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CONSUMPTION OF *ULVA LACTUCA* (CHLOROPHYTA) BY THE OMNIVOROUS MUD SNAIL *ILYANASSA OBSOLETA* (SAY)[1]

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Marine invertebrate grazing on temperate macroalgae may exert a significant "top-down" control on macroalgal biomass. We conducted two laboratory experiments to test (1) if consumption by the omnivorous mud snail *Ilyanassa obsoleta* (Say) on the macroalga *Ulva lactuca* Linnaeus was a function of food quality (nitrogen content) and (2) if grazing on benthic macroalgae occurred at significant rates in the presence of alternative food sources in the sediment (detritus, larvae, benthic microalgae). Grazing rates were higher for N-enriched macroalgae; however, all snails lost weight when grazing on macroalgae alone, indicating that *U. lactuca* was a poor food source. The presence of sediment from two sites, a sandy lagoon and an adjacent organic-rich muddy tidal creek, did not affect consumption of macroalgae in microcosm experiments, and the grazing snails were capable of significantly reducing macroalgal biomass associated with both sediment types. Grazing rates by this omnivore were as high as 10.83 mg wet weight·individuals^{-1}·d^{-1} and were similar to those recorded for herbivorous species. *In situ* loss rates calculated from average grazing rates per individual and snail abundances (up to 3.5 g dry weight·m^{-2}·d^{-1}) also were comparable with those calculated for herbivorous species. This level of grazing could remove up to 88% of new macroalgal growth at the lagoon site where the N supply was relatively low but had a much smaller effect (18% of new growth) at the high-nutrient creek site. Snails facilitated macroalgal growth at both sites by increasing tissue N content by 40%–80%. Consumption and digestion of macroalgae aided in the recycling of nutrients temporarily bound in the algae and resulted in enrichment of surficial sediments. Increased N sequestration in the sediments also was associated with an interruption of snail burrowing behavior due to persistent anoxia in sediments rich in decaying algal material. Our data suggest that in shallow lagoons where mud snails and benthic macroalgae coexist, grazing may influence N retention in macroalgal biomass.

Key index words: **grazers; herbivores; *Ilyanassa*; nitrogen; nutrients; *Ulva***

Abbreviations: **DO, dissolved oxygen**

The mud snail *Ilyanassa obsoleta* is an abundant neogastropod in coastal lagoons of eastern North America and often coexists with the opportunistic green macroalga *Ulva lactuca* (Crisp 1969, Curtis and Hurd 1979). In sheltered areas of intertidal and subtidal waters down to a depth of 10 m, *Ulva* sp. can cover up to 85%–100% of the substrate (Sfriso et al. 1992, Harlin and Rines 1993). *Ilyanassa obsoleta* is often found clinging to the drifting and attached macroalgae (Scheltema 1964, Edwards and Welsh 1982) and is relatively tolerant of the wide range of salinities, temperatures, and oxygen conditions usually associated with algal mats (Jenner 1956, Scheltema 1964, Curtis and Hurd 1981, Norkko and Bonsdorff 1996). These snails typically form and reform aggregations that range from several hundred to 23,000 snails·m^{-2} (Scheltema 1961, Brown 1969, Curtis and Hurd 1981, Collins 1983). Despite its dominance in shallow coastal ecosystems and its association with benthic macroalgae, we know little about mud snail consumption of macroalgae and the extent to which its grazing influences *in situ* macroalgal biomass.

Mud snails are omnivores, primarily consuming surficial sediment containing detritus, larvae, diatoms, and other benthic microalgae (Jenner 1956, Scheltema 1964, Wetzel 1977, Haines and Montague 1979, Conner et al. 1982). One reason that *I. obsoleta* is numerically dominant in many areas may be its ability to limit recruitment of other invertebrates (gastropods, polychaetes, amphipods, isopods) by consuming settling larvae in the sediment (DeWitt and Levinton 1985, Hunt et al. 1987). Anatomically and physiologically, *I. obsoleta* has all the functional adaptations associated with a carnivorous lifestyle (Brown 1969) and has a rapid, though short-lived, attraction to carrion (Crisp 1969, Curtis and Hurd 1979). At the same time, it is the only neogastropod known also to possess a mucoprotein crystalline style within its stomach—a structure associated with an herbivorous diet (Brown 1969, Curtis 1980). Mud snails lose and regain their crystalline styles on a daily basis (Curtis 1980); when the style is absent snails can digest carrion, and when it is present snails can only digest particles of vegetation (Brown 1969). Macroalgae have been found in the gut of *I. obsoleta* (Curtis and Hurd 1981), although it is not known how large a component of their diet it comprises. If snails consume significant quantities of macroalgae that also occur at high densities, they may play a role in reducing macroalgal biomass in shallow estuaries and lagoons. On the other hand, snails may enhance macroalgal growth by increasing the availability of nitrogen (N), the limiting nutrient for most

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temperate macroalgae. Excretion of nitrogenous wastes by feeding invertebrates provides pulses of nitrogen that fertilize growing algae (Williams and Carpenter 1988, Valiela et al. 1997, Hauxwell et al. 1998). In addition, the burrowing behavior of mud snails (Norkko and Bonsdorff 1996) may release N from the sediments and make it available for algal uptake (Fong et al. 1997).

This study examines in a set of laboratory experiments whether the mud snail is a significant consumer of *U. lactuca*. Our motivation for this study was our observation that extensive blooms of *U. lactuca* occurred seasonally in the tidal creeks of a shallow barrier island lagoon, whereas algal biomass was consistently low in the lagoon immediately adjacent to the mouth of the creeks. Macroalgal N content was lower in the lagoon than in the creeks, and *I. obsoleta* biomass was higher on the sandy sediments of the lagoon than on the muddy creek bottom (Giannotti 1999). We first tested if grazing of *U. lactuca* occurred in the absence of other food sources and if this was dependent on the food quality (N content) of the algae. We hypothesized that as with other algal herbivores (Mattson 1980, Hauxwell et al. 1998), *I. obsoleta* grazing rates would increase with higher algal N content. We then tested how this grazing impact would be affected by the presence of alternative food sources under more realistic conditions, by incubating the snails and algae in intact sediment cores with an overlying water column. We hypothesized that algal biomass in the lagoon microcosms would be significantly reduced by snail grazing because the lagoon water and sediments were N deficient and macroalgal growth rates were too slow to compensate for consumption by snails. Conversely, we hypothesized that algal biomass in the tidal creek microcosms would be less affected by grazing because alternative food sources were available in the highly organic sediments and growth rates of the N-enriched algae were rapid.

MATERIALS AND METHODS

Study site and experimental period. Samples for this study were collected from two locations in Hog Island Bay, a shallow lagoon on the eastern shore of Virginia that is part of the Virginia Coast Reserve Long Term Ecological Research Site: 1) a tidal creek ("creek") on the southern end of Hog Island and 2) in the open waters of Hog Island Bay immediately adjacent to the creek ("lagoon"). The tidal creek drains a *Spartina alterniflora* salt marsh of approximately 22 years of age (Walsh 1998). Two laboratory experiments were conducted on samples collected in August and September 1998.

Herbivory versus macroalgal N content. This experiment was designed to test if grazing of *I. obsoleta* on *U. lactuca* was a function of macroalgal N content. Macroalgae were collected from the lagoon in the vicinity of Hog Island and were transported back to the laboratory in seawater from the site. The algae were acclimated to experimental conditions in a growth chamber (PGR-15, Conviron, Winnipeg, Canada) for 10 days in low-nutrient artificial seawater at the *in situ* temperature (20–22° C) and salinity (35–37 ppt) on a 12:12 light:dark cycle to allow for nutrient depletion of macroalgal tissue before fertilization began (McGlathery et al. 1997). Light was provided by fluorescent and incandescent lamps at a level (450 μmol photons·m^{-2}·s^{-1}) known to saturate *Ulva* photosynthesis (Henley and Ramus 1989). The N content (% dry weight [dw]) of the algae collected in the field was 1.09 ± 0.11. After acclimation, half the algae were fertilized for 7 days with NH_4Cl and half were not fertilized and served as controls. For the enriched algae, N was added daily from a stock solution in sufficient quantity to saturate macroalgal growth demand at the desired 4% N content. The addition was based on macroalgal growth rates determined in a previous laboratory experiment (Giannotti 1999). To determine grazing rates on the "high-N" and "low-N" algae, the algae were subdivided into 1.0-g wet weight (ww) segments (free of visible epiphytes) and placed in Plexiglass cylinders (length, 10 cm; diameter, 5 cm; volume, 196 mL) closed at the ends with 0.5-mm mesh Nytex netting. For each treatment, four replicate cylinders had algae alone to account for growth changes during the incubation period and four contained algae plus one *I. obsoleta* of similar size (initially starved for 24 h and allowed to acclimate to the aquaria for 24 h). The cylinders were immersed in artificial seawater in separate tanks, and fertilization of the high-N algae continued during the 7-day experiment to maintain the treatment differences in macroalgal N content. Grazing rate was calculated as algal mass (ww) loss in the snail + algae treatments corrected for the average algal growth rate for each treatment during that same time period. At the end of the experiment, the algae were freeze dried and ground for determination of tissue N content on a Carlo-Erba Elemental Analyzer (NA 2500, Rodano, Italy).

Snail–macroalgal interactions. Once we established that *I. obsoleta* grazed on *U. lactuca* in the absence of alternative food sources, our goal in the next experiment was to determine grazing rates in more realistic conditions when sediment food sources also were present. To do this, we used intact sediment cores with an overlying water column from the two sites that differed in potential food sources: highly organic (~4% of dw) muddy sediments from the tidal creek containing both detritus and microalgae and organic-poor (<0.5% of dw) sandy sediments from the lagoon primarily containing microalgae.

The microcosm experiment was conducted in the growth chamber under the same conditions as for the previous experiment. Seawater and sediment cores (diameter, 9.5 cm; sediment height, 14 cm) were collected from the two sites on a falling tide. Mud snails and macroalgae from each site also were collected, stored in separate containers, and transported back to the laboratory with the cores. Snails were collected haphazardly by blindly tossing a small plot (1/16 m^2) and collecting the snails within each toss. The water depth in the microcosms was maintained at approximately 10 cm above the sediment surface. Several additions of deionized water were needed to maintain salinity at 35–40 ppt, which is well within the tolerance range of *I. obsoleta* (Curtis and Hurd 1981). To keep dissolved oxygen (DO) levels in our cores consistent with those measured in the tidal creeks, we did not aerate the cores or change the overlying water. This experimental design also allowed diurnal variations in DO driven by sediment and algal metabolism to occur as they did in the field (Giannotti 1999).

The treatments for the experiment were as follows: sediment + algae, sediment + snails, and sediment + algae + snails. Each treatment was run in triplicate for each site. For the + algae treatments, approximately 1.0 g ww of *U. lactuca* from a single sheet found at each of the two sites was placed into each microcosm after determining initial weights (patted dry and left to air dry for 10 min). This is equivalent to 48 g dw·m^{-2}, which is within the biomass range measured in the field (Giannotti 1999). A portion of the initial algal sample from each site was freeze dried and ground for later analysis of tissue N content. The number of snails ($n = 4$) used in the microcosms was representative of the mean density of all lagoon and creek snail populations over the summer months of 1998 (mean, 235 individuals·m^{-2}) scaled down to the area of substrate within the microcosm. An initial laboratory experiment showed no relationship between snail size and the amount of consumption (Giannotti 1999), so snail size (age) was not a factor in selecting snails to be used in the experiment. Initial wet weights of the snails also were recorded after patting the snails dry and leaving them for 20 min,

during which time they sealed their opercula and expelled any water contained inside their shells. This served as a means for standardizing the procedure each time.

Changes in biomass of the algae and the snails were measured on days 7, 12, and 24 as changes in wet weight. Specific growth rates were calculated as the increase in algal wet weight assuming exponential growth:

$$\mu = (\ln B_t - \ln B_o) \cdot t^{-1} \quad (1)$$

where B_o and B_t are the algal biomass before and after t days of growth.

Diurnal changes in salinity, water temperature, and DO were recorded at 30-min intervals during the light:dark cycle six times throughout the 24-day experiment (three times going from light to dark and three times from dark to light). Because the experiment was designed to measure the grazing impact of *I. obsoleta* on *U. lactuca* and not to quantify the impact of algae and snails on nutrient supply, we did not measure water column nutrient concentrations.

At the end of the experiment (day 24), all algae were collected, briefly rinsed in deionized water, patted dry, and freeze dried for 48 h for tissue N analysis. Dried tissue was ground using a mortar and pestle, and N content was determined as described previously. Sediments from each core were sectioned into three layers (0–2, 2–5, and 5–10 cm), finely ground, freeze dried, and analyzed for N content on the elemental analyzer. Triplicate subsamples were run for each sediment layer.

Treatment differences in mean changes in algal biomass, snail biomass, and %N were analyzed with a two-way analysis of variance. Bonferroni adjustments were applied to weekly changes in biomass to account for making multiple measurements on the same cores over time. A standard t-test was used in analyzing tissue %N between treatments in the fertilization experiment, changes in snail biomass, and algal growth rate comparisons between lagoon and creek cores. Differences were accepted as significant at $P < 0.05$.

RESULTS

Mud snails consumed *U. lactuca* in the absence of alternative food sources during the 7-day incubation period. The difference in %N of macroalgal tissue between our treatments was smaller than intended (0.96% N vs. 1.3% N; $t = 3.46$, $P = 0.014$), probably due to higher than expected growth rates in the N-enriched algae during the experiment. It is likely that the N content of the macroalgae in the high-N treatment fluctuated during the day in response to the pulsed nutrient addition and rapid growth rates. Nonetheless, grazing on *U. lactuca* by the mud snails was significantly higher on the N-enriched algae (consumption of 0.085 ± 0.03 g ww vs. net growth 0.018 ± 0.019 g ww for N-poor algae; $t = 10.86$, $P = 0.017$). Our results therefore represent conservative estimates of the effect of algal N content on herbivory, and we would expect a greater difference in grazing intensity with the higher N content that was observed in the *U. lactuca* in the field (up to 4% N) (Giannotti 1999).

All snails lost weight during the experiment (snails consuming low N algae = 0.03 ± 0.014 g ww; snails consuming high N = 0.03 ± 0.009 g ww). However, the change in snail biomass was equal in both the high- and low-N treatments, suggesting that at these tissue N levels the macroalgae in both treatments were a poor food source for the snails.

Grazing mud snails in the microcosm experiment also reduced *U. lactuca* biomass in the presence of alternative food sources in the sediment (Fig. 1a). Grazing rates varied from 0.74 to 10.83 mg ww·individual^{-1}·d^{-1} for the snails in the lagoon microcosms and 0 to 9.32 mg ww·individual^{-1}·d^{-1} for snails in the creek microcosms. The time course showed that the main grazing impact occurred early in the experiment (Fig. 1b). Significant grazing losses were observed only during the first week in the lagoon microcosms and throughout the experiment in the creek microcosms. Calculated over the 24-day experiment, consumption of *U. lactuca* by snails in muddy tidal creek microcosms was more than double that in the sandy lagoon microcosms (4.42 vs. 1.65 mg ww·individual^{-1}·d^{-1}; $F_{2,10} = 126.28$, $P < 0.001$), suggesting that alternative food sources by themselves did not reduce grazing rates. At the end of the experiment, total biomass loss due to grazing at the two sites was significantly related to algal tissue N content (data not shown; $R^2 = 0.863$, $P < 0.02$).

In the absence of snails, specific growth rates of *U. lactuca* were significantly higher in the creek cores over the course of the experiment than in the lagoon cores (Fig. 1a; $t = 3.45$, $P = 0.026$). However, growth rates were highest during the first week and were similar for both sites (Fig. 1b; 0.061 ± 0.017 d^{-1} and 0.045 ± 0.009 d^{-1} for the lagoon and creek cores, respectively).

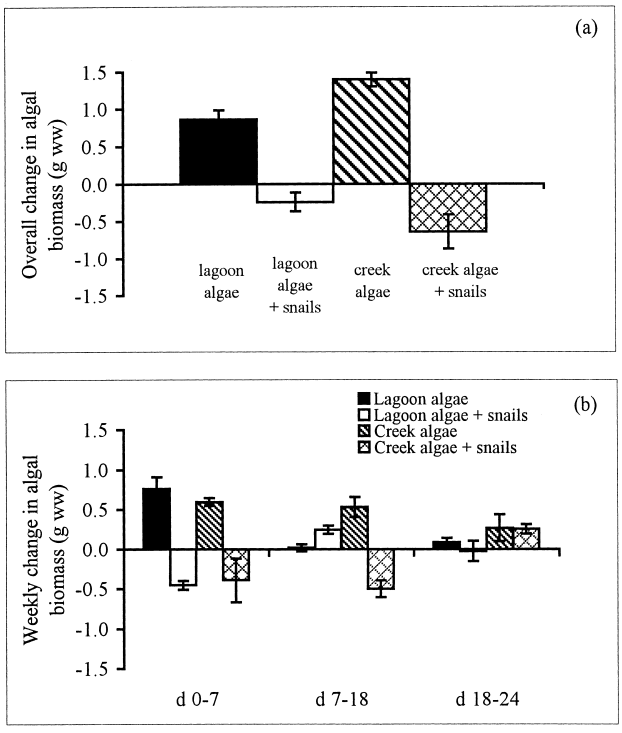

FIG. 1. (a) Changes in *Ulva lactuca* biomass (g ww) in cores from the lagoon and the creek at the end of the 24-day core experiment. (b) Weekly changes in *U. lactuca* biomass (g ww) over time in the core experiment. Error bars represent the standard error of the mean ($n = 3$).

The presence of snails resulted in a 40%–80% enrichment of the macroalgal N content (Table 1); the greatest effect was in the sandy lagoon cores where the N supply from the sediments was extremely low.

In contrast to the grazing experiment on algae alone, snails did not lose weight uniformly in the 24-day microcosm experiment in the presence of alternative food sources. It was only in the presence of algae in the creek cores that there was significant weight loss (Fig. 2a; $F_{2,10} = 37.93$, $P < 0.001$), and this occurred during the first week of the experiment (Fig. 2b). Snail biomass loss was approximately 2.5 times greater in the creek cores than in the lagoon cores.

Snails in the tidal creek microcosms with *U. lactuca* were exposed to prolonged periods of anoxia (Fig. 3a). Even though there was no water exchange in the microcosms, these periods of anoxia were of similar duration and magnitude as those that occurred in the field (Giannotti 1999). Diurnal measurements of DO showed that creek microcosms containing algae and snails remained anoxic, whereas lagoon microcosms showed an increase in DO during the day due to macroalgal photosynthesis. In the lagoon microcosms, DO production was similar regardless of whether algae were present alone or with snails (Fig. 3, a and b). However, in the creek cores, benthic respiration coupled with macroalgal respiration at night clearly exceeded macroalgal production of oxygen during the day and resulted in DO levels that were consistently below those cores containing *U. lactuca* only (Fig. 3b) or snails with no algae (Fig. 3c). This prolonged anoxia resulted in 4 snail deaths (out of 12) within the first 48 h of experimentation and illustrates the severity of the physicochemical conditions associated with the macroalgal mat. We did not replace the snails because this loss represented a true response to conditions of the experiment; however, snails that expired during the experiment were omitted from data presentations and statistical analyses.

The N content of the surface sediments (0–2 cm) in the microcosms from the tidal creek was significantly different between treatments (Fig. 4; $F_{2,8} = 4.372$, $P = 0.006$). There were no differences in the deeper sediment layers (2–10 cm) (Fig. 4; $F_{2,16} = 0.654$, $P = 0.53$). However, the higher N content in the surface sediments of the algae + snail treatment suggests that consumption and digestion of macroalgae facilitates the recycling of N in these creeks. Nitrogen levels in the lagoon cores were undetectable for all treatments.

TABLE 1. Nitrogen content (% of dw) of *Ulva lactuca*.

Treatment	Lagoon	Creek
Initial	2.45 ± 0.126	2.45 ± 0.126
Final (24 days)		
+ Algae	0.91 ± 0.034	1.07 ± 0.102
+ Algae + snails	1.64 ± 0.306	1.47 ± 0.034

Values are means ± SE.

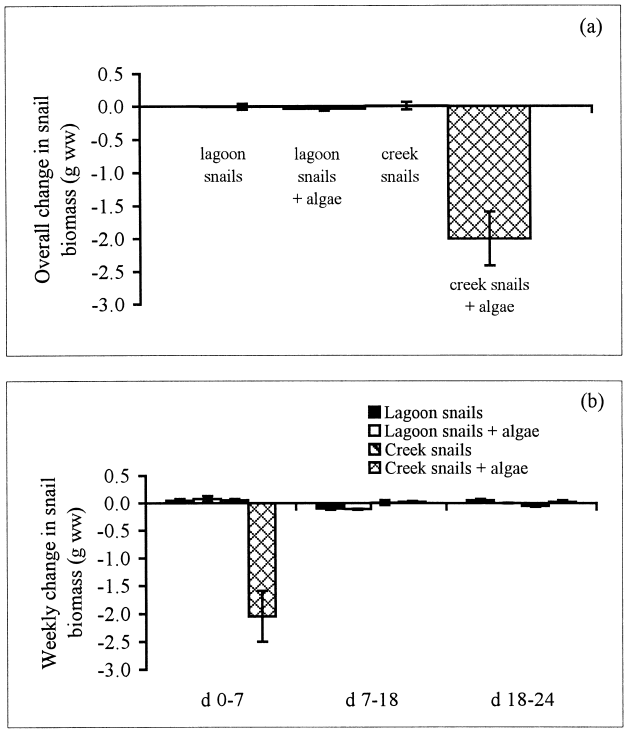

FIG. 2. (a) Changes in *Ilyanassa obsoleta* biomass (g ww) in cores from the lagoon and the creek at the end of the 24-day experiment. (b) Weekly changes in *I. obsoleta* biomass (g ww) over time during the experiment. Error bars represent the standard error of the mean ($n = 3$).

DISCUSSION

Our results provide clear evidence that the mud snail *I. obsoleta* is a direct and significant consumer of *U. lactuca*. Consumption was related to the nutritional quality (N content) of the macroalgal tissue and occurred even in the presence of alternative food sources in the sediment. These results are consistent with other studies showing increased grazing on plants of higher N content for fish, amphipods, intertidal gastropods, and many terrestrial organisms (Mattson 1980, Mickenberg and Ottenheim 1990, Yates and Peckol 1993, McGlathery 1995, Hauxwell et al. 1998). Even though food sources in addition to macroalgae are an important and critical part of the *I. obsoleta* diet (Wetzel 1977, Curtis and Hurd 1979, Haines and Montague 1979, Conner et al. 1982), we did not find any direct evidence that the presence of these food sources inhibited consumption of macroalgae. To the contrary, individual grazing rates were highest on algae overlying sediments rich in decaying organic matter over the 24-day microcosm experiment.

The grazing rates calculated per individual from the core experiment were similar to those reported for other invertebrate consumers of macroalgae. Because other studies have been done over a short time period (4–5 days) either in the laboratory or in the field, it is most appropriate to compare these rates with the rates determined during the first week of

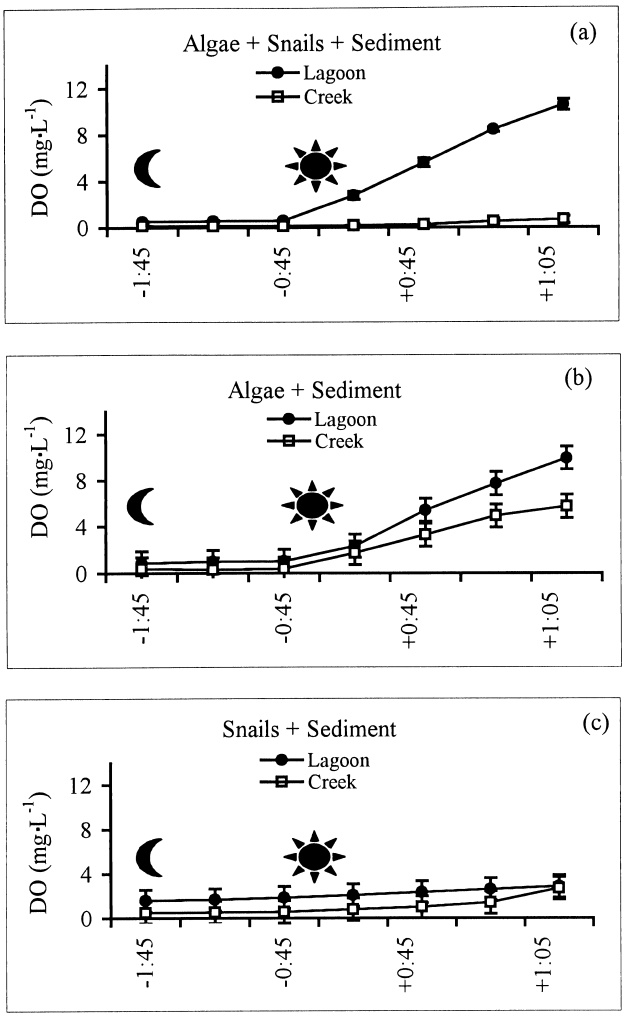

FIG. 3. Diurnal fluctuations in dissolved oxygen ($mg \cdot L^{-1}$) among different treatments and sample sites of the core experiment: (a) snails + algae + sediment, (b) algae + sediment, and (c) snails + sediment. Lights in the growth chamber were turned on at time 0:00. Error bars represent the standard error of the mean ($n = 3$ for each treatment).

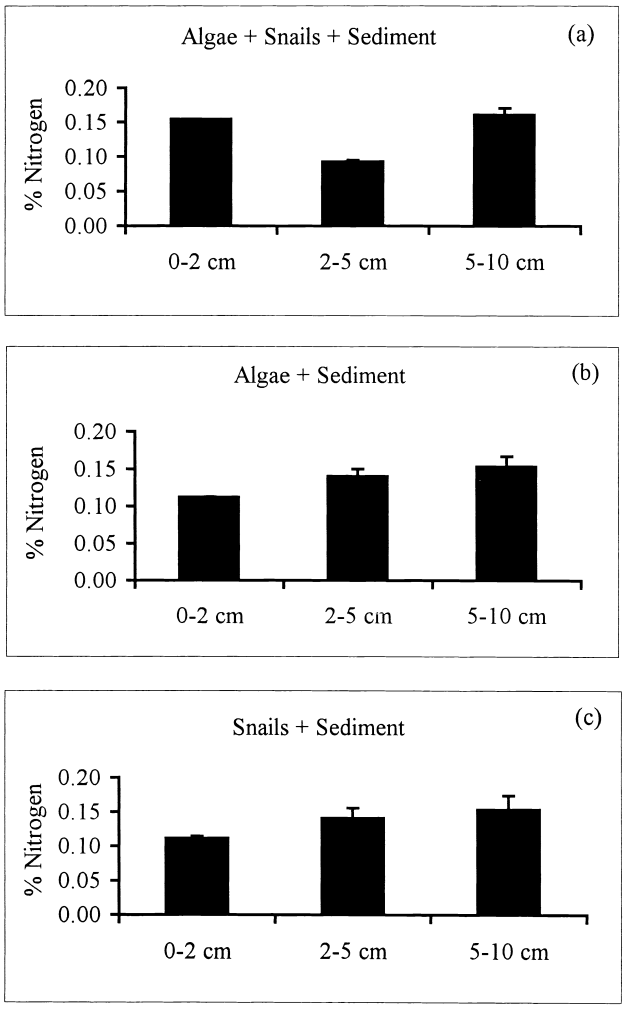

FIG. 4. Sediment nitrogen content (% of dw) of creek cores at the end of the 24-day experiment for the treatments: (a) snails + algae + sediment, (b) algae + sediment, and (c) snails + sediment. Error bars represent the standard error of the mean ($n = 3$ for each treatment).

our microcosm experiment (10.83 and 9.32 mg $ww \cdot individual^{-1} \cdot d^{-1}$ for the lagoon and creek cores, respectively). In a recent field study of isopod (*Idotea baltica*) grazing on another chlorophyte, *Cladophora vagabunda*, Hauxwell et al. (1998) measured average grazing rates of 7.3 mg $ww \cdot individual^{-1} \cdot d^{-1}$ in cages suspended in the water column. An earlier laboratory study on isopod grazing by Nicotri (1980) found grazing rates on several different macroalgal species to range from 0.2 to 8.1 mg $ww \cdot individual^{-1} \cdot d^{-1}$ (2.9 mg $ww \cdot individual^{-1} \cdot d^{-1}$ for *Ulva* sp.). We are aware of only one other study on gastropod grazing in a soft-bottom subtidal system in which Fong et al. (1997) showed that the California horn snail (*Cerithidea californica*) was not a significant consumer of *Ulva expansa* but instead enhanced macroalgal growth by increasing N availability. However, for the intertidal gastropod *Littorina littorea*, Yates and Peckol (1993) measured consumption rates of 7.9 mg $ww \cdot individual^{-1} \cdot d^{-1}$ on *Fucus vesiculosis* from a high-nitrogen subestuary of Waquoit Bay, Massachusetts. It is clear that even though *I. obsoleta* is an omnivore and cannot survive by consuming macroalgae alone (Curtis and Hurd 1979), its grazing intensity is similar to that of herbivorous species.

Given the high consumption rates of individual snails, it is possible that at high densities *I. obsoleta* may have an important influence on macroalgal biomass in the field. To our knowledge, there are no studies on the potential impact of *I. obsoleta* grazing on macroalgal biomass. We made such a calculation based on our laboratory grazing rates and measurements of snail densities at the two locations (lagoon and creek) at our study site in Hog Island Bay. Average monthly snail densities ranged from around 50 to 1136 $individuals \cdot m^{-2}$ at the lagoon site and from 0 to 200 $individuals \cdot m^{-2}$ at the creek site during June 1997 to August 1998 (Giannotti 1999). Using the grazing rates from

our microcosm experiment, we calculated that the maximum potential grazing intensity was 12.3 g ww·m^{-2}·d^{-1} at the lagoon site and 1.9 g ww·m^{-2}·d^{-1} at the creek site. Potential grazing losses were lower at the creek site largely because of the relatively low snail abundance at this site. Our calculated rates are similar to those calculated by Hauxwell et al. (1998) using a similar approach for crustacean (isopod, amphipod) grazers on *C. vagabunda* in Waquoit Bay, Massachusetts. In that study, grazing rates varied from nearly 0 to 2.5 g dw·m^{-2}·d^{-1}, compared with 0 to 3.5 g dw·m^{-2}·d^{-1} in our study (using a measured ww:dw ratio of 3.5 for *U. lactuca*). In Waquoit Bay, grazing was sufficient to lower macroalgal biomass in mid-summer in subestuaries subject to low-moderate nutrient loading (Hauxwell et al. 1998). This also may be true for the lagoon site where snail densities were high and the N supply was relatively low (Giannotti 1999). Based on our experimental growth rates and using the maximum number of snails at each site, we calculated that grazing could remove about 88% of new macroalgal growth at the lagoon site compared with 18% at the creek site.

Mud snails are considered to be among the most tolerant benthic invertebrates of the variation in oxygen levels associated with macroalgal mats (Norkko and Bonsdorff 1996). However, the 33% mortality and rapid weight loss of snails in the creek microcosms with macroalgae suggest that the persistent anoxia may have contributed to the decline in snail biomass either directly or indirectly by altering their normal feeding physiology and metabolism. In the creek microcosms and field populations, snails were observed on top of the macroalgal mat or attached to the side of the microcosms. By forcing snails up off the sediment, anoxia may have inhibited detritivory and prevented the snails from consuming a potentially important component of their dietary needs. Because mud snails tended to lose weight when consuming only macroalgae, this behavioral modification could account for their weight loss relative to microcosms without algae where snails would be feeding on sediment sources. This is supported by several studies of gut contents showing that *I. obsoleta* do not consume macroalgae alone (Brown 1969, Curtis and Hurd 1981, Conner et al. 1982, Feller 1984) but instead require nutrients from both plant and animal sources to grow, survive, and reproduce (Curtis and Hurd 1979).

Although grazing resulted in a significant loss of macroalgal biomass, the presence of feeding snails facilitated the growth of macroalgae by increasing macroalgal tissue N content, especially at the sandy lagoon site. Fong et al. (1997) found that horn snails also increased the availability of N for *U. expansa* and suggested that they did this by facilitating the regeneration and release of N sequestered in sediment. Others have found that pulses of N from consumers can increase algal tissue content (Williams and Carpenter 1988). Because no new N was supplied during our microcosm experiment, the only possible sources available to sustain macroalgal growth were diffusion of regenerated N from the sediments, snail excretion, and internal N stores in macroalgal tissue. At the lagoon site, measurements of nutrient exchange across the sediment–water interface have shown that these sandy sediments were a sink rather than a source of dissolved inorganic nitrogen (Tyler et al. 2001). Thus, it is reasonable to attribute the enrichment effect at the lagoon site to snail excretion. Alternatively, diffusion of N across the sediment–water interface is likely to be more important for muddy sediments rich in organic material (McGlathery et al. 1997). The higher growth rates and slightly higher tissue N content of algae from the creek microcosms maintained in the absence of snails suggest that in addition to snail excretion, N diffusing from the organic sediments may have helped sustain macroalgal growth. However, at both sites the supply of regenerated N, either from snail excretion or diffusion from the sediments, was insufficient to meet growth demand, and macroalgae drew on internal N stores, especially at the lagoon site where sediment N supply was lower. This agrees with other studies that have shown the importance of tissue N reserves in sustaining macroalgal growth when external N supplies are insufficient (McGlathery 1995, Pedersen and Borum 1996, Borum 1996).

The enrichment of surficial sediments in the creek microcosms with macroalgae suggests that where grazing intensity is high, consumption and excretion of nitrogenous wastes by snails may play an important role in recycling nutrients temporarily bound in macroalgal tissue. Fong et al. (1997) showed the opposite effect with the California horn snail *C. californica* where snails did not graze on the algae and instead reduced sediment nitrogen content. In addition to the obvious difference in grazing and excretion between the two snail species, this discrepancy probably also reflects behavioral differences. Release of N from the sediment to the water column by the California horn snail was attributed to burrowing and reworking of the sediments (Fong et al. 1997). The absence of burrowing due to anoxic conditions associated with the organic-rich creek sediments in the present study may have been at least in part responsible for the build-up of N in surface sediments; we did not see a similar effect in the sandy lagoon microcosms that remained oxic throughout the experiment. Thus, in addition to direct loading of labile organic matter to the sediments, an indirect effect of anoxia related to the physical breakdown of the algal mat is increased N sequestration in the sediments. This effect, however, may only be temporary as continued decomposition of algal detritus will increase nutrient concentrations in sediment pore waters and promote the release of dissolved N to the water column along steep diffusion gradients.

In conclusion, this study shows that the omnivorous mud snail is as significant a consumer of benthic macroalgae as any of the reported herbivorous invertebrates, even though it cannot survive on macroalgae

alone. As such, the mud snail plays an important role in the recycling of nutrients temporarily bound in macroalgal tissue. At low to moderate nutrient loading and high snail densities, direct consumption of live macroalgae may be sufficient to reduce macroalgal biomass significantly. This impact will likely be diminished where nutrient loading rates are high, as in the tidal creeks, because the presence of anoxic conditions in dense macroalgal mats reduces snail abundance and limits grazing activity.

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Borum, J. 1996. Shallow waters and land/sea boundaries. *In* Jørgensen, B. B. & Richardson, K. [Eds.] *Eutrophication in Coastal Marine Ecosystem.* American Geophysical Union, Washington, DC, pp. 179–204.

Brown, S. C. 1969. The structure and function of the digestive system of the mud snail *Nassarius obsoletus* (Say). *Malacolog.* 9: 447–500.

Collins, L. S. 1983. *Effects of a Deposit-Feeding Mud Snail,* Ilyanassa obsoleta *(Say, 1822) (Mollusca: Gastropoda), on Bivalve Population Dynamics in an Estuarine Intertidal Sandflat (Delaware Bay, USA).* Ph.D. Thesis, University of Delaware, Newark, Delaware. 113 pp.

Conner, M. S., Teal, J. M. & Valiela, I. 1982. The effect of feeding by mud snails, *Ilyanassa obsoleta* (Say), on the structure and metabolism of a laboratory benthic algal community. *J. Exp. Mar. Biol. Ecol.* 65:29–45.

Crisp, M. 1969. Studies on the behavior of *Nassarius obsoletus* (Say) (Mollusca, Gastropoda). *Biol. Bull.* 136:355–73.

Curtis, L. A. 1980. Daily cycling of the crystalline style in the omnivorous, deposit-feeding estuarine snail *Ilyanassa obsoleta. Mar. Biol.* 59:137–40.

Curtis, L. A. & Hurd, L. E. 1979. On the broad nutritional requirements of the mud snail, *Ilyanassa (Nassarius) obsoleta* (Say), and its polytrophic role in the food web. *J. Exp. Mar. Biol. Ecol.* 41:289–97.

Curtis, L. A. & Hurd, L. E. 1981. Nutrient procurement strategy of a deposit-feeding estuarine neogastropod, *Ilyanassa obsoleta. Est. Coast. Shelf Sci.* 13:277–85.

DeWitt, T. H. & Levinton, J. S. 1985. Disturbance, emigration and refugia: how the mud snail, *Ilyanassa obsoleta* (Say), affects the habitat distribution of an epifaunal amphipod, *Microdeutopus gryllotalpa* (Costa). *J. Exp. Mar. Biol. Ecol.* 92:97–113.

Edwards, S. F. & Welsh, B. L. 1982. Trophic dynamics of a mud snail [*Ilyanassa obsoleta* (Say)] population on an intertidal mudflat. *Est. Coast. Shelf Sci.* 14:663–86.

Feller, R. J. 1984. Dietary immunoassay of *Ilyanassa obsoleta*, the eastern mud snail. *Biol. Bull.* 166:96–102.

Fong, P., Desmond, J. S. & Zedler, J. B. 1997. The effect of a horn snail on *Ulva expansa* (Chlorophyta): consumer or facilitator of growth? *J. Phycol.* 33:353–9.

Giannotti, A. L. 1999. *Grazing Control of the Marine Macroalga* Ulva *sp. by the Mud Snail* Ilyanassa obsoleta *in a Barrier Island Lagoon System of the Virginia Coast Reserve.* MS Thesis, University of Virginia, Charlottesville, Virginia. 93 pp.

Haines, E. B. & Montague, C. L. 1979. Food sources of estuarine invertebrates analyzed using $^{13}C/^{12}C$ ratios. *Ecology* 60:48–56.

Harlin, M. M. & Rines, H. M. 1993. Spatial cover of eight common macrophytes and three associated invertebrates in Narragansett Bay and contiguous waters, Rhode Island, USA. *Bot. Mar.* 36:35–45.

Hauxwell, J., McClelland, J., Behr, P. J. & Valiela, I. 1998. Relative importance of grazing and nutrient controls of macroalgal biomass in three temperate shallow estuaries. *Estuaries* 21:347–60.

Henley, W. J. & Ramus, J. 1989. Photoacclimation of *Ulva rotundata* (Chlorophyta) under natural irradiance. *Mar. Biol.* 103:261–6.

Hunt, J. H., Ambrose, Jr., W. G. & Peterson, C. H. 1987. Effects of the gastropod, *Ilyanassa obsoleta* (Say), and the bivalve, *Mercenaria mercenaria* (L.), on larval settlement and juvenile recruitment of infauna. *J. Exp. Mar. Biol. Ecol.* 108:229–40.

Jenner, C. 1956. Occurrence of a crystalline style in *Nassarius. Biol. Bull.* 3:304.

Mattson, W. J. 1980. Herbivory in relation to plant nitrogen content. *Annu. Rev. Ecol. Syst.* 11:119–61.

McGlathery, K. J. 1995. Nutrient and grazing influences on a subtropical seagrass community. *Mar. Ecol. Prog. Ser.* 122:239–52.

McGlathery, K. J., Krause-Jensen, D., Rysgaard, S. & Christensen, P. B. 1997. Patterns of ammonium uptake within dense mats of the filamentous macroalga *Chaetomorpha linum. Aquat. Bot.* 59: 99–115.

Mickenberg, O. P. J. M. & Ottenheim, J. J. E. W. 1990. Effect of leaf nitrogen content of tomato plants on preference and performance of a leaf mining fly. *Oecologia* 83:291–8.

Nicotri, M. E. 1980. Factors involved in herbivore food preference. *J. Exp. Mar. Biol. Ecol.* 42:13–26.

Norkko, A. & Bonsdorff, E. 1996. Rapid zoobenthos community responses to accumulations of drifting algae. *Mar. Ecol. Prog. Ser.* 131:143–57.

Pedersen, M. F. & Borum, J. 1996. Nutrient control of algal growth in estuarine waters. Nutrient limitation and the importance of nitrogen requirements and nitrogen storage among phytoplankton and species of macroalgae. *Mar. Ecol. Prog. Ser.* 142:261–72.

Scheltema, R. S. 1961. Metamorphosis of the veliger larvae of *Nassarius obsoletus* (Gastropoda) in response to bottom sediment. *Biol. Bull.* 120:92–109.

Scheltema, R. S. 1964. Feeding habits and growth in the mud snail *Nassarius obsoletus. Ches. Sci.* 5:161–6.

Sfriso, A., Pavoni, B., Marcomini, A. & Orio, A. A. 1992. Macroalgae, nutrient cycles, and pollutants in the lagoon of Venice. *Estuaries* 15:517–28.

Tyler, A. C., McGlathery, K. J. & Anderson, I. C. 2001. Macroalgal mediation of dissolved organic nitrogen fluxes in a temperate coastal lagoon. *Est. Coast. Shelf Sci.* (in press).

Valiela, I., McClelland, J., Hauxwell, J., Behr, P. J., Hersh, D. & Foreman, K. 1997. Macroalgal blooms in shallow estuaries: controls and ecophysiological and ecosystem consequences. *Limnol. Oceanogr.* 42:1105–18.

Walsh, J. P. 1998. *Low Marsh Succession Along on Over-Wash Salt Marsh Chronosequence.* Ph.D. dissertation. University of Virginia, Charlottesville, Virginia. 211 pp.

Wetzel, R. L. 1977. Carbon resources of a benthic salt marsh invertebrate *Nassarius obsoletus* (Say) (Mollusca: Nassariidae). *In* Wiley, M. [Ed.] *Estuarine Processes.* Academic Press, New York, pp. 293–308.

Williams, S. L. & Carpenter, R. C. 1988. Nitrogen-limited primary productivity of coral reef algal turfs: potential contribution of ammonium excreted by *Diadema antillarum. Mar. Ecol. Prog. Ser.* 47:145–52.

Yates, J. L. & Peckol, P. 1993. Effects of nutrient availability and herbivory on polyphenolics in the seaweed *Fucus vesiculosus. Ecology* 74:1757–66.