

Figure 1. Sediment chlorophyll *a* concentration (mg m^{-2}) (mean \pm standard error) measured inside and outside cages plotted versus nitrogen load ($\text{kg N ha}^{-1} \text{yr}^{-1}$) in four estuaries of Waquoit Bay.

species composition and abundance of crabs and fish that consume microalgae or perturb sediments.

We assessed the magnitude of grazing by measuring the difference in chlorophyll *a* concentration inside and outside cages at the end of the study period. Grazers removed significant, nearly constant amounts of microalgal biomass (mean = $49.2 \pm 8.7 \text{ mg m}^{-2}$) irrespective of nitrogen load ($t = 890.5^*$, Fig. 1). Because of the cage effects, we can only tentatively conclude that grazers consume important amounts of microalgal chlorophyll, but our results document top-down control in agreement with previous findings in which removal of macroherbivores significantly increased microalgal biomass (8, 9).

Chlorophyll *a* increased with nitrogen load, but the amount of chlorophyll removed by grazer populations in each estuary remained constant. This suggests that the proportion of biomass grazed decreased as nitrogen load increased. This potential decrease in the significance of grazer impact as nitrogen load increases is similar to what was found in studies of amphipod grazing on macroalgal biomass within Waquoit Bay (10, Haux-

well, unpubl. data). These findings suggest that the relative importance of top-down and bottom-up controls in coastal marine systems may change as the systems become subject to nutrient enrichment, a phenomenon that has been documented in freshwater systems (11). As coastal ecosystems become increasingly eutrophic (12, 13), it may be that there will be a shift towards situations where top-down controls are overwhelmed by bottom-up controls. This is an important issue in coastal ecology, and our data are only suggestive. Further studies are needed to verify the results presented here.

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Control of Periphyton on *Zostera marina* by the Eastern Mudsnail, *Ilyanassa obsoleta* (Say), in a Shallow Temperate Estuary

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The presence of epiphytes on eelgrass (*Zostera marina*) reduces irradiation reaching eelgrass blades and decreases eelgrass productivity (1, 2). Grazers (gastropods, amphipods, and isopods) may, however, increase eelgrass productivity (3, 4) by preferentially consuming epiphytes. To quantify grazer effects on epiphytes, we evaluated the consumption of periphyton (epiphytic microalgae, bacteria, microfauna, and detritus) on eelgrass leaves by the gastropod *Ilyanassa obsoleta* (Say) in Jehu Pond (average depth ~ 1.2 m below MLLW), an estuary of Waquoit Bay, Massachusetts.

We first related epiphyte biomass to snail density in the field. We then measured rates of periphyton removal by snails in the laboratory. Lastly, we extrapolated the laboratory grazing rates to field densities of snails to estimate the potential effect of *I. obsoleta* on eelgrass periphyton in the estuary.

We identified sites in the estuary containing relatively high, medium, and low snail densities (164, 100, and 52 snails m^{-2}) in early August 1997, by randomly sampling snail density using 12 quadrats (0.25 m^2) and 10 benthic grabs (0.0225 m^2). The

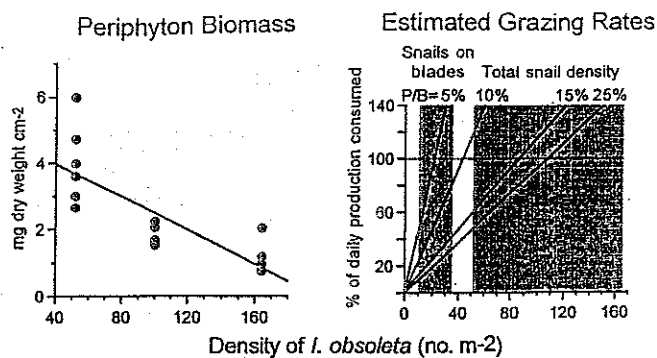


Figure 1. Left panel: Biomass of periphyton measured on *Zostera marina* leaves, plotted vs. density of *Ilyanassa obsoleta*. Points show values obtained for different blades within areas where snail density was measured. Periphyton biomass = $-0.025 \times \text{density of } I. \text{ obsoleta} + 4.971$, $F = 28.586^{**}$, $r^2 = 0.632$, $P < 0.0001$ (Model I linear regression assuming the Berkson case [9]). Right panel: Estimated percentage of daily periphyton production consumed by *I. obsoleta* at varying densities, for eelgrass shoot density and epiphyte load measured in early August 1997. Possible production/biomass ratio (P/B) values are estimated as 5%–25% to represent the range of potential epiphytic production scenarios. Right-most shaded area corresponds to the range of total snail densities for which field periphyton biomass was measured (see left panel). Left-most shaded area represents snail densities on eelgrass leaves. Vertical reference lines denote mean snail densities. Horizontal reference line indicates the level of consumption above which net periphyton biomass is reduced by *I. obsoleta*.

proportion of total snail density on eelgrass blades vs. on sediment was determined for each quadrat. To measure epiphyte biomass from each site, five to seven leaf blades were harvested from randomly chosen shoots. To rule out variability in epiphyte biomass with leaf age, only the third blade in every shoot sampled was harvested. Periphyton was removed from both sides of each blade and weighed after drying overnight at 80°C.

Periphyton biomass decreased with increasing density of *I. obsoleta* (Fig. 1, left), suggesting control of periphyton biomass by this grazer. *I. obsoleta* density in the eelgrass bed ranged from 20 to 240 indiv. m⁻² (mean \pm SE = 101.2 ± 23.3 indiv. m⁻²). Of the total density of snails in each quadrat, $21\% \pm 7\%$ (mean \pm SE) were on eelgrass blades.

To measure periphyton grazing rates by *I. obsoleta*, we enclosed individual snails with eelgrass leaves colonized with periphyton. These experiments were run in clear plastic cages (15 cm \times 15 cm \times 3.5 cm) in a laboratory running seawater system. Initial periphyton biomass on 10-cm sections of blade was quantified by scraping periphyton from one randomly selected side of the blade and weighing it after drying at 80°C overnight. Use of periphyton from only one side of a blade to calculate the total epiphyte biomass per blade was validated by comparing the biomass on internal vs. external faces of eighteen 10-cm blade sections from different leaves. The mean epiphyte biomass did not differ between the two faces (t -test, $P = 0.529$), showing that the initial values of epiphyte biomass are similar for either side of a blade. To run the experiments, a section of blade was pinned scraped-side down to the bottom of each cage. Snails previously acclimated in the laboratory for 1–2 d with an excess of periphyton food (to simulate field conditions) were then placed in each cage (36 replicates) and allowed to graze for 24 h. Final epiphyte

biomass was obtained by scraping periphyton from the side of each leaf section that was available to the snail. *I. obsoleta* removed 11.3 ± 0.8 mg dry weight of periphyton day⁻¹ indiv.⁻¹ (mean \pm SE) from eelgrass blades, which corresponds to $58.9\% \pm 5.8\%$ of the periphyton biomass on each blade section.

We extrapolated our laboratory measurements to field densities of snails to assess the possible effect of grazing by *I. obsoleta* on the estimated epiphytic production in Jehu Pond. Using our measured mean consumption rate, field measurements of mean eelgrass shoot density (127.3 ± 29.2 shoots m⁻² [unpubl. data]) and epiphyte load (0.0318 ± 0.0110 g shoot⁻¹ [unpubl. data]) and compiled literature estimates of the turnover rate of *Z. marina* periphyton (production:biomass ratio P/B = 5%–25% [5, 6]), we calculated the percentage of daily periphyton production (DPP) potentially consumed by varying densities of *I. obsoleta* (Fig. 1, right). The right-most shaded reference area in Figure 1 indicates the range of total snail densities for which field periphyton biomass was measured (in Fig. 1, left), and represents an upper limit on the ability of this grazer to consume periphyton. The left-most shaded area represents snail densities found on eelgrass leaves during sampling, used as a lower limit on our consumption estimate. If one considers the range of total snail densities, *I. obsoleta* could consume from 50% to >100% of DPP, depending on the actual P/B value. Using the densities of snails found on leaves, *I. obsoleta* could consume >100% of DPP, but only at low P/B values (~5%). These estimates suggest that *I. obsoleta* may be a control on periphyton biomass at certain snail densities, and at P/B values that occur in the field.

I. obsoleta is an important consumer of *Z. marina* epiphytes. By consuming significant epiphyte biomass, *I. obsoleta* may also influence eelgrass itself, as grazing rates similar to ones obtained here have resulted in increased eelgrass productivity in laboratory and mesocosm studies (7, 8). Periphyton may be a significant food source in this seagrass system; over 100% of daily production can potentially be consumed in sites where densities of *I. obsoleta* on eelgrass blades are high. Therefore, *I. obsoleta* can be an agent establishing top-down control of epiphytes as well as an important mechanism that influences eelgrass productivity and survivorship.

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