

Long-term succession of benthic infauna communities on constructed *Spartina alterniflora* marshes

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ABSTRACT: Benthic infauna communities were characterized along a chronosequence (1 to 28 yr old) of 7 constructed *Spartina alterniflora* Loisel marshes and 7 natural (reference) marshes to identify patterns of succession following salt marsh creation. Infauna density and species richness (per 7.07 cm² core) achieved equivalence to comparable reference marshes within 8 yr following marsh creation. Taxa with dispersing larval stages (e.g. *Streblospio benedicti*, *Capitella* sp.) achieved equivalence within 3 yr following marsh creation. Taxa that lack a planktonic dispersal stage, such as tubificid oligochaetes and *Manayunkia aesturina*, were slower to develop. Densities of *Manayunkia* did not achieve equivalence to natural marshes until 8 yr after marsh creation. Twenty-five yr elapsed before oligochaete densities of constructed marshes were similar to natural marshes. In constructed marshes, densities of surface-deposit feeders, dominated by *Streblospio* and *Manayunkia*, achieved equivalence to natural marshes within 8 yr following marsh creation. Subsurface-deposit feeders, consisting mostly of oligochaetes, did not become equivalent to natural marshes for 25 yr. Predictable trajectories, described by an asymptotic increase over time, existed for total species, species richness, and surface- and subsurface-deposit feeders. Oligochaetes and *Manayunkia*, which produce non-dispersing larvae, exhibited linear trajectories over time. In constructed marshes, total density and density of dominant taxa and trophic groups were strongly correlated with soil characteristics, especially organic C, N, bulk density and macro-organic matter (MOM, the living and dead root and rhizome mat). Non-linear regressions using soil organic C and MOM explained 38 to 40% of the variation in constructed marsh infauna density. The regressions suggest that a threshold of 0.5% soil organic C (500 g m⁻², 0 to 10 cm) and 500 g MOM m⁻² (0 to 10 cm) is needed to support infauna densities comparable to densities found in natural marshes. Taxon richness of constructed marshes was more strongly related to vegetation characteristics, especially macro-organic matter quality (e.g. lignin) than soil characteristics. Development of benthic infauna communities following marsh construction requires longer than the 5 yr monitoring period required by many wetland mitigation plans, and as much as 25 yr are needed for some attributes (e.g. oligochaetes) to achieve equivalence.

KEY WORDS: Wetland creation · Restoration · Rehabilitation · Ecosystem development · Chronosequence · Reference wetland · Salt marshes · North Carolina

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INTRODUCTION

Benthic and aquatic invertebrates are frequently used as indicators of ecosystem health to assess biotic integrity of aquatic and wetland ecosystems (Lenat 1988, Lang et al. 1989, Karr 1991, Kerans & Karr 1994, Spieles & Mitsch 2000). In estuarine wetlands, benthic

invertebrates also are used to assess the development of secondary production and food web support following salt marsh creation and restoration (Moy & Levin 1991, Sacco et al. 1994, Levin et al. 1996, Scatolini & Zedler 1996, Simenstad & Thom 1996, Minello & Webb 1997, Craft et al. 1999, Talley & Levin 1999). Most studies to date indicate that infauna community composi-

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tion is slow to develop, requiring years to achieve equivalence to natural marshes (LaSalle et al. 1991, Moy & Levin 1991, Minello & Zimmerman 1992, Sacco et al. 1994, Levin et al. 1996, Scatolini & Zedler 1996, Minello & Webb 1997) and some (tubificid) oligochaetes are especially slow to develop (Moy & Levin 1991, Levin et al. 1996). Levin et al. (1996) reported that 4 yr after marsh construction, oligochaetes, which comprised more than 50% of the infauna in a nearby natural marsh, were rare or absent from the constructed marsh. The slow rate of colonization by infauna, and oligochaetes in particular, is attributed to the absence of a planktonic dispersal stage (Levin et al. 1996) as well as low organic-matter content of constructed marsh soils (Moy & Levin 1991, Levin et al. 1996, Craft 2000, Broome et al. 2001).

In spite of the importance of benthic infauna as an indicator of structural/functional equivalence following salt marsh creation and restoration, little is known about long-term succession of the community. Posey et al. (1997) and Alphin & Posey (2000) reported that benthic infauna communities of 3 *Spartina alterniflora* constructed marshes in South Carolina, ranging in age from 6 to 24 yr old, had qualitatively similar species composition as natural marshes, although in these studies, natural marshes were not directly compared. Comparison of 16 mo to 10 yr old *Salicornia*-vegetated marshes in southern California also indicated relatively rapid development of the infauna community (Talley & Levin 1999). In this study, densities of infauna, with the exception of tubificid oligochaetes, achieved equivalence to natural *Salicornia* marshes within 5 to 10 yr following marsh creation. Craft et al. (1999) reported that two 20 to 25 yr old constructed *S. alterniflora* Loisel marshes contained infaunal density, diversity and trophic structure comparable to 2 natural reference marshes sampled at the same time. However, this study did not determine whether infauna populations were self-sustaining on these marshes, nor was it possible from this study to identify trajectories of successional development over time.

We compared infauna community composition along a chronosequence of 7 constructed *Spartina alterniflora* marshes that varied in age from 1 to 28 yr to elucidate patterns of development of (1) density and taxon richness, (2) dominant taxa and (3) feeding groups, and (4) to identify the relationship between infauna community development and edaphic (soil & vegetation) factors following salt marsh construction. Each constructed marsh was

paired with a natural reference marsh that was sampled at the same time to provide a benchmark for assessing the degree of convergence towards full or complete equivalence.

Our measured parameters characterize the development of infauna structure (e.g. density, taxon richness) following marsh construction. Wetland managers, however, are more interested in restoring functional attributes such as food web support that are assessed by other measurements such as infauna biomass and secondary production. Thus, it is important to recognize that measurements of infauna density serve as an index of functional development of benthic infauna communities.

MATERIALS AND METHODS

Site description. We used the chronosequence approach to evaluate succession of benthic infauna following salt marsh construction. In this study, we sampled benthic invertebrates from 7 constructed marshes that had similar tidal inundation, salinity, vegetation and soils but differed with respect to age (Table 1). Between 1970 and 1997, salt marsh wetlands were constructed along the North Carolina coast for a variety of purposes, including dredge spoil and shoreline stabilization, and mitigation of wetland loss (Fig. 1). Marshes were constructed by grading to intertidal elevation, then planting at elevations between mean sea level (MSL) and mean high water with cordgrass *Spartina alterniflora* (Broome et al. 1988). Tidal amplitude ranged between 1.0 and 1.2 m MSL at all sites.

The strength of the chronosequence approach is that it 'compresses' time, avoiding the need for long-term repeated measurements on a single site. A limitation of the approach is that, because of variable disturbance histories, differences among sites may be incorrectly attributed to ecosystem development rather than past

Table 1. Characteristics of constructed and natural salt marshes. Marshes were constructed for mitigation on dredge spoil (Marshes 1 and 2), research (Marsh 3), mitigation on graded upland soil (Marsh 4), shoreline stabilization (Marsh 5) and dredge spoil stabilization (Marshes 6 and 7). Age and size refer to constructed marshes

Marsh	Age (yr)	Size (ha)	Salinity (g l ⁻¹)	Geomorphic position
(1) DOT	1	0.9	20–30	Back barrier flats
(2) Consultant	3	1.0	17–32	Back barrier flats
(3) Port	8	1.0	18–30	Back barrier flats
(4) Dill's Creek	13	0.3	14–33	Submerged upland
(5) Pine Knoll	24	0.3	20–30	Back barrier fringe
(6) Marine Lab	26	0.2	20–30	Back barrier flats
(7) Snow's Cut	28	0.8	5–20	Riverine

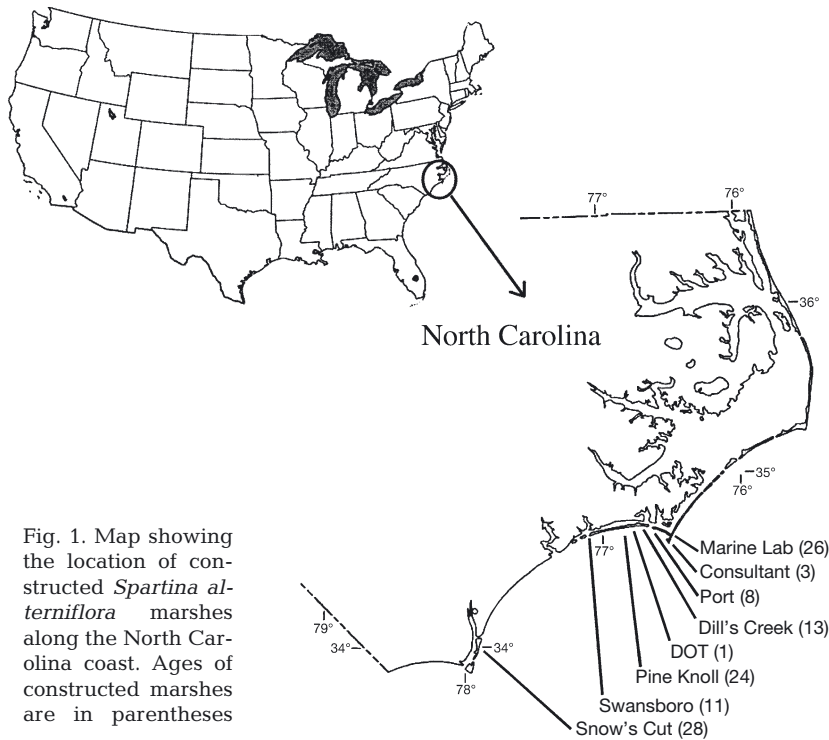


Fig. 1. Map showing the location of constructed *Spartina alterniflora* marshes along the North Carolina coast. Ages of constructed marshes are in parentheses

disturbance events (Pickett 1994). However, because our constructed marshes are relatively young (<30 yr old), we are familiar with changes, including disturbance history, of the 7 sites during their existence.

At each site, a nearby natural marsh with the same environmental conditions and vegetation was paired with the constructed marsh to serve as a reference site for comparison. Reference wetlands are used to set performance goals for created and restored wetlands (Brinson & Rheinhardt 1996). By pairing each constructed marsh with its own reference marsh, we were able to minimize the effects of geomorphic position (see Table 1) that might affect benthic invertebrate succession. Soils of the constructed marshes were classified as typic psammaquents (high sand content) (USDA 1999). Natural marsh soils were classified as typic psammaquents or typic hydraquents (high clay content) (USDA 1999).

Sample collection and analysis. Infauna were sampled in June 1998 by collecting 3 cm diameter by 5 cm deep cores from each marsh. The small diameter and shallow depth of the corer likely biases sampling towards smaller organisms and leads to under-representation of larger organisms (Alphin & Posey 2000). By collecting a greater number of cores ($n = 25$) throughout the marsh, we were able to capture the spatial variability caused by the patchiness of infauna communities that may not be accounted for by studies that collect larger but fewer cores (for example, $n = 7$ per marsh as in Alphin & Posey 2000).

Twenty-five cores were collected from each marsh in June 1998. Sampling was stratified with 10 samples randomly collected from the levee ('tall' *Spartina*) zone and 15 samples collected from the marsh interior or marsh plain (medium to 'short' *Spartina*). Cores were preserved with 10% buffered formaldehyde and Rose Bengal (to stain the organisms) in the field, then washed through a 250 μm sieve with deionized water in the lab (Sacco et al. 1994). Organisms retained on the screen were sorted, identified to the lowest possible taxon, counted, and stored in 70% ethyl alcohol. Dominant taxa consisted of the polychaetes *Manayunkia aestuarina*, *Streblospio benedicti*, and *Capitella* sp. Oligochaeta, Nematoda and Nereidae were not identified below this level. Whereas a 250 μm mesh sieve retains most of benthic infauna, it does not quantitatively sample nematodes that are usually sampled using a 63 μm mesh sieve.

Thus, the results of our nematode dataset are biased towards the larger ones retained by the 250 μm mesh sieve.

Infauna trophic structure was determined by classifying the organisms into the following groups: surface-deposit feeders (*Manayunkia aestuarina*, *Streblospio benedicti*, Nereidae), subsurface-deposit feeders (Oligochaeta, *Capitella* sp.) and carnivores based on feeding strategy of Sacco et al. (1994). Some taxa (e.g. nematodes), because of unknown or variable feeding habits, were classified as 'unknown' in the feeding category. Table 2 contains the complete list of infauna taxa along with their trophic classification.

Characteristics of below-ground biomass and soil of constructed marshes were used to identify relationships between infauna succession and edaphic factors. Biomass and soil samples were collected from 10 of the 25 infauna sampling points (5 levee and 5 marsh plain samples each) at the same time that infauna were sampled. At each sampling point, 2 cores each 8.5 cm diameter by 10 cm deep were collected. Below-ground biomass (macro-organic matter) was collected by washing 1 core on a 2 mm mesh diameter screen, collecting the roots remaining on the screen and drying them at 70°C. Macro-organic matter quality was characterized by measuring water-soluble extractives, cellulose and lignin, as described by Ryan et al. (1990). The second soil core was weighed (for bulk density), then dried and sieved through a 2 mm mesh diameter screen and analyzed for organic C, nutrients (N, P) and

Table 2. Taxa identified, trophic group classification and mean proportional density of benthic infauna in constructed and natural marshes

Taxon	Trophic group	Proportional density (%)	
		Constructed marsh	Natural marsh
Oligochaeta	Subsurface ^a	16.6	32.8
Polychaeta:			
<i>Manayunkia aestuarina</i>	Surface ^b	11.4	12.2
<i>Streblospio benedictii</i>	Surface	7.1	9.1
<i>Capitella</i> sp.	Subsurface	9.7	4.7
Nereidae	Surface	3.3	4.1
Cirratulidae	Surface	0.02	0.1
<i>Glycera</i> sp.	Carnivore	0	0.1
Maldanidae	Subsurface	0	0.01
Orbiniidae	Subsurface	0.1	0.4
Phyllodocidae	Carnivore	0.02	0.1
<i>Polydora ligni</i>	Surface	0.3	0.05
Sabellidae	Surface	0	0.02
<i>Spionid</i> sp.	Surface	0.2	0.05
Nematoda	Unknown	29.7	19.5
Crustacea:			
Barnacle	Surface	0.1	0.01
<i>Cyathura polita</i>	Surface	0.1	0.1
Gammaridae	Surface	0.1	0.2
Harpacticoid Copepoda	Unknown	1.1	1.8
<i>Leptochelia</i> sp.	Surface	4.7	4.0
Ostracoda	Unknown	0.5	3.1
<i>Sesarma</i> sp.	Surface	0.03	0.01
<i>Uca</i> sp.	Surface	0.1	0.1
Crab larvae	Unknown	0.9	0.1
<i>Edotea</i> sp.	Surface	0.03	0.3
Arachnida:			
Acarina	Unknown	0.4	0.3
Insecta:			
Collembola	Surface	0.01	0.03
Ceratopogonidae	Surface	0.9	0.2
Dolichopodidae	Carnivore	0.3	0.1
Dipteran larvae	Surface	0.1	0.03
Homoptera	Surface (grazer)	0.2	0.01
Tabanidae	Carnivore	0.02	0.01
Mollusca:			
Bivalva	Unknown	3.0	0.5
Gastropoda	Surface	7.5	4.0
<i>Melampus</i> sp.	Surface (grazer)	0.7	0.01
Cnidaria (Coelenterata):			
Anemone	Carnivore	0.6	0.3
Platyhelminthes:			
Turbellaria	Carnivore	0.4	1.5
Rhynchocoela (Nemertea)	Carnivore	0.02	0.1

^aSubsurface-deposit feeders
^bSurface-deposit feeders

particle size. Organic C and N were measured using a Perkin-Elmer 2400 CHN analyzer. Total P was measured as orthophosphate after digestion in nitric-perchloric acid (Sommers & Nelson 1972). Sand, silt and clay were determined by the hydrometer method (Gee & Bauder 1986).

Statistical analysis. Pair-wise *t*-tests were used to test for differences in ecological attributes between constructed and natural marsh pairs (SAS 1996). Where appropriate, test results were interpreted based

on the assumption of unequal variances. All tests of significance were made at $\alpha = 0.05$. Regression analysis was used to describe relationships between the measured attributes and constructed marsh age (SAS 1996). Correlation analysis, regression analysis and canonical correlation analyses were used to explore relationships between edaphic characteristics of below-ground vegetation (macro-organic matter quantity and quality—lignin, cellulose, water-soluble extractives) and soil (bulk density, sand, silt, clay, organic C, N, P)

and benthic infauna community composition (SAS 1996). Prior to analysis, the data were tested for homogeneity of variance (*F*-max test) and log-transformed (log [x+1]) if needed (Sokal & Rohlf 1995). A total of 70 macro-organic matter, soil (0 to 10 cm depth) and infauna samples (0 to 5 cm depth) were used in the analysis.

RESULTS

Total density, taxon richness and dominant taxa

The 1 and 3 yr old constructed marshes contained significantly fewer individuals and were less taxon rich than their natural marsh counterparts (Table 3). Infauna density in the 1 yr old constructed marsh was 15% (19 500 ind. m⁻²) of levels found in the natural marsh (126 000 ind. m⁻²), whereas the 3 yr old constructed marsh contained half the number of infauna (52 000 ind. m⁻²) as the comparable reference marsh (95 000 ind. m⁻²). Taxon richness (per 7.07 cm² core) in the 1 and 3 yr old constructed marshes was only 30 to 55% of levels found in comparable reference marshes (Table 3). Total taxa identified per marsh were also lower in the 1 (8), 3 (13) and 8 (17) yr old constructed marshes as compared to the comparable reference marshes (16 to 24) (Table 3). There was no difference in infauna density and taxon richness between older constructed marshes and reference marshes (Table 3).

Density of the 6 dominant taxa, oligochaetes, *Manayunkia aestuarina*, *Streblospio benedicti*, *Capitella* spp., Nereidae and nematodes, were all significantly lower in the 1 yr old constructed marsh than in the comparable reference marsh (Tables 2 & 3). The 3 yr old constructed marsh contained significantly fewer oligochaetes, *M. aestuarina* and Nereidae than the comparable reference marsh (Tables 2 & 3). The 8, 13 and 24 yr old constructed marshes also contained fewer

oligochaetes than comparable reference marshes. Densities of *S. benedicti* and *Capitella* sp. achieved equivalence to natural marshes relatively quickly, after 3 yr (Table 4).

Similar to total density, density of non-dominant 'other' taxa was significantly lower in the 1 and 3 yr old constructed marshes (Table 4). In these constructed marshes, the density of non-dominant taxa was 10% (1200 m⁻²) of levels found in comparable reference marshes (11 000 to 12 000 ind. m⁻²). Low density of 'other' taxa in 1 and 3 yr old constructed marshes was attributed to large numbers of the gastropod, the mud snail *Ilyanassa* sp., a surface-deposit feeder, in the reference marshes (4.4 to 9% of all organisms) but was absent, or nearly so, from the constructed marshes (0.2 to 0.3%).

Oligochaetes were the dominant taxon in natural marshes (19 to 45%) and in constructed marshes older than 10 yr (16 to 48%) and the tubificid *Monopylephorus* spp. was the most abundant oligochaete. Nematodes were the second most abundant taxon, accounting for 7 to 35% in natural marshes and 7 to 64% in constructed marshes. *Manayunkia aestuarina* (0 to 31%), *Streblospio benedicti* (1 to 18%), *Capitella* sp. (<1 to 19%) and Nereidae (<1 to 6%) were present in lesser numbers in constructed and natural marshes.

Trophic composition

Densities of infauna trophic groups were lower in the youngest constructed marshes as compared to comparable reference marshes. The 1 yr old constructed marsh contained significantly fewer surface- and subsurface-deposit feeders and organisms of unknown feeding preferences than the reference marsh (Table 5). The 3 yr old constructed marsh contained fewer surface-deposit feeders, subsurface-deposit feeders and carnivores, and the density of subsurface-

Table 3. Mean total density, taxon richness and density of oligochaetes and *Manayunkia estuarina* of constructed (Con.) and natural (Nat.) *Spartina alterniflora* marshes. Multiply values by 1000 to express as density in number m⁻²

Marsh	Age (yr) ^a	Density (no. m ⁻² × 10 ³)		Taxon richness (no. 7.07 cm ⁻²)		Oligochaetes (no. m ⁻² × 10 ³)		<i>Manayunkia</i> (no. m ⁻² × 10 ³)	
		Con.	Nat.	Con.	Nat.	Con.	Nat.	Con.	Nat.
DOT	1	19	126*	2.6 (8) ^b	9.0* (19)	0.2	35*	0	17*
Consultant	3	52	95*	4.5 (13)	8.0* (16)	2.7	31*	1	7*
Port	8	102	96	8.8 (17)	8.3 (24)	9.2	38*	4	0.1
Dill's Creek	13	145	128	8.6 (16)	8.0 (16)	24	39*	11	2
Pine Knoll	24	106	135	8.6 (20)	6.9 (20)	24	61*	5	14
Marine Lab	26	118	125	9.2 (20)	8.6 (20)	16	24	37	33
Snow's Cut	28	137	157	7.2 (18)	7.8 (21)	67	58	42	42

^aAge of the constructed marsh; ^bnumber of taxa identified per marsh
 *Significantly greater density (p < 0.05) in the natural marsh versus the paired constructed marsh according to Student's *t*-test

Table 4. Mean density (no. m⁻²) of *Streblospio benedicti*, *Capitella*, Nereidae, Nematoda and combined all 'Other' taxa of constructed (Con.) and natural (Nat.) *Spartina alterniflora* marshes

Marsh	Age (yr) ^a	<i>Streblospio</i>		<i>Capitella</i>		Nereidae		Nematoda		Other	
		Con.	Nat.	Con.	Nat.	Con.	Nat.	Con.	Nat.	Con.	Nat.
DOT	1	1700	14500*	3800	9000*	100	7000*	12500	33500*	1200	10700*
Consultant	3	1700	14500*	7700	5000	1700	6000*	30500	19500	1200	12000*
Port	8	800	1300	10700	900**	5000	2400**	20000	34000	52500	18500**
Dill's Creek	13	25000	23000	4200	3000	8400	5900	3300	22000	40000	33000
Pine Knoll	24	1000	1000	11100	5100**	2300	3100	23500	11500**	38500	40000
Marine Lab	26	9000	9500	11900	6300	7100	7200	17000	28000	20500	17500
Snow's Cut	28	100	18000*	200	13100*	100	4100*	9000	12500	19000	9500

^aAge of the constructed marsh
*Significantly greater density ($p < 0.05$) in the natural marsh versus the paired constructed marsh according to Student's *t*-test
**Significantly lower density ($p < 0.05$) in the natural marsh versus the paired constructed marsh according to Student's *t*-test

deposit feeders and carnivores was significantly lower in the 8 yr old constructed marsh than in the natural marsh (Table 5). Surface-deposit feeders developed quickly following marsh construction as a result of colonization by *Streblospio benedicti*. Subsurface-deposit feeders, which consisted mostly of non-dispersing (tubificid) oligochaetes, were slower to develop than other feeding groups. Only the 26 and 28 yr old constructed marshes had densities of subsurface-deposit feeders that were comparable to reference marshes (Table 5).

Subsurface-deposit feeders were the dominant trophic group in natural marshes, accounting for 25 to 49% of total density. In natural marshes, surface-deposit feeders, unknown feeding groups and carnivores accounted for 14 to 47%, 10 to 40% and 0 to 1% of the total, respectively. Constructed marshes contained a greater proportion of unknown feeding groups (9 to 68%), mostly nematodes that may be surface-deposit feeders, subsurface-deposit feeders or carnivores.

Trajectories of infauna succession

Density and taxon richness of infauna were low in young constructed marshes but, over time, converged towards equivalence to natural marsh infauna communities (Fig. 2). Both invertebrate density and taxon richness were significantly related to constructed marsh age ($r^2 = 0.89$ to 0.90 , $p < 0.001$), achieving equivalence to natural marshes after 8 yr. Of the 6 dominant taxa, oligochaetes and *Manayunkia aestuarina* exhibited a predictable increase in numbers over time (Fig. 3). Density of *M. aestuarina* increased linearly with constructed marsh age ($r^2 = 0.65$, $p < 0.05$) and achieved or exceeded equivalence to natural marshes after 8 yr. Oligochaetes also exhibited a linear increase with marsh age ($r^2 = 0.57$, $p < 0.05$), but densities did not achieve equivalence to natural marshes until after 25 yr (Fig. 3b). Other dominant taxa, *Streblospio benedicti*, *Capitella* sp., Nereidae and nematodes, did not exhibit a predictable increase in density over time. Rather, density of these taxa increased quickly,

Table 5. Mean density (no. m⁻²) of surface-deposit feeders, subsurface-deposit feeders, carnivores and unknown feeding groups of constructed (Con.) and natural (Nat.) *Spartina alterniflora* marshes

Marsh	Age (yr) ^a	Surface feeders		Subsurface feeders		Carnivores		Unknown	
		Con.	Nat.	Con.	Nat.	Con.	Nat.	Con.	Nat.
DOT	1	2000	46000*	4000	44000*	300	400	13500	36500*
Consultant	3	10500	37000*	10500	35500*	0	300*	30500	21000
Port	8	40000	14000**	21500	42000*	100	1800*	41000	38000
Dill's Creek	13	79000	43500**	28500	43500*	0	0	37000	41000
Pine Knoll	24	41000	55000	36500	67000*	200	200	28000	13500**
Marine Lab	26	70500	60500	28500	31500	500	900	19000	34500
Snow's Cut	28	57000	70500	67000	71500	200	100	13500	14500

^aAge of the constructed marsh
*Significantly greater density ($p < 0.05$) in the natural marsh versus the paired constructed marsh according to Student's *t*-test
**Significantly lower density ($p < 0.05$) in the natural marsh versus the paired constructed marsh according to Student's *t*-test

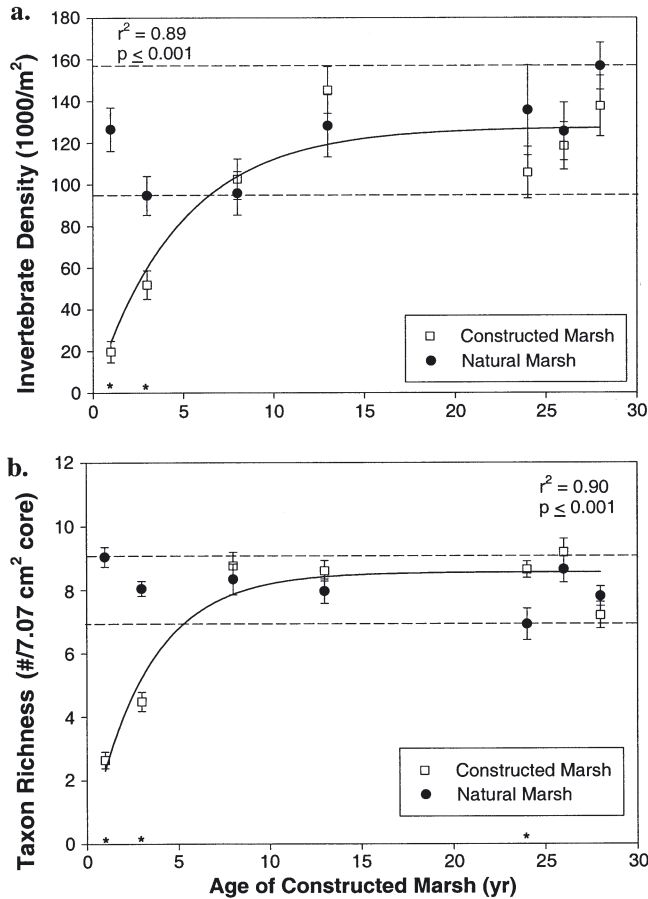


Fig. 2. (a) Density (no. m⁻² ± SE) and (b) species richness (taxa 7.07 cm⁻² core ± SD) of benthic infauna along a chronosequence of constructed salt marshes and natural reference marshes. Asterisks (*) indicate that the constructed and paired reference marsh are significantly different ($p < 0.05$) according to Student's *t*-test. Dashed lines represent the range of values measured in the natural marshes

achieving or exceeding equivalence to natural marshes within 7 yr following marsh construction (Table 4).

Proportional density of oligochaetes increased along the chronosequence of constructed marshes, from 1% of the total in the 1 yr old marsh to 48% in the 28 yr old marsh. Proportional density of *Manayunkia aestuarina*, another taxon with non-dispersing larvae, also increased with constructed marsh age. *M. aestuarina* were absent from the 1 yr old constructed marsh but increased to 31% of the total in the 26 and 28 yr old marshes. Other taxa such as nematodes and *Capitella* sp. were most abundant in the youngest constructed marshes and decreased with marsh age. Proportional density of nematodes, for example, was greatest (64%) in the 1 yr old constructed marsh and lowest (7%) in the 28 yr old marsh. Similarly, proportional density of *Capitella* sp. was 19% in the 1 yr old constructed marsh, decreasing to <1% in the 28 yr old constructed

marsh. Overall, proportional density of oligochaetes was 2 times greater (32%) in natural marshes than in constructed marshes (16%) (Table 2). Constructed marshes, in contrast, contained relatively more *Capitella* sp. and Nematoda than natural marshes (Table 2).

Density of surface- and subsurface-deposit feeding infauna were also significantly related to constructed marsh age ($r^2 = 0.71$ to 0.73). The number of surface-deposit feeders increased over time, achieving or exceeding equivalence to natural marshes within 10 yr following marsh construction (Fig. 4a). Subsurface-deposit feeders developed at a slower rate than surface-deposit feeders (Fig. 4b) and did not achieve equivalence to natural marshes until 25 yr after marsh construction.

The proportion of unknown feeding groups decreased with constructed marsh age, from 68% in the 1 yr old marsh to 9% in the 28 yr old marsh. Conversely, the proportion of surface-deposit feeders in-

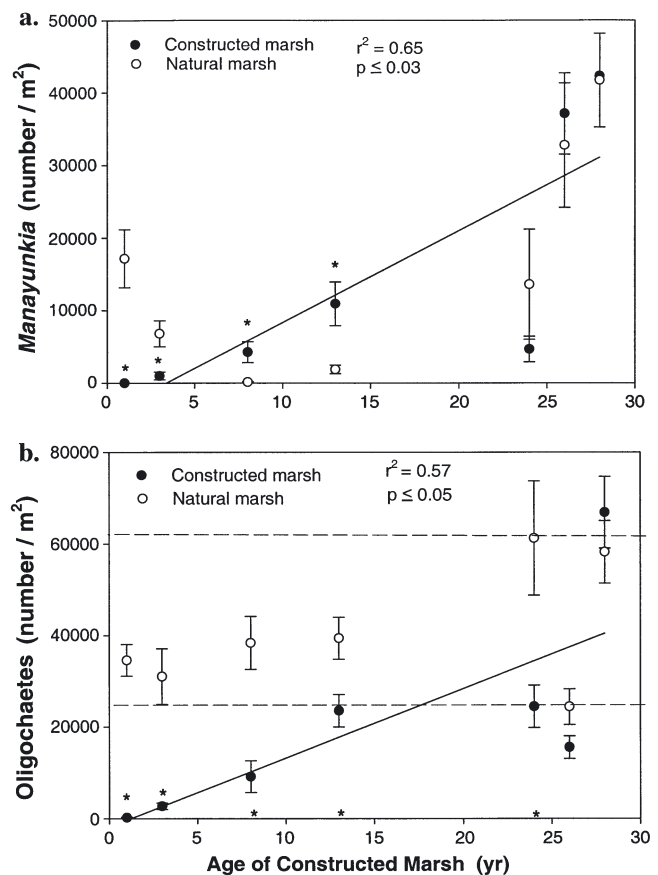


Fig. 3. Density (no. m⁻² ± SE) of (a) *Manayunkia aestuarina* and (b) oligochaetes along a chronosequence of constructed salt marshes and natural reference marshes. Asterisks (*) indicate that the constructed and paired reference marshes are significantly different ($p < 0.05$) according to Student's *t*-test. Dashed lines represent the range of values measured in the natural marshes

creased from 10% in the 1 yr old constructed marsh to 39–59% in constructed marshes greater than 5 yr old. No clear trend was identified with respect to the proportion of subsurface-deposit feeders and constructed marsh age.

Trajectories describing successional development of oligochaetes and *Manayunkia aestuarina* were linear, whereas trajectories for surface- and subsurface-deposit feeders was best described by a non-linear (exponential rise to maximum) curve. Because oligochaetes are a major component of the subsurface-deposit feeding trophic group, one would expect that both groups would be represented by a similarly shaped curve. Thus, the asymptotic increase in density of subsurface-deposit feeders over time must be caused by rapid colonization by other subsurface-deposit-feeding taxa such as *Capitella* sp. (Table 4). Increased numbers of surface-deposit feeders relative to *M. aestuarina* (a surface-deposit feeder) was attributed to rapid colonization of constructed marshes by another surface-deposit feeder, *Streblospio benedicti*. It is interesting to note that a linear-regression model best described successional development of taxa (oligochaetes, *M. aestuarina*) that lack a planktonic dispersal stage. A curvilinear model was better for describing succession of infauna trophic groups because these groups contain taxa with both dispersing and non-dispersing larvae.

Edaphic factors and infauna community composition

Trajectories of infauna succession were linked to development of other ecological attributes such as plant biomass, soil organic C, N, silt and clay, which increase over time following marsh construction (Craft et al. 1999, 2003). For example, soil bulk density and macro-organic matter (0 to 10 cm depth) were significantly correlated with attributes of the infauna community, including total density, taxon richness, domi-

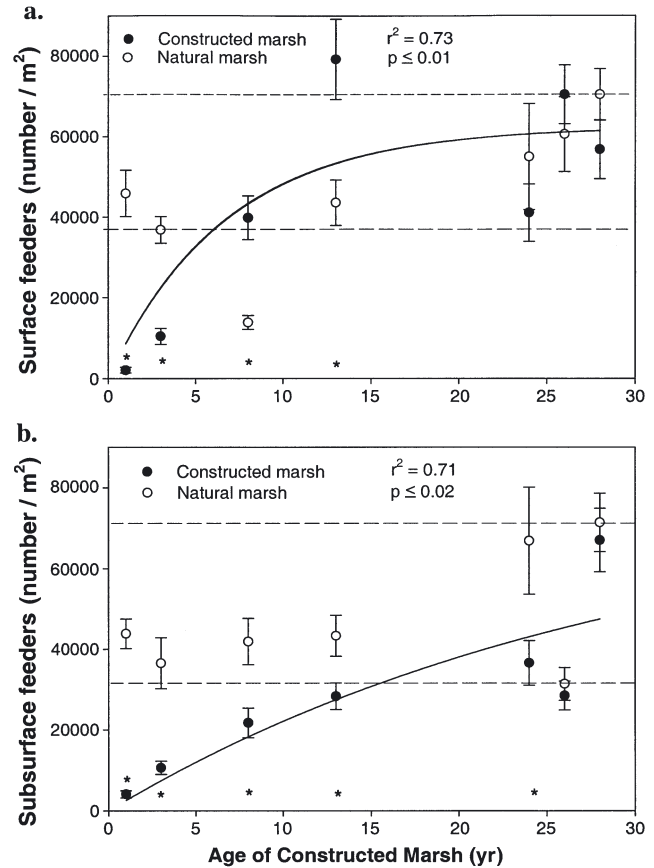


Fig. 4. Density (no. $m^{-2} \pm SE$) of (a) subsurface-deposit feeders and (b) surface-deposit feeders along a chronosequence of constructed salt marshes and natural reference marshes. Asterisks (*) indicate that the constructed and paired reference marsh are significantly different ($p < 0.05$) according to Student's *t*-test. Dashed lines represent the range of values measured in the natural marshes

nant taxa (oligochaetes, *Manayunkia aestuarina*) and trophic groups (surface- and subsurface-deposit feeders) (Table 6). Soil characteristics including organic C, N, silt and clay (0 to 10 cm depth), which increase dur-

Table 6. Significant ($p < 0.05$) correlation coefficients between benthic infauna community composition and soil-belowground biomass characteristics of constructed *Spartina alterniflora* marshes ($n = 70$). MOM = macro-organic matter

	Density	Taxon richness	Oligochaetes	<i>Manayunkia aestuarina</i>	<i>Streblospio benedicti</i>	Surface feeders	Subsurface feeders
Bulk density	-0.58	-0.45	-0.55	-0.61	-	-0.61	-0.55
Organic carbon	0.45	0.45	0.51	0.61	-	0.52	0.45
Total nitrogen	0.45	-	0.48	0.62	-	0.51	0.49
Sand	-0.50	-	-0.50	-0.55	-0.48	-0.53	-0.49
Silt	0.51	-	0.53	0.57	0.55	0.52	0.52
Clay	0.47	-	0.44	0.50	0.38	0.53	0.43
MOM	0.51	0.44	0.46	0.51	-	0.47	0.47
Lignin	-	0.38	-	-	-	-	-
Extractives	-	-0.36	-	-	-	-	-

ing salt marsh ecosystem development, were also positively associated with infauna community development (Table 6). There was no correlation between infauna density and aboveground biomass or stem density of *Spartina* based on comparison of mean values from each marsh (Craft et al. 2003). In constructed marshes, density of *Streblospio benedicti* was positively correlated with silt and clay content and negatively correlated with sand, but was not correlated with other soil characteristics such as bulk density, C or N (Table 6). Taxon richness of infauna also was correlated with quality of accumulating macro-organic matter. Taxon richness was positively associated with lignin, which increased with constructed marsh age and negatively correlated with water-soluble extractives that were greater in MOM of young constructed marshes.

Similar to the simple correlations, canonical correlation analysis revealed that infauna density was associated mostly with soil characteristics whereas taxon richness was more strongly associated with macro-organic matter quality. The first canonical variable, which was highly correlated with infauna density ($r = 0.98$), was positively correlated with macro-organic matter ($r = 0.64$), soil organic C ($r = 0.62$), N ($r = 0.60$), silt ($r = 0.71$) and clay ($r = 0.65$), and negatively correlated with bulk density ($r = -0.79$) and sand ($r = -0.70$). The second canonical variable, which represented taxon richness ($r = 0.93$), was positively correlated with lignin ($r = 0.60$) and cellulose ($r = 0.42$) and negatively correlated with water-soluble extractives ($r = -0.74$).

Macro-organic matter and soil organic C were the best single variables for predicting infauna density following marsh construction. Macro-organic matter and soil organic C (0 to 10 cm depth) explained 40 and 38% of the variation, respectively, in infauna density of individual soil cores ($n = 70$), and a non-linear model fit the data better than a linear model (Fig. 5). Based on the regressions, it appears that approximately 500 g MOM m^{-2} or 0.5% C ($500 g m^{-2}$) is sufficient to support constructed marsh infauna densities that are comparable to densities measured in our natural marshes (Fig. 5). Above these 'threshold' concentrations, infauna densities remain relatively uniform across a broad range of MOM (500 to 4000 $g m^{-2}$) and soil organic C (0.5 to 8%) levels.

Non-linear regression of soil organic C and MOM were also the single best predictors of taxon richness and density of oligochaetes, surface-deposit feeders and subsurface-deposit feeders. Organic C explained 42% ($p < 0.0001$) of the variation in taxon richness, whereas MOM explained 52% of the variation ($p < 0.0001$). The non-linear model based on soil organic C also was useful for predicting density of oligochaetes ($r^2 = 0.33$, $p < 0.05$), subsurface deposit

feeders ($r^2 = 0.32$, $p < 0.05$) and surface deposit feeders ($r^2 = 0.40$, $p < 0.01$).

DISCUSSION

Infauna succession

Total density and taxon richness of benthic infauna achieved equivalence to natural marshes within 8 yr following marsh construction (Fig 2). Our findings suggest relatively rapid development of benthic infauna numbers, which is supported by other studies of constructed estuarine marshes. For example, macrofauna density in marshes of Winyah Bay (South Carolina) were 4 times greater in an 8 yr old *Spartina alterniflora* marsh (19 943 ind. m^{-2} measured in 1988) as compared to a 4 yr old marsh (4628 ind. m^{-2}) (LaSalle et al. 1991). Repeated sampling of 3 Winyah Bay marshes (established in 1977, 1981 and 1988, respectively) in 1993 and 1998 revealed that, whereas infauna density var-

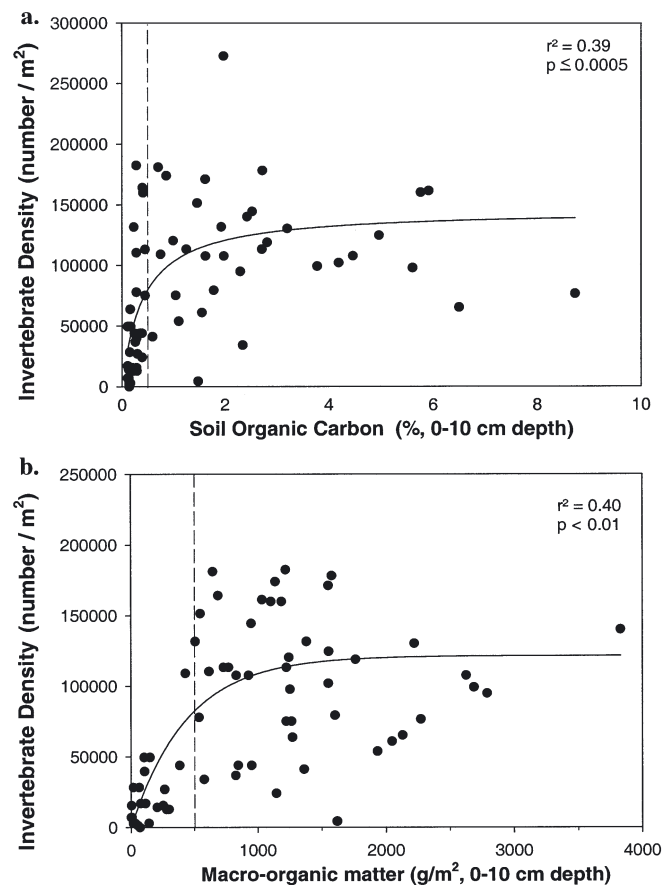


Fig. 5. Relationship between infauna density (no. m^{-2}) and (a) % soil organic C (0 to 10 cm depth) and (b) macro-organic matter ($g m^{-2}$, 0 to 10 cm depth) in constructed salt marshes. $N = 70$ samples

ied between years, proportional density of dominant species was constant regardless of marsh age or year of sampling (Alphin & Posey 2000). Infauna communities of *Salicornia*-vegetated marshes created in southern California also developed quickly, within 5 to 10 yr (Talley & Levin 1999).

Some studies, however, suggest that infaunal communities develop much more slowly. Sacco et al. (1994) reported that 16 yr after creation, some constructed marshes contained fewer numbers of infauna than comparable natural marshes. Craft et al. (1999) sampled infauna 10 yr apart on 2 constructed and 2 natural *Spartina alterniflora* marshes in North Carolina. Density of infauna increased between 1986 and 1995 in both constructed marshes, but held steady in the 2 natural marshes. In contrast, repeated annual sampling by Simenstad & Thom (1996) over a 3 yr period following construction of a brackish-water (0 to 15 ppt) *Carex lyngbyei* estuarine marsh in Puget Sound, Washington, yielded no clear evidence of increasing density and succession of infauna communities. In the west coast study, it is possible that the young age of the marsh (4 yr) and the short (3 yr) sampling interval made it difficult to identify trajectories of benthic infauna succession on this marsh.

Streblospio benedicti and *Capitella* sp. quickly colonized constructed marshes. Density of these taxa achieved equivalence to natural marshes within 5 yr following marsh creation (Table 4). Previous studies noted that *S. benedicti* and *Capitella* sp. are early colonizers of constructed *Spartina alterniflora* marshes (Moy & Levin 1991, Levin et al. 1996, Posey et al. 1997, Alphin & Posey 2000). *Capitella* sp. produces planktotrophic larvae that readily disperse (Levin et al. 1996) and, therefore, are among the first to colonize a site. *S. benedicti* produces both planktotrophic and lecithotrophic (non-dispersing) larvae (Levin & Huggett 1990). In this study, we did not identify larval forms of *S. benedicti*, but rapid colonization by this species following marsh construction is consistent with immigration by the planktonic form. *Manayunkia aestuarina* and tubificid oligochaetes, in contrast, lack a planktonic dispersal stage (Levin et al. 1996) and, therefore, these taxa may be slower to colonize the marsh. In our study, *Monopylephorus* sp., a non-dispersing tubificid, was the most abundant oligochaete taxon and, as a result, there were significantly fewer oligochaetes in constructed marshes less than 25 yr old as compared to natural marshes (Table 3). *Manayunkia* densities were lower only in the 1 and 3 yr old constructed marshes (Table 3). Levin et al. (1996) observed that a 4 yr old constructed *S. alterniflora* marsh in North Carolina contained fewer oligochaetes than a nearby natural marsh. Tubificid oligochaetes also were less abundant in 16 mo to

10 yr old created *Salicornia* marshes than in natural *Salicornia* marshes of southern California (Talley & Levin 1999).

Some studies of older constructed marshes, however, suggest that oligochaete and *Monopylephorus* spp. densities achieve equivalence faster than the time scales reported above. Alphin & Posey (2000), for example, reported that *Monopylephorus* spp. was the dominant taxon in 3 constructed marshes ranging in age from 6 to 19 yr old. Similarly, a literature review of salt marshes constructed on dredged material revealed no difference in the density of oligochaetes between constructed and natural marshes (Streever 2000). In the review paper, however, abundance of polychaetes and crustaceans was significantly greater in natural versus constructed marshes.

In contrast to subsurface deposit-feeding oligochaetes and the surface deposit-feeder *Manayunkia*, whose densities exhibited linear trajectories over time (Fig. 3), density of surface and subsurface deposit feeders increased asymptotically (Fig. 4). Also, trajectories of surface and subsurface deposit feeders exhibited better 'goodness-of-fit' versus time than trajectories of individual taxa. Faster pace of development of surface- and subsurface deposit feeders relative to oligochaetes and *Manayunkia* reflects rapid colonization of constructed marshes by other surface and subsurface deposit-feeding organisms. For example, densities of the subsurface deposit feeder, *Capitella* sp., achieved or exceeded equivalence to natural marshes within 3 yr following marsh construction. Density of surface deposit-feeders, *Streblospio benedicti*, Nereidae and bivalves, also quickly achieved or exceeded equivalence to natural marshes (Table 2). Subsurface deposit feeders developed more slowly than surface deposit feeders (Fig. 4b). Other studies noted that densities of subsurface deposit feeders are slow to develop following marsh construction, primarily because of slow development of subsurface deposit-feeding tubificid oligochaetes (Sacco et al. 1994, Levin et al. 1996) caused, possibly, by low MOM and soil organic matter (Moy & Levin 1991, Minello & Zimmerman 1992, Sacco et al. 1994, Levin et al. 1996, Craft 2000).

Infauna density of our natural and constructed marshes greater than 5 yr of age ranged from 96 000 to 157 000 organisms m⁻². These values are higher than densities reported for other natural and constructed marshes of the southeastern US coast, but comparable to densities in *Spartina foliosa* and *Salicornia*-vegetated marshes in southern California (Levin et al. 1998, Talley & Levin 1999) (Table 7). High infauna densities in this study relative to other atlantic coast studies reflects (1) smaller sieve size (250 µm) used in this study relative to other studies (LaSalle et al. 1991, Alphin & Posey 2000) and (2) nematodes that were

Table 7. Comparison of benthic infauna densities (no. m⁻²) of constructed and natural *Spartina alterniflora* marshes

	Constructed marshes	Natural marshes
LaSalle et al. (1991) (4 and 8 yr old, >0.500 µm)	5 000–20 000	Not measured
Moy & Levin (1991) (1–3 yr old, >300 µm)	19 600 (450 000) ^a	15 000 (760 000) ^a
Minello & Zimmerman (1992) (2–5 yr old, >500 µm)	1 900–56 000	13 000–70 000
Sacco et al. (1994) (1–16 yr old, >250 µm)	16 000–49 000	18 000–69 000
Levin et al. (1996) (1–4 yr old, >300 µm)	6 000–47 000	37 000–65 000
Levin et al. (1998) (<i>S. foliosa</i> marshes, >300 µm)	Not measured	122 000
Craft et al. (1999) (21, 25 yr old, >250 µm)	31 000–102 000	19 000–31 000
Talley & Levin (1999) ^b (5–10 yr old, >300 µm)	88 000–290 000	22 000–117 000
Alphin & Posey (2000) (6–25 yr old, >500 µm)	3 000–13 000	Not measured
This study (1–28 yr old, >250 µm)	19 000–145 000	96 000–157 000

^aNumbers in parentheses are meiofauna, organisms retained on a 63–300 µm sieve
^b*Salicornia*-vegetated marsh

qualitatively enumerated in this study but were not counted in other studies (Sacco et al. 1994, Levin et al. 1996).

Three marsh sites (Dill's Creek, Pine Knoll, Snow's Cut) sampled as part of this study in 1998 were compared with infauna data collected by Sacco et al. (1994) in 1986. Both studies used similar sampling methods and sieve size (250 µm). Total density measured in 1998 was much greater (106 000 to 157 000 ind. m⁻²) than in 1986 (17 500 to 69 900 ind. m⁻²), partially because we quantitatively enumerated nematodes, whereas Sacco et al. (1994) did not. However, densities of individual taxa (e.g. oligochaetes, *Manayunkia*, *Streblospio benedicti*) also were lower in Sacco et al.'s (1994) study as compared to this study. Overall, taxonomic and trophic composition was similar in the constructed marshes and their natural marsh counterparts in 1986 and 1998, except for the Dill's Creek constructed marsh, which was 2 yr old in 1986 and contained essentially no oligochaetes at that time. Alphin & Posey (2000) also sampled the Snow's Cut constructed marsh in November 1998. Taxonomic composition of the infauna community was similar to results of Sacco et al. (1994) and this study except that a tanaid (*Heterotanais* sp.) was the dominant taxa, accounting for 46% of total density.

Density of some taxa was consistently greater in several constructed marshes. For example, the 8 yr old

constructed marsh had significantly more *Capitella* sp., Nereidae and 'other' taxa as compared to the natural marsh, and the 24 yr old marsh contained more *Capitella* sp. and nematodes (Table 4). Levin et al. (1996) tracked infauna community succession on the same 8 yr old constructed marsh for 4 yr following marsh construction, and found that *Capitella* sp. was the first taxon to colonize the site. Some studies suggest that density of *Capitella* sp. is positively related to percent sand (see Zipperer 1996 and Toomey 1997, cited in Levin & Talley 2000) but we did not observe a similar relationship in this study. In the 8 yr old constructed marsh, another factor that may contribute to greater density of *Capitella* sp., Nereidae and other taxa may be the construction of a tidal creek in this marsh (but not in other marshes) that facilitates tidal flushing and promotes soil oxygenation and recruitment. The 24 yr old constructed marsh also was sampled by Craft et al. (1999) in 1995 and, in that study, the

constructed marsh also contained significantly more *Capitella* sp., but not nematodes, than the nearby reference marsh.

Edaphic factors and succession

In constructed marshes, infauna density was strongly associated with below-ground biomass and soil properties, especially bulk density and organic C (Table 6). Regression analysis revealed that soil organic C and MOM (0 to 10 cm depth) were the single best predictors of infauna density (Fig. 5) and taxon richness ($r^2 = 0.42$ and 0.52 , respectively). Other studies of constructed and natural salt marshes report that infauna density is positively associated with below-ground biomass (Lana & Guiss 1992, Craft 2000, Levin & Talley 2000) and soil organic C (Sarda et al. 1995, Levin et al. 1998, Craft 2000, Levin & Talley 2000). In a comprehensive review paper, Levin & Talley (2000) reported that infauna density is most frequently associated with soil organic matter. For example, in natural and constructed southern California marshes vegetated with *Spartina foliosa* and *Salicornia*, soil organic matter was positively associated with total density and density of oligochaetes and polychaetes. Canonical correspondence analysis of the same dataset revealed that soil organic content was the dominant component of the

first principal axis explaining infauna community variation (Levin & Talley 2000). In a study of *Salicornia*-vegetated constructed marshes of southern California, infauna density of some macrofaunal taxa was positively related to soil organic matter (SOM), whereas in natural marshes density of some taxa was negatively related to SOM (Talley & Levin 1999). Reduced densities of infauna in constructed marshes has been attributed to low soil organic C and high bulk density, which provides food, refuge and ease-of-burrowing, and is characteristic of older, high organic matter natural marsh soils (Moy & Levin 1991, Levin et al. 1996).

Total density and density of individual taxa (oligochaetes, *Manayunkia aestuarina*, *Streblospio benedicti*) and trophic groups (surface and subsurface deposit feeders) also was significantly associated with particle size (Table 6). Density of *S. benedicti* was much greater in the 13 yr old constructed marsh than its natural marsh counterpart as compared to all other marshes (Table 4). Constructed and natural marsh soils from the 13 yr old site also contained more silt plus clay (constructed marsh = 38%, natural marsh = 66%, 0 to 10 cm depth), than the other constructed (6 to 11%) and natural marshes (4 to 52%). Sacco et al. (1994) also observed greater densities of *S. benedicti* in these 2 marshes than in 5 other constructed and natural and marsh pairs, which all had coarser, sandier soils. Other published studies found that infauna density is positively correlated with fine-grained sediment (Lana & Guiss 1991) and negatively correlated with percent sand (Levin & Talley 2000). Levin & Talley (2000) reported that, in *Spartina foliosa* marshes, density of total macrofauna and enchytraeid oligochaetes were inversely correlated with percent sand, whereas in *Salicornia*-vegetated marshes, the reverse was true.

In contrast to infauna density, which was positively related to organic matter quantity, taxon richness was more strongly related to quality of MOM. Canonical correlation analysis revealed that taxon richness was positively correlated with lignin ($r = 0.60$) and cellulose ($r = 0.42$), and negatively correlated with water-soluble extractives ($r = -0.74$) in MOM. Lignin is relatively unpalatable to heterotrophic organisms (Melillo et al. 1982, Stevenson 1994), so the positive correlation between infauna density and lignin may be attributed to physical rather than nutritional properties of macro-organic matter. Lignin decomposes slowly, persisting in the soil, enhancing soil structure that possibly contributes to development of infauna communities.

We also measured aboveground characteristics of *Spartina* in the same marshes. Because *Spartina* was sampled at the end of the growing season (October) rather than in the summer (June), when infauna, MOM and soils were sampled, we were unable to quantitatively evaluate the effects of aboveground biomass and

stem density on infauna succession. Comparison of mean values from the 7 constructed marshes, however, indicated that infauna density was correlated with soil properties (organic C, total N) but not with aboveground biomass or stem density (Craft et al. 2003). Similar to infauna density, aboveground biomass of *S. alterniflora* also required 8 yr to achieve equivalence to natural marshes (Craft et al. 2003), and the 1 and 3 yr old constructed marshes contained significantly less biomass (300 to 700 g m⁻²) than comparable natural marshes (900 to 1200 g m⁻²). Belowground biomass took longer to develop, as 15 yr elapsed before belowground biomass of constructed marshes developed to levels found in natural marshes (Craft et al. 2003). These findings suggest that belowground biomass (MOM) of *Spartina* is more important than aboveground biomass for development of infauna communities.

Other published studies evaluating relationships between infauna communities and edaphic conditions report few correlations between above-ground characteristics of marsh vegetation but much stronger correlations with below-ground characteristics. Levin & Talley (2000) cite a variety of studies where infauna density and density of various taxa were positively correlated with below-ground biomass of both constructed marshes (Levin & Talley 2000) and natural marshes (Osenga & Coull 1983, Rader 1984, Lana & Guiss 1992, Levin & Talley 2000). In some studies, however, several infauna taxa were negatively correlated with belowground biomass (Capehart & Hackney 1989, Levin & Talley 2000).

CONCLUSIONS

Most attributes of infauna community structure and function achieved equivalence to natural marshes within 8 yr following marsh construction. Oligochaetes and subsurface-deposit feeders, however, required much longer (25 yr) before densities developed to levels that were comparable to natural marshes. Development of oligochaetes and subsurface deposit feeders depended on accumulation of sufficient soil organic matter (0.5% or 500 g m⁻²) and macro-organic matter (500 g m⁻²) to support densities found in natural marshes. The 'success' of most wetland creation projects is evaluated on the basis of vegetation attributes such as percent cover measured after a 5 yr period. Slow development of the benthic infauna community, especially oligochaetes, following salt marsh construction suggests that wetland managers should consider the pace of development of infauna communities when setting performance criteria for salt marsh mitigation projects.

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