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COMPARISON OF WETLAND STRUCTURE AND FUNCTION ON GRAZED AND UNGRAZED SALT MARSHES

JUDY READER

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Abstract: Macrophyte productivity, soil development, and benthic invertebrate communities were compared on grazed and ungrazed salt marshes to examine the effects of grazing by feral ponies on wetland structure and function. The marshes had similar geomorphology (embayment), elevation (streamside and backmarsh), tidal inundation (1 m), salinity (25–35 ppt), soil type (Carteret series), and plant species composition (*Spartina alterniflora* Loisel) but differed with respect to the presence or absence of ponies. Over a two year period, above and belowground (0–30 cm depth) biomass were significantly lower in the grazed marsh (aboveground = 196–400 g/m^2, belowground = 828–1049 g/m^2) than the ungrazed marsh (aboveground = 588–671 g/m^2; belowground = 4,921–6,730 g/m^2). Reduction in *Spartina* biomass at the grazed marsh resulted in less soil organic carbon, nitrogen, and phosphorus than at the ungrazed marsh. There was no difference in C:N ratios at the two marshes, but N:P ratios were higher in the ungrazed marsh (9:1–19:1) than the grazed marsh (6:1–11:1), suggesting that more N is available for marsh organisms at the ungrazed site. Total benthic infauna density did not differ between the grazed (31,265 organisms/m^2) and ungrazed (45,511 organisms/m^2) marshes. However, the density of subsurface deposit feeders was significantly lower in the grazed marsh (10,370 organisms/m^2) than in the ungrazed marsh (16,877 organisms/m^2), perhaps as a result of lower soil organic matter and reduced food availability. Our findings suggested that herbivory by feral ponies co-ops primary productivity that would otherwise enter the detritus based salt marsh food web. This hypothesis should be tested using manipulative studies (e.g. exclosures) that exclude the ponies from areas of the marsh.

Key Words: Grazing; herbivory; invertebrates; North Carolina; salt marsh.

INTRODUCTION

Wetlands are the transitional areas between aquatic and terrestrial environments and are among the most productive ecosystems on this planet (Niering, 1985). Coastal wetlands are a critical component of estuarine systems, providing habitat

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(Bellrose and Trudeau, 1988; Odum et al., 1988; Race and Christie, 1982), and detritus for marsh and estuarine organisms (Lugo and Brinson, 1979; Marinucci, 1982), serving as sinks for sediment (Frey and Bason, 1978), nutrients (Craft et al., 1993) and organic carbon (Armentano and Menges, 1986), and buffering uplands from erosion through the action of wind and waves (Rosen, 1980; Knutson, 1988). Distribution of plant communities within a salt marsh are generally associated with tidal inundation, frequency and amplitude (McKee and Patrick, 1988), salinity (Webb, 1983), and the severity of anoxic conditions (Linthurst and Seneca, 1980). *Spartina alterniflora* Loisel, the smooth cordgrass, is highly adapted to the high tidal amplitude, frequent inundation, and high salinity characteristic of coastal wetlands (Daehler and Strong, 1994; Furbish and Albano, 1994).

Carrot Island in the Rachel Carson National Estuarine Research Reserve, North Carolina, is home to a populations of feral ponies (*Equus caballus*). Like some other barrier islands (e.g., Chincoteague National Wildlife Refuge in Virginia, Cumberland Island in Georgia), these ponies are most likely the descendants of domesticated horses that were permitted to graze on the island 50 or more years ago (Mohlenbrock, 1994). Many coastal wetlands were utilized for the grazing of livestock, such as cattle, horses, and sheep, for many years (Reimold et al., 1975). Over time, the descendants of the domesticated horses became feral and have developed special adaptations to the harsh conditions of the coastal wetlands, including smaller stature and thicker coat (Mohlenbrock, 1994).

Herbivory by ungulates can have a severe and varying impact on salt marsh structure and function. Some of the detrimental effects of grazing include the reduction of net aboveground primary productivity (Reimold et al., 1975), belowground biomass (Smith and Odum, 1981), and epibenthic invertebrate populations (Reimold et al., 1975). Rate of regrowth and the quality of vegetation in the marsh may decrease because of the trampling effect of horses (Chabreck, 1968; Jensen, 1985). Large herbivores can impact the salt marsh vegetation by: 1) direct grazing and defoliation of the plants, 2) trampling, 3) feces deposition, 4) urine deposition, and 5) the complete removal of plants through uprooting (Jensen, 1985). Salt marsh vegetation must be able to tolerate defoliation, root systems must be strong and established to avoid uprooting, plants must regrow rapidly following clipping, have a high toleration of fecal and urine deposits, and have large belowground biomass (Jensen, 1985) to withstand the impact of grazing.

The effects of feral horses on salt marshes has been examined at the Cumberland Island National Seashore in Georgia (Turner, 1987). This study examined the effects of clipping (foraging) and trampling of *S. alterniflora* by the horses. The grazing effects were significant, with moderate grazing resulting in a 25% decrease in net aboveground primary productivity. The grazing of these feral horses was not uniform across the marsh site. The reduction of net aboveground primary production in the salt marsh was mainly attributed not to clipping, but the combination of clipping and trampling by the feral horses (Turner, 1987). Trampling can lead to a significant loss of soil structure under moist conditions (Jensen, 1985) and in a salt marsh, moisture is a persistent condition. Since wetlands act as buffers for erosion, the heavy grazing by horses may result in decreasing the effectiveness of these wetlands as buffer zones. The heavy grazing results in lower net aboveground primary productivity which can lead to a decrease in the marsh soil accretion rate, since the rate of accretion is tied to sediment deposition, which is directly proportional to the stem density of marsh vegetation (Gleason et al., 1979).

At Assateague Island National Seashore (established in 1965), the grazing effects of the population of feral horses has been studied in terms of selective herbivory (Furbish and Albano, 1994). The lower salt marshes at Assateague Island consist of a mixture of two plants, *S. alterniflora* and *Distichilis spicata* L. The horse population was found to graze in the marsh nearly 50% of the time throughout the year and fed primarily on *S. alterniflora.* The selective grazing on *S. alterniflora* favored the expansion of *D. spicata* which, over time, colonized about half of the lower marsh (Furbish and Albano, 1994).

Although the effects of grazing on marsh primary production have been documented, little is known about how grazing affects the flow of detritus and carbon to marsh consumers, as well as marsh soil development. We compared macrophyte productivity, soil bulk density and nutrients and benthic infauna community composition in a grazed and ungrazed *S. alterniflora* marsh at Rachel Carson National Estuarine Research Reserve, North Carolina to investigate the effects of grazing on salt marsh structure and function. We hypothesized that grazing resulted in reduced above- and below-ground biomass production of *S. alterniflora.* Furthermore, we hypothesized that the removal of *S. alterniflora* biomass by herbivory will result in reduced inputs of organic matter to the soil, leading to lower concentrations of soil organic matter and nitrogen as well as reduced numbers of detritus feeding benthic invertebrates in the soil.

METHODS

Site Description

Rachel Carson is a National Estuarine Research Reserve (NERRS) site located near Beaufort along the central coast of North Carolina, Carteret County, between Bogue Sound and Back Sound (Fig. 1). Two sites, an ungrazed marsh (Middle Island Marsh) and a marsh grazed by feral ponies (Carrot Island) were sampled. Rachel Carson provided a unique opportunity to study the effects of equine grazing because the grazed site, Carrot Island, was home to wild ponies quarantined on the island because of the presence of equine infectious anemia in the herd, while Middle Island Marsh contained no ponies. The grazed site was chosen on the basis of evidence (presence of ponies, manure piles, cropped *Spartina*) indicating that the ponies were utilizing the marsh. Ponies were present in and around the grazed site when we sampled during June and October 1995 and again in October 1996. Herbivory by ponies was especially prevalent in October 1996 as evidenced by fresh manure piles and freshly cropped *Spartina.*

On the grazed and ungrazed islands, we chose marsh sites that were similar with respect to vegetation type, salinity, tidal inundation, soil type, geomorphic position and elevation. Both sites were dominated by *S. alterniflora* Loisel. Both marshes were regularly flooded with tidal inundation of 1 m determined at high tide during our first sampling visit in June 1995. Both marshes had similar surface water salinity (measured using a refractometer) that varied between 25–35 ppt during our three sampling visits in 1995 and 1996. Soils at both sites were classified as Carteret series (mixed, thermic typic psammaquents (USDA, 1987). Both sites were located along a small embayment in the interior of the island (Fig. 1),

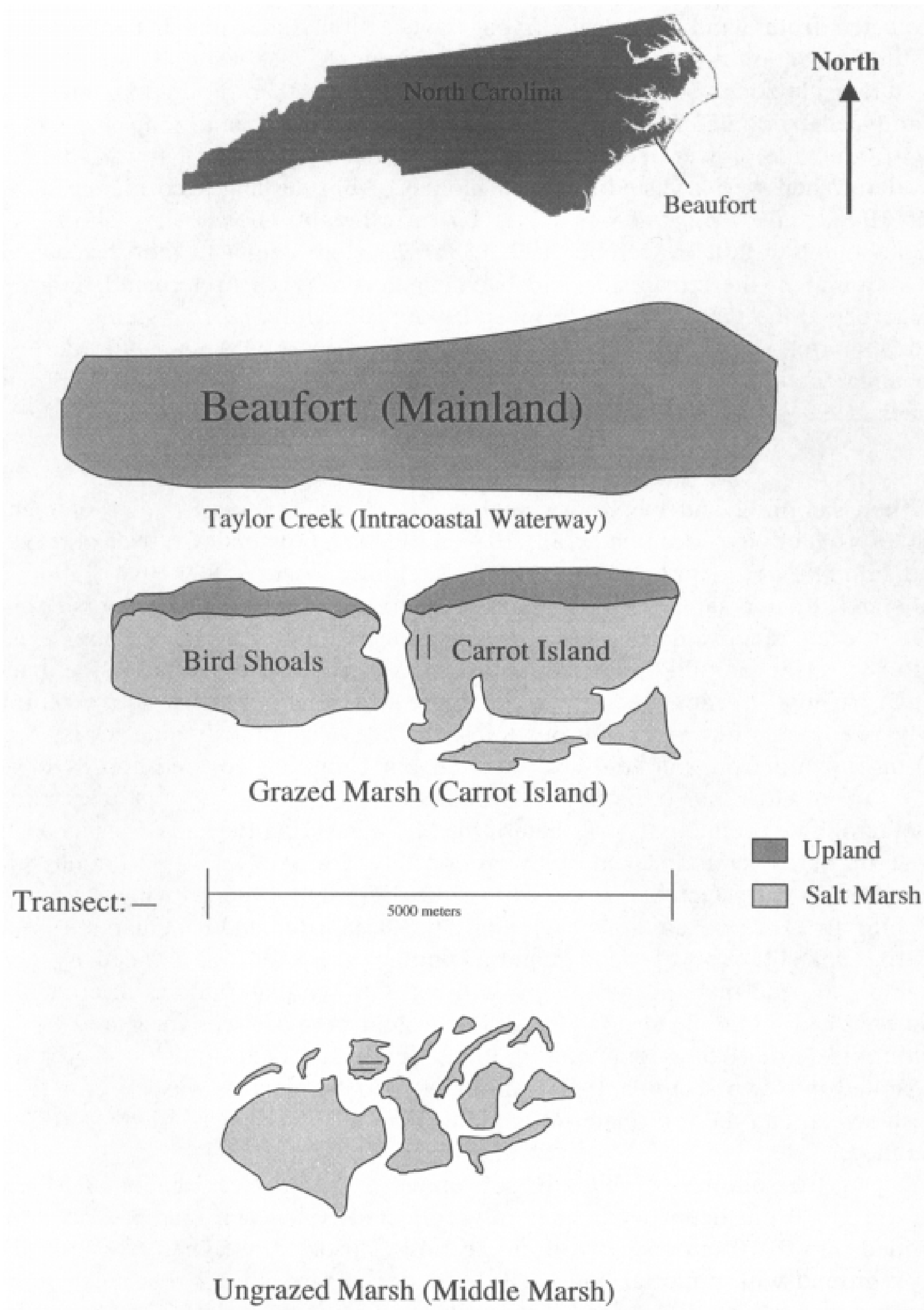

Figure 1. Location of the grazed and ungrazed salt marshes at Rachel Carson NERRS, North Carolina. The grazed and ungrazed sites, although similar in scale, are not drawn in geographic relation to each other.

protected from wind and boat driven wave action. Each marsh contained two distinct elevation zones, streamside and backmarsh, that were sampled (Fig. 1). A streamside zone, 5–10 m wide, higher in elevation than the interior marsh and dominated by "tall" *Spartina,* was sampled. The backmarsh zone was broader (30–50 m wide), lower in elevation and dominated by *Spartina* that was somewhat shorter. When we harvested *Spartina* biomass from the ungrazed marsh in 1995 and 1996, "tall" *Spartina* was 1.2 to 1.7 m in height whereas the "short" form was about 1 m tall. In October 1995, *Spartina* stem height in the grazed marsh was similar in the streamside and backmarsh zones, 0.8 to 1 m tall. Increased herbivory at the grazed site in October 1996, resulted in *Spartina* stems that were much shorter, 0.2–0.4 m tall, than the previous year (1995). In 1996, there was no apparent difference in stem height between the streamside and backmarsh zones at the grazed site because of intensive cropping by the ponies.

Sampling Methodology

Field sampling and laboratory analyses followed previous studies of macrophyte productivity (Broome et al., 1986), soil development (Craft et al., 1988), and infaunal community structure and function (Sacco et al., 1994). Biomass, soils and infauna sampling were stratified into streamside and backmarsh zones. Within each zone, samples were randomly selected using a random number generator to select sampling points along a 100 m long transect parallel to the marsh-estuary fringe. Because the streamside zone was relatively narrow, we sampled only five meters outward from our transect. In the backmarsh zone, we sampled 20 m outward from our transect. In total, our sampling covered approximately 2,500 m^2 of each marsh.

Macrophyte productivity was determined by measuring the end of season standing crop of aboveground and belowground biomass. Aboveground biomass was measured in early October at the end of the 1995 and 1996 growing seasons by clipping five 0.25 m^2 quadrats each along the streamside and backmarsh transects (10 per marsh). Aboveground material within each plot was clipped by hand. Living and dead material were separated and the live material was dried at 70°C and weighed to the nearest 0.1 g. Belowground biomass was measured by collecting one core (8.5 cm diameter $\times$ 30 cm depth) from each quadrat. Cores were separated into two sections, 0–10 cm and 10–30 cm depths, washed on a 2 mm mesh screen and the root material remaining on the screen was dried at 70°C and weighed.

During the summer of 1995, 10 soil cores (5 streamside, 5 backmarsh), each 8.5 cm $\times$ 30 cm deep, were randomly collected from each marsh. Cores were divided into 0–10 cm and 10–30 cm sections, air-dried, weighed (for bulk density), ground with a mortar and pestle, and sieved through a 2 mm mesh screen. Organic matter was determined through loss on ignition at 450°C for 8 hr (Craft et al., 1988). Organic carbon and total nitrogen were analyzed with a Perkin-Elmer CHN analyzer. National Institute of Standards and Technology (NIST) standards were used to ensure that proper recovery levels were obtained. For nitrogen (N) analysis, the average value for peach leaves (NIST #1547) was 2.935 $\pm$ 0.01%, compared to the "true" value of 2.945%, a 99.7% recovery rate. Total phosphorus (P) was measured in nitric-perchloric acid digests (Sommers and Nelson, 1972) following Murphy and Riley (1962). The recovery of P in estuarine sediment (NIST #1646a) was 259.65 μg/g, compared to the "true" value of 265 μg/g, a 98% recovery rate. Extractable phosphorus was measured in Mehlich 3 extracts (Mehlich, 1984). All analyses were corrected for soil moisture content using a correction factor obtained by oven drying sub-samples overnight at 105°C.

Benthic infauna were sampled by randomly collecting 30 cores (3 cm diameter by 5 cm deep), 15 each from streamside and backmarsh zones, during July of 1995. Cores were preserved and stained in the field using 10% buffered formalin containing Rose Bengal. Samples were sieved through a 250 μm screen with deionized water and the organisms remaining on the screen were sorted and stored in 70% ethyl alcohol. Taxonomic identification to the lowest taxa was performed by John Sacco. Trophic structure of benthic infauna was determined based on feeding strategy. Infauna were separated into four groups: surface feeders, subsurface deposit feeders, carnivores, and other feeding types following Sacco et al. (1994).

Statistical Analyses

Data were analyzed using Statistical Analysis Systems (SAS, 1982). Prior to statistical analysis, infauna data were log transformed to comply with the assumptions of analysis of variance (ANOVA), that the data are normally distributed and have homogeneous variance (Zar, 1996). A three-way ANOVA based on the site (grazed, ungrazed), depth (0–10 cm, 10–30 cm), and year (1995, 1996) was used to evaluate the effects of grazing on above- and below-ground biomass. Soil data was examined using a two-way ANOVA, based on site and depth. ANOVA means were compared using the Ryan-Einot-Gabriel-Welsch (REGWQ) multiple range test. All the comparisons were tested for significance at the 0.05 alpha level. Student's *t* test was used to test the null hypothesis that benthic infauna community composition (density, number of species, trophic and taxonomic composition) did not differ between the grazed and ungrazed marshes.

RESULTS

Macrophyte Productivity

Analysis of variance revealed that both above- and below-ground biomass were significantly lower in the grazed marsh (Fig. 2). Aboveground biomass was significantly lower in the grazed marsh during 1995 ($p < 0.05$, 400 ± 66 g/m^2) and 1996 ($p < 0.01$, 196 ± 25 g/m^2) as compared to the ungrazed marsh (1995 = 588 ± 28 g/m^2, 1996 = 671 ± 37 g/m^2). Aboveground biomass at the grazed site was significantly less in 1996 than 1995 ($p < 0.05$), perhaps a result of increased grazing pressure. There was no difference in aboveground biomass at the ungrazed marsh between 1995 and 1996.

Belowground biomass (0–10 cm and 10–30 cm) was also significantly lower in the grazed marsh during 1995 ($p < 0.05$) and 1996 ($p < 0.01$) (Fig. 2). Root biomass (0–10 cm) at the grazed site was 638–790 g/m^2 as compared to 1,306–2,839 g/m^2 at the ungrazed marsh. Belowground biomass in the 10–30 cm depth was also significantly less in the grazed marsh ($p < 0.01$) (190–259 g/m^2) than in the ungrazed marsh (3,615–3,891 g/m^2). Most root biomass in both marshes was concentrated in the 0–10 cm depth, which is a common characteristic of environments where the soils are periodically anoxic and oxygen is limiting.

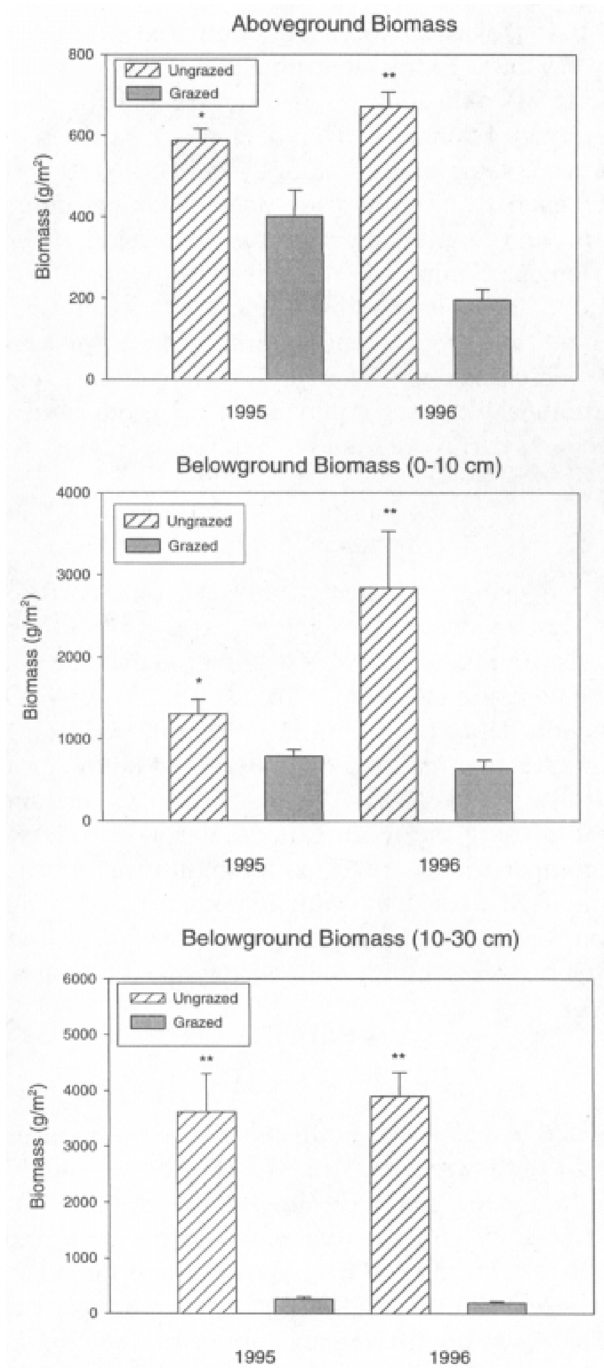

Figure 2. Mean (n=10) above- and belowground (0–10 cm, 10–30 cm) end-of-season biomass at the Rachel Carson NERRS grazed and ungrazed marshes in 1995 and 1996.
*, **; Significantly greater ($p<0.05$ and 0.01 respectively) than the grazed marsh based on ANOVA.

Soil Development and Organic Matter/Nutrient Pools

Soil bulk density was higher ($p < 0.05$) and organic matter, soil organic carbon, nitrogen and phosphorus were lower ($p < 0.05$) at the grazed marsh than at the ungrazed marsh (Table 1). Bulk density was 1.21–1.35 g/cm^3 at the grazed site

Table 1. Mean (n = 10) bulk density, organic matter, organic carbon, total nitrogen, phosphorus, extractable P, C:N and N:P ratios, and nutrient pools (0–30 cm depth) (± one standard error) of grazed and ungrazed marsh soils at Rachel Carson NERRS. Means followed by the same letter within a given parameter are not significantly different (p = 0.05), according to the Ryan-Einot-Gabriel-Welsch Multiple Range Test.

Parameter	Depth (cm)	Grazed	Ungrazed
Bulk density (g/cm^3)	0–10	1.21 ± 0.05 a	0.75 ± 0.06 b
	10–30	1.35 ± 0.08 a	0.70 ± 0.02 b
Organic matter (%)	0–10	1.37 ± 0.21 c	4.48 ± 0.56 b
	10–30	1.09 ± 0.23 c	8.51 ± 0.58 a
Organic carbon (%)	0–10	0.61 ± 0.06 c	2.02 ± 0.25 b
	10–30	0.49 ± 0.10 c	3.83 ± 0.26 a
Nitrogen (%)	0–10	0.04 ± 0 b	0.15 ± 0.02 a
	10–30	0.03 ± 0.01 b	0.20 ± 0.01 a
Phosphorus (μg/g)	0–10	158 ± 1 c	332 ± 20 a
	10–30	65 ± 5 d	232 ± 14 b
Extractable P ($\mu g/m^3$)	0–10	49 ± 3 a	46 ± 4 a
	10–30	12 ± 1 b	11 ± 1 b
C:N (atom)	0–10	16.3 ± 0.5 b	16.2 ± 0.4 b
	10–30	18.3 ± 1.5 a, b	22.1 ± 0.6 a
N:P (atom)	0–10	6.1 ± 0.2 c	9.4 ± 0.8 b
	10–30	11.1 ± 2.3 a, b	19.3 ± 1.0 a
C pool (g/m^2)	0–30	2018 ± 241 b	6839 ± 400 a
N pool (g/m^2)	0–30	135 ± 12 b	387 ± 19 a
P pool (g/m^2)	0–30	37 ± 2 b	56 ± 2 a

and 0.70–0.75 g/cm^3 at the ungrazed marsh. Reduction in above and belowground biomass caused by cropping resulted in lower organic matter (1.1–1.4%), carbon (0.5–0.6%), nitrogen (0.03–0.04%), and phosphorus (65–158 μg/g), as compared to the ungrazed marsh (Table 1). The grazed marsh also contained significantly ($p < 0.05$) smaller soil N, P, and organic C pools (0–30 cm depth) than the grazed marsh (Table 1). Nitrogen, phosphorus, and organic C pools in the grazed marsh were one third to one half the size of nutrient pools in the ungrazed marsh (Table 1). Extractable phosphorus did not differ between the grazed (12–49 $\mu g/cm^3$) and the ungrazed (11–46 $\mu g/cm^3$) marshes. There were no clear differences in bulk density and nitrogen with depth in the grazed and ungrazed marsh (Table 1). However, extractable and total P decreased with depth in both marshes. In the ungrazed marsh, organic matter and carbon increased with depth ($p < 0.05$), the result of increased root biomass (Fig. 2) and, hence, organic matter inputs to the 10–30 cm depth.

Comparison of soil C:N ratios revealed no differences between grazed and ungrazed marshes (Table 1). Soil C:N in both marshes increased with depth, reflecting decreased availability of N in subsurface marsh soils. Soil N:P ratios, in contrast, were higher in the ungrazed marsh ($p < 0.05$) suggesting that proportionally more N was available to marsh organisms in the ungrazed marsh (Table 1). The low N:P ratios (<30) suggested that N was the primary limiting nutrient in these marshes.

Benthic Infauna

No significant differences existed between the grazed and ungrazed marshes in relation to the total density of benthic invertebrates. Ungrazed marsh averaged 45,511 ± 9,125 organisms/m^2, while the grazed marsh contained 31,265 ± 4,570 organisms/m^2. Mean number of species per core and marsh species richness also did not differ between the ungrazed marsh (6.30 ± 0.42 species/core, 20 species/marsh) and the grazed marsh (6.10 ± 0.51 species/core, 21 species/marsh).

Comparisons of the six numerically dominant taxa revealed that *Oligochaeta, Manayunkia,* and *Capitella* were significantly higher ($p < 0.05$) in the ungrazed marsh (11,643 ± 2,419 organisms/m^2, 12,025 ± 2,844 organisms/m^2 and 3,070 ± 651 organisms/m^2, respectively) than in the grazed marsh (6,126 ± 1,655 organisms/m^2, 283 ± 127 organisms/m^2 and 1,132 ± 311 organisms/m^2, respectively) (Fig. 3a). *Streblospio* and *Nematoda,* in contrast, were more abundant ($p < 0.05$) in the grazed marsh (4,711 ± 934 organisms/m^2 and 9,521 ± 1,966 organisms/m^2, respectively) than in the ungrazed marsh (2,363 ± 566 organisms/m^2 and 4,103 ± 1,415 organisms/m^2).

Analyses of trophic groups revealed that the density of subsurface deposit feeders was significantly lower ($p < 0.01$) in the grazed marsh (10,370 ± 2,009 organisms/m^2) than in the ungrazed marsh (16,877 ± 2,745 organisms/m^2) (Fig. 3b). Density of surface deposit feeders also was lower ($p < 0.05$) in the grazed (9,196 ± 1,570 organisms/m^2) than the ungrazed marsh (23,017 ± 5,772 organisms/m^2). No differences existed in carnivore density between the grazed and ungrazed marshes. The trophic group, "Other," which consisted mostly of nematodes, was significantly higher ($p < 0.05$) in the grazed marsh (11,642 ± 2,207 organisms/m^2) than in the ungrazed marsh (5,560 ± 1,853 organisms/m^2).

DISCUSSION

During the 1995 and 1996 growing seasons, the grazed site had significantly less above- and below-ground *S. alterniflora* biomass than the ungrazed marsh and other natural and restored salt marshes in North Carolina (Craft et al., in press). In our study, aboveground biomass in the grazed marsh at Rachel Carson was reduced by 23–40%. Our results were similar to the findings of Reimold et al. (1975), where the biomass was reduced by nearly half in the grazed site, and Turner (1987), who observed a 20–50% reduction in aboveground biomass because of cropping and trampling by horses. In our study, belowground productivity (0–10 cm depth and 10–30 cm depth) also was reduced because of grazing as fewer roots were needed to support the reduced aboveground vegetation under grazed conditions. Previous studies suggested that the effects of grazing on salt marsh vegetation depended on the length of time the grazers forage in the marsh (Bazely and Jefferies, 1986; Hik and Jefferies, 1990). The longer the grazers, in this case lesser snow geese, spent in the marsh feeding, the greater the impact on vegetation (Bazely and Jefferies, 1986; Hik and Jefferies, 1990).

Comparison of plant biomass in ungrazed *Spartina* marshes revealed that the grazed marsh contained less above- and belowground biomass than "tall" *S. alterniflora* marshes along the U.S. Atlantic and Gulf coasts (Table 2). In 1995, aboveground biomass in the grazed marsh was comparable to ungrazed "short" *S. alterniflora* marshes. However, in 1996 following intensive grazing, both

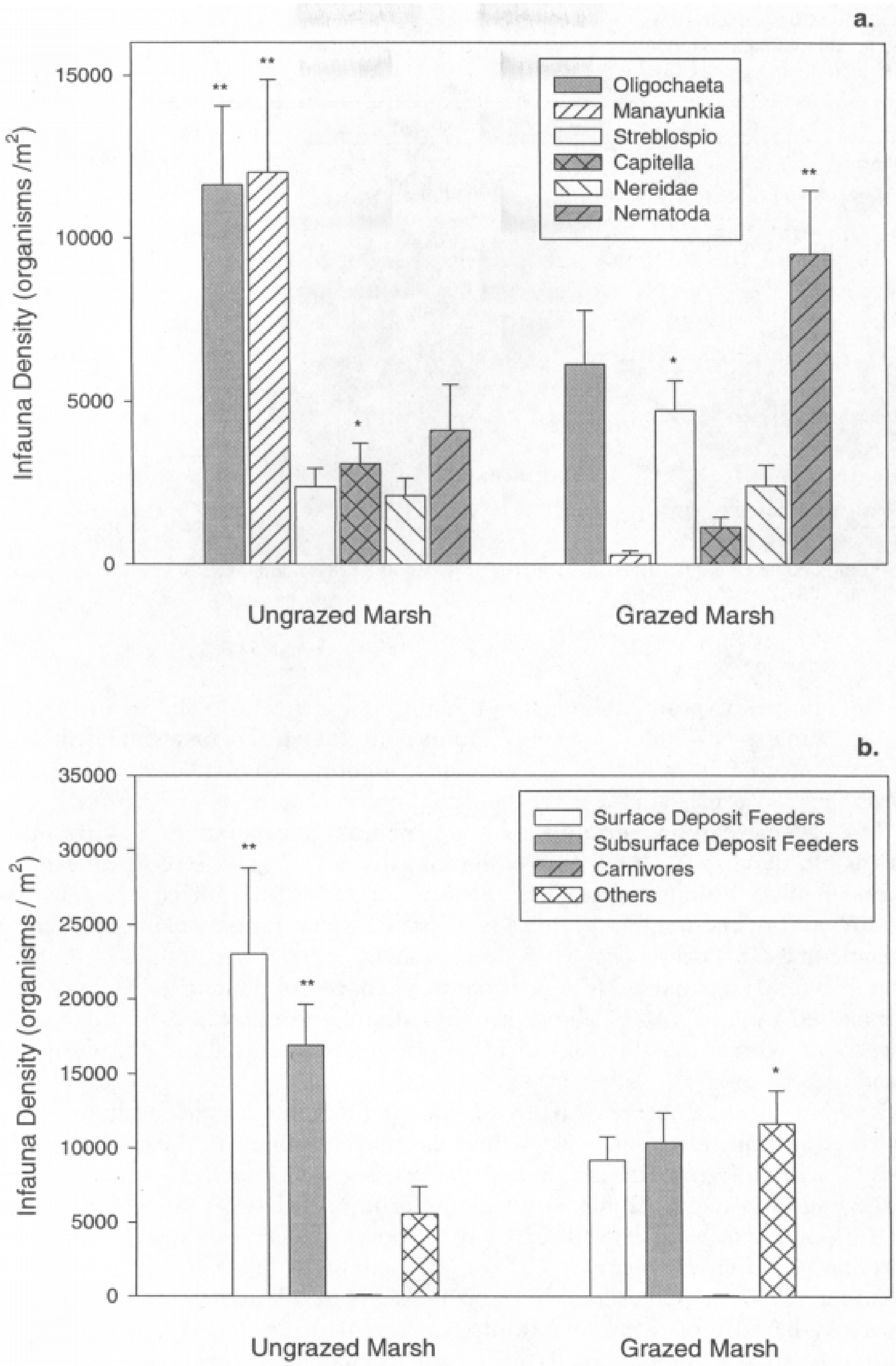

Figure 3. Mean (n=30) density of a) the six dominant taxa and b) trophic groups of benthic infauna at the grazed and ungrazed marsh at Rachel Carson NERRS.
*, **; Grazed and ungrazed marshes are significantly different ($p<0.05$ and 0.01, respectively) based on ANOVA.

Table 2. Comparison of *Spartina alterniflora* biomass, macro-organic matter (MOM) soil nutrients and benthic infauna communities in our grazed marsh and in natural *S. alterniflora* marshes along the U.S. atlantic and gulf coasts.

	Grazed Marsh[1]	Natural Marshes	
Biomass[2]			
Aboveground (g/m²	196–400	Tall form:	363–2335
		Short form:	259–592
MOM (0–30 cm; g/m²)	828–1049	Tall form:	1,574–6,730
		Short form:	925–11,200
Soil (0–30 cm)[3]			
Organic C (%)	0.53		0.2–16.4
Nitrogen (%)	0.03		0.04–1.17
C:N (wt:wt)	18		12–20
Phosphorus (μg/g)	96		128–833
Benthic infauna[3]			
Density	31,260		5,000–102,200
Species richness	20		3–43

[1] This study.
[2] From Broome et al. (1975), Turner (1976), Howes et al. (1981) and table 7 of Craft et al. (in press).
[3] From table 7 of Craft et al. (in press).

above- and below-ground biomass in the grazed marsh was lower than in "short" *Spartina* marshes (Table 2). Lower biomass in the grazed marsh than in either ungrazed "tall" or "short" *Spartina* marshes during 1996 suggests that grazing by ponies had a measurable effect on standing crop biomass of *Spartina.*

Soil organic carbon, nitrogen, and phosphorus concentrations (0–10 cm and 10–30 cm depths) and pools were significantly lower ($p < 0.05$) in the grazed marsh than in the ungrazed marsh. Soil organic C in the grazed marsh was on the low end of the range reported for ungrazed *S. alterniflora* marshes along the Atlantic and Gulf coasts (Table 2). Total N and P were lower in the grazed marsh than in ungrazed marshes. It is possible that reduced organic matter inputs to the soil caused by cropping of aboveground material and reduced production of belowground biomass resulted in lower soil organic C and nutrients in the grazed marsh.

Soil organic C (3.2%), N (0.18%), and P (265 μg/g) concentrations in the ungrazed marsh (0–30 cm) were within the range reported for Atlantic and Gulf coast *S. alterniflora* marshes (Table 2). Likewise, soil organic C, N, and P pools in the ungrazed marsh (Table 1) were similar to organic C (1,900–12,300 g/m²), N (130–520 g/m²) and P (40–270 g/m²) pools in other salt marshes in North Carolina (Craft et al., in press).

Turner (1987) hypothesized that grazing leads to a shift from a detrital to an herbivory-based food web. Our results suggested that reduced macrophyte productivity and soil nutrient pools may lead to changes in benthic infauna community structure and function. Both grazed and ungrazed marshes had infauna density and species richness that were within the range reported for Atlantic and Gulf coast *S. alterniflora* marshes (Table 2). However, the ungrazed marsh had significantly greater numbers of surface and subsurface deposit than the grazed marsh. Reimold et al. (1975) observed that the density of the fiddler crab, *Uca* spp., a surface deposit feeder, was significantly lower in grazed than ungrazed marshes. It is possible that the reduction in subsurface deposit feeders in the grazed marsh is caused by reduced organic matter inputs to the soil as much of the marsh primary production was shifted to the herbivorous ponies.

CONCLUSIONS

Our observational data suggested that grazing resulted in changes in salt marsh structure and function at Rachel Carson NERRS. Grazing reduced macrophyte biomass by cropping aboveground material, resulting in reduced belowground production and biomass accumulation. The reduction in macrophyte biomass led to reduced inputs and, perhaps, reduced accumulation of soil organic matter and nutrients and density of subsurface deposit feeding invertebrates in the soil. This study, like many others investigating the effects of herbivory on salt marshes, was dependent on a single examination between a grazed and ungrazed marsh, exclusive of experimental manipulations (Beeftink, 1966). Our conclusions should be tested using exclosures barring grazers from portions of the marsh to examine changes in *Spartina* biomass, soil characteristics, and infauna community composition in response to grazing.

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