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THE EFFECT OF FEEDING BY MUD SNAILS, *ILYANASSA OBSOLETA* (Say), ON THE STRUCTURE AND METABOLISM OF A LABORATORY BENTHIC ALGAL COMMUNITY

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Abstract: Eastern mud snails, *Ilyanassa obsoleta* (Say), in densities of 0, 80, and 160 snails · m^{-2} were placed in flow-through laboratory microcosms containing 5 cm of frozen and sieved sediments. Other microcosms were raked once daily to a depth of 10 mm. All these containers were incubated for 5 wk and regularly sampled for plant pigments and light and dark transfer of oxygen and carbon dioxide. Feeding at the low density significantly increased chlorophyll standing stock. Respiration and gross photosynthesis increased by an even greater percentage compared to ungrazed controls. Standing stocks of algal pigments, respiration, and photosynthesis were depressed in microcosms which received the 160-snail or raking treatments.

The dominant benthic algae in the containers were pennate diatoms. Grazed containers contained a larger percentage of non-motile as compared to motile forms.

Sediments fertilized with ammonium at a rate equivalent to excretion of six snails, showed increased chlorophyll content equal to the 80-snail treatment. Daily raking inhibited this effect.

We conclude that low densities of *Ilyanassa obsoleta* stimulate algal growth by accelerating nitrogen cycling and selectively removing specific components of the diatom community. At high snail densities these effects are overwhelmed by overgrazing and sediment stirring.

INTRODUCTION

Grazing herbivores can have dramatic effects on plant community biomass and species composition in both terrestrial (J. L. Harper, 1969) and marine environments (Connell, 1975). Grazing herbivorous marine gastropods have little direct influence on established macroalgae, but can exert a significant grazing pressure on the microflora and influence algal succession in the rocky intertidal zone (Castenholz, 1961; Dayton, 1975; Lubchenco, 1978). Marine gastropods can selectively feed on certain diatom species and affect the composition of the benthic microflora. Nicotri (1977) found those "canopy" species that form long chains of moderate-sized cells protruding from the

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rock surface are selectively grazed in preference to those cells tightly attached to the rock. Snails grazing on soft substrata can also change the composition of the microflora. Fenchel & Kofoed (1976) found a shift in size distribution of diatom cells towards smaller cells in grazed sediments after 8 days.

While heavy grazing pressure can drastically reduce standing stocks of plant communities, some grazers may stimulate primary production. Low levels of grazing by crayfish (Flint & Goldman, 1975) stimulate production of periphyton. Benthic microepiflora are stimulated by grazing of amphipods (Hargrave, 1970), fish (Cooper, 1973), and hydrobiid snails (Fenchel & Kofoed, 1976).

Decomposition of litter as well as other benthic microbial processes show stimulation by grazing (Fenchel, 1972). This stimulation could be caused by physical stirring of the sediment community during the detritivore's feeding which may increase availability of nutrients to bacterial cells.

Pace *et al.* (1979) tested the ability of the common Eastern mud snail *Ilyanassa obsoleta* (= *Nassarius obsoletus* Say) to stimulate the benthic microbial community of a Georgia salt marsh at densities of 480 and 1580 $\cdot$ m^{-2}. They concluded that these densities of grazers led to reduced productivity. However, a daily removal of 5–10% of the standing chlorophyll (by their migration into lens paper used to collect diatoms) increased microflora productivity.

Ilyanassa obsoleta is one of the predominant deposit-feeders in intertidal and subtidal sandflats, mudflats, and salt marshes along much of the Atlantic coast of the United States and in isolated Pacific Coast bays. *Ilyanassa* subsists mainly on benthic algae although it is also known to scavenge larger dead animal remains (Scheltema, 1964; Brown, 1969). Labelling experiments have shown that *Ilyanassa* ingests and assimilates sediment bacteria and algae, but not *Spartina* detritus (Wetzel, 1977).

The benthic algal community in Great Sippewissett Marsh, Massachusetts is dominated by pennate diatoms, which exhibit two life forms. The motile, free-living forms of the epipelon migrate daily to the sediment water interface, while the epipsammon are mostly attached to sand particles (Round, 1971). The mobile Biraphidineae vary from relatively immobile, e.g. *Amphora* spp. (Round, 1979), to diurnally migrating, e.g. *Hantzschia virgata* (Palmer & Round, 1967).

The other two sections (Araphidineae and Monoraphidineae) of pennate diatoms are mostly non-migratory, though M.A. Harper (1969) has shown that they can move slowly from sand grain to sand grain. They are found in salt marsh either attached to sand grains or epiphytic on the green alga, *Enteromorpha*.

These non-migratory forms have generally been considered to be unimportant due to continual deposition of sediments by tides (Williams, 1962; Sullivan, 1975; Pace *et al.*, 1979) and because the lens paper method commonly used for diatom collection (Eaton & Moss, 1966) discriminates against non-migratory forms. Yet when methods are used which sample both epiphytic and epipsammic species, the latter are found in abundance in salt marshes (Lee *et al.*, 1975), shallow bays (Rao & Lewin, 1976), and tidal flats (Riznyk, 1973). These araphidaceous and monoraphidaceous diatoms could

have an important role at Great Sippewissett Marsh. The yearly accretion of sediment is 1.5 mm (Valiela & Teal, 1979), but the top centimeter of the surface sediments is frequently reworked by resident invertebrates, reducing the problem of burial.

METHODS

The sediment, collected from creek bottom and mud flat habitat in Great Sippewissett Salt Marsh was a mixture of sand and silt with an organic content of 2% carbon by dry weight. After collection it was passed through a 2-mm sieve, then frozen and thawed twice to remove macrofauna and meiofauna. Subsequent microscopic examination of the sediment failed to show these organisms.

We collected 20–25 mm long *Ilyanassa obsoleta*, which averaged 2.4 g, from Great Sippewissett Marsh. We added 0, 6, or 12 individuals to the microcosms, equivalent to 0, 80, and 160 snails $\cdot$ m^{-2}. This is within the range of densities of *Ilyanassa* found locally, 0 to 700 $\cdot$ m^{-2}. Higher densities inhibited production as found by Pace *et al.* (1979). The stirring regimen of the sediment was chosen to imitate that produced by the range of snail densities used (Connor, 1980).

The experiments were conducted in gas-tight, flow-through, Plexiglas microcosms (29.2 × 26.2 × 14.2 cm) described by Connor (1980). We added 5 cm depth of homogenized sediment and 5-μm mesh filtered sea water to each microcosm to give a final depth of 10 cm and placed them under an array of fluorescent "grow" lights. Water flowed in continuously to provide one turnover every 2 h. The chambers received an average illumination of 30 $\mu E \cdot m^{-2} \cdot s^{-1}$, approximately the saturation light intensity for several benthic diatoms reported by Admiraal (1977). The microcosms were allowed to incubate for 2 wk on a 14–10 h light–dark cycle before experiments began. During the course of the experiment, chlorophyll content averaged 17.1 $\mu g \cdot cm^{-2}$, within the usual range for Great Sippewissett Marsh (Estrada *et al.*, 1974).

After 7 days incubation, we sampled the microcosms three times before beginning four duplicate treatments. Snails were added to four containers, two containers were left untreated, and two containers were raked once daily to a depth of 5–10 mm with tines 10 mm apart (Table I). We sampled the microcosms four times during the next 15 days. To eliminate any possible effects of the containers, we switched snails between 0 and 6-snail treatments and also switched 12-snail and raking treatments. The microcosms were then sampled four times in the next 14 days.

At each sampling date, snails were removed and placed in separate containers in filtered sea water. The microcosms were drained and sealed for measurement of community metabolism by light and dark incubations for determination of oxygen and carbon dioxide concentrations. Duplicate gas samples were taken from each microcosm at the beginning and end of 12–20 h dark and light incubations. Gas concentrations were analyzed using the thermal conductivity detector of a Hewlett Packard gas chromatograph (Model 5730A). At the end of the incubations, we measured sediment temperature and pH and resumed treatments.

At each sampling triplicate cores 9 mm in diameter and 1 cm deep were taken from each microcosm and extracted with 5 ml of 90% methanol (Fenchel & Straarup, 1971). The samples were shaken and stored overnight in the dark at 4 °C, centrifuged and scanned for absorbance from 400 to 800 nm. Peak height was determined at 760 nm (bacterial chlorophyll), 666 nm (chlorophyll), 615 nm (phycocyanin), and 440 nm (phaeopigments), and converted to pigment biomass per square centimeter (Connor, 1980).

TABLE 1

Experimental design for determining the effect of four treatments on sediment metabolism in laboratory microcosms.

	Day										
Tank	0	4	6	11	15	18	21	25	28	32	35
1					0-Snail				6-Snail		
2					6-Snail				0-Snail		
3	Pre-treatment				6-Snail				0-Snail		
4					0-Snail				6-Snail		
5	Incubation				Raked				12-Snail		
6					12-Snail				Raked		
7					12-Snail				Raked		
8					Raked				12-Snail		

We compared the deviations of individual treatments from general trends in two ways. The community metabolism and pigment data were analyzed by a mixed-model, three-way analysis of variance (ANOVA) (treatment × tank × day) on data normalized by subtracting the tank averages before treatments began to remove systematic variation due to initial tank differences.

For some of these sample days we took surface cores (0–1 cm) for determining the composition of the benthic diatom community. The cores were oxidized with sulfuric acid, potassium permanganate, and oxalic acid (Hasle & Fryxell, 1970). We then washed the cleaned frustules and mounted them in Hyrax. Diatom populations in each sample were identified to genus and enumerated from a random sample of between 500 and 1000 valves which were observed using oil-immersion, phase-contrast optics at a magnification of 1000×. The permanent slides have been deposited at Hellerman Diatom Herbarium, North Dartmouth, Massachusetts: HDSM 1551-1586.

We also measured the effect of nitrogen fertilization and stirring on algal growth in nine plastic containers (9.3 × 9.3 cm) filled with sieved, frozen, stirred sediments to a depth of 3 cm and 125 ml of 5-μm mesh filtered sea water. The containers were incubated for 1 wk under "grow" lights, then sampled daily for 5 days for algal pigments. At this point we began three treatments in triplicate using a randomized blocks design: control, fertilized and fertilized with daily raking. All containers received 10 ml of filtered sea water daily. Both fertilization treatments also received 35 μM of NH_4Cl, an

amount equivalent to the excretion rate of six snails (5.7 $\mu g\ N \cdot cm^{-2}$; Connor, 1980). Three of the six fertilized containers were also raked daily as in the other experiments. We sampled all containers four times in the next week for algal pigments.

Pigment concentrations were assayed as before and normalized by subtracting pre-treatment means for each container. The normalized data were subjected to a three-way ANOVA (treatment × tank × day).

RESULTS

COMMUNITY METABOLISM

There was a slight difference in the visual appearance of the microcosms. The untreated tanks were covered by a brownish film. When snails were present or

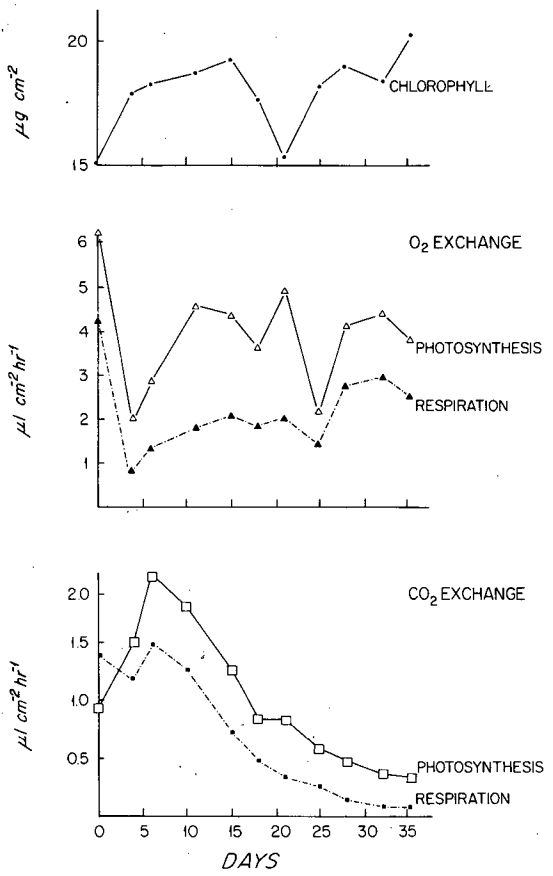

Fig. 1. Average chlorophyll standing stocks and rates of photosynthesis and respiration for all experimental microcosms during the experiment.

sediments were stirred, this film was absent. The redox discontinuity layer was at ≈6 mm in all containers.

Since we switched treatments to eliminate microcosm effects, temporal trends in the microcosms were considered during the experiment by pooling all containers (Fig. 1). Before treatments started (Days 0–6), measured parameters in the microcosms were much more variable than they were subsequently. Once treatments started, dark O_2 uptake and chlorophyll concentration gradually increased.

CO_2 exchange rates in both light and dark declined during the experiment corresponding to a rising pH in the tanks. When the average CO_2 light and dark exchange rates for the microcosms are plotted against average sediment pH, there is a significant correlation between the two (Fig. 2; $P < 0.05$), as expected from carbonate equilibrium calculations. Both sulfate reduction and denitrification occur in marsh sediments and probably caused the rise in pH and also changed the alkalinity thereby confounding bicarbonate calculations.

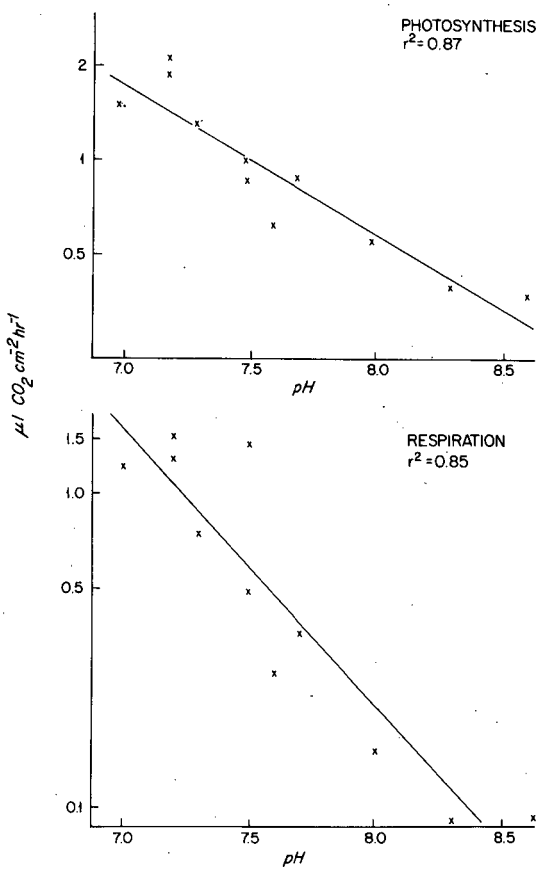

Fig. 2. The effect of pH on light and dark carbon dioxide transfer in flow-through experimental microcosms.

Since 0- and 6-snail treatments were switched in the middle of the experiment, we plotted these four microcosms separately (Figs. 3–5). At nearly every sampling period, microcosms containing six snails had higher gas transfer rates or chlorophyll standing stocks. In the figures this appears as a flip-flop in behavior of individual tanks. The response of photosynthetic and respiration rates to snail addition was rapid, peaking after 1 wk and then declining (Fig. 3). Chlorophyll concentrations showed no clear temporal pattern (Fig. 5).

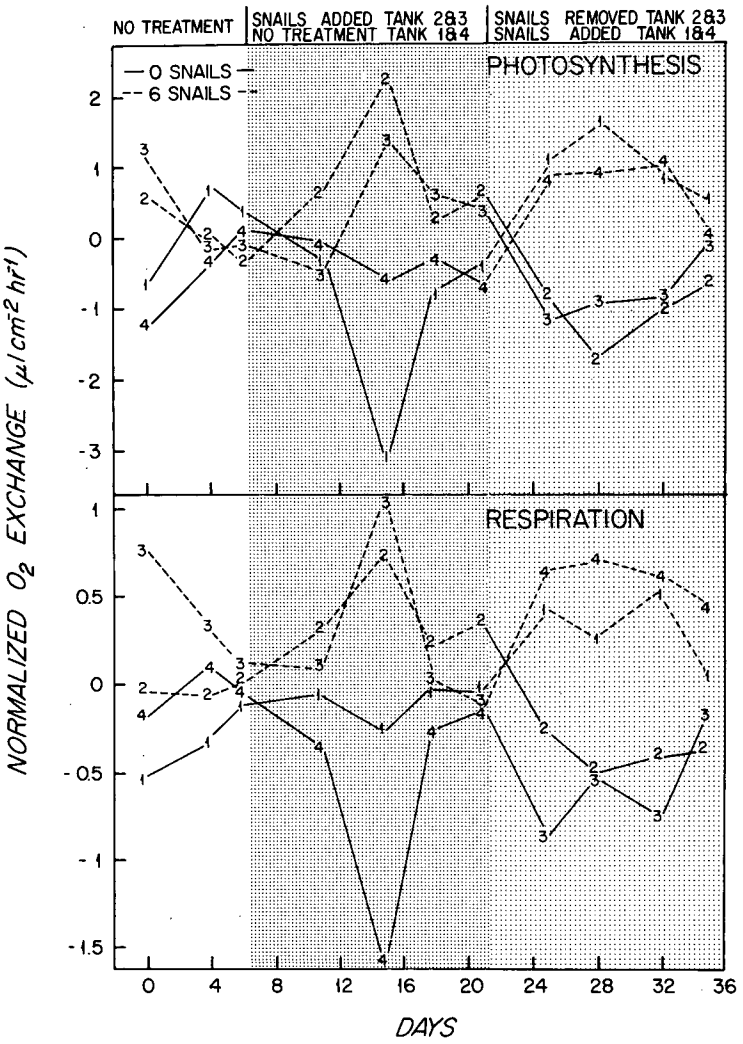

Fig. 3. The effect of snail grazing on respiration (dark oxygen uptake) and photosynthesis (light–dark oxygen production) in laboratory microcosms: the deviations from the daily and tank means are plotted; average tank means are respiration, 2.37 $\mu l \cdot cm^{-2} \cdot h^{-1}$ and photosynthesis, 4.55 $\mu l \cdot cm^{-2} \cdot h^{-1}$.

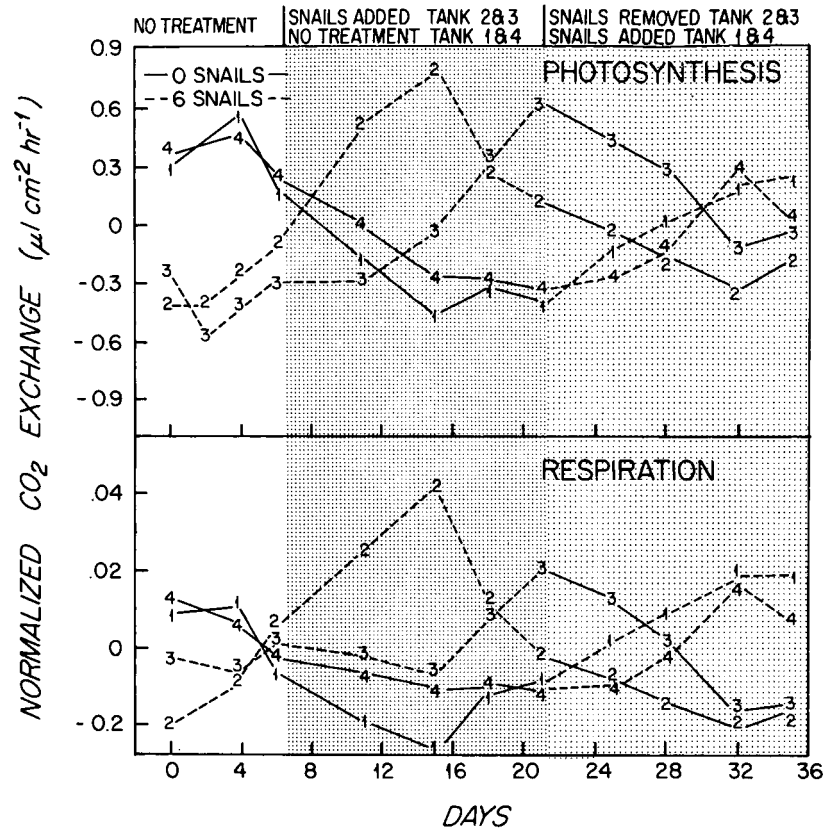

Fig. 4. The effect of snail grazing on respiration (dark carbon dioxide production) and photosynthesis (light–dark carbon dioxide uptake) in laboratory microcosms: the deviations from the daily and tank means are plotted; average tank means are respiration, 0.65 $\mu l \cdot cm^{-2} \cdot h^{-1}$ and photosynthesis, 1.01 $\mu l \cdot cm^{-2} \cdot h^{-1}$.

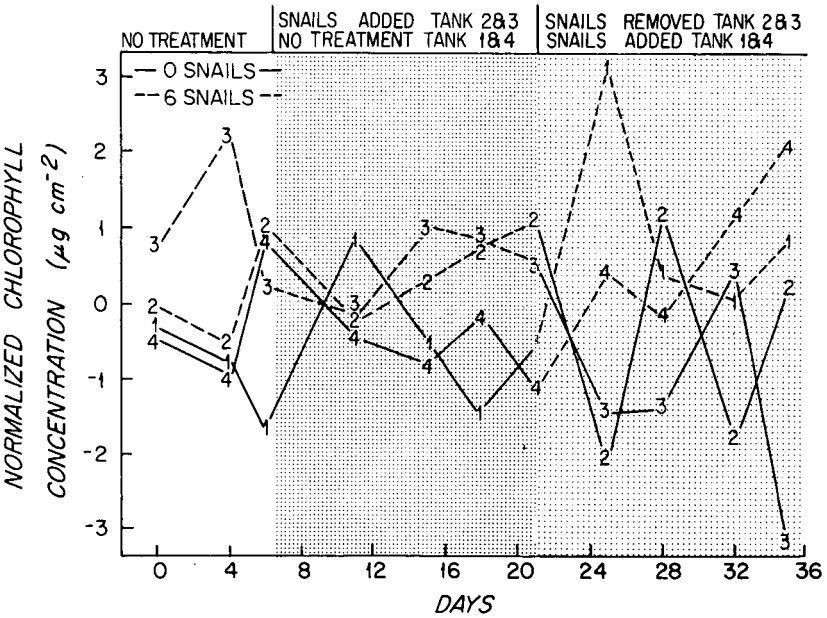

Fig. 5. The effect of snail grazing on sediment chlorophyll concentrations in laboratory microcosms: the deviations from the daily and tank means are plotted; average tank mean is 18.6 $\mu g \cdot cm^{-2}$.

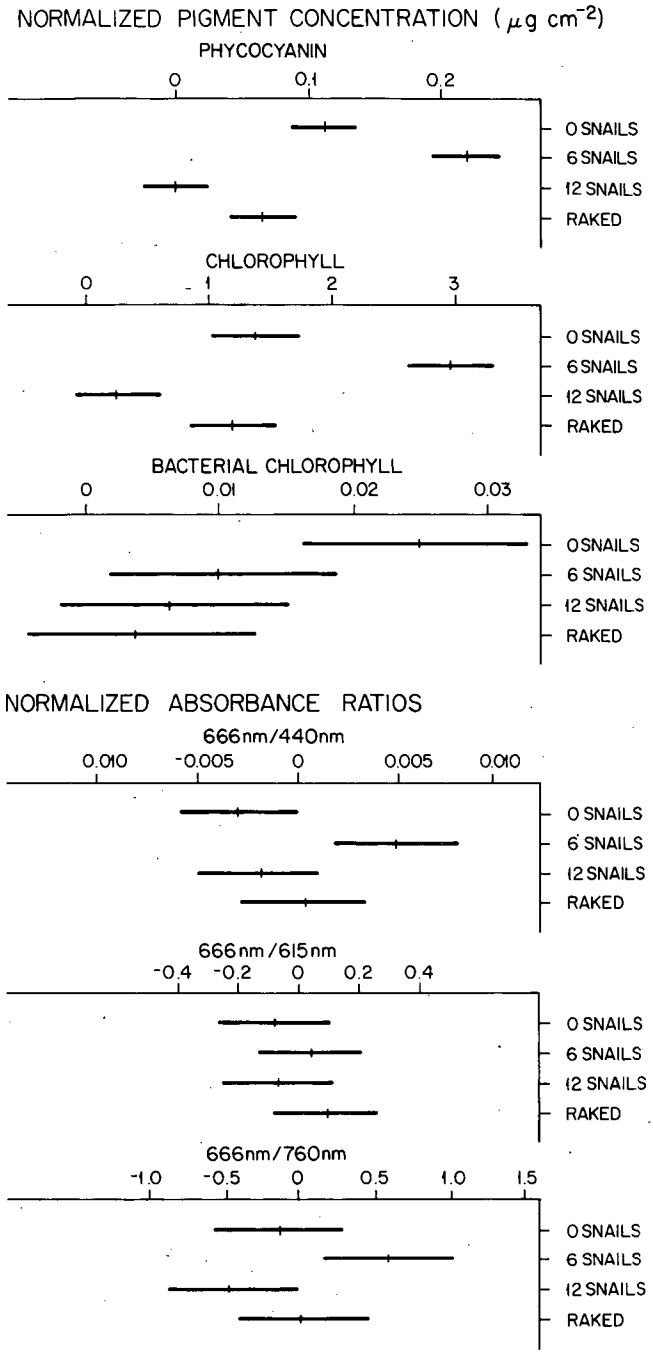

Fig. 6. The effect of four treatments on sediment pigment concentrations and ratios in laboratory microcosms: plotted are the pooled data for two tanks sampled in triplicate four times during a 15-day period and, after treatments were switched, four more times during a 14-day period; all values have been normalized by subtracting tank pre-treatment means; horizontal lines denote 2 SE computed from the interaction component of a three-way ANOVA (day × treatment × tank); average pre-treatment tank means are phycocyanin, 1.39 $\mu g \cdot cm^{-2}$; chlorophyll, 17.1 $\mu g \cdot cm^{-2}$; bacterial chlorophyll, 0.37 $\mu g \cdot cm^{-2}$; 666/440 = 0.183; 666/615 = 11.7 and 666/760 = 9.33

Feeding by six snails increased rates of respiration and photosynthesis compared with zero-snail controls. The 6-snail microcosms in the dark showed an average of 41% higher O_2 uptake, 38% more CO_2 release, and in the light 42% higher O_2 release and 35% more CO_2 uptake than 0-snail controls. But chlorophyll biomass was only 9% higher (Fig. 5) and phycocyanins only 7% higher (Fig. 6) in the tanks with 6 snails as compared to untreated tanks. All these differences were significant at $P < 0.05$.

Phycocyanin and chlorophyll concentrations were depressed below the untreated values in the raking treatment and even more so in the heavily grazed 12-snail treatment (Fig. 6). Both densities of snail grazing and the raking treatment reduced bacterial chlorophyll levels below those of untreated tanks. The ratio of absorbance at 666 nm to other absorbance peaks was always greater in the 6-snail treatment, and in the case of 666 nm/440 nm, significant at $P < 0.05$. None of the other pigment ratios were statistically different from one another.

As with standing stock measurements, doubling the snail densities reduced photosynthetic and respiration rates below those of untreated tanks as measured by O_2 exchange (Fig. 7). The raking treatment had the same effect as 12 snails. Dark O_2

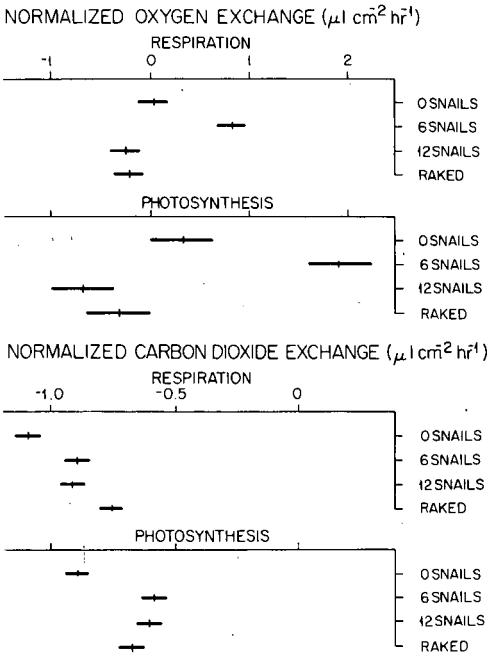

Fig. 7. The effect of four treatments on respiration and photosynthesis in laboratory microcosms: plotted are the pooled data for two tanks sampled four times during a 15-day period and, after treatments were switched, four more times during a 14-day period; all values have been normalized by subtracting tank pre-treatment means; horizontal lines denote 2 SE computed from the interaction component of a three-way ANOVA (day × treatment × tank); average pre-treatment tank means are CO_2 respiration, 1.35 $\mu l \cdot cm^{-2} \cdot h^{-1}$; photosynthesis, 1.50 $\mu l \cdot cm^{-2} \cdot h^{-1}$, O_2 respiration, 2.11 $\mu l \cdot cm^{-2} \cdot h^{-1}$ and photosynthesis, 3.72 $\mu l \cdot cm^{-2} \cdot h^{-1}$.

uptake was slightly depressed, and gross photosynthesis was significantly depressed ($P < 0.05$) compared to untreated tanks.

The CO_2 data are less clear-cut because of the pH effect. Generally untreated tanks had a slightly higher pH than all treated tanks, particularly the raked containers, where the pH was often 0.1–0.2 units lower than any other tank. Since dissolved CO_2/HCO_3 is higher at low pH, light and dark CO_2 exchanges were higher in all treated microcosms, but these rates are only a small percentage of the rates measured by oxygen exchange.

COMMUNITY STRUCTURE

Pennate diatoms were by far the dominant benthic algal group, although blue-green algae were present. Microscopic observations showed that ≈ 65–80% of the 5×10^9 diatoms $\cdot$ cm^{-2} were viable.

The clearest pattern in community composition emerged when diatoms were grouped by class, the highly migratory Naviculineae (Biraphidineae) compared to the mostly attached classes of Achnanthineae (Monoraphidineae) and Fragilarineae (Araphidineae). Both grazing treatments resulted in a much higher proportion of non-migratory cells, especially very small (2–10 μm) *Fragilaria pinnata*, than in untreated containers. The raking treatment had an intermediate proportion of migratory biraphidaceous species (Fig. 8).

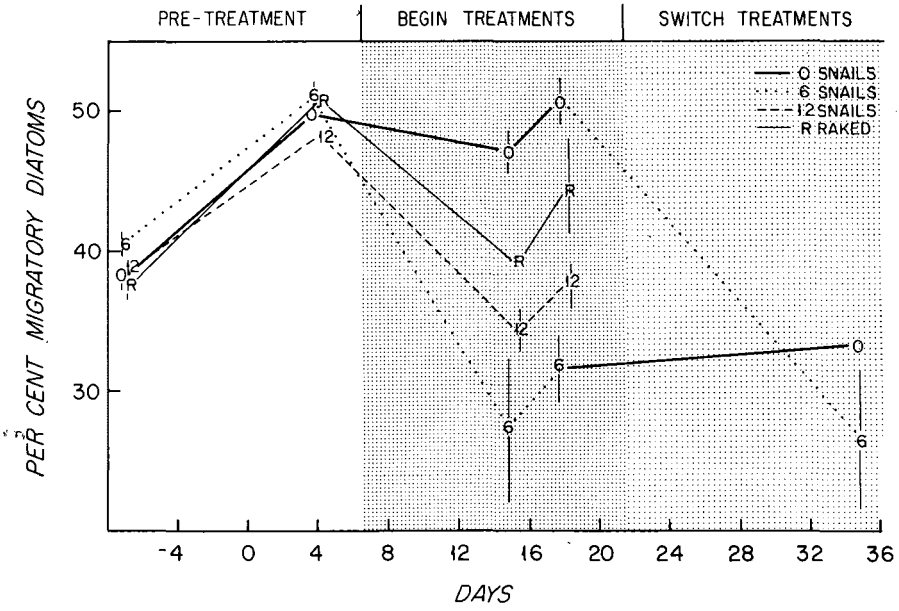

Fig. 8 The effect of four treatments on the dominance of the benthic diatom community in laboratory microcosms by migratory diatoms: vertical bars show the range from duplicate treatments.

FERTILIZATION

The fertilized, unstirred containers had significantly higher ($P < 0.05$) standing stocks than controls of all photosynthetic pigments measured (phaeopigments, phycocyanin, chlorophyll, and bacterial chlorophyll; Fig. 9). Those fertilized containers

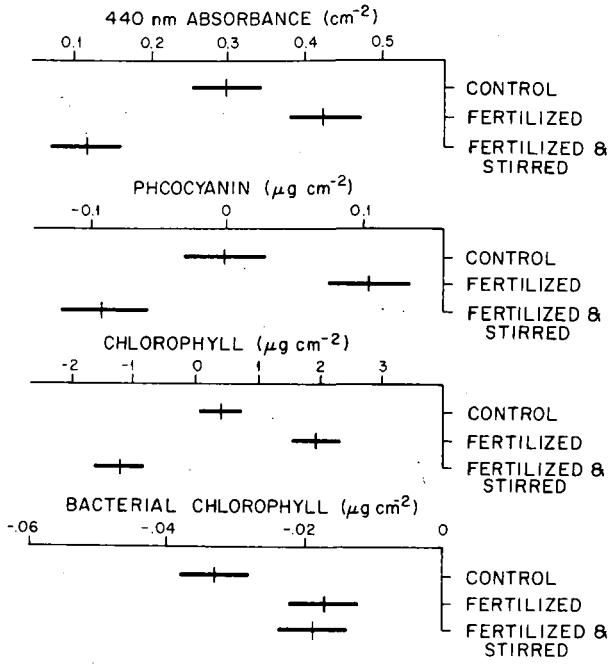

Fig. 9. The effect of three treatments on sediment pigment concentrations in laboratory microcosms: plotted are the normalized means of three tanks sampled in duplicate four times during a 7-day period; horizontal lines denote 2 SE computed from the interaction component of a three-way ANOVA (treatment × tank × day); average pretreatment means for all tanks are 440 nm absorbance, 3.4 · cm^{-2}; phycocyanin, 1.7 μg · cm^{-2}; chlorophyll, 22.7 μg · cm^{-2} and bacterial chlorophyll, 0.39 μg · cm^{-2}.

which were also raked contained significantly lower standing stocks of all pigments except bacterial chlorophyll, for which their levels equalled the unstirred, fertilized containers.

Discussion

These results show a stimulation of sediment algal productivity and standing stock by low levels of snail feeding and an inhibition at higher snail densities. There are several possible mechanisms which can account for these results, including feeding-induced changes in the benthic diatom community, fertilization effects through nutrient regeneration, and stirring effects.

Flint & Goldman (1975) and Cooper (1973) hypothesized a successional mechanism for stimulation of periphyton or edaphic algae by low grazing intensities. They suggest that older, senescent plants are removed from the substratum so that the community remains in a more highly productive state. At higher grazing intensities, primary producers can no longer compensate for the increased removal of cells. Such an argument could be made for this system. Besides increased productivity in lightly grazed containers, there is a significantly higher ratio of 666/440 nm absorbance in grazed containers compared to controls (Fig. 6). Margalef (1967) characterized this ratio as an indicator of phytoplankton succession, a lower value (more pheopigments) indicating a later successional stage or more senescing cells.

Other indications of a change in algal community composition due to grazing were found. The ratio of 666 nm absorbance to the two other photosynthetic pigments was slightly increased by the 6-snail treatment (Fig. 6). Within the pennate diatoms, the dominant benthic algal group, grazing caused a shift from larger, migratory, epipelic forms to smaller, non-migratory forms. This change could have two components: selective removal of large migratory cells and increased growth of small, uneaten cells. Snails do selectively feed on migratory cells (Connor, 1980), but the decreased percentage of Naviculineae in the 6-snail as compared to the 12-snail treatments suggests that both processes are occurring (Fig. 8). Otherwise, there should be fewer migratory cells in the 12-snail microcosms.

This community shift to smaller, non-migratory cells could increase production in two ways. Small cells generally grow faster than larger ones (Round, 1971), and the investment of a large portion of the carbon budget of migratory cells in mucus strands needed for movement could decrease the growth efficiency of these cells compared to non-migratory cells. Besides leaving less carbon for photosynthetic machinery, a thick, polysaccharide mat will inhibit photosynthesis below it by absorbing light, like a forest canopy. Removal of the canopy by grazing would allow increased growth of non-migratory species.

Snails affect nutrient regeneration as can be seen by comparing the nitrogen budget of 0- and 6-snail treatments in the fertilization experiment (Table II). Given sufficient light, edaphic diatom communities show seasonal nitrogen limitation (Sullivan & Daiber, 1975; Van Raalte *et al.*, 1976). O_2 uptake rates were 3.75 $\mu l \cdot cm^{-2} \cdot h^{-1}$ for the 0-snail treatment and 5.35 $\mu l \cdot cm^{-2} \cdot h^{-1}$ for the 6-snail treatment. Assuming a photosynthetic ratio of 1 and a C/N molar ratio of 6.63 (Redfield *et al.*, 1963), the difference in daily production is 3.7 $\mu g\ N \cdot cm^{-2}$. Approximately 5.7 $\mu g\ N \cdot cm^{-2}$ is available daily from snail excretion (Connor, 1980). Fertilizing containers at that rate under the same light and temperature regimes increased chlorophyll concentration by an average of 1.5 $\mu g \cdot cm^{-2}$ in 7 days, equivalent to the increase found in the 6-snail microcosms. The amount of nitrogen excreted by low densities of grazing snails is sufficient to account for the increased production found.

The increase in chlorophyll concentration in grazed microcosms may either be due to an increase in chlorophyll/carbon, characteristic of improved growth (Eppley &

Renger, 1974), or be a function of mobilization of non-algal nitrogen pools by snails. Alternatively, the algal community changes discussed above could influence chlorophyll standing stock or ratios. Fertilization, alone, is not sufficient to explain the changes in algal community composition (Connor, 1980), and our experiments were not able to distinguish the extent to which these two mechanisms are responsible for the effects on algal productivity increases.

TABLE II

A, comparison of the nitrogen budgets for the stimulation of algal photosynthesis by *Ilyanassa* grazing with the amount of nitrogen available from snail excretion: snail excretion from Connor (1980). B, comparison of the differences in chlorophyll standing stock due to snail grazing and fertilization with ammonium chloride.

A	Daily production ($\mu g\ N \cdot cm^{-2}$)	Daily excretion ($\mu g\ N \cdot cm^{-2}$)
6 snails	12.2	5.7
0 snails	8.5	0
Difference	3.7	5.7

B	Average chlorophyll standing stock ($\mu g \cdot cm^{-2}$)
6 snails	19.3
0 snails	17.8
Difference*	1.5
Difference between fertilized ($5.7\ \mu g\ N \cdot cm^{-2} \cdot day^{-1}$) and unfertilized microcosms**	1.5

* Twenty-nine day average.
** Seven-day average.

The declines in algal productivity may also have more than one mechanism. At some grazing intensity the stimulation due to nutrient regeneration and changes in algal community composition must be inhibited by simple overgrazing, but the inhibition at 12-snail densities may also be due to stirring which mixes live cells below the surface where they receive less light. Raking sediments daily inhibited photosynthesis, respiration, and standing stock of chlorophyll and also inhibited chlorophyll stimulation due to fertilization. In tundra ponds, sediment disturbance by grazing benthic invertebrates may be removing more cells than by grazing (Stanley, 1976).

Dayton (1975) noted that effects of molluscan grazers in the rocky intertidal are similar to those of mammalian grazers in terrestrial systems. The similarity becomes even more striking on soft bottoms where the secondary effects of grazers are more apparent. Trampling and dung deposition are important secondary effects of grazing herbivores (J. L. Harper, 1969). They create heterogeneity in the physical environment

and increase vegetational diversity. As we have seen, both have correlates in the feeding of snails which stir and fertilize sediments as part of their feeding behavior.

One of the most dramatic examples of the secondary effects of herbivory is the change of the East African landscape from forest to grassland by herds of elephants (Laws, 1970). Like elephants, *Ilyanassa* are orders of magnitude larger than the plants they eat. Their stirring effects (trampling) as they move through the environment are substantial. But because of substratum fluidity and the short distances required to mix plant cells below the photic zone, *I. obsoleta*'s secondary grazing processes are disproportionately important in benthic soft bottom communities. Benthic diatoms are presented with a variety of selective pressures by snail grazing: snails selectively feed on unattached, migratory cells (Connor, 1980); their movement can bury surface cells or bring deeper cells to the surface; their mucus trail probably affects the resuspension of sediments below it; surviving cells are provided a rich source of nutrients by snail excretion which can stimulate their growth.

The variety of components that make up grazing by *Ilyanassa* probably ensures that the overall effects on community structure and metabolism reported here are a complicated function of snail density. At low densities acceleration of nutrient cycling by snails' grazing and excretion stimulate photosynthesis. At high densities nutrient cycling is overwhelmed by stirring inhibition and simple overgrazing.

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