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TWENTY-FIVE YEARS OF ECOSYSTEM DEVELOPMENT OF CONSTRUCTED *SPARTINA ALTERNIFLORA* (LOISEL) MARSHES

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Abstract. Wetland creation and restoration are frequently used to replace ecological functions and values lost when natural wetlands are degraded or destroyed. On many sites, restoration of ecological attributes such as secondary production, habitat/species diversity, and wetland soil characteristics do not occur within the first decade, and no long-term studies exist to document the length of time required to achieve complete restoration of wetland dependent functions and values. Characteristics of community structure (macrophyte aboveground biomass, macro-organic matter [MOM], benthic invertebrates) and ecosystem processes (soil development, organic C, N, and P accumulation) of two constructed *Spartina alterniflora* (Loisel) marshes (established 1971 and 1974) and paired natural *S. alterniflora* marshes in North Carolina were periodically measured during the past 25 yr. On constructed marshes, the macrophyte community developed quickly, and within 5 to 10 yr, aboveground biomass and MOM were equivalent to or exceeded corresponding values in natural marshes. After 15–25 yr, benthic infauna density and species richness were greater than in the natural marshes. Soil bulk density decreased, and organic C and total N increased over time in constructed marshes, but after 25 yr, soil organic C and N reservoirs were much smaller than in a 2000-yr-old natural marsh. Organic C accumulation was similar in constructed and natural marshes with 12–24% of the net primary production buried annually. Nitrogen accumulation was much higher in constructed marshes ($7–12\ g \cdot m^{-2} \cdot yr^{-1}$) than in natural marshes ($2–5\ g \cdot m^{-2} \cdot yr^{-1}$), reflecting the open biogeochemical cycles and paucity of N in these young ecosystems. Different ecological attributes develop at different rates, with primary producers achieving equivalence during the first 5 yr, followed by the benthic infauna community 5–10 yr later. Accumulation of soil nutrients to levels similar to those of reference marshes may require more time.

Key words: benthic infauna; biomass; community structure; ecosystem processes; marshes, reference; organic matter and nutrients; salt marsh; soils; Spartina alterniflora; *trophic composition; wetland creation and restoration.*

Introduction

Establishment of salt marsh cordgrass (*Spartina alterniflora* Loisel) has been used increasingly to restore or construct estuarine wetland habitat for (1) stabilizing dredged material (Lindau and Hossner 1981, Seneca et al 1985); (2) reducing shoreline erosion (Broome et al. 1986); and (3) mitigating wetland loss from surface mining (Broome et al. 1988*a, b,* Rulifson 1991), oil spills (Seneca and Broome 1992) and urban development (Langis et al. 1991, Moy and Levin 1991, Zedler 1992, Gibson et al. 1994). In particular, the accelerating urbanization of coastal environments has resulted in the increased use of wetland construction as a tool for replacing natural marshes destroyed by development activities (Race and Christie 1982, Stockton and Richardson 1987, Zedler 1992).

Studies measuring macrophyte biomass indicate that constructed *S. alterniflora* marshes often achieve parity with natural marshes within 5–10 yr after establishment (Seneca et al. 1985, Broome et al. 1986). Broome et al. (1986) reported that, within four growing seasons, above- and belowground biomass of *S. alterniflora* were comparable to a nearby natural marsh. However, other measures of *S. alterniflora* structure such as stem height may not develop as rapidly. A *Spartina foliosa* salt marsh in California constructed to provide habitat for the endangered light footed clapper rail (*Rallus longirostris levipes*) had a much shorter canopy (few plants were 60 cm tall) than nearby natural marshes where most of the plants were taller than 60 cm (Zedler 1993). As a result, the clapper rail did not utilize the marsh for breeding because the nests in shorter canopy of the restored marsh were inundated by the tides (Zedler 1993).

Other attributes of wetland structure, such as epibenthic infauna and benthic infauna, develop more slowly than the plant community. Studies of constructed salt marshes ranging in age from 4 to 17 years old report lower epifauna and infauna densities and fewer

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subsurface deposit feeders than in natural marshes (Moy and Levin 1991, Sacco et al. 1994, Levin et al. 1996, Scatolini and Zedler 1996). Many of these studies suggest that low soil organic matter content may limit infauna colonization in constructed *S. alterniflora* marshes (Sacco et al. 1988, 1994, Moy and Levin 1991, Levin et al. 1996).

Biogeochemical processes such as organic matter and nutrient accumulation, denitrification, and tidal export of nutrients may require even longer to develop to levels comparable to natural wetlands (Craft et al. 1988, 1989, 1991*b*, Langis et al. 1991, Thompson et al. 1995). Langis et al. (1991) reported that a 4-yr-old constructed *S. foliosa* marsh in San Diego Bay contained much lower soil organic C and N pools than an adjacent natural marsh. Craft et al. (1988) reported that, after 15 yr, constructed *S. alterniflora* marshes contained significantly lower soil nutrient (N, P, organic C) reservoirs than in nearby natural marshes.

Studies of constructed salt marshes marshes suggest that several important ecological attributes (wetland soil development, benthic infauna) develop slowly such that, after 15 yr, these wetlands remain functionally inferior to natural marshes (Craft et al. 1988, Sacco et al 1994). Although, it seems likely that, given sufficient time, correctly designed constructed salt marshes will become similar to natural marshes, it is not clear how much time is required for these ecosystems to achieve levels of community structure and ecosystem function equivalent to natural counterparts. If wetland construction is to be used as an effective tool for mitigating the loss and degradation of natural wetlands, it is critical to determine whether these constructed ecosystems can successfully replace the structural and functional attributes that are lost when natural wetlands are degraded or destroyed.

We made periodic measurements of macrophyte biomass production, soil development, and infauna community composition of two 20 to 25 year old constructed *S. alterniflora* marshes and paired natural marshes to evaluate the long-term development of wetland structure and function of constructed salt marshes. The constructed marshes (Pine Knoll Shores, shown in Fig. 1; Snow's Cut) are among the oldest successful plantings in the United States and were the focus of considerable research on macrophyte productivity, soil development and benthic infauna communities during the first 10–15 yr after establishment.

Methods

Site description

Salt marsh community structure (macrophyte biomass, benthic infauna) and ecosystem processes (wetland soil development, organic C, N, and P accumulation) were measured in two constructed *S. alterniflora* marshes (Pine Knoll Shores, Snow's Cut) and in paired natural *S. alterniflora* marshes in North Carolina (Fig. 2). Pine Knoll Shores was established in 1974 for shoreline erosion control along Bogue Sound whereas Snow's Cut (established 1971) was established for stabilization of dredged material. The Pine Knoll Shores marshes are ~0.3 ha in size each whereas the Snow's Cut marshes ranged in size from 0.8–1.0 ha. These are separated from each other by the Cape Fear River. Tidal amplitude is 1.0 m at Pine Knoll Shores and 1.2 m at Snow's Cut. Surface water salinities are 25–35 g/kg at Pine Knoll Shores and 7–10 g/kg at Snow's Cut. The constructed marsh soils are classified as Carteret series (Typic psammaquents). The Pine Knoll Shores natural marsh soil is Carteret series also whereas the Snow's Cut natural marsh soil is classified as Lafitte series (Typic medisaprist) (USDA 1975).

At both sites, an extensive record of data on macrophyte productivity (Seneca et al. 1985, Broome et al. 1986), soils (Craft et al. 1988), and benthic invertebrates (Sacco et al. 1988, 1994) was used to evaluate the development of salt marsh structure and function over time (Table 1).

Sampling methodology

We followed the methodology used in previous studies of these sites to measure macrophyte biomass (Broome et al. 1986), macro-organic matter (MOM, the living and dead root and rhizome mat), soil nutrient pools and rates of nutrient accumulation (Craft et al. 1988), and infauna community composition (Sacco et al 1994). Aboveground biomass was measured by clipping 10 randomly selected 0.25-m^2 quadrats from each marsh at the end of the growing season (early October) in 1995 and 1996. Live material was separated from dead material, dried at 70°C, and weighed. Macro-organic matter was measured in 1995 and 1996 by collecting one core (8.5-cm-diameter by 30-cm-deep) from each quadrat after the aboveground material was clipped. The cores were separated into 0–10 and 10–30 cm depths and washed on a 2-mm mesh diameter screen. The material remaining on the screen was dried (70°C) and weighed.

We collected a second soil core (8.5 cm diameter by 30 cm deep) from each quadrat (10 per marsh) at the same time we sampled biomass in 1995. The cores were sectioned into 0–10 and 10–30 cm depths, air-dried, weighed, ground, and sieved through a 2-mm mesh diameter screen. Bulk density was calculated by weighing the air-dried cores and applying a correction factor determined by drying a subsample at 105°C. The air-

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FIG. 1. The Pine Knoll Shores constructed marsh shortly after planting with *S. alterniflora* transplants in 1974 (top) and after three years (1977; middle) and 21 years (1995; bottom).

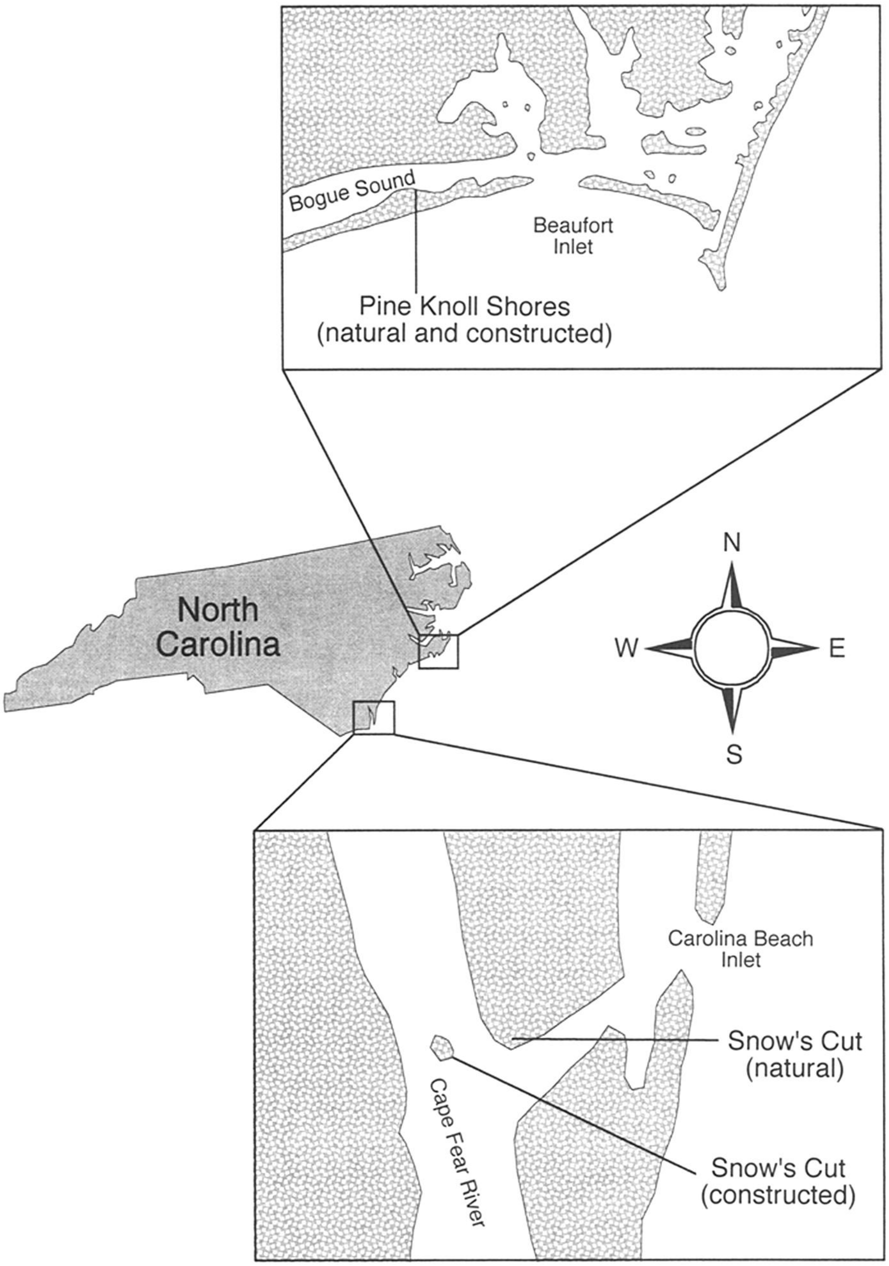

FIG. 2. Locations of the constructed (established 1971 and 1974) and natural reference salt marshes in North Carolina, USA.

dried soil was analyzed for organic matter content, organic C, total N, total P, and extractable P. Organic matter was measured by loss on ignition at 450°C (Craft et al. 1988). Total C and N were measured using a Perkin-Elmer CHN analyzer (Perkin-Elmer Corp., Foster City, California). Total P was measured in nitric-perchloric acid digests (Sommers and Nelson 1972) using the method of Murphy and Riley (1962). Extractable P was determined by the Mehlich 3 method (Mehlich 1984). Nutrient pools in the upper 30 cm of constructed and natural marshes were calculated using bulk density and nutrient concentration measurements. Rates of organic matter, C, N, and P accumulation in the constructed marshes were calculated by subtracting the soil C, N, and P pools (0–30 cm) in 1984 (Craft et al. 1988) from the C, N, and P pools in 1995 and dividing by 11 years. Organic matter, C, N, and P accumulation in the natural marshes were determined by ^{210}Pb dating (gamma spectrometry of the 46.5 keV photopeak) of 2 cm depth increments sectioned from intact soil cores (Craft and Reader 1997).

Benthic infauna were sampled to a depth of 5 cm

TABLE 1. Ecological attributes measured to evaluate salt marsh structure and function on constructed and natural *S. alterniflora* marshes.

Ecological attribute	Number of years after construction that marshes were sampled
Aboveground biomass	Pine Knoll: 1–10†, 21, 22‡ Snow's Cut: 2–5, 12§, 25, 26‡
Macro-organic matter	Pine Knoll: 1–10†, 11‖, 21, 22‡ Snow's Cut: 2–5, 12§, 14‖, 25, 26‡
Soil bulk density, organic C, total N and P	Pine Knoll: 11‖, 21‡ Snow's Cut: 14‖, 25‡
Infauna density, diversity, trophic structure	Pine Knoll: 12¶, 21‡ Snow's Cut: 15¶, 25‡

Sources: † Broome et al. (1986); ‡ this study; § Seneca et al. (1985); ‖ Craft et al. (1988) ¶ Sacco et al. (1994).

using a stainless steel corer 3 cm in diameter. The small core diameter likely biases sampling towards smaller organisms and leads to underrepresentation of larger organisms. Thirty cores were randomly collected from each marsh in June 1995, the same time of year as previous infauna sampling at these sites (Sacco et al. 1994). Cores were preserved with 10% buffered formalin and Rose Bengal (to stain the organisms) in the field and washed through a 250 μm sieve with deionized water. The organisms retained on the screen were sorted, identified to the lowest possible taxon, counted, and stored in 70% ethyl alcohol. Infauna trophic structure was determined by classifying the organisms into groups (surface feeders, subsurface deposit feeders, and carnivores) based on feeding strategy (Sacco et al. 1994).

Statistical analyses

Student's *t* test and Analysis of Variance (ANOVA-1995 and 1996 data sets) were used to test the null hypothesis that measured parameters did not differ between the paired constructed and natural marshes (SAS 1990). A two-way ANOVA based on marsh type (constructed vs. natural) and year (1995 vs. 1996) was used to test for differences in aboveground biomass. A three-way ANOVA based on marsh type, year, and depth (0–10 cm, 10–30 cm) was used to test for differences in macro-organic matter (MOM). Soil bulk density and nutrient concentrations in constructed and natural marshes were tested using a two-way ANOVA based on marsh type and depth. The Ryan-Einot-Gabriel-Welsch Multiple Range Test (REGWQ) was used to compare marsh type by year (aboveground biomass), marsh type by year by depth (belowground biomass) and marsh type by depth (bulk density and nutrients) means (SAS 1990). Student's *t* test was used to compare soil nutrient pools (0–30 cm) and benthic infauna community composition in constructed and natural marshes. Student's *t* tests also were used to compare changes in marsh soil characteristics between 1984 and 1995. All tests of significance were made at an alpha level of 0.05 unless otherwise stated.

RESULTS AND DISCUSSION

Comparison of constructed and natural marshes 20–25 years after establishment

Macrophyte productivity.—There were no differences in aboveground biomass and MOM between the Pine Knoll Shores and Snow's Cut constructed and natural marshes 22–26 yr after constructed marsh establishment (Fig. 3). However, aboveground biomass (870 ± 52 g/m^2) and MOM (3825 ± 87 g/m^2) averaged across years and marshes at Snow's Cut was substantially higher than at the Pine Knoll Shores marshes (aboveground = 643 ± 52 g/m^2, MOM = 2336 ± 197 g/m^2). Higher aboveground biomass and MOM in the Snow's Cut marshes likely reflects increased productivity subsidized by freshwater flow, sediment, and nutrients from the Cape Fear River (Good et al. 1982). The Pine Knoll Shores marshes are fringing (shoreline) marshes located on the backside of a barrier island and do not receive as large a large volumes of freshwater and associated sediment and nutrients as the Snow's Cut marshes. In our natural and constructed marshes, most MOM was in the 0–10 cm depth. Typically, salt marshes concentrate most roots and rhizomes in the surface soil (Broome et al. 1986, Craft et al. 1988) in order to obtain oxygen for respiration (NRC 1995).

Soil bulk density and nutrient concentrations.— Except for extractable P, there was no difference in the measured soil parameters (bulk density, organic matter, organic C, N, P, C:N, and N:P between the constructed and natural marshes at Pine Knoll Shores [Table 2]). Extractable P was higher (10–30 cm depth only) in the constructed marsh than the natural marsh (Table 2) and may reflect increased P loadings from lawns and septic fields adjacent to the marsh. The soils at Pine Knoll Shores are mineral soils (Typic Psammaquents; Craft et al. 1988) with relatively high bulk density (>1.00 g/cm^3) and low organic matter (<3%), organic C (<1.4%), and N (<0.10%). At both marshes, bulk density increased and organic matter and nutrients decreased with depth in most cases (Table 2).

In contrast to Pine Knoll Shores, the constructed

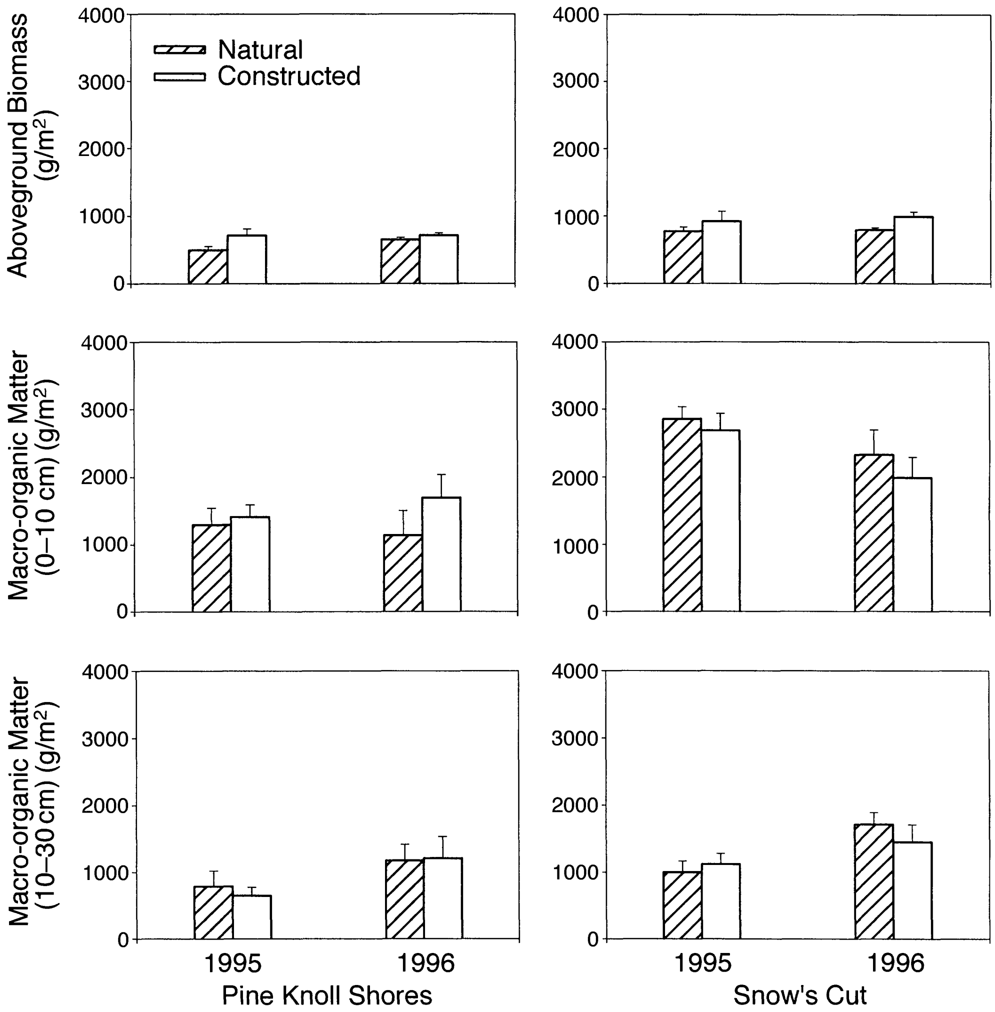

FIG. 3. Mean +1 SE aboveground and macro-organic matter (MOM; at depths of 0–10 cm and 10–30 cm) end-of-season biomass in constructed and natural marshes in 1995 and 1996 (n = 10).

marsh at Snow's Cut had significantly higher bulk density and lower organic matter, organic C, and N than the natural marsh (Table 2). Except for the 10–30 cm depth, where the natural marsh had more total P, there was no significant difference in soil P between the constructed and natural marshes at this site (Table 2). The natural marsh at Snow's Cut is a deep (>3 m) organic soil (Typic Medisaprist) with low bulk density (<0.30

TABLE 2. Mean bulk density, organic matter, organic carbon, nitrogen, phosphorus, extractable P, C:N, and N:P (± 1 SE) in constructed and natural marsh soils.

Location	Marsh type	Depth (cm)	Bulk density (g/cm³)	Organic matter (%)	Organic C (%)	Nitrogen (%)
Pine Knoll	Constructed	0–10	1.05 ± 0.10[a]	2.26 ± 1.27[a,b]	1.02 ± 0.57[a,b]	0.07 ± 0.04[a,b]
		10–30	1.39 ± 0.05[b]	1.37 ± 0.39[b]	0.62 ± 0.18[b]	0.02 ± 0.01[b]
	Natural	0–10	1.00 ± 0.06[a]	3.06 ± 0.38[a]	1.38 ± 0.17[a]	0.09 ± 0.02[a]
		10–30	1.39 ± 0.06[b]	0.91 ± 0.32[b]	0.41 ± 0.14[b]	0.01 ± 0.01[b]
Snow's Cut	Constructed	0–10	0.56 ± 0.10[b]	8.91 ± 2.01[c]	4.01 ± 0.90[c]	0.26 ± 0.10[c]
		10–30	1.08 ± 0.05[c]	1.13 ± 0.22[d]	0.51 ± 0.10[d]	0.03 ± 0.01[d]
	Natural	0–10	0.31 ± 0.02[a]	21.23 ± 2.04[b]	9.55 ± 0.92[b]	0.49 ± 0.02[b]
		10–30	0.27 ± 0.03[a]	41.80 ± 5.75[a]	18.81 ± 2.59[a]	0.73 ± 0.07[a]

Note: Means (n = 10) within the same location followed by the same superscript letter are not significantly different (P > 0.05) according to the Ryan-Einot-Gabriel-Welsch Multiple Range Test.

TABLE 3. Mean (± 1 SE; n = 10) benthic infauna density, number of taxa, species richness, and Shannon's diversity index (H) of constructed and natural marshes.

Location	Marsh type	Density (no. organisms/m²)	Number of taxa (no. organisms/7.07 cm²)	Species richness (no. taxa/ marsh)	Shannon's Index (H)
Pine Knoll	Constructed	32 210 ± 4470*	5.78 ± 0.37***	17	1.96
	Natural	18 670 ± 3620	2.83 ± 0.26	15	1.09
Snow's Cut	Constructed	102 200 ± 18 570***	5.70 ± 0.44	23	1.44
	Natural	30 520 ± 8180	4.80 ± 0.42	18	1.92

Asterisks indicate that mean values were significantly greater than those in the natural marshes according to Student's t test: *$P < 0.05$; ***$P < 0.001$.

g/cm³) and high organic matter content (>20%). Carbon-14 dating of the basal peat indicates that organic matter deposition and wetland formation began ~2500 yr BP (C. B. Craft, *unpublished data*). In the natural marsh, bulk density, organic matter, organic C, and N were constant or increased from the 0–10 cm to the 10–30 cm depth, whereas, in the constructed marsh, bulk density increased and organic matter, organic C, and N decreased with depth (Table 2). Lower organic matter and N content in the surface soil of the natural marsh likely reflects increased tidal exchange and sediment deposition caused by widening and deepening of the Cape Fear river channel in 1889 (Hackney and Yelverton 1990) as well as construction of Snow's Cut (part of the Intercoastal waterway) during the 1930s (see Fig. 2). In both Snow's Cut marshes, total and extractable P generally decreased from the 0–10 cm to the 10–30 cm depth (Table 2).

Carbon : nitrogen ratios at both Pine Knoll Shores and Snow's Cut were lower in the 0–10 cm depth (14–23) and generally increased in the 10–30 cm depth (Table 2). Carbon : nitrogen ratios >20 are indicative of microbial immobilization of available soil N whereas C:N <20 suggests that microbial needs are satisfied and sufficient N is available for plant uptake (Tisdale et al. 1985). With the exception of the Snow's Cut constructed marsh, the C:N ratios of our marsh soils suggest that, below the 10-cm depth, limited N is available for plant uptake. Nitrogen : phosphorus ratios ranged from 1 to 39 and, except for the Snow's Cut natural marsh, generally decreased with depth (Table 2). Nitrogen : phosphorus ratios >30–35 indicate P limitation whereas N:P <30–35 indicate N limitation (Verhoeven et al. 1996). The low N:P ratios (1–17) in most of our marshes suggest that N is the primary limiting nutrient in these ecosystems, as has been documented by salt marsh fertilization studies (Sullivan and Daiber 1974, Broome et al. 1975, Valiela and Teal 1975). The high N:P ratios of the natural marsh at Snow's Cut (17–39) suggest that this marsh, like many freshwater marshes, may be P limited. But, like the high soil organic matter and N content in this marsh, the high N:P ratio may be a relic from the past when this marsh was less saline and inundated by freshwater.

TABLE 2. Extended.

Phosphorus (μg/g)	Extractable P (μg/cm³)	C:N (atomic mass ratio)	N:P (atomic mass ratio)
477 ± 45[a,b]	102 ± 8[a,b]	14:1 ± 2[a]	7:1 ± 3[a]
417 ± 36[b]	107 ± 6[a]	31:1 ± 5[b,c]	1:1 ± 1[a]
574 ± 33[a]	72 ± 8[b]	21:1 ± 2[a,b]	3:1 ± 1[a]
474 ± 28[a,b]	24 ± 5[c]	48:1 ± 12[c]	1:1 ± 1[a]
446 ± 77[b,c]	40 ± 4[a]	18:1 ± 1[a]	11:1 ± 1[a]
96 ± 13[d]	38 ± 5[a]	18:1 ± 1[a]	7:1 ± 1[a]
632 ± 23[a,b]	33 ± 4[a]	23:1 ± 1[b]	17:1 ± 1[b]
411 ± 14[c]	12 ± 1[b]	29:1 ± 2[b]	39:1 ± 4[c]

Benthic infauna.—Infauna density was significantly higher in the constructed marshes than in the natural marshes (Table 3). At Pine Knoll Shores, infauna density in the constructed marsh was 70% higher in the natural marsh, whereas, at Snow's Cut, total density was 330% higher than in the natural marsh. The high density of infauna in the Snow's Cut constructed marsh may be due to its increased accessibility and recruitment of these organisms. The constructed marsh is located within the channel of the Cape Fear River (see Fig. 2) where tidal and river currents may enhance recruitment of planktonic larvae and swimming adults from upstream. The natural marsh also is tidally influenced but is not positioned to interact with the volume of water that the constructed marsh receives.

The Pine Knoll Shores constructed marsh also contained significantly more taxa than the natural marshes (Table 3). Previous shorter-term studies indicate that infauna species richness develops relatively quickly in constructed marshes. Levin et al. (1996) reported that, 4 yr after establishment, a constructed salt marsh had species richness that was similar to a natural reference marsh. The constructed marsh at Snow's Cut had the highest species richness (23), whereas species richness was lowest in the Pine Knoll Shores natural marsh (15). Shannon's diversity index (H) ranged from 1.09 at the Pine Knoll Shores natural marsh to 1.96 at the constructed marsh with no clear difference between the constructed and natural marshes.

Comparison of the six dominant taxa revealed that, at Pine Knoll Shores, the constructed marsh contained higher numbers of *Manayunkia, Streblospio, Capitella,*

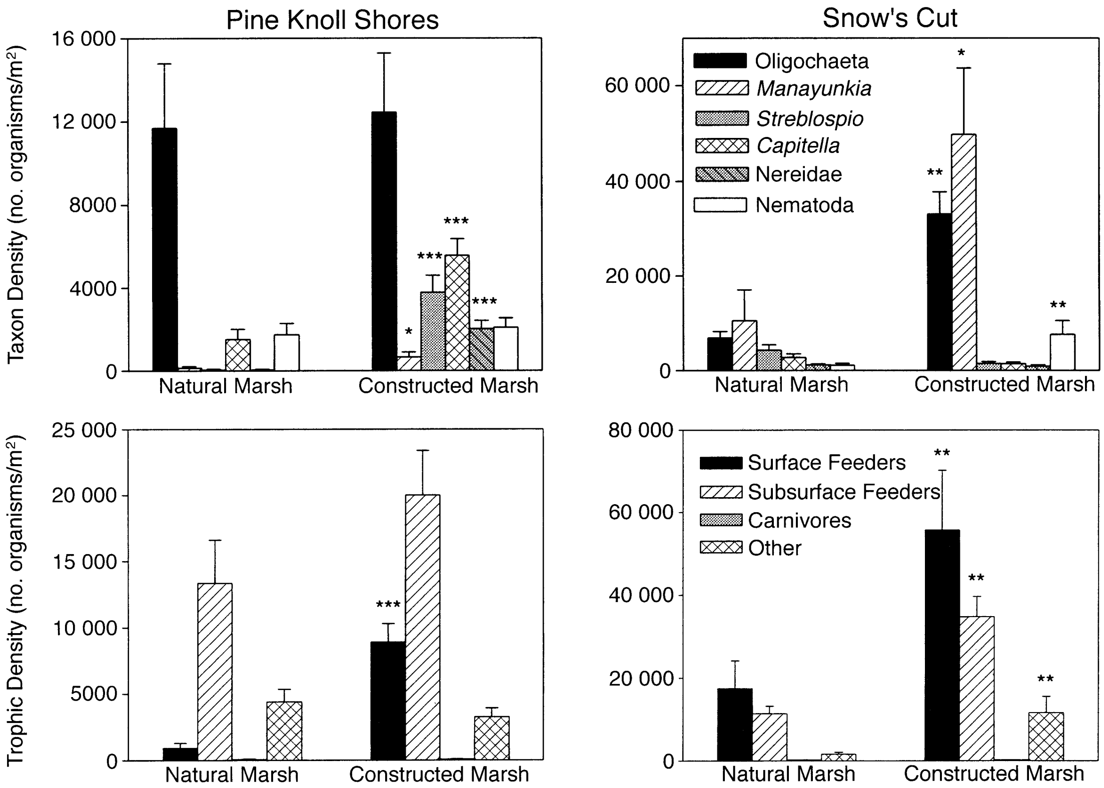

FIG. 4. Mean density (+1 SE) of the six dominant taxa and trophic composition of benthic infauna in constructed and natural marshes in 1995. Significant differences according to Student's t test are indicated: $*P < 0.05$; $**P < 0.01$; $***P < 0.001$.

and *Nereidae* than the natural marsh (Fig. 4). There was no difference in the number of oligochaetes, which were the dominant taxa in both marshes, or numbers of nematodes between the marshes at Pine Knoll Shores. At Snow's Cut, the constructed marsh contained greater numbers of *Manayunkia,* oligochaetes, and nematodes (Fig. 4). In both Snow's Cut marshes, *Manayunkia* was the dominant taxa followed by oligochaetes. Levin et al. (1996) observed that a 4-yr-old constructed salt marsh had greater numbers of *Streblospio* and *Manayunkia,* whereas oligochaetes were dramatically underrepresented as compared to the natural marsh. Infauna that produce planktonic larvae (e.g., *Streblospio, Capitella*) are early colonizers of salt marshes, whereas organisms that are direct developers (e.g., nondispersing adults including oligochaetes and *Manayunkia*) are slower to colonize (Levin et al. 1996). Even after 17 yr, constructed marshes often have lower numbers of oligochaetes (Sacco et al. 1994).

Comparison of trophic groups revealed that both constructed marshes had significantly higher densities of surface deposit feeders than the natural marshes (Fig. 4). At Pine Knoll Shores, the density of surface deposit feeders was 10 times higher in the constructed marsh ($8900/m^2$) than in the natural marsh ($900/m^2$). Likewise, the constructed marsh at Snow's Cut contained three times as many surface ($56\,000/m^2$) and subsurface deposit feeders ($34\,800/m^2$) as the natural marsh (surface feeders = $17\,500/m^2$, subsurface feeders = $11\,400/m^2$). There was no difference in the density of subsurface deposit feeders between the Pine Knoll Shores marshes (Fig. 4). Previous studies of younger (<17 yr old) constructed marshes report lower densities of subsurface deposit feeders and attribute this to lower organic matter and coarser texture of the soil (Moy and Levin 1991, Sacco et al. 1994, Levin et al. 1996). Our results suggest that sufficient soil organic matter is present in our 20- to 25-yr-old constructed marshes to support infauna communities that are comparable to those of natural salt marshes.

The proportion of subsurface deposit feeders was similar in constructed and natural marshes and accounted for 58–65% of the total density at Pine Knoll Shores and 46–49% at Snow's Cut. We also observed no difference in the proportion of surface deposit feeders (39–48%) in the Snow's Cut marshes. However, the constructed marsh at Pine Knoll Shores contained a much higher proportion of surface deposit feeders (32%) than the natural marsh (5%). The natural marsh at this site is undergoing lateral erosion as evidenced by undercutting at the water's edge and deposition of shell fragments on the marsh surface. It is possible that high wave energy and deposition of shell material make

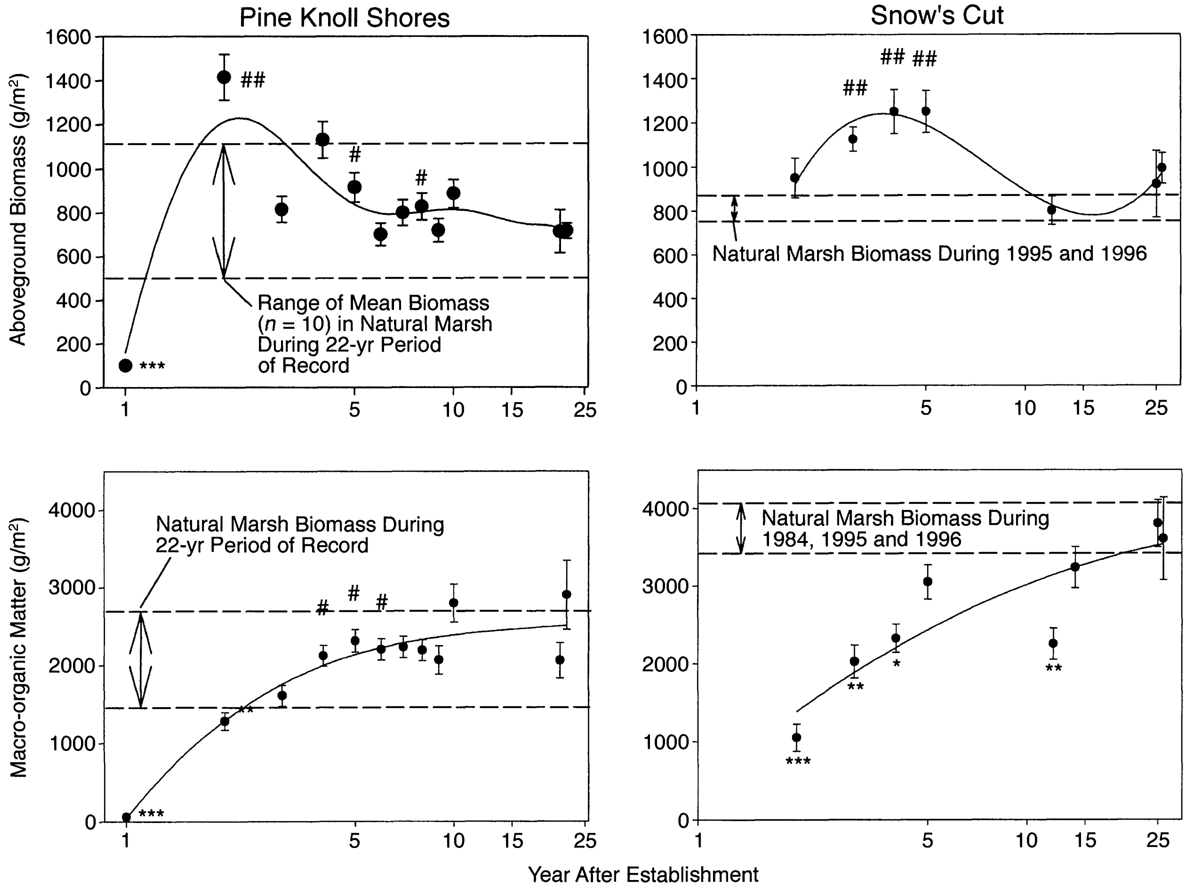

FIG. 5. Patterns of development of end-of-season (a) aboveground standing crop biomass and (b) macro-organic matter (MOM) in constructed and natural marshes during the 22–26 yr period of record. A polynomial function was used to fit the curves. Data are from Seneca et al. (1985), Broome et al. (1986), Craft et al. (1988), and this study. Values that are significantly greater that those in the natural marsh for the same year according to Student's t test are indicated as follows: $^{\#}P < 0.05$; $^{\#\#}P < 0.001$. Values that are significantly less than those in the natural marsh for the same year according to Student's t test are indicated by: $^{*}P < 0.05$; $^{**}P < 0.01$.

it difficult to maintain a large population of surface deposit feeders in this marsh.

We were unable to categorize the trophic status of some taxa, so these organisms were grouped as "other." Comparison of this "other" category revealed no difference between the constructed and natural marshes at Pine Knoll Shores. However, the constructed marsh at Snow's Cut had significantly higher densities of "Others" (Fig. 4), which was due primarily to increased numbers of nematodes and infauna such as mites (*Acarina*) and springtails (*Collembola*). Taxa in the "other" group that were common in both constructed and natural marshes also included Harpacticoid copepods, gastropods, and Tanaids.

Development of ecological attributes over time on constructed marshes

In the constructed marshes, aboveground biomass of *Spartina* developed quickly, becoming equivalent to nearby natural marshes within two to three growing seasons (Fig. 5). Macro-organic matter required longer to become equivalent to natural marshes. Three to five years elapsed before constructed marshes developed MOM stocks equivalent to natural marshes (Fig. 5). Interestingly, once the macrophyte community became established, the constructed marshes had greater aboveground biomass than the natural marshes. At Pine Knoll Shores, both aboveground biomass and MOM were significantly higher in the constructed marsh, although intermittently, during the first 10 yr (Fig. 5). The Snow's Cut constructed marsh also had significantly higher aboveground biomass than in the natural marsh during the first 3–5 yr. Previous studies of constructed marshes in North Carolina reported that aboveground biomass typically develops to levels comparable to natural marshes within 1–3 yr, whereas belowground biomass and MOM require longer, usually 3–5 yr (Broome et al. 1986, Broome and Craft, *in press*). This study, however, is the first to document the development and maintenance of *S. alterniflora* aboveground biomass and MOM on constructed marshes that are nearly a quarter of a century old.

TABLE 4. Mean (n = 10) bulk density, organic C, total N, and total P (0–30 cm) of constructed marsh soils in 1984 and 1995 (1984 data are from Craft et al. [1988]).

Marsh	Year	Bulk density (g/cm³)	Organic C (%)	Total N (%)	Total P (μg/g)
Pine Knoll Shores	1984	1.40 ± 0.02†	0.31 ± 0.02*	0.02 ± 0.001†	434 ± 22
	1995	1.28 ± 0.05	0.75 ± 0.18	0.04 ± 0.01	437 ± 25
Snow's Cut	1984	1.06 ± 0.02*	0.95 ± 0.07†	0.04 ± 0.002**	138 ± 9*
	1995	0.90 ± 0.06	1.67 ± 0.33	0.11 ± 0.02	213 ± 30

Note: Statistical significance of the difference between 1984 and 1995 mean values was assessed according to Student's t test: †$P < 0.10$; *$P < 0.05$; **$P < 0.01$.

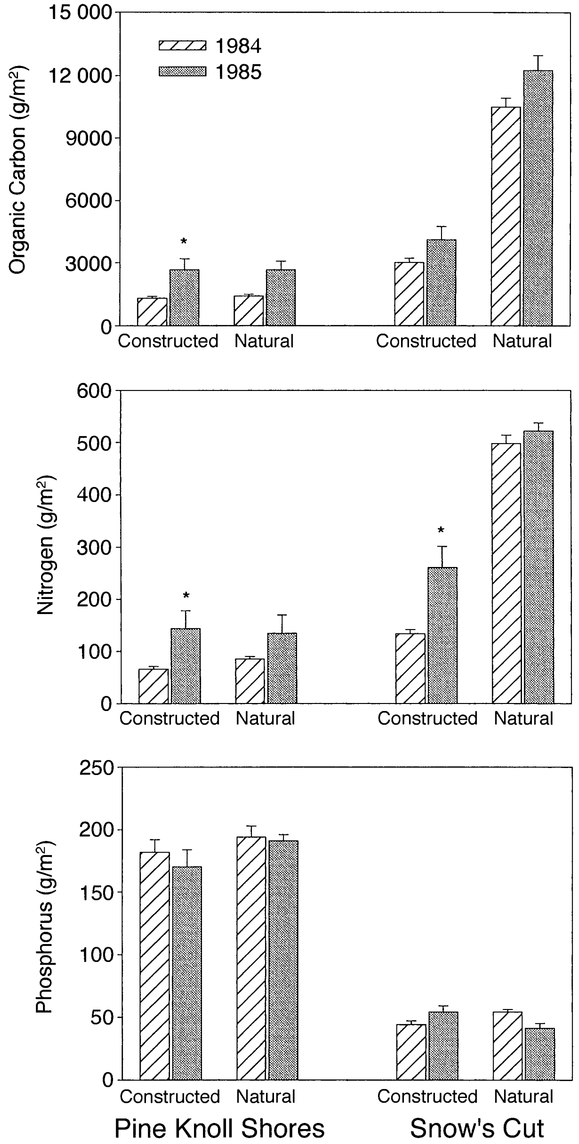

FIG. 6. Mean (+1 SE) organic C, total N, and P pools (0–30 cm depth) of constructed and natural marsh soils in 1984 and 1995. An asterisk (*) indicates a significant increase ($P < 0.05$) in the pool size between 1984 and 1995 according to Student's t test. The 1984 data are from Craft et al. (1988).

In the constructed marshes, soil bulk density decreased and organic C and N increased between 1984 and 1995 (Table 4). An important attribute of wetland soil development is the accumulation of organic matter and nutrients (Friedman and Dewitt 1978, Craft et al. 1988) and the concomitant decrease in bulk density resulting from the low particle density of organic matter (Craft et al. 1993). The amount of organic C and total N sequestered in constructed marsh soils increased between 1984 and 1995 (Fig. 6). Both marshes exhibited a significant increase in the amount of N stored, whereas organic C storage increased significantly only at Pine Knoll Shores. Constructed and natural marsh phosphorus pools did not change between 1984 and 1995 (Fig. 6) which is not surprising since N, not P, tends to be the primary limiting nutrient in salt marsh ecosystems (Broome et al. 1975, Sullivan and Daiber 1974, Valiela and Teal 1974). An interesting difference between the two sites was the large amount of P sequestered at the Pine Knoll Shores marshes (Fig. 6). These marshes contain substantial amounts of oyster shells in the soil (0.04% to 0.13% carbonate-C) (Craft et al. 1991*a*) that serve as a substrate for sorption of P from the water column (Craft et al. 1988).

Comparison of the two natural marshes revealed that the Snow's Cut marsh contained four to five times more organic C (10.5–12.3 kg/m²) and N (500–520 g/m²) than the marsh at Pine Knoll Shores (organic C = 1.4–2.7 kg/m², N = 85–135 g/m²) (Fig. 6). The soils underlying the Snow's Cut marsh are 2500 yr-old Histosols with low soil bulk density (0.28 g/cm³), high organic C (14%), and peat depth of 2.5–3 m (see *Results and discussion: Soil bulk density and nutrient concentrations*). In contrast, the natural marsh at Pine Knoll Shores is a geologically young wetland as evidenced by the high soil bulk density (1.28 g/cm³), low organic C (<1%), and absence of organic rich soil horizons (Table 4).

Even though the Snow's Cut natural marsh contained larger reservoirs of soil organic C and nutrients, organic C accumulation was similar in the paired constructed and natural marsh soils (Table 5). The percentage of net primary production buried annually in the soil also was similar in the two marsh types. Nitrogen accumulation, however, was two to five times higher in the constructed marshes (Table 5). Young

TABLE 5. Net primary production (NPP) and organic C, total N, and total P accumulation in constructed and natural marsh soils. Numbers in parentheses are the percentages of NPP buried annually.

Marsh	NPP† ($g\ C\cdot m^{-2}\cdot yr^{-1}$)	Organic C ($g\cdot m^{-2}\cdot yr^{-1}$)	Total N ($g\cdot m^{-2}\cdot yr^{-1}$)	Total P ($g\cdot m^{-2}\cdot yr^{-1}$)
Pine Knoll Shores				
Constructed‡	601	125 (21)	7.1	0
Natural‡	607	115 (19)	4.5	0
Snow's Cut				
Constructed‡	803	99 (12)	11.5	0.9
Natural‡	658	159 (24)	2.2	0
Natural§	···	91 (14)	3.9	0.3

† NPP is calculated as [aboveground standing crop biomass (mean of 1995 and 1996) + 1.1 × (belowground biomass)] × 0.40. Assumptions are that belowground productivity is 1.1 × aboveground standing crop (based on the increase in belowground biomass from October 1974 to October 1975 in the restored marsh and aboveground standing crop measured in October 1975; from Broome et al. 1986) and carbon content of biomass is 40%.

‡ Accumulation rates of constructed and natural marshes are calculated as the difference in organic C and total N and P pools between 1984 and 1995 divided by 11 years (from Fig. 7).

§ Long-term (100 yr) accumulation rates of the old natural marsh (Snow's Cut) are calculated based on accretion rates determined by ^{210}Pb (2.3 mm/yr) and soil bulk density (0.28 g/cm^3), organic C (14.2%), total N (0.61%), and total P (522 μg/g) (0–30 cm). Long-term accumulation rates based on ^{210}Pb could not be calculated for the Pine Knoll Shores natural marsh because of the non-monotonic decrease in ^{210}Pb with depth.

ecosystems typically are open with respect to nutrient cycling and become more closed as succession proceeds and nutrients accumulate in biomass and soil organic matter (Odum 1969, Vitousek and Reiners 1975, Craft 1997). This theory is supported by higher soil N accumulation in constructed marshes as well as significant uptake of NH_4-N and PO_4-P during tidal inundation of these wetlands (Craft et al. 1989). There was little or no accumulation of phosphorus in constructed and natural marshes at both sites (Table 5) which probably reflects the abundant soil P reservoirs (Fig. 6) that provide ample P to support biological activity.

Comparison of benthic infauna communities revealed that, in 1986, there was no difference in infauna densities between the constructed and natural marshes (Table 6). Other studies, however, reported significantly lower densities of benthic infauna in constructed than natural marshes 3–16 yr after marsh establishment (Moy and Levin 1991, Sacco et al. 1994, Levin et al. 1996, Scatolini and Zedler 1996). By 1995, infauna densities were significantly greater in the constructed marshes than in the natural marshes (Table 6). With the exception of surface deposit feeders at Pine Knoll Shores (in 1995), there was no difference in infauna trophic composition between constructed and natural marshes or between the 1986 and 1995 sampling years (Table 6). In 1995, both marshes at Pine Knoll Shores were dominated by subsurface deposit feeders, but the constructed marsh contained more surface deposit feeders than the natural marsh (Table 6), especially the polychaetes *Streblospio benedicti* and *Nereis* spp. Con-

TABLE 6. Mean (± 1 SE) benthic infauna density and trophic composition (surface and subsurface deposit feeders) of constructed and natural marshes in 1986 and 1995 (1986 data are from Sacco et al. [1994]).

Marsh	Year	Density (no. organisms/m^2)	Surface deposit feeders (%)	Subsurface deposit feeders (%)
Pine Knoll Shores				
Constructed	1986	20 470 ± 2480	45 ± 13	55 ± 17
Natural	1986	18 130 ± 2390	62 ± 20	38 ± 16
Constructed	1995	32 210 ± 4470*	28 ± 4***	62 ± 10
Natural	1995	18 670 ± 3620	5 ± 2	71 ± 17
Snow's Cut				
Constructed	1986	49 410 ± 6310	41 ± 18	59 ± 18
Natural	1986	69 200 ± 9170	66 ± 24	34 ± 6
Constructed	1995	102 200 ± 18 570***	54 ± 14	34 ± 5
Natural	1995	30 520 ± 8180	57 ± 22	37 ± 6

Note: Statistical significance of differences from the natural marsh were assessed according to Student's t test: *$P < 0.05$; ***$P < 0.001$.

structed salt marshes often contain a greater proportion of surface deposit feeders than natural marshes, perhaps because the low organic content and high bulk density of constructed marsh soils do not provide the food, refuge, and ease of burrowing characteristic of older, higher organic matter natural marshes (Moy and Levin 1991, Levin et al. 1996).

Regression analysis of data from this study and from previously published work revealed that, in constructed marshes, infauna density increased with increasing soil organic C ($P = 0.001$) and also with marsh age ($P = 0.05$) (Fig. 7a and b). The goodness-of-fit of both regressions was due, in large part, to the increase in organic C and infauna density in our two constructed marshes between 1984–1986 and 1995. There also was a significant relationship between soil C:N and marsh age (Fig. 7c; $P = 0.01$). Generally, C:N decreased with increasing marsh age and achieved equivalence to natural marshes after 10–25 yr.

Comparison with natural Spartina alterniflora *marshes*

Comparison of ecological attributes in our constructed marshes and natural *S. alterniflora* marshes of the U.S. Atlantic and Gulf coasts revealed that the constructed marshes possessed similar aboveground biomass, MOM, and soil C:N (Table 7). However, soil organic C, N, and P concentrations (0–30 cm depth) were lower than in natural *Spartina* marshes. Rates of organic C, N, and P accumulation in constructed marshes were higher than in natural marshes of North Carolina but lower than in *Spartina* marshes in Louisiana (Table 7). Higher organic C and nutrient accumulation in Louisiana natural marshes likely reflects increased sediment and nutrient deposition from riverine sources (e.g., Mississippi River) (DeLaune et al. 1981) and the resultant increase in *Spartina* productivity and organic matter accumulation. In the constructed marshes, benthic infauna density was similar to or higher than in natural marshes on the Atlantic and Gulf coasts (Table 7) whereas species richness was comparable to natural marshes. These findings suggest that, after 20–25 yr, constructed marshes possess macrophyte productivity, benthic infauna communities and organic C and nutrient accumulation similar to natural marshes. However, soil nutrient reservoirs are smaller in constructed marshes than in many older natural *Spartina* marshes.

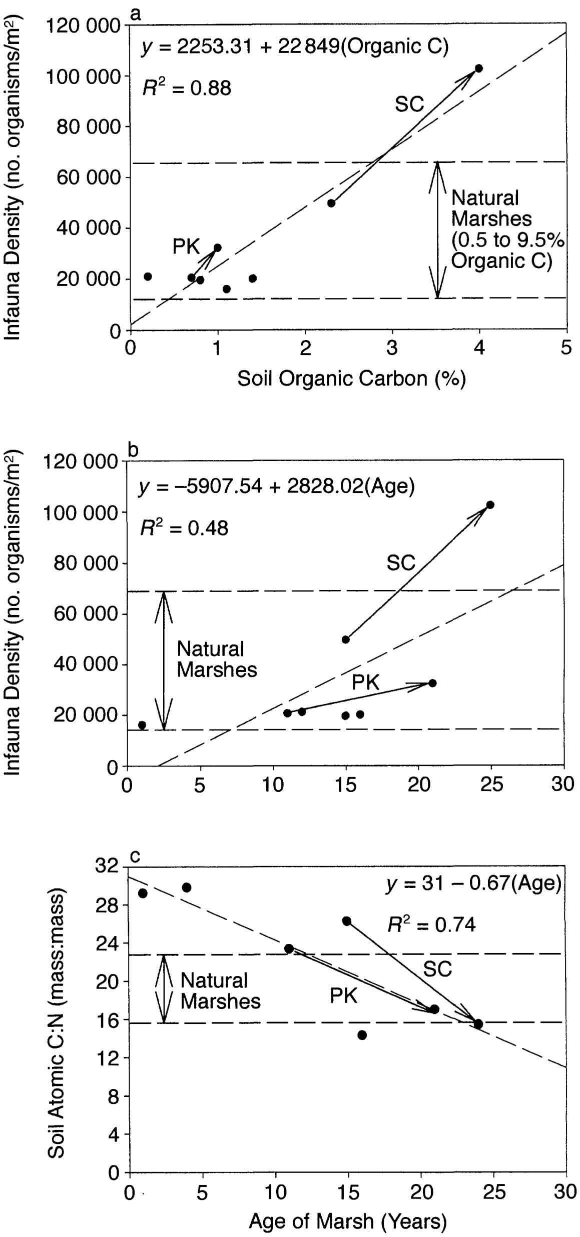

FIG. 7. Regressions of (a) infauna density (0–5 cm) vs. soil organic C (0–10 cm), (b) infauna density (0–5 cm) vs. marsh age, and (c) soil C:N (0–10 cm) vs. marsh age in constructed marshes. Arrows represent the change in infauna density, soil organic C and soil C:N between 1984–1986 and 1995 at the constructed marsh sites. Additional soil organic C data (0–5 cm) in regressions (a) and (b) are from Sacco et al. (1994) and assume that soil organic matter is 45% carbon. Additional soil C:N data are from Craft et al. (1988).

CONCLUSIONS

Succession theory predicts that various ecological attributes change over time. Such predictions include increased biomass and nonliving organic matter, and closure of nutrient cycles over time (Odum 1969). Information collected during 25 yr of ecosystem development on constructed salt marshes supports several of these predictions, including increased nonliving organic matter and nutrient (N) conservation in the older constructed marshes and in natural marshes. Likewise, young constructed marshes have more open nutrient cycles than natural marshes as evidenced by the higher rates of N accumulation. Biomass accumulation of macrophytes, however, is greatest during the early-to-middle stages instead of the later stages of ecosystem development. Once macrophytes become established

TABLE 7. Comparison of *Spartina alterniflora* biomass, macro-organic matter (MOM) soil nutrients, and benthic infauna communities in 20–25 year old constructed marshes (NC) and natural *S. alterniflora* marshes along the coasts of North Carolina (NC), the Southeast (SE: Delaware, Maryland, Virginia, South Carolina, Georgia), the Northeast (NE: New Jersey, Connecticut, Massachusetts), and the Gulf of Mexico (Florida, Mississippi, Louisiana, Texas), USA.

	Constructed	Natural marshes			
	NC†	NC	SE	NE	Gulf
Biomass					
Aboveground (g/m²)‡	713–992	363–1930	568–2335	592–1592	428–2000
MOM (0–30 cm; g/m²)§	2059–3609	1574–6730	2100	2520–11 400	
Soil (0–30 cm)‖					
Organic C (%)	0.7–1.7	0.5–15.7	0.2–28		1.2–16.4
Nitrogen (%)	0.04–0.11	0.04–0.65			0.46–1.17
Atomic C:N (mass : mass)	18–25	18–20			12.0–20.0
Phosphorus (μg/g)	213–437	128–786			500–833
Soil accumulation¶					
Organic C ($g \cdot m^{-2} \cdot yr^{-1}$)	99–125	21–159			183–393
Nitrogen ($g \cdot m^{-2} \cdot yr^{-1}$)	7.1–11.5	1.3–4.5			11.0–23.1
Phosphorus ($g \cdot m^{-2} \cdot yr^{-1}$)	0–0.9	0–0.4			0.7–2.3
Benthic infauna#					
Density	32 210–102 200	5000–84 500	1000–19 900		2900–70 000
Species richness	17–23	6–18	3–21		8–43

† This study.

‡ "Tall" *Spartina*; from Broome et al. (1975), Steever et al. (1976), Turner (1976), Valiela et al. (1976), White et al. (1978), DeLaune et al. (1979), Morris et al. (1990), Craft and Reader (1997), and this study.

§ From Valiela et al. (1976), Gallagher and Plumley (1979), Smith et al. (1979), Craft and Reader (1997), and this study.

‖ From Broome et al. (1975), Coultas and Gross (1975), Darmody and Foss (1978), DeLaune et al. (1979, 1981), Lindau and Hosner (1981), Hatton et al. (1982), Craft et al. (1988), Griffin and Rabenhorst (1989), Moy and Levin (1991), Osgood and Zieman (1993), Sacco et al. (1994), Craft and Reader (1997), and this study.

¶ From DeLaune and Patrick (1980), DeLaune et al. (1981), Hatton et al. (1982), Smith et al. (1983), Craft et al. (1993), Craft and Reader (1997), and this study.

From Cammen (1976) (0–13 cm), Rader (1984) (0–10 cm), LaSalle et al. (1991) (0–10 cm), Moy and Levin (1991) (0–4 cm), Minello and Zimmerman (1992) (0–5 cm), Minello et al. (1994) (0–5 cm), Sacco et al. (1994) (0–5 cm), Havens et al. (1995) (no depth given), Levin et al. (1996) (0–6 cm), Craft and Reader (1997) (0–5 cm), Levin et al. (1998) (0–6 cm), and this study (0–5 cm).

(usually in the first 1–3 yr), biomass accumulation peaks during the first decade of marsh development, similar to the aggradation phase of forest succession (Bormann and Likens 1979). Development of the benthic infauna community lags behind the producer community, but 15–25 yr after marsh establishment, species and trophic composition are similar to natural marshes whereas densities are higher than in natural marshes.

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LITERATURE CITED

Bormann, F. H., and G. E. Likens. 1979. Catastrophic disturbance and the steady state in northern hardwood forests. American Scientist **67**:660–669.

Broome, S. W., and C. B. Craft. *In press.* Reclamation of coastal marsh areas. *In* R. I. Barnhisel, W. L. Daniels, and R. G. Darmody, editors. Reclamation of drastically disturbed lands. American Society of Agronomy special publication. American Society of Agronomy, Madison, Wisconsin, USA.

Broome, S. W., C. B. Craft, and E. D. Seneca. 1988*b*. Creation and development of brackish-water marsh habitat. Pages 197–205 *in* J. Zelazny and J. C. Feierabend, editors. Increasing our wetland resources. National Wildlife Federation, Washington, D.C., USA.

Broome, S. W., E. D. Seneca, and W. W. Woodhouse, Jr. 1986. Long-term growth and development of transplants of the salt-marsh grass *Spartina alterniflora.* Estuaries **9**:63–74.

Broome, S. W., E. D. Seneca, and W. W. Woodhouse, Jr. 1988*a*. Tidal salt marsh restoration. Aquatic Botany **32**:1–22.

Broome, S. W., W. W. Woodhouse, Jr., and E. D. Seneca. 1975. The relationship of mineral nutrients to growth of *Spartina alterniflora* in North Carolina: II. The effects of N, P and Fe fertilizers. Soil Science Society of America Proceedings **39**:301–307.

Cammen, L. M. 1976. Abundance and production of macroinvertebrates from natural and artificially established salt marshes in North Carolina. American Midland Naturalist **96**:487–493.

Coultas, C. L., and E. R. Gross. 1975. Distribution and properties of some tidal marsh soils of Apalachee Bay, Florida. Soil Science Society of America Proceedings **39**:914–919.

Craft, C. B. 1997. Dynamics of nitrogen and phosphorus retention during wetland ecosystem succession. Wetlands Ecology and Management **4**:177–187.

Craft, C. B., S. W. Broome, and E. D. Seneca. 1988. Nitrogen, phosphorus and organic carbon pools in natural and transplanted marsh soils. Estuaries **11**:272–280.

Craft, C. B., S. W. Broome, and E. D. Seneca. 1989. Exchange of nitrogen, phosphorus and organic carbon between transplanted marshes and estuarine waters. Journal of Environmental Quality **18**:206–211.

Craft, C. B., and J. M. Reader. 1997. Restored salt marshes: evolution of wetland structure and function over time. Final report to NOAA, National Estuarine Research Reserve System. November 30, 1997. Office of Coastal and Ocean Resource Management, NOAA, Silver Spring, Maryland, USA.

Craft, C. B., E. D. Seneca, and S. W. Broome. 1991*a*. Loss on ignition and Kjeldahl digestion for estimating organic carbon and total nitrogen in estuarine marsh soils: calibration with dry combustion. Estuaries **14**:175–179.

Craft, C. B., E. D. Seneca, and S. W. Broome. 1991*b*. Porewater chemistry of natural and created marsh soils. Journal of Experimental Marine Biology and Ecology **152**:187–200.

Craft, C. B., E. D. Seneca, and S. W. Broome. 1993. Vertical accretion in microtidal regularly and irregularly flooded estuarine marshes. Estuarine Coastal and Shelf Science **37**: 371–386.

Darmody, R. G., and J. E. Foss. 1978. Tidal marsh soils of Maryland. Maryland Agricultural Experiment Station MP 930. University of Maryland. College Park, Maryland, USA.

DeLaune, R. D., R. J. Buresh, and W. H. Patrick, Jr. 1979. Relationship of soil properties to standing crop biomass of *Spartina alterniflora* in a Louisiana marsh. Estuarine and Coastal Marine Science **8**:477–487.

DeLaune, R. D., and W. H. Patrick, Jr. 1980. Rate of sedimentation and its role in nutrient cycling in a Louisiana salt marsh. Pages 401–412 *in* P. Hamilton and K. B. Macdonald, editors. Estuarine and wetland processes with emphasis on modeling. Plenum Publishing, New York, New York, USA.

DeLaune, R. D., C. N. Reddy, and W. H. Patrick, Jr. 1981. Accumulation of plant nutrients and heavy metals through sedimentation processes and accretion in a Louisiana salt marsh. Estuaries **4**:328–334.

Friedman, R. M., and C. B. DeWitt. 1978. Wetlands as carbon and nutrient reservoirs: a spatial, historical and societal perspective. Pages 175–185 *in* P. E. Greeson, J. R. Clark, and J. E. Clark, editors. Wetland functions and values: the state of our understanding. American Water Resources Association, Minneapolis, Minnesota, USA.

Gallagher, J. L., and F. G. Plumley. 1979. Underground biomass profiles and productivity in Atlantic coastal marshes. American Journal of Botany **66**:156–161.

Gibson, K. D., J. B. Zedler, and R. Langis. 1994. Limited response of cordgrass (*Spartina foliosa*) to soil amendments in a constructed marsh. Ecological Applications **4**:757–767.

Good, R. E., N. F. Good, and B. R. Frasco. 1982. A review of primary production and decomposition dynamics of the belowground marsh component. Pages 139–157 *in* V. S. Kennedy, editor. Estuarine comparisons. Academic Press, New York, New York, USA.

Griffin, T. M., and M. C. Rabenhorst. 1989. Processes and rates of pedogenesis in some Maryland tidal marsh soils. Soil Science Society of America Journal **53**:862–870.

Hackney, C. T., and F. C. Yelverton. 1990. Effects of human activities and sea level rise on wetland ecosystems in the Caper Fear River estuary, North Carolina, USA. Pages 55–61 *in* D. F. Whigham, R. E. Good, and J. Kvet, editors. Wetland ecology and management: case studies. Kluwer, Dordrecht, The Netherlands.

Hatton, R. S., W. H. Patrick, Jr., and R. D. DeLaune. 1982. Sedimentation, nutrient accumulation and early diagenesis in Louisiana Barataria Basin coastal marshes. Pages 255–267 *in* V. S. Kennedy, editor. Estuarine comparisons. Academic Press, New York, New York, USA.

Havens, K. J., L. M. Varnell, and J. G. Bradshaw. 1995. An assessment of ecological conditions in a constructed tidal marsh and two natural reference tidal marshes in coastal Virginia. Ecological Engineering **4**:117–141.

Langis, R., M. Zalejko, and J. B. Zedler. 1991. Nitrogen assessments in a constructed and a natural salt marsh of San Diego Bay. Ecological Applications **1**:40–51.

LaSalle, M. W., M. C. Landin, and J. G. Sims. 1991. Evaluation of the flora and fauna of a *Spartina alterniflora* marsh established on dredged material in Winyah Bay, South Carolina. Wetlands **11**:191–208.

Levin, L. A., T. S. Talley, and J. Hewitt. 1998. Macrobenthos of *Spartina foliosa* (Pacific cordgrass) salt marshes in southern California: community structure and comparison to a Pacific mudflat and a *Spartina alterniflora* (Atlantic smooth cordgrass) marsh. Estuaries **21**:129–141.

Levin, L. A., D. Talley, and G. Thayer. 1996. Succession of macrobenthos in a created salt marsh. Marine Ecology Progress Series **141**:67–82.

Lindau, C. W., and L. R. Hossner. 1981. Substrate characterization of an experimental marsh and three natural marshes. Soil Science Society of America Proceedings **45**: 1171–1176.

Mehlich, A. 1984. Mehlich 3 soil test extractant: a modification of Mehlich 2 extractant. Communications in Soil Science and Plant Analysis **15**:1409–1416.

Minello, T. J., and R. J. Zimmerman. 1992. Utilization of natural and transplanted Texas salt marshes by fish and decapod crustaceans. Marine Ecology Progress Series **90**: 273–285.

Minello, T. J., R. J. Zimmerman, and R. Medina. 1994. The importance of edge for natant macrofauna in a created salt marsh. Wetlands **14**:184–198.

Morris, J. T., B. Kjerfve, and J. M. Dean. 1990. Dependence of estuarine productivity on anomalies in sea level rise. Limnology and Oceanography **35**:926–930.

Moy, L. D., and L. A. Levin. 1991. Are *Spartina* marshes a replaceable resource? A functional approach to evaluation of marsh creation efforts. Estuaries **14**:1–16.

Murphy, J., and J. P. Riley. 1962. A modified single solution method for the determination of phosphate in natural waters. Analytica Chimica Acta **27**:31–36.

NRC (National Research Council). 1995. Wetlands characteristics and boundaries. National Academy Press, Washington, D.C., USA.

Odum, E. P. 1969. The strategy of ecosystem development. Science **164**:262–270.

Osgood, D. T., and J. C. Zieman. 1993. Factors controlling aboveground *Spartina alterniflora* (smooth cordgrass) tissue element composition and production in different-age barrier island marshes. Estuaries **16**:815–826.

Race, M. S., and D. R. Christie. 1982. Coastal zone development: mitigation, marsh creation and decision making. Environmental Management **6**:317–328.

Rader, D. N. 1984. Salt marsh benthic invertebrates: small-scale patterns of distribution and abundance. Estuaries **7**: 413–420.

Rulifson, R. A. 1991. Finfish utilization of man-initiated and adjacent natural creeks of South Creek estuary, North Carolina using multiple gear types. Estuaries **14**:447–464.

Sacco, J. N., F. L. Booker, and E. D. Seneca. 1988. Comparison of the macrofaunal communities of a human initiated salt marsh at two and fifteen years of age. Pages 282–285 *in* J. Zelazny and S. Feierabend, editors. Increasing our wetland resources. National Wildlife Federation, Washington, D.C., USA.

Sacco, J. N, E. D. Seneca, and T. Wentworth. 1994. Infaunal

community development of artificially established salt marshes in North Carolina. Estuaries **17**:489–500.
SAS Institute. 1990. SAS user's guide. SAS Institute, Cary, North Carolina, USA.
Scatolini, S. R., and J. B. Zedler. 1996. Epibenthic invertebrates of natural and constructed salt marshes of San Diego Bay. Wetlands **16**:24–37.
Seneca, E. D., and S. W. Broome. 1992. Restoring tidal marshes in North Carolina and France. Pages 53–78 *in* G. W. Thayer, editor. Restoring the nation's marine environment. Maryland Sea Grant College, College Park, Maryland, USA.
Seneca, E. D., S. W. Broome, and W. W. Woodhouse, Jr. 1985. The influence of duration-of-inundation on development of a man-initiated *Spartina alterniflora* Loisel marsh in North Carolina. Journal of Experimental Marine Biology and Ecology **94**:259–268.
Sommers, L. E., and D. W. Nelson. 1972. Determination of total phosphorus in soils: A rapid perchloric acid digestion procedure. Soil Science Society of America Proceedings **36**:902–904.
Smith, C. J., R. D. DeLaune, and W. H. Patrick, Jr. 1983. Carbon dioxide emission and carbon accumulation in coastal wetlands. Estuarine Coastal and Shelf Science **17**:21–29.
Smith, K. K., R. E. Good, and N. F. Good. 1979. Production dynamics for above and belowground components of a New Jersey *Spartina alterniflora* tidal marsh. Estuarine and Coastal Marine Science **9**:189–201.
Steever, E. Z., R. S. Warren, and W. A. Niering. 1976. Tidal energy subsidy and standing crop production of *Spartina alterniflora.* Estuarine and Coastal Marine Science **4**:473–478.
Stockton, M. B., and C. J. Richardson. 1987. Wetland development trends in coastal North Carolina, USA, from 1970 to 1984. Environmental Management **11**:1–9.
Sullivan, M. J., and F. C. Daiber. 1974. Response in production of cordgrass, *Spartina alterniflora,* to inorganic nitrogen and phosphorus fertilizer. Chesapeake Science **15**: 121–123.
Thompson, S. P., H. W. Paerl, and M. C. Go. 1995. Seasonal patterns of nitrification and denitrification in a natural and a restored salt marsh. Estuaries **18**:399–408.
Tisdale, S. L., W. L. Nelson, and J. D. Beaton. 1985. Soil fertility and fertilizers. Macmillan Publishing, New York, New York, USA.
Turner, R. E. 1976. Geographic variations in salt marsh macrophyte production: a review. Contributions in Marine Science **20**:47–68.
USDA-SCS (United States Department of Agriculture Soil Conservation Service). 1975. Soil Taxonomy. Agricultural Handbook No. 436. U.S. Government Printing Office, Washington, D.C., USA.
Valiela, I., and J. M. Teal. 1974. Nutrient limitation in salt marsh vegetation. Pages 547–563 *in* R. J. Reimold and W. H. Queen, editors. Ecology of halophytes. Academic Press, New York, New York, USA.
Valiela, I., J. M. Teal, and N. Y. Persson. 1976. Production and dynamics of experimentally enriched salt marsh vegetation: belowground biomass. Limnology and Oceanography **21**:245–252.
Verhoeven, J. T. A., W. Koerselman, and A. F. M Meuleman. 1996. Nitrogen or phosphorus limited growth in herbaceous wet vegetation: relations with atmospheric inputs and management regimes. Trends in Ecology and Evolution **11**: 494–497.
Vitousek, P. M., and W. A. Reiners. 1975. Ecosystem succession and nutrient retention: a hypothesis. BioScience **25**: 376–381.
White, D. A., T. E. Weiss, J. M. Trapani, and L. B. Thien. 1978. Productivity and decomposition of the dominant salt marsh plants in Louisiana. Ecology **59**:751–759.
Zedler, J. B. 1992. Restoring cordgrass marshes in southern California. Pages 7–52 *in* G. W. Thayer, editor. Restoring the nation's marine environment. Maryland Sea Grant College, College Park, Maryland, USA.
Zedler, J. B. 1993. Canopy architecture of natural and planted cordgrass marshes: selecting habitat evaluation criteria. Ecological Applications **3**:123–138.