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Why are there few algae on snail shells? The effects of grazing, nutrients and shell chemistry on the algae on shells of *Helisoma trivolvis*

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SUMMARY

1. Freshwater snails often lack visible growths of algae on their shells. We tested three possible mechanisms that may account for this (grazing, snail-derived nutrients and chemical defences), using the ramshorn snail *Helisoma trivolvis*.
2. The experiments were carried out in floating plastic enclosures in a pond and comprised seven treatments. Grazing treatments were: a lone snail (ungrazed, as self-grazing does not occur), *Helisoma* with conspecifics, *Helisoma* with the co-occurring pond snail *Physa* sp., empty shells with *Helisoma*, and ungrazed empty shells. Nutrient effects were possible in all treatments with occupied shells (lone snail; *Helisoma* with conspecifics, and with *Physa*) versus absent in other treatments. Testing for chemical defences compared algae on fresh empty shells, weathered shells (outer organic periostracum layer absent) and boiled fresh shells (with denaturization of susceptible proteins).
3. Diatoms dominated algal assemblages on snail shells. Although the upright diatom *Gomphonema gracile* was abundant on all shells, it was dominant on the shells of snails housed with other snail grazers (either *Helisoma* or *Physa*).
4. Only the lone snail (nutrients but no grazing) showed higher algal biomass, so presumably any nutrient effect in the treatments with grazers was masked. Both *Helisoma* and *Physa* were observed apparently grazing on *Helisoma* shells, and consequently algal biomass in multi-snail treatments was similar to that on empty shells. Scanning electron microscopy revealed that algal density was highest near the aperture of live snails, but not empty shells; this is consistent with a nutrient addition effect. There was no evidence of chemical defences against algal growth.
5. In soft-bottomed freshwater habitats with abundant snails, shells of living snails provide nutrient-augmented substrata that may indirectly boost overall snail production.

Keywords: algal ecology, biofouling, diatoms, periphyton

Introduction

Molluscs may act as ecosystem engineers in both marine and freshwater habitats because of the production of sizeable shells (reviewed by Gutiérrez *et al.*, 2003). Shells provide a hard substratum for the settlement and establishment of a wide range of organisms, including both microscopic and macroscopic algae, and macroinvertebrates, such as chironomid larvae, hydropsychid caddisflies, barnacles, bryozoans, sponges and polychaetes (references in Gutiérrez *et al.*, 2003; Vasconcelos *et al.*, 2007). Mollusc shells, particularly in the form of bivalve beds, also provide protection from predation, desiccation and disturbance (Vance, 1978; Witman, 1985; Beekey, McCabe & Marsden, 2004a), and can influence the settling and retention of fine mineral and organic

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particles in the benthos (Commito *et al*., 2005). In fine sediments, the hard substrata provided by snail and bivalve shells can increase local species abundance (benthic macroinvertebrates: Botts, Patterson & Schloesser, 1996) and richness (discussed in Gutiérrez *et al*., 2003).

Although the mollusc shells increase habitat availability, the occupation of shells by live molluscs or hermit crabs can have additional biological effects (e.g. Botts, Patterson & Schloesser, 1996; Creed, 2000). Nutrients released by filter-feeding bivalves have been implicated in increasing algal growth (of some filamentous algae, Francoeur *et al*., 2002; of algal biomass, Spooner & Vaughn, 2006) on bivalve shells and higher invertebrate densities within bivalve beds (Beekey, McCabe & Marsden, 2004b; Spooner & Vaughn, 2006). In contrast, movement and habitat choice by hermit crabs, gastropods and bivalves can reduce epibiont (algal and invertebrate) assemblages on shells through abrasion and desiccation (Bell, 2005; Spooner & Vaughn, 2006).

The growth of epibionts on the shells or external surface of organisms can be detrimental to the host (Lauer & Spacie, 2000; Buschbaum & Saier, 2001; Chan & Chan, 2005), especially if the epibionts are large. Mechanisms may include increased drag in currents or waves (Schmitt, Osenberg & Bercovitch, 1983; Wahl, 1996; Gonzalez, Stotz & Aguilar, 2001), the inability to access protective crevices, and competition for food and nutrients (but see Buschbaum & Saier, 2001). Alternatively, epibionts may benefit the host by providing camouflage (Feifarek, 1987), a supplementary food source (Cox & Wagner, 1989) or protection (Brooks, 1988), or may have no measurable effect (Donovan *et al*., 2002).

Whereas the growth of epibionts has been noted on many types of marine shells (e.g. Vance, 1978; Black & Peterson, 1987; Creed, 2000; Bell, 2005) and on freshwater bivalves (Curry, Everitt & Vidrine, 1981; Francoeur *et al*., 2002; Vaughn, Spooner & Hoagland, 2002; Spooner & Vaughn, 2006), the shells of many freshwater snails apparently have only very sparse algal growth, although they may host diatoms (e.g. Keating & Prezant, 1998). A lack of fouling organisms on submerged surfaces can result from short exposure period, disturbance and defence (Wahl & Sönnichsen, 1992). Short exposure probably does not apply to freshwater snails, which are relatively long-lived and do not moult. However, shell age may affect the distribution of algae on individual shells because the older portions have been exposed for longer to colonists and possibly because any anti-biofouling chemicals have been leached. Disturbances include burrowing in soft sediments (e.g. in marine snail shells occupied by hermit crabs; Creed, 2000), grazing (Wahl & Sönnichsen, 1992) and abrasion associated with high flow. Potential defence mechanisms of gastropods include anti-biofouling chemicals (marine mussels: Bers *et al*., 2006) and microtopographic characteristics of shells (marine mussels: Scardino *et al*., 2003; Bers & Wahl, 2004). In contrast, factors that can promote algal growth on submerged substrata, including mollusc shells, are high availability of nutrients and light, and favourable surface microtopography (Scardino *et al*., 2003; Bers & Wahl, 2004).

Common species of pond snails (*Helisoma* spp. and *Physa* spp.) generally lack visible growth of algae on their shells. We investigated potential factors affecting the growth of algae on the shells of the ramshorn snail *Helisoma trivolvis* (Say). Specifically, we investigated experimentally whether various biological (grazing and nutrients) and chemical (of the outer periostracum layer) factors affect the growth of periphyton on the shells. We also investigated whether the distribution of algae on the snail shells was consistent with the effect of relative shell age or with the location of possible nutrient input.

Methods

Helisoma trivolvis is a widespread North American snail common in still water and occasionally in slow flowing streams. The planispiral shell grows to about 20 mm in diameter (Eversole, 1978) and the snail feeds primarily on algae (Smith, 1989) and detritus.

The experiment was carried out in an experimental pond at the Aquatic Research Facility on the University of Oklahoma campus. The pond used for the experiment was fishless and has been periodically used for holding freshwater mussels. Rain water inputs to the pond were augmented by well water to maintain a constant water level. The conductivity of the pond water averaged 495 $\mu S\ cm^{-1}$ and pH averaged 9.1 during the experiment. *Helisoma trivolvis* and *Physa* sp. occur in the pond, but *Helisoma* for the experiment were collected from a nearby farm pond, where they were extremely crowded because of drought-induced low water level.

Chemical and structural effects of shells were assessed in three treatments: (i) empty shells (snails were removed to prevent grazing or nutrient effects; one shell/replicate); (ii) weathered shells (periostracum absent and calcite layers exposed; two shells/replicate) and (iii) boiled shells (which may denature proteins in the outer periostracum layer of the shell; two shells/replicate).

Grazing and nutrient effects were assessed by comparing empty shells (treatment 1 above) with: (iv) empty shells with conspecific grazers (one shell and three *Helisoma*/replicate); (v) lone snails (nutrient effects, but no grazing by other snails; one *Helisoma*/replicate); (vi) snails with grazing conspecifics (three *Helisoma*/replicate) and (vii) snails with an additional species of grazing snail: *Physa* sp. (two *Helisoma* and three *Physa*/replicate)

Live snails from the farm pond and empty, weathered (white) shells from the shoreline were collected on 3 October 2005. Empty weathered shells were kept dry and live snails were held in a greenhouse tank for 1 week before the experiment. Fresh empty shells were obtained by freezing snails for an hour, after which the body mass was easily pulled out. The aperture of all shells without snails was sealed with a low temperature melting point glue (Glu-Stix, Merchant General Corporation, Oldsmar, FL, U.S.A.) to prevent algal growth on the shell interior. *Physa* snails were obtained from greenhouse tanks, using stocks sourced from the experimental pond during the previous year.

Treatments were housed individually in small 950-mL plastic containers (approximate dimensions: 10 cm L × 10 cm W × 9 cm D; water depth of 6 cm). Densities of one to three *Helisoma* in the containers equate to densities in the published range of 100–300 snails m^{-2} (Eversole, 1978). *Helisoma* density was not measured at the collection site because of snail crowding during water draw-down; the pond subsequently dried.

Windows cut in all four sides of the containers were covered with nylon 1-mm mesh screen to allow water circulation but retain snails. Each container was floated with a closed-Styrofoam collar and groups of 12 containers were arranged in each of four floating racks, which were anchored to the pond bottom. Container lids were fitted with mesh and were initially used to ensure that snails did not escape and that 'wild' snails did not enter. We stopped using the lids after 1 week because snails stayed below the water level. A flattened fired-clay disk was placed in each container as a weight and substratum for algae, and containers were inoculated with a benthic algal slurry obtained from greenhouse tanks to augment natural algal colonization. Containers and racks were set up 1 week before the experiment.

Treatments were replicated six times and treatment locations were assigned randomly among the racks. Extra replicates of single snail and shell treatments provided samples for scanning electron microscopy (SEM); replicates of multiple snail treatments could be used for both SEM ($n = 2$) and chlorophyll-*a* analysis ($n = 5$).

The experiment started on 10 October 2005 and was harvested on 8 November 2005. Because unoccupied shells floated, these shells were held near the bottom by a narrow rubber band around the clay discs. Snails were initially offered a 0.3-g pellet of fish food to supplement their diet; one-half of the food quantity was added to containers without live, grazing snails. Although snails in holding tanks readily consumed food pellets, food was not noticeably eaten in the containers and feeding was discontinued on the fourth day of the experiment. During the experiment, the green filamentous alga *Mougeotia* sp. formed an extensive mat over the pond surface. To reduce mat accumulation in the racks and containers, the racks and containers were periodically lowered below the water surface and most of the mat was floated off. The mat disappeared during cool weather in the later part of the experiment. Screens on the containers were cleaned weekly.

At harvest, snail shells to be analysed for chlorophyll-*a* biomass in multi-*Helisoma* treatments were selected by using the snail in a randomly selected quadrat within the container. Shells for chlorophyll and taxonomic analysis of the diatom assemblage were foil wrapped, labelled and frozen in small plastic bags. Additional snails and shells were randomly selected for SEM and placed in 20-mL glass scintillation vials with pond water and refrigerated overnight. All samples were labelled with container number and were analysed without knowledge of the corresponding treatment. Snails used as grazers were returned to greenhouse tanks.

Chlorophyll-*a* concentration was used to quantify algal biomass. Snails were removed from shells prior to chlorophyll extraction. Chlorophyll-*a* concentration

was determined using ethanol extraction (Sartory & Grobbelaar, 1984) of entire shells in combination with a calculation of shell surface area. Shell diameter was measured with digital callipers and diameters were converted to area using a regression between diameter and shell area [regression equation: area = 11.053 − (1.204 × diameter) + (0.77 × diameter^2), R^2 = 0.889]. This equation was derived using 12 *Helisoma* shells that encompassed the size range of experimental snails. Surface area was measured as the weight gain of a coating of salt (particle layer technique, Bergey & Getty, 2006).

The algal assemblage composition was described using a relative abundance technique (Biggs, 1995) for four replicates of each of the seven treatments. Following chlorophyll extraction, shells were submerged in 30% hydrogen peroxide, which both removed and cleaned diatoms, but also limited our analysis of the algal community to diatoms. After sample rinsing, diatoms were mounted in Naphrax (Northern Biological Supply, Ipswich, England), and slides were scanned at 1000×. Each species was ranked on a relative scale of 1 (= small and rare) to 5 (= abundant and highest biomass). Hence, the dominant species was scored as 5, subdominant species received a score of 4, and common (especially large) species were scored as 3. Because both species density and cell biovolume were used in scoring, relative abundance scores reflected the relative total biovolumes of the taxa.

Shells for SEM were fixed in cacodylate-buffered gluteraldehyde, snails were removed and drain holes were drilled into the shells, then shells were treated with 2% osmium and run through a graded series of ethanol. Shells were critical point dried (Autosamdri-814; Tousimis, Rockville, MD, U.S.A.). The ventral, drilled surfaces of the dried shells were glued to aluminium stubs and the dorsal surfaces viewed using a Zeiss DSM-960A SEM (Oberkochen, Germany). Shells were photographed four times – the surface of the outer whorl near the aperture, the junction of the outer and adjacent whorl, a whorl junction near the centre, and the outer whorl near the tail. Malfunction of the critical point drier during sample processing resulted in the loss of most of the shells for SEM analysis. The remaining six shells were three shells of snails housed with grazing snails (= 'grazed') and three shells from the empty shell treatments (one each of empty, weathered and boiled; = 'ungrazed'). Regional diatom density on shells was estimated by counting the number of diatoms within a delineated circular area of approximately 70 000 μm^2 on the photographs.

Data analysis

Chlorophyll data were analysed using a randomized block ANOVA design, with rack location as the blocking variable. Tukey's multiple comparison test was used to determine differing treatments. No data transformations were needed.

Non-metric multidimensional scaling (NMDS) was used to assess diatom communities graphically. Analysis was limited to the 11 most common taxa, which had a cumulative rank score of 25 or more across the 28 samples. The NMDS analysis was based on the Curtis-Bray similarity matrix constructed using non-transformed rank data. Clusters of samples on the NMDS plots were delineated by cluster analysis (CLUSTER, using group average linkage). Diatom assemblages among treatments were compared with analysis of similarities (ANOSIM). A species contribution to similarity analysis (SIMPER) was used to identify taxa contributing to differences among sample groups. Analyses were performed with PRIMER, version 5 (Primer-E Ltd, Plymouth Marine Laboratory, Plymoth, U.K.). Because of the low sample number, analysis of diatom densities from SEM was limited to diatom densities on grazed versus ungrazed shells using ANOVA and graphical analysis of patterns of diatom distribution.

Results

Algal biomass on shells was low and differed among the snail treatments (ANOVA: $F_{6,23} = 3.228$, $P = 0.019$; Fig. 1). Differences among racks, the blocking variable, were insignificant ($F_{3,23} = 1.055$, $P = 0.387$). The highest algal biomass occurred on the shells of lone snail shells, which presumably were bathed in recycled nutrients from snail and were not grazed. Treatments with empty shells and no grazers had low algal biomass, irrespective of treatments that affected the periostracum (i.e. fresh empty shells versus shell weathering or boiling). The algal biomass in two of the three treatments with grazers was intermediate between the biomass of empty shells and the biomass of single snail shells. During the experiment, *Helisoma* was frequently observed grazing on

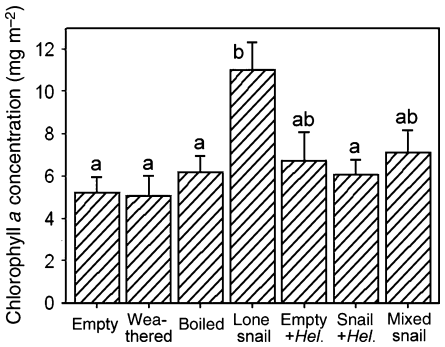

Fig. 1 Algal biomass on snail shells after colonization in a pond enclosures. Three treatments had lone empty shells: empty, weathered and boiled; the lone snail had a single live snail and the three multi-snail treatments were an empty shell with *Helisoma* and *Helisoma* with either conspecifics or *Physa*. Different letters show significant differences.

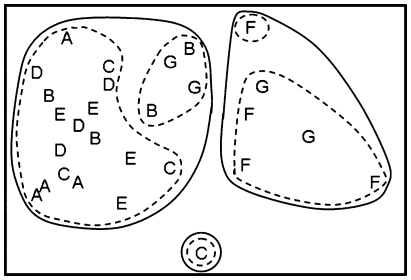

Fig. 2 Non-metric multidimensional scaling scatter plot of algal assemblages, with superimposed group-average clustering from Curtis-Bray similarities. Solid-lines show 75% similarity; dashed lines show 80% similarity. A, fresh empty shells; B, weathered shells; C, boiled shells; D, lone snail; E, empty shell plus three *Helisoma*; F, three *Helisoma*; G, *Helisoma* plus *Physa*. Stress = 0.14.

the shells of conspecifics. *Physa* also grazed on *Helisoma* shells and was frequently seen grazing the sides of the containers. Snails did not graze on their own shells.

Although there were remnants of the filamentous algal mat in the containers at the end of the experiment, there was no noticeable growth of filamentous algae on any of the snails or shells. Based on this observation, and the viewing of shells by SEM, we concluded that algal assemblages were dominated by diatoms. Diatom assemblages were dominated by *Gomphonema gracile* Ehr. emend. V. H. and chains of *Fragilaria virescens* Ralfs. Other common species were *Nitzschia denticula* Grun., *Synedra ulna* (Nitz.) Ehr. and *Synedra delicatissima* W. Sm. (Table 1).

Diatom assemblages on the shells differed among treatments (ANOSIM: $R = 0.337$, $P = 0.01$; see Fig. 2). Of the 21 possible pairwise comparisons among the seven treatments, seven pairs had clear differences in species assemblages ($R > 0.50$; Table 2). Each of the different pairs was between snails in multi-snail treatments (multiple *Helisoma* or *Helisoma* plus *Physa*), and the other treatments. The among-treatment differences resulted from differences in species' ranks

Table 2 Diatom assemblage SIMPER dissimilarity values between treatment pairs

	Empty	Boiled	Weathered	Empty + H	Lone	Snail + H
Boiled	18.4					
Weathered	21.0	20.7				
Empty + H	14.4	16.6	15.1			
Lone	16.3	19.4	15.2	13.2		
Snail + H	33.6*	26.6	28.6*	28.9*	31.5*	
Snails + P	31.0*	24.6	21.6	24.2*	24.7*	19.5

H, *Helisoma*; P, *Physa*.
Higher numbers indicate greater dissimilarity. Pairs with SIMPER R values >0.50 (different but possibly overlapping; Clarke & Gorley, 2001) are denoted with an '*'.

Table 1 Rank abundance of the eight most abundant diatom species on *Helisoma* shells. The maximum rank is 20 (= scoring the highest rank of five in each of the four replicates)

	Empty	Weathered	Boiled	Lone snail	Empty + *Helisoma*	Snails + *Helisoma*	Snail + *Physa*
Fragilaria virescens	20	18	18	18	20	10	9
Gomphonema gracile	11	17	16	13	15	20	20
Nitzschia denticula	12	11	14	13	13	15	16
Synedra delicatissima	11	13	9	15	13	9	8
Synedra ulna	16	9	12	14	13	6	5
Nitzschia cf. *amphibioides* Hust.	8	3	10	5	7	7	9
Achnanthidium minutissimum (Kutz.) Czarnecki	7	4	8	4	6	4	7
Encyonopsis microcephala (Grun.) Krammer	7	5	5	5	5	3	3

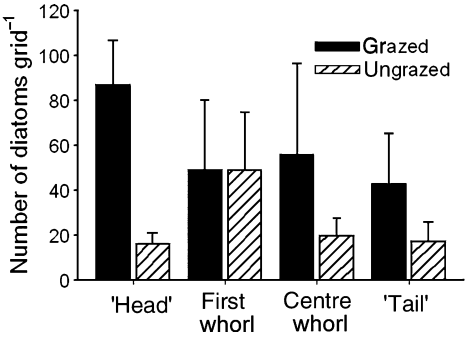

Fig. 3 Diatom distribution on grazed and ungrazed *Helisoma* shells. Mean (+1 SE) counts of diatoms within a template placed on scanning electron microscopy (SEM) photographs taken of four positions of each shell ($n = 3$).

rather than differences in the presence or absence of species. Assemblages of the two multi-snail treatments had more *G. gracile*, and less *F. virescens* and *S. ulna*, than treatments without multiple grazers (in six out of seven pairs with $R > 0.50$; species contributions analysis of SIMPER; Table 1). Assemblages on the shells in the lone snail treatment did not differ from assemblages on any of the empty shells treatments.

Based on counts of diatoms in SEM photographs of the six shells, diatom density was twice as high on grazed, occupied shells as on ungrazed, empty shells (mean number of diatoms/grid: grazed = 56, ungrazed = 26; ANOVA: $F_{1,16} = 4.557$, $P = 0.044$, $n = 3$; Fig. 3). Regionally, grazed shells showed a pattern of higher diatom density on the whorl near the aperture ('head-end') than was found on ungrazed shells (means of 87 and 16 diatoms per grid, respectively; Fig. 3). Bacteria, fungal filaments and short algal filaments were also visible on the photographs.

Discussion

In soft-bottomed ponds, hard substrata may be limited to the surfaces of live or dead plants and animals. Here, snail shells may provide a habitat for a different algal assemblage than occur on the sediment surface. Although sediment was not sampled in this study, the dominant diatoms from the snail shells are periphytic rather than epipelic (living in or on fine sediments). Similarly, the algal assemblage on the shells of lake-dwelling freshwater mussels differed from the assemblage in the fine sediments (Francoeur *et al.*, 2002).

Algal biomass on snail shells was affected by the snail itself. Algal biomass was highest on the shells of snails caged individually. Potential mechanisms to explain this higher biomass on these occupied shells are: (i) prevention of grazing; (ii) nutrient release by the inhabiting snail and (iii) optimization of habitat by the snail (including selection of sunlight and prevention from burial). Of the three mechanisms, the interplay of two (prevention from grazing and nutrient release) is likely to have produced the higher algal biomass. Release from grazing resulted from the inability of snails to graze their own cases. Snail grazing reduces algae through consumption, which in *Helisoma* is non-selective among diatom species (Smith, 1989), and through non-consumptive removal of algae caused by other snails moving over the shell. If grazers control algae on snail shells, ungrazed shells should have more algae that grazed snails. However, only the lone snail among the ungrazed shells had more algae than grazed shells. The other ungrazed shells (which were all empty) had low algal abundance; hence, grazing did not correlate directly with algal abundance. The second mechanism, nutrient release by grazing snails, may enhance algal growth on their own shells. Nutrient release from filter-feeding bivalves (Spooner & Vaughn, 2006) has similarly been associated with increased algal biomass on shells. The third mechanism, optimization of habitat for algal growth, did not apply to our experiment because all experimental containers had the same light conditions and lacked fine sediments, which prevented shell burial. Other studies have shown behavioural effects: living snails prevent burial and thereby support more epibionts than empty shells (Creed, 2000) and differential movement in the sediments influences the relative amount of epibionts in co-occurring species (Creed, 2000; Spooner & Vaughn, 2006).

The algal biomass on shells was also influenced by the presence of other snails, and was lower in treatments with multiple live snails than in the lone-snail treatment. Housing snails together enabled mutual grazing on shells and, indeed, both conspecifics and *Physa* were frequently seen on *Helisoma* shells. In addition to grazing, non-consumptive physical disturbance by snails may also have reduced algal biomass on shells. Wahl & Sönnichsen (1992) found the same relationship in the marine snail *Littorina littorea* (L.); that is, singly caged snails had more epibionts (invertebrates and algae) on their shells, whereas epibiont cover was much lower on

shells in cages with multiple snails. Further, epibiont density declined as snail density increased in both their field experiment and at their field sites. As in our study, the inverse relationship between epibiontic algae and snail density was attributed to the effects of snails on shells, including grazing and possibly non-consumptive loss. Conspecific grazing has also been described for caddisflies: *Agapetus fuscipes* Curtis (Cox & Wagner, 1989), *Gumaga nigricula* (McL.) (Bergey & Resh, 1994) and *Glossosoma intermedium* (Klapálek) (Cavanaugh, Haro & Jones, 2004), which graze on the portable cases constructed by the larvae.

Diatom distribution on shells may be affected by the snail itself. Diatoms were more abundant on the shell near the head of live snails than on the same location on empty shells. Although this might be as a result of defensive behaviour of the inhabitant in response to attempts at grazing by other snails, no such behaviour was observed. The aperture of the shell is also where nutrients are released in snails. Torsion, the twisting of the body during development in snails, results in a cavity into which the head can retract and that also contains the excretory and digestive outlets. Thus, a higher diatom density near the head is consistent with local nutrient enrichment. The front of the shell is the youngest part of the shell and the relatively high algal abundance there compared with older parts of the shell indicates that nutrient enrichment has a stronger influence on algal biomass than time for colonization. In larval Trichoptera, the site of nutrient enrichment and the older part of the case are at the same place. Thus, the sand-grain and silk cases of the caddisfly *G. nigricula* have a higher algal biomass at the rear than near the front of their tubular cases (Bergey & Resh, 1994) and our results from snail shells indicate that nutrient enrichment, rather than greater age, might have caused the higher algal biomass at the end of the caddisfly cases.

Many sessile marine macroalgae and invertebrates are apparently free of biofouling organisms. When tested, chemical or whole-body extracts of biofouler-free organisms often have anti-biofouling properties (e.g. macroalga, da Gama *et al.*, 2002; corals, Targett *et al.*, 1983; Maida, Sammarco & Coll, 2006; sponges, Nogata *et al.*, 2003; ascidians, McClintock *et al.*, 2004). Some of these biofouling extracts inhibit diatoms (Targett *et al.*, 1983; Maida *et al.*, 2006). Bacteria living on the surface of organisms may also contribute to antifouling by larger organisms (reviewed by Armstrong, Boyd & Burgess, 2000 and Dobretsov, Dahms & Qian, 2006). Mollusc shells are a biogenic, non-living surface and evidence for anti-fouling chemicals is sparse, being limited to activity against barnacles, marine bacteria and diatoms by extracts of the shell of the blue mussel *Mytilus edulis* L. (Bers *et al.*, 2006). Chemical anti-fouling has not been reported in gastropods. For instance, Wahl & Sönnichsen (1992) found no anti-fouling effects by extracts of the shell of the snail *L. littorea*. We found no evidence of chemical defences in *Helisoma* shells; although we tested biofouling of fresh (intact periostracum), weathered (no periostracum) and boiled (possibly denatured proteins in the periostracum) shells directly rather than testing with chemical extracts. Extract bioassays have not been performed with freshwater snails and such assays are needed to assess further any potential chemical defences by snail shells.

Although epibionts on mollusc shells can have detrimental effects on their host, it is unlikely that diatom epibionts on *Helisoma* shells were harmful. The short stature of the algal assemblage would have minimal physical effects and, rather than competing for food and resources, the diatom epibionts apparently provided a food resource for the host species (but not the individual host), as well as other snail species. Conversely, snails provided the algae with a suitable substratum and nutrients. Our experimental design could not be used to test whether snails actually benefited from grazing on shells because the large area of hard substrata in the containers, the walls of which also supported algal growth.

Snails can be very abundant in ponds, wetlands and lakes and, hence, biological interactions involving snail shells could have ecosystem effects. In our experiment, snail shells provided substrata for algal growth and, because there is no apparent behavioural defence of the shell, also provided added grazing substratum for other snails. Algal food can be a limiting resource for snails (Osenberg, 1989) and we suggest that the shells of living snails can increase algal food and overall production in ponds. This effect would be larger in ponds with high snail densities and limited hard substrata. Further studies are needed to determine whether algal production on snail shells is ecologically significant.

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