grazers which were present in the enclosures may also have influenced the epiphyton. Many species of Trichoptera and Ephemoptera are known to be important grazers of epilithon in stream habitats (Jacoby 1987; Lamberti et al. 1987; Peterson 1987; Hill and Knight 1988), but their importance in lentic systems is unclear. Grazing by chironomid larvae, cladocerans, and oligochaetes in lentic habitats would appear to have little impact on periphyton standing crop (Mason and Bryant 1975; Cattaneo 1983; Cuker 1983b; Cattaneo and Kalff 1986) though it may effect epiphyton species composition. Yet, as significant treatment effects were found in this experiment, it can be concluded that freshwater pulmonate snails are important grazers in the lentic habitat studied.

Nutrient turnover due to snails will have also benefited some epiphytic taxa, e.g. green algae (Fairchild et al. 1989). The initial increase of coccal green algae under snail grazed conditions may have been due to this, as well as to their ability to survive grazing (Porter 1976; van Aardt and Wolmarans 1981; Underwood and Thomas 1990). Small diatom taxa (e.g. *Cocconeis placentula*), which can both avoid ingestion and survive digestion by snails (Underwood and Thomas 1990) would also be in a position to benefit from increased nutrient availability and reduced competition from larger taxa (Power 1990; Pringle 1990). These advantages may explain the increases in *C. placentula* cell densities in the snail treatments.

Changes in epiphyton structure and species composition during the experiment can be attributed to successional and seasonal changes as well as to differences in grazing regime. Differences in diversity, mean number of species and species composition of snail-grazed and non-snail-grazed epiphyton were less marked than in similar laboratory-based experiments (Underwood and Thomas 1990). This could have been due to non-molluscan grazing pressure influencing species composition as well as to the longer time period of this experiment. Principal component analysis indicated that the greatest amount of variation in epiphyte communities was due to temporal changes. These would have included increases in cyanobacteria during the summer (Cattaneo 1983; Morin 1986), successional changes in community structure (Hoagland et al. 1982; Roemer et al. 1984) and in changes to the nutrient and temperature regimes which favour cyanobacteria (Tilman et al. 1986).

Interactions between snail species in the enclosures

The observed patterns of egg laying, adult post-oviposition mortality, and juvenile growth and mortality agree with published results on the life cycles of freshwater pulmonates (Eisenberg 1970; Calow 1978; Gaten 1986; Lam and Calow 1989). It is known that intra- and interspecific competition for food is an important factor in determining snail densities (Eisenberg 1970; Brown 1982; Lam and Calow 1989; Osenburg 1989). The enclosures probably provided a set amount of food, and although final numbers were similar, the age structure and composition of the snail populations were different. This may have been due to differences in food preference and competitive ability between species and between adults and juveniles of different size classes (Brown 1982; Thomas et al. 1985; Lodge 1986; Underwood and Thomas 1990; Bronmark et al. 1991).

Conclusions

This experiment demonstrated that freshwater snails can significantly enhance the growth of *C. demersum* and affected epiphyton populations under highly variable natural conditions. As an increase in macrophyte biomass increases the probability of a plant surviving into a second season (Arber 1963), such enhancement could have longer term ecological importance. Increased macrophyte growth will also result in an increased surface area of epiphyton, upon which snails feed, as well as sites for shelter and oviposition. There is evidence indicating that grazed periphyton assemblages are more productive than ungrazed assemblages (Gregory 1983; Jacoby 1987; Lamberti et al. 1987) and therefore if increased epiphyton production compensates for lower algal biomass, snails may enhance the food resources available to them.

The significant effect that snails can have on epiphyton and macrophytes may effect other species of invertebrate. Strongly interacting grazers can modify the environment in favour of species whose grazing activities are not great enough to maintain their own food supply (Dethier and Duggins 1984; Feminella and Resh 1991). It is possible that some of the smaller species of snails and ephemeroptera may benefit from the activities of the more strongly interacting, pulmonate snail species. This hypothesis remains to be tested in lentic conditions.

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References

Aram RH (1970) Studies on the population biology of *Lymnaea peregra* (Mull.) and *Planorbis planorbis* (L.). Unpublished D. Phil Thesis, University of Sussex, UK

Arber A (1963) Water plants, a study of aquatic angiosperms. Reprint J. Cramer Weinheim. Hafner, New York

Bronmark C (1985) Interactions between macrophytes, epiphytes and herbivores: an experimental approach. Oikos 45:26–30
Bronmark C (1989) Interactions between epiphytes, macrophytes and freshwater snails: a review. J Moll Stud 55:299–311
Bronmark C, Rundle SD, Erlandsson A (1991) Interactions between freshwater snails and tadpoles: competiton and facilitation. Oecologia 87:8–18
Brown KM (1982) Resource overlap and competition in pond snails: an experimental analysis. Ecology 63:412–422
Calow P (1978) The evolution of life-cycle strategies in fresh-water gastropods. Malacologia 17:351–364
Cattaneo A (1983) Grazing on epiphytes. Limnol Oceanogr 28:124–132
Cattaneo A, Kalff J (1986) The effect of grazer size manipulation on periphyton communities. Oecologia 69:612–617
Coen LD (1988) Herbivory by crabs and the nature of algal epibionts on caribbean host corals. Oecologia 75:198–203
Cuker BE (1983a) Grazing and nutrient interactions in controlling the activity and composition of the epilithic algal community in an arctic lake. Limnol Oceanogr 28:133–141
Cuker BE (1983b) Competition and coexistance among the grazing snail *Lymnaea,* Chironomidae, and microcrustacea in an arctic epilithic lacustrine community. Ecology 64:10–15
Dethier MN, Duggins DO (1984) An "indirect commensalism" between marine herbivores and the importance of competitive hierarchies. Am Nat 124:205–219
Eisenberg RM (1970) The role of food in the regulation of the pond snail, *Lymnaea elodes*. Ecology 51:680–684
Fairchild GW, Sherman JW, Acker FW (1989) Effects of nutrient (N,P,C) enrichment, grazing and depth upon littoral periphyton of a softwater lake. Hydrobiologia 173:69–83
Feminella JW, Resh VH (1991) Herbivorous caddisflies, macroalgae, and epilithic microalgae: dynamic interactions in a stream grazing system. Oecologia 87:247–256
Gaten E (1986) Life cycle of *Lymnaea peregra* (Gastropoda: Pulmonata) in the Leicester Canal, UK with an estimate of annual production. Hydrobiologia 135:45–54
Gauch HG Jr (1984) Multivariate analysis in community ecology (Cambridge Studies in Ecology 1) Cambridge University Press, Cambridge
Gregory SV (1983) Plant herbivore interactions in stream systems. In: Barnes JR, Minshall GW (eds) Stream ecology: Application and testing of general ecological theory. Plenum Press, New York London, pp 157–189
Hill WR, Knight AW (1988) Concurrent grazing effects of two stream insects on periphyton. Limnol Oceanogr 33:15–26
Hoagland KD, Roemer SC, Rosowski JR (1982) Colonization and community structure of two periphytic assemblages, with emphasis on the diatoms (Bacillariophyceae). Am J Bot 69:188–213
Hootsmans MJM, Vermaat JE (1985) The effects of periphyton grazing by three epifaunal species on the growth of *Zostera marina* L. under experimental conditions. Aquat Bot 22:83–88
Hossell JC, Baker JH (1979) A note on the enumeration of epiphytic bacteria by microscopic methods with particular reference to two freshwater plants. J Appl Bacteriol 46:87–92
Howard RK, Short FT (1986) Seagrass growth and survivorship under the influence of epiphyte grazers. Aquat Bot 24:287–302
Jacoby JM (1985) Grazing effects on periphyton by *Theodoxus fluviatilis* (Gastropoda) in a lowland stream. J Freshw Ecol 3:265–274
Jacoby JM (1987) Alterations in periphyton characteristics due to grazing in a cascade foothill stream. Freshw Biol 18:495–508
Kairesalo T, Koskimies I (1987) Grazing by oligochaetes and snails on epiphytes. Freshw Biol 17:317–324
Kesler DH (1981) Periphyton grazing by *Amnicola limosa:* an enclosure exclosure experiment. J Freshw Ecol 1:51–59
Lam PKS, Calow P (1989) Intraspecific life-history variation in *Lymnaea peregra* (Gastropoda: Pulmonata) 1. Field study. J Anim Ecol 58:571–588
Lamberti GA, Ashkenas LR, Gregory SV, Steinman AD (1987) Effects of three herbivores on periphyton communities in laboratory streams. J N Am Benthol Soc 6:92–104
Lodge DM (1985) Macrophyte-gastropod associations: observations and experiments on macrophyte choice by gastropods. Freshw Biol 15: 695–708
Lodge DM (1986) Selective grazing on periphyton: a determinant of freshwater gastropod microdistributions. Freshw Biol 16:831–841
Lodge DM, Kelly P (1985) Habitat disturbance and the stability of freshwater gastropod populations. Oecologia 68:111–117
Lowe RL, Hunter RD (1988) Effects of grazing by *Physa integra* on periphyton community structure. J N Am Benthol Soc 7:29–36
Mat I (1988) Ecophysiological aspects of nitrogen metabolism in the freshwater snail *Biomphalaria glabrata.* D. Phil Thesis, University of Sussex, UK
Mason CF, Bryant RJ (1975) Periphyton production and grazing by chironomids in Alderfen Broad, Norfolk. Freshw Biol 5:271–277
Morin JO (1986) Initial colonization of periphyton on natural and artifical apices of *Myriophyllum heterophyllum* Michx. Freshw Biol 16:685–694
Osenberg CW (1989) Resource limitation, competition and the influence of life history in a freshwater snail community. Oecologia 79:512–519
Peterson CG (1987) Gut passage and insect grazer selectivity of lotic diatoms. Freshw Biol 18:455–460
Porter KG (1976) Enhancement of algal growth and productivity by grazing zooplankton. Science 192:1332–1333
Power ME (1990) Resource enhancement by indirect effects of grazers: Armoured Catfish, algae and sediment. Ecology 71:897–904
Pringle CM (1990) Nutrient-spatial heterogeneity: effects on community structure, physiognomy, and diversity of stream algae. Ecology 71:905–920
Pyke DA, Thompson JN (1986) Statistical analysis of survival and removal rate experiments. Ecology 67:240–245
Roemer SC, Hoagland KD, Rosowski JR (1984) Development of a freshwater periphyton community as influenced by diatom mucilages. Can J Bot 62:1799–1813
Rogers KH, Breen CM (1981) Effects of epiphyton on *Potamogeton crispus* L. leaves. Microb Ecol 7:351–363
Rogers KH, Breen CM (1983) An investigation of macophyte, epiphyte, and grazer interactions. In Wetzel RG (Ed) Periphyton of Freshwater ecosystems. Junk, The Hague
Subramaniam J (1990) The biochemical ecology of freshwater communities with particular reference to the neuston. D.Phil Thesis, University of Sussex, UK
Tilman D, Kiesling R, Sterner R, Kilham SS, Johnson FA (1986) Green, bluegreen and diatom algae: taxonomic differences in competititve ability for phosphorus, silicon and nitrogen. Arch Hydrobiol 106: 473–485
Thomas JD (1987) An evaluation of the interactions between freshwater pulmonate snail hosts of human schistosomes and macrophytes. Phil Trans R Soc London B 315:75–125
Thomas JD (1990) Mutualistic interactions in freshwater modular systems with molluscan components. Adv Ecol Res 20:125–178
Thomas JD, Tait AI (1984) Control of the snail hosts of schistosomiasis by environmental manipulation: a field and laboratory appraisal in the Ibadan area, Nigeria. Phil Trans R Soc London B305:201–253
Thomas JD, Nwanko DI, Sterry PR (1985) The feeding strategies of juvenile and adult *Biomphalaria glabrata* (Say) under simulated natural conditions and their relavance to ecological theory and snail control. Proc R Soc London B 266:177–209

Thomas JD, Kowalczyk C, Somasundaram B (1989) The biochemical ecology of *Biomphalaria glabrata*, a snail host of *Schistosoma mansoni*: Short chain carboxylic and amino acids as phagostimulants. Comp Biochem Physiol 93A: 899–911

Underwood GJC (1991a) Note: Colonization and invasion of leaves of the aquatic macrophyte *Ceratophyllum demersum* L. by epiphytic bacteria. Microb Ecol 21:267–275

Underwood GJC (1991b) Growth enhancement of the macrophyte *Ceratophyllum demersum* in the presence of the snail *Planorbis planorbis*: the effect of grazing and chemical conditioning. Freshw Biol 26:325–334

Underwood GJC, Baker JH (1991) The effect of various aquatic bacteria on the growth and senescence of duckweed *(Lemna minor)*. J Appl Bacteriol 70:92–196

Underwood GJC, Thomas JD (1990) Grazing interactions between pulmonate snails and epiphytic algae and bacteria. Freshw Biol 23:505–521

van Aardt WJ, Wolmarans CT (1981) Evidence for non-assimilation of *Chlorella* by the african freshwater snail *Bulinus (Physopsis) globosus*. S Afr J Sci 77 319–320

Zar JH (1984) Biostatisical analysis. 2nd edn. Prentice Hall Int Inc, New Jersey