Relationships of Nitrogen Loadings, Residential Development, and Physical Characteristics with Plant Structure in New England Salt Marshes

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ABSTRACT: We examined the vascular plant species richness and the extent, density, and height of Spartina species of ten Narragansett Bay, Rhode Island (United States) fringe salt marshes which had a wide range of residential land development and N-loadings associated with their watersheds. Significant inverse relationships of tall S. alterniflora with species richness and with the extent and density of S. patens and short S. alterniflora were observed. Extent and density of S. patens and extent of short S. alterniflora were positively and significantly related with plant species richness. Marsh elevation and area did not significantly correlate with plant structure. Flood tide height significantly and inversely correlated with S. patens, but did not significantly relate to S. alterniflora or plant species richness. Marsh width significantly and positively correlated with plant species richness and S. patens and inversely correlated with tall S. alterniflora. Significant inverse relationships were observed for N-load, % residential development, and slope with S. patens, short S. alterniflora, and species richness, and significant positive relationships with tall S. alterniflora. The marsh slope and width were significantly correlated with N-load and residential development that made it difficult to determine to what extent anthropogenic stressors were contributing to the variation in the plant structure among the marshes. At five marshes with similar slopes, there were significant inverse relationships of N-load with S. patens (density and extent) and a positive relationship with tall S. alterniflora (extent). Although there were no significant relationships of slope with the plant metrics among the five sites, other physical factors, such as the flood tide height and marsh width, significantly correlated with the extent and density of Spartina species. Significant relationships of N-load with plant structure (albeit confounded by the effect of the physical characteristics) support the hypothesis of competitive displacement of dominant marsh plants under elevated nitrogen. It is likely that the varying plant structure in New England marshes is a response to a combination of natural factors and multiple anthropogenic stressors (e.g., eutrophication and sea level rise).

Background

Although salt marshes are often considered nitrogen (N) poor (Valiela and Teal 1974), nonpoint source pollution to coastal waters has dramatically risen in recent decades and the N status of critical habitats such as wetlands may also be affected by these increased nutrient loads (Carpenter et al. 1998; Deegan 2002). Recent research in New England salt marshes has shown increasing stable N isotopic ratios in salt marsh biota that has been attributed to increasing wastewater contributions from adjacent watersheds (McClelland and Valiela 1998; Valiela et al. 2000a; McKinney et al. 2001; Wigand et al. 2001). It has been demonstrated in fertilization studies at a few New England sites that Spartina patens, which is the superior competitor when N is limiting, is out-competed and

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displaced by *Spartina alterniflora* under N-enriched conditions (Levine et al. 1998; Emery et al. 2001). These fertilization studies suggest that under nutrient-enriched conditions where *S. alterniflora* is both the best competitor for N and most tolerant of physical stresses an entire salt marsh could become dominated by this one species (Levine et al. 1998; Emery et al. 2001). It has generally been demonstrated, although not specifically in salt marsh plant communities, that there is decreasing plant species diversity in macrophyte-based ecosystems with increasing nutrient availability (Tilman 1984, 1987; Goldberg and Miller 1990).

The New England salt marsh plant structure is described as a patchy mosaic of *S. alterniflora* (short and tall forms), *S. patens, Distichlis spicata, Juncus* gerardii, Salicornia europea, and bare patches that are influenced by elevation, tidal inundation, salinity, sediment oxygen levels, interspecific competition, and availability of N (Redfield 1972; Nixon

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1982; Bertness and Ellison 1987; Bertness 1991, 1992; Emery et al. 2001). In the classical zonation paradigm, the low marsh is dominated by mostly homogenous stands of S. alterniflora, which is bounded at its upper limit by the extent of the mean high tide (Nixon 1982). A consistent elevation for the limits of growth relative to a tidal datum plane could not be demonstrated along the Atlantic and Gulf Coasts suggesting that the upper limit and the extent of S. alterniflora may be influenced by biotic interactions (e.g., competition) as well as tidal inundation (McKee and Patrick 1988). In the low marsh, N enrichment and sediment oxidation can cause the conversion of patches of short S. alterniflora to the tall form (Valiela et al. 1975; Howes et al. 1986). Tall S. alterniflora is often found under N-enriched conditions and near the borders of creeks that drain the marsh (Redfield 1972; Valiela et al. 1975; Howes et al. 1986). S. alterniflora productivity has been shown to be directly related to N concentrations in some fertilization studies (Valiela et al. 1973, 1975) and field surveys (Nixon and Oviatt 1973).

In contrast to the low vascular plant species richness associated with the low marsh zone, the plant structure of the high marsh zone is dynamic and complex (Miller and Egler 1950; Niering and Warren 1980; Roman et al. 2000). In New England salt marshes, the high marsh zone is characterized by both monotypic patches and mixtures of *S. patens*, *D. spicata*, *J. gerardii, Iva frutescens, Panicum virgatum, Phragmites australis*, and forbs (i.e., herbs other than grasses) (Niering and Warren 1980).

Eutrophication especially the over-enrichment of N, is identified as a major stressor associated with human activities (Vitousek et al. 1997). In this field survey, we test the hypothesis that elevated Nloads associated with human activities alter plant species richness, and the extent, density, and height of *Spartina* species. In addition to the anthropogenic stressors of watershed N loads and land use changes, we also examined marsh slope, area, width, and elevation, and flood tide heights to address the relationship of these other factors to the plant structure.

Methods

We used a comparative survey approach to examine the plant structure of salt marshes with similar geomorphology and sea exchange, but various land development in the adjoining watersheds. To minimize natural confounding effects among subestuaries we chose 10 sites that had similar geological bedrock and tidal flushing in the main basin of Narragansett Bay, Rhode Island (Fig. 1; Mc-Kinney et al. 2001). Tidal ranges estimated from tidecharts averaged 1.3 m with a range of 1.2–1.4

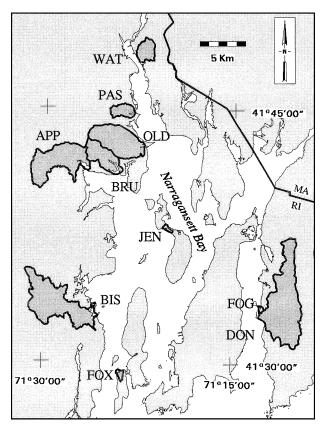


Fig. 1. Map of the locations of the salt marshes and adjacent watersheds in Narragansett Bay, Rhode Island, that were included in the comparative survey.

m among the 10 subestuaries. The slope of the marsh landscape and marsh elevations were estimated using standard surveying techniques. Transects were run approximately perpendicular to the shoreline in each marsh, starting at the landward edge and continuing to the cove. A standard surveyor's level (Berger Instruments) was used to determine the relative elevation at the beginning, middle, and end of each plant belt along the transect. For plant belts that were more than a few meters from beginning to end, additional elevation measurements were made every couple of meters. All elevations were referenced to National Geodetic Vertical Datum of 1929 (NGVD29) by using a previously established elevation benchmark near each of the 10 marshes (Thursby and Abdelrhman 2004).

The flood tide height above the marsh surface was measured in the *S. alterniflora* at the marsh-sea edge using tidal flooding gauges. PVC pipes (7.6 cm in diameter \times 2 m in length) were drilled with 1-cm holes every 5-cm along both the length and circumference of the pipe. At each marsh, a drilled pipe was set along the marsh-sea edge of each tran-

TABLE 1. Marsh slopes, watershed description, and calculated nitrogen loadings for 10 Narragansett Bay fringe marshes and associated watersheds. Sites are listed from lowest to highest marsh N-load. JEN = Jenny Pond; FOX = Fox Hill Salt Marsh; FOG = Fogland Marsh; DON = Mary Donovan Marsh; PAS = Passeonkquis Cove; BRU = Brush Neck Cove; BIS = Bissel Cove; OLD = old Mill Creek; WAT = Watchemoket Cove; and APP = Apponaug Cove.

			Watershed	Calculated Nitrogen Loads			oads
Site	$\begin{array}{c} \text{Marsh Slope} \\ (\text{cm } \text{m}^{-1}) \end{array}$	Watershed Area (ha)	Percent Residential	Marsh Area (ha)	Total N-load (kg N yr ⁻¹)	Percent Wastewater	Marsh N-load (kg N ha ⁻¹ yr ⁻¹)
JEN	0.7	41	4.0	11.85	29	37.4	2
FOX	0.7	62	0.3	10.04	103	2.3	10
FOG	0.9	30	14.9	4.43	280	25.0	63
DON	1.5	2,975	10.0	29.00	11,593	30.2	400
PAS	3.5	314	65.4	4.10	9,917	82.2	2,418
BRU	5.3	781	61.8	9.16	22,344	81.9	2,440
BIS	2.3	2,296	22.1	3.85	11,235	62.6	2,922
OLD	2.3	1,505	44.5	9.63	31,587	79.1	3,282
WAT	9.7	402	56.0	1.97	11,920	70.0	6,037
APP	6.5	1,738	43.3	3.17	32,472	74.5	10,253

sect (n = 3), and filled with 500 ml of sphagnum peat moss in August 2000 during a spring tide. Height of the flooding tide was measured as the height of the rise of the peat moss in the PVC pipe plus the height of the erosional edge at the end of each transect. The measurement of the flood tide height for each marsh is the average of the three transect values.

The sub-watersheds and areas of the marshes were delineated using 15 min (1:24,000 scale) United States Geological Survey (USGS) topographic maps (Table 1). The watershed information was processed using the Environmental Systems Research Institute (ESRI) ARC/INFO software package. The data layer for land use and land cover was developed from 1995 aerial photography (1:24,000 scale) coded to Anderson modified level 3 (Anderson et al. 1976) to one half-acre minimum polygon resolution. In previous reports we described natural land types (% forested, % brushland, and % inland wetland) and human altered land (i.e., % residential, % agricultural, % industrial and commercial, % recreational) in the subwatersheds adjoining the marshes (McKinney et al. 2001; Wigand et al. 2001). Since percent residential lands dominated the land types altered by humans in this urbanized region (Wigand et al. 2001), we used this land type for our correlations with the marsh plant structure in this study.

To estimate the N loading to the Narragansett Bay marshes, we used a nitrogen loading model (NLM) developed and verified for Cape Cod, Massachusetts (Valiela et al. 1997, 2000a), and also used for estimating nitrogen loads for Nantucket, Massachusetts, and Narragansett Bay, Rhode Island (Cole et al. 2004). The NLM estimates coastal nitrogen loads from atmospheric deposition, fertilizer, and wastewater (via septic systems, using values for per capita contributions of nitrogen) in watersheds by multiplying the surfaces of various land use types (e.g., natural vegetation, agricultural land, turf, residential land, and impervious surfaces) by an appropriate coefficient and subsequently correcting the loads for nitrogen losses in various compartments (e.g., vegetation and soils, vadose zone, aquifer). The estimate of the N-load to the marsh was then calculated as the sum of the loads from atmospheric deposition, fertilizer, and wastewater (corrected for losses) and divided by the marsh area in hectares.

Sewer information for the watersheds was obtained from a GIS data layer that was compiled in 1995 from available regional and municipal sewer authority maps. According to this information, in three of the ten Narragansett Bay marsh watersheds studied, less than 20% of their wastes are sewered. At the time of the study, the balance of residential waste in these three watersheds and all of the waste from the other seven watersheds is treated in domestic septic systems. We recognized the existence of a nitrogen pollution gradient in Narragansett Bay and the possibility that this marine N-load also affects marsh plant structure (Nixon and Oviatt 1973; Oviatt et al. 1977). However, the highest concentrations of dissolved N in Narragansett Bay are associated with watersheds having the highest percent residential land use. Since it is primarily land-associated human activities that generate non point pollution of surface waters (Vitousek et al. 1997), we concentrated our efforts on relating estimated N-loads from the watershed and percent residential development to plant structure of the marshes.

The extent (distance parallel to the upland edge) of the marsh was estimated in the field, and three transects were set approximately equidistant across the marsh and ran perpendicular from the upland edge (e.g., beginning at the seaward edge of the *Iva frutescens* zone) to the cove edge in each of the 10 marshes. For two consecutive years, using

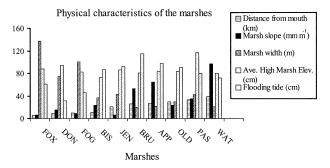


Fig. 2. Some physical characteristics, including marsh slope, width, elevation, and flooding tide of the sites (listed from the mouth to the head of Narragansett Bay).

a tape measure, the length (at least one meter) of each discrete plant belt (single or mixed species) along a transect and the entire length of the transect were measured in meters. Discrete plant belts are defined by a change in plant species composition or in the dominant plant species along the transect, for example from S. patens to short form S. alterniflora, or from short form S. alterniflora to mixed S. patens-D. spicata. Tall form S. alterniflora was observed on the cove or creek edge (but sometimes present at the interface of the high marsh) and was generally about twice as tall as the short form S. alterniflora at any particular marsh site. A circular 0.1 m² quadrat was randomly dropped within each discrete plant belt to estimate percent cover of each plant species. Percent plant cover was the average estimate of separate observations by two indiv for each quadrat.

To normalize for varying marsh widths (distance perpendicular to the upland edge) among the ten sites, the extent of a plant species on the marsh landscape was reported as a percentage. The percent extent of a plant species along a transect was determined by the sum along the transect of the products of percent plant cover and belt length divided by the total transect length. Extent of the *Spartina* species was averaged for the three transects each year (1998 and 1999) and reported as an annual average. During 1999, we measured shoot height and density for the *Spartina* species in each quadrat. Shoot heights of 10 random plants for each *Spartina* species were measured with a meter stick to the nearest mm, and a destructive subsample $(0.013 \text{ m}^2; 11.5 \text{ cm square})$ of the dominant *Spartina* species from each quadrat was harvested to measure density of plants. *Spartina* species shoot height and density were averaged across belts on each transect and reported as an average value (the average of the three transects).

Vascular plant species richness was determined from the 2-yr transect data using a jackknife procedure that takes into account the total number of observed species plus the occurrence of rare species and allows for the construction of the variance associated with the estimation (Heltshe and Forrester 1983). Each of the six transects sampled over the 2-yr period was evaluated as a sampling unit to calculate species richness at each site. We also reported the cumulative presence or absence of vascular plant species at the sites over the 2-yr period. Species denoted as present could be present either 1 or 2 yr. In addition to the observations of plant species from the transect sampling, observations of stands of P. australis and Spartina species not found on the transects were included in the cumulative record of species occurrences at the sites.

Using correlation analyses we examined the relationships between distance from the mouth along the north-south axis of Narragansett Bay and flood tide height and marsh width, slope, area, and elevation. We correlated percent residential development, N-loads, and marsh slope, area, width, and flooding tide with the extent, height, and density of the co-dominant Spartina species and plant species richness. In addition, we examined the interspecific relationships of the tall S. alterniflora (extent, height, density) with S. patens and short S. alterniflora. The probability for significance is reported at p < 0.05. Finally, we used stepwise multiple regression to examine the relationships of Nload, percent residential development, and the physical characteristics with the metrics of plant structure. Predictor variables for the stepwise multiple regression were considered for addition to the model in the order of highest partial correlations with the dependent variable entered first, and the criteria of p < 0.15 to add to the model.

TABLE 2. Relationships between the physical characteristics of the Narragansett Bay marshes (n = 10). * indicates p < 0.05.

	Distance from Mouth (km)	Marsh Slope (cm m ⁻¹)	Marsh Width (m)	Marsh Area (ha)	Marsh Elevation (cm)
Marsh slope (cm m ⁻¹)	0.77*				
Marsh width (m)	-0.78*	-0.65*			
Marsh area (ha)	-0.46	-0.45	0.29		
Marsh elevation (cm)	0.19	-0.15	0.13	0.17	
Flooding time (cm)	0.54	0.36	-0.69*	-0.49	-0.21

Results

The GIS analysis showed a gradient of low to high % residential land use (ranging from 0.3% to 65%) associated with the watersheds of the ten marsh sites (Table 1). Similarly, there was a wide range of watershed nitrogen loadings, from 2.5 Kg N ha⁻¹ y⁻¹ to 10,250 Kg N ha⁻¹ y⁻¹, and fraction of wastewater, from 2% to 82% (Table 1). As one would expect, the percentage of wastewater nitrogen calculated by the NLM model significantly (p < 0.05; r = 0.90) correlated with the percentage of residential development in the marsh watersheds. High marsh elevation was similar among the marshes (Fig. 2), but the marsh slope and width were significantly correlated with the distance from the mouth of the bay (Table 2). Marsh width was significantly (p < 0.05) and inversely correlated with both marsh slope (r = -0.65) and flooding tide (r = -0.69). Marshes at the head of the bay had steeper slopes and shorter widths (Fig. 2). The average marsh width or transect length among the ten sites was 52.6 \pm 12.5 m. Marsh area ranged from about 3 hectares at Apponaug Cove to about 29 hectares at Mary Donovan Marsh with no significant relationship with distance from the mouth of the bay (Tables 1 and 2).

Plant species richness ranged from 3.8 ± 1.0 at WAT to 12.5 ± 1.9 at DON (Table 3). The high marsh plant patches were dominated by S. patens, but in addition, short S. alterniflora, D. spicata, S. europaea, L. nashii, and J. gerardii were observed in discrete monotypic or mixed species patches. The low marsh was dominated by S. alterniflora. During the 2-yr period S. alterniflora and S. patens were present at all of the sites, although, not always located on the transects. From the transect data of the ten sites, average plant density was tall S. alterniflora: 550 \pm 89 shoots m⁻², short S. alterniflora: 1,058 \pm 247 shoots m⁻², and S. patens: 4,638 \pm 1,370 shoots m^{-2} (Table 3). Average height of the Spartina shoots across the marshes was tall S. alterniflora: 107 \pm 6.1 cm, short S. alterniflora: 55 \pm 3.8 cm, and S. patens: 44 ± 2.8 cm (Table 3). Short S. alterniflora was observed at all sites except Watchemoket Cove (WAT), and the frequency of occurrence of the short form was greatest at Jenny Pond (JEN) and Fox Hill Salt Marsh (FOX). No tall S. alterniflora was observed at FOX and the average height of the short S. alterniflora at FOX was 46 cm (Table 3). P. *australis* was observed at all of the sites except JEN. Not including the Spartina species and P. australis, the D. spicata (present at 8 sites), S. europaea (6 sites), and L. nashii (6 sites) were the next most prevalent species (Table 4).

Among the 10 sites, significant inverse relationships were observed between the extent of tall S.

$^{\circ}$ Starry (rati) Subsylection Density (part) Served: (a) Density (part) Served: (b) Density (b) <thdensity (c)<="" th=""> Density (c)</thdensity>	Cove; OLD = Old Mill Creek; WAT = Watchemoket										
$ \begin{array}{c ccccccccccccccccccccccccccccccccccc$		Species Richness	Density S. $patens$ Shoots m ⁻²	Density (tall) S. alterniflora Shoots m ⁻²	Density (short) S. alterniflora Shoots m^{-2}	% Extent S. patens	% Extent (tall) S. alterniflora	% Extent (short) S. alterniftora	Shoot Height S. patens	Shoot Height (tall) S. alterniflora	Shoot Height (short) S. alterniftora
$ \begin{array}{c ccccccccccccccccccccccccccccccccccc$		7.8 ± 1.0	4,992	377	1,914	14.4	2.0	21.6	32	83	41
$ \begin{array}{cccccccccccccccccccccccccccccccccccc$		11.7 ± 1.5	12,823	0	2,325	23.9	0	22.8	35	NA	46
$ \begin{array}{cccccccccccccccccccccccccccccccccccc$		10.7 ± 2.0	9,552	553	1,507	19.4	1.5	4.6	36	67	46
$\begin{array}{cccccccccccccccccccccccccccccccccccc$		12.5 ± 1.9	7,674	628	1,733	21.4	2.5	3.0	46	94	52
$ \begin{array}{cccccccccccccccccccccccccccccccccccc$		10.7 ± 1.5	5,878	528	528	13.8	7.8	0.5	56	108	54
$ \begin{array}{cccccccccccccccccccccccccccccccccccc$		9.5 ± 2.3	1,658	678	754	5.1	7.9	7.2	47	115	68
$\begin{array}{cccccccccccccccccccccccccccccccccccc$		6.8 ± 1.0	1,771	5.78	908	7.5	6.7	8.9	43	86	52
0 0 18.7 0 NA 125 716 4.7 11.4 3.8 53 136		7.8 ± 1.0	2,035	352	126	11.2	11.7	1.2	51	120	75
716 4.7 11.4 3.8 53 136		3.8 ± 1.0	0	728	0	0	18.7	0	NA	125	NA
		5.8 ± 1.0	0	1,080	716	4.7	11.4	3.8	53	136	63

marsh N-lo; BIS = Bisse	marsh N-load. JEN = Jenny Pond; FOX = Fox Hill BIS = Bissel Cove; OLD = Old Mill Creek; WAT =	anny Pond;) = Old Mi	FOX =		Marsh; FO(hemoket C	<pre>fill Salt Marsh; FOG = Fogland Marsh; DON = Mary = Watchemoket Cove; and APP = Apponaug Cove.</pre>	Marsh; D(DN = Mary naug Cove.	Donovan N	Aarsh; PAS =	- Passeonko	Salt Marsh; FOG = Fogland Marsh; DON = Mary Donovan Marsh; PAS = Passeonkquis Cove; BRU = Brush Neck Cove; Watchemoket Cove; and APP = Apponaug Cove.	U = Brush	Neck Cove;
Site	Althaea officinalis	Aster subulatus	Cladium spp.	Distichlis spicata	Juncus gerardii	Limonium nashii	Panicum virgatum	Phragmites australis	Plantago maritima	Salicornia europaea	Sairpus sp.	Solidago sempervirens	Typha angustifolia	Unknown Species
JEN	0	1	0	1	0	1	1	0	0	1	0	0	0	0
FOX	0	0	0	1	1	1	0	1	1	1	1	0	0	1
FOG	0	0	0	1	1	1	0	1	0	1	0	1	0	0
DON	0	0	0	1	1	1	0	1	0	1	0	1	1	0
PAS	1	0	1	1	0	0	0	1	0	0	1	0	1	0
BRU	0	0	0	1	0	1	0	1	0	1	0	1	0	0
BIS	0	0	0	1	0	1	0	1	0	1	0	0	0	0
OLD	0	0	0	1	0	0	0	1	0	0	0	1	0	0
WAT	0	0	0	0	0	0	0	1	0	0	1	0	0	0
APP	0	0	0	0	0	0	1	1	0	0	0	0	0	0

TABLE 4. The cumulative presence or absence of plant species excluding Spartina for 1998 and 1999 are reported. Presence of a species is denoted by a 1 and absence by a 0, and species denoted by a 1 may have been present during one or two years. S. alterniflora and S. patens were present at all the sites. Sites are listed from lowest to highest

alterniflora and the extent and density of both *S. patens* and short *S. alterniflora* as well as species richness (Table 5). Significant positive relationships were observed between the extent of tall *S. alterniflora* and the average heights of *S. patens* and short *S. alterniflora* (Table 5). Extent and density of *S. patens* and extent of short *S. alterniflora* were positively and significantly related with plant species richness (Table 5).

We observed significant relationships of some physical characteristics with the N-load and percent residential development among the 10 sites. Correlation analyses showed significant (p < 0.05) positive relationships of slope with percent residential development (r = 0.74) and N-loads (r = 0.79). There was a significant (p < 0.05; r = -0.72) inverse relationship of marsh width with percent residential development.

Marsh area and elevation did not significantly correlate with any measures of plant structure in this study. The flooding tide measurements significantly and inversely correlated with the density and extent of S. patens, but did not significantly relate to S. alterniflora or plant species richness (Table 6). Marsh width significantly and positively correlated with plant species richness and the extent and density of S. patens, and inversely correlated with the extent and density of tall S. alterniflora (Table 6). Significant inverse relationships of slope, Nload, and percent residential development with S. patens (density and extent) and density of short S. alterniflora and, in contrast, significant positive relationships with the extent and height of tall S. alterniflora were observed (Table 6). Significant inverse relationships of slope and N-load with plant species richness and significant positive relationships with the density of tall S. alterniflora were observed (Table 6). A significant inverse relationship of percent residential development with the extent of short S. alterniflora and significant positive relationships with the heights of short S. alterniflora and S. patens were also observed (Table 6).

Stepwise multiple regression analysis showed Nload as the strongest variable relating to plant species richness and density of tall *S. alterniflora*, with no significant effect of adding percent residential development or the physical characteristics to the predictive model (Table 7). Percent residential development was the strongest variable in a stepwise multiple regression analysis relating to shoot heights of *S. patens* and short *S. alterniflora* and density of short *S. alterniflora*, with no significant effect of adding N-load or the physical characteristics to the predictive model. Together N-load and percent residential development related with height of tall *S. alterniflora* with no significant effect of adding any of the physical characteristics to the stepwise

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TABLE 5. Relationships of various plant metrics of *Spartina* and species richness, as well as interspecific *Spartina* relationships. (* p < 0.05; n = 10 for all variables, except length: n = 9).

	Species Richness	Density S. patens Shoots m ⁻²	Density (tall) S. alterniflora Shoots m^{-2}	Density (short) S. alterniflora Shoots m ⁻²	% Extent S. patens	% Extent (tall) S. alterniflora	% Extent (short) S. alterniflora
Density S. patens shoots m^{-2}	0.83*						
Density (tall) S. alterniflora shoots m^{-2}	-0.49	-0.69*					
Density (short) S. alterniflora shoots m ⁻²	0.63*	0.80*	-0.51				
% extent S. patens	0.87*	0.95*	-0.66*	0.80*			
% extent (tall) S. alterniflora	-0.79*	-0.83*	0.54	-0.92*	-0.87*		
% extent (short) S. alterniflora	0.22	0.49	-0.62	0.79*	0.44	-0.65*	
Height S. patens	-0.21	-0.58	0.57	-0.82*	-0.53	0.83*	-0.80*
Height (tall) S. alterniflora	-0.45	-0.61	0.62	-0.76*	-0.62	0.79*	-0.63
Height (short) S. alterniflora	-0.35	-0.67	0.35	-0.83*	-0.62	0.87*	-0.60

regression model. Marsh slope was the strongest variable relating to percent extent of tall *S. alterniflora* with no significant effect on the regression model by adding N-load, percent residential development, or the other physical characteristics. Stepwise multiple regression analysis showed mixed models of anthropogenic stressors and physical characteristics for the dependent variables: density and extent of *S. patens* and extent of short *S. alterniflora* (Table 7).

To minimize the confounding effect of slope observed in the set of 10 marsh sites, a sub-set of five sites (Bissel Cove, Mary Donovan Marsh, Fogland Marsh, Old Mill Creek, and Passeonkquis Cove) with more similar slopes (ranging from 0.9-3.5 cm m^{-1} ; Table 1) than the entire set was analyzed to examine for relationships of N-load, percent residential development, and physical characteristics with the plant structure. Among these five sites there were no significant relationships of marsh slope or percent residential development with plant extent, density, or species richness. Correlation analyses showed significant inverse relationships of N-load with density and percent extent of S. Patens, density of short S. alterniflora, and a significant positive relationship with the percent extent of tall S. alterniflora (Table 8). Measurements of the flooding tide were significantly and positively related with the percent extent of tall *S. alterniflora*, and, inversely related with extent of *S. patens* and density of short *S. alterniflora* (Table 8). Marsh width was significantly and positively related with the density of *S. patens* and inversely related with the percent extent of the tall *S. alterniflora*.

Discussion

As described in earlier reports for New England and summarized here for Rhode Island (Fig. 3), with increasing percent residential development and percent of wastewater nitrogen load to coastal waters, the stable nitrogen isotopic ratios of marsh biota, S. alterniflora and Geukensia demissa (ribbed mussel), increases (McClelland and Valiela 1998: Valiela et al. 2000a; McKinney et al. 2001; Wigand et al. 2001). Compared with atmospheric deposition ($\delta^{15}N$ of +2 to +8%) and fertilizer ($\delta^{15}N$ of -3 to +3%), nitrogen derived from wastewater $(\delta^{15}N \text{ of } +10 \text{ to } +22\%)$ is relatively enriched in N¹⁵ (Kreitler et al. 1978; Gormley and Spalding 1979; Kreitler and Browning 1983; Arevena et al. 1993), which results in enriched stable nitrogen isotopic ratios in biota when the percentage of wastewater that is processed increases. The enriched stable nitrogen isotopic ratios of the Narragansett Bay biota suggest that wastewater nitrogen is a source of nitrogen to these organisms.

TABLE 6. Relationships of anthropogenic stressors (N-load and percent residential development) and marsh physical characteristics (slope, width, and elevation) with plant structure. (* p < 0.05; n = 10 for all variables, except length: n = 9)

% Residential	$\frac{\text{Marsh Slope}}{(\text{cm m}^{-1})}$	Marsh Width (m)	Flooding Tide (cm)
0100	-0.71*		
	0.71	0.70*	-0.52
-0.66*	-0.73*	0.96*	-0.67*
0.50	0.67*	-0.65*	0.22
-0.88*	-0.74*	0.79*	-0.45
-0.72*	-0.85*	0.88*	-0.67*
0.77*	0.89*	-0.75*	0.4
-0.69*	-0.54	0.50	0.07
0.82*	0.74*	-0.61	0.29
0.74*	0.78*	-0.56	0.34
0.73*	0.66	-0.62	0.52
	$\begin{array}{c} 0.50 \\ -0.88^{*} \\ -0.72^{*} \\ 0.77^{*} \\ -0.69^{*} \\ 0.82^{*} \\ 0.74^{*} \end{array}$	$\begin{array}{ccccc} 0.50 & 0.67* \\ -0.88* & -0.74* \\ -0.72* & -0.85* \\ 0.77* & 0.89* \\ -0.69* & -0.54 \\ 0.82* & 0.74* \\ 0.74* & 0.78* \end{array}$	$\begin{array}{cccccccccccccccccccccccccccccccccccc$

	N-load	% Residential	Marsh Slope (cm m ⁻¹)	Marsh Width (m)	Flooding Tide (cm)
Species richness	Xa				
Density S. patens shoots m^{-2}	Xa			X^a	
Density (tall) S. alterniflora shoots m^{-2}	Xa				
Density (short) S. alterniflora shoots m ⁻²		\mathbf{X}^{a}			
% extent S. patens			\mathbf{X}^{a}	X^a	
% extent (tall) S. alterniflora			\mathbf{X}^{a}		
% extent (short) S. alterniflora		\mathbf{X}^{a}		X^{b}	X^a
Height S. patens (cm)		\mathbf{X}^{a}			
Height (tall) S. alterniflora (cm)		X^{b}			
Height (short) S. alterniflora (cm)		\mathbf{X}^{a}			

TABLE 7. Summary of the stepwise multiple regression analyses for relationships between N-load, percent residential development, and physical characteristics with plant metrics. Probability is reported as ^a p < 0.05 and ^b p < 0.10.

In the present study, we observed significant relationships of N-load and percent residential development with plant species richness and density and height of dominant plant species, but the effect of these anthropogenic stressors was confounded by the effect of slope, flooding tide, and marsh width on plant structure. Slope significantly correlated with N-load as well as percent residential development making it difficult to conclude the degree to which N-load is contributing to the varying plant structure among the sites. Although marsh width is a physical characteristic of the marsh, human activities over the past century-for example, filling in and road building-might have altered the natural boundaries and widths of the marshes. Likewise, human activities (i.e., global warming) may contribute to apparent sea-level rise and consequently flooding conditions of New England marshes (Warren and Niering 1993; Donnelly and Bertness 2001).

When just five sites with similar slopes were examined for relationships of N-load with plant structure, we observed significant relationships of Nload with density of *S. patens* and short *S. alterniflora* and percent extent of *S. patens* and tall *S. alterniflora*. This is similar to the results when all ten marshes were included in the correlation analyses. Marsh width and flooding tide were also strongly related to some of the plant metrics among the subset of five marshes. Because the N-load effect is confounded by the effect of physical characteristics, even among the marshes of similar slopes, it is unclear whether (and to what extent) nitrogen enrichment contributes to the variation in plant structure among the marshes in Narragansett Bay.

In marsh fertilization experiments in New England, S. patens is outcompeted by S. alterniflora under nitrogen enrichment (Levine et al. 1998; Bertness and Pennings 2000; Emery et al. 2001). Under increasing N-loads (albeit confounded by slope and flooding tide) in this baywide survey, the extent and density of S. patens is reduced and that of tall S. alterniflora is increased. We also noticed a reduction in the extent and density of the short form of S. alterniflora at the same sites where the S. patens was in decline, although the height of both species significantly increased with increasing extent of tall S. alterniflora. We suggest two alternative explanations for the decline of the short S. alterniflora. One explanation is that the short S. alterniflora becomes tall S. alterniflora due to nitrogen enrichment (Valiela et al. 1975), or a second explanation is that the tall S. alterniflora displaces the short S. alterniflora. Researchers have shown that short S. alterniflora can become tall when fertilized by nitrogen (Valiela et al. 1975). In common garden experiments, Gallagher et al. (1988) suggest that there are distinct genotypes associated with some tall and short forms. Reduction in density and extent along with increases in heights of S. patens and short S. alterniflora suggest that competition for light under increasing N-loads and the

TABLE 8. Relationships of N-load, marsh slope, width, and flooding tide with plant structure at five Narragansett Bay sites (* p < 0.05; n = 5).

	$\begin{array}{c} \text{N-load} \\ \text{KgN ha}^{-1} \text{ y}^{-1} \end{array}$	$\begin{array}{c} \text{Marsh Slope} \\ (\text{cm } \text{m}^{-1}) \end{array}$	Marsh Width (m)	Flooding Tide (cm)
Species richness	-0.80	-0.27	0.68	-0.84
Density S. patens shoots m^{-2}	-0.94*	-0.53	0.92*	-0.86
Density (tall) S. alterniflora shoots m^{-2}	-0.62	-0.28	0.54	-0.65
Density (short) S. alterniflora shoots m ⁻²	-0.89*	-0.72	0.83	-0.90*
% extent S. patens	-0.92*	-0.58	0.84	-0.94*
% extent (tall) S. alterniflora	0.94*	0.70	-0.92*	0.89*
% extent (short) S. alterniflora	-0.02	-0.35	0.09	0.02

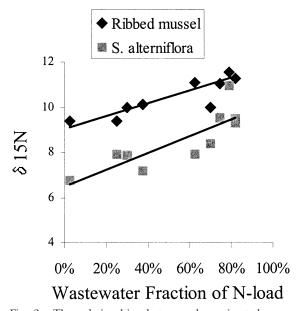


Fig. 3. The relationships between the estimated percent wastewater in the watershed N-loads of 10 Narragansett Bay marsh sites and the stable nitrogen isotopic ratios in ribbed mussels (*Geukensia demissa*) and *Spartina alterniflora* leaf tissue. (See McKinney et al. 2001; Wigand et al. 2001 for further description of the data.)

extent of tall *S. alterniflora* may also contribute to plant structure.

In New England salt marshes, high species richness is often described for the high marsh zone where *S. patens* is usually the dominant plant (Miller and Egler 1950; Niering and Warren 1980; Roman et al. 2000). The results of this survey showed significant positive relationships of *S. patens* with plant species richness and inverse relationships of tall *S. alterniflora* with species richness. When wastewater inputs from watersheds cause nitrogen enrichment in salt marshes, *S. patens* as well as other sensitive plant species may be displaced by tall *S. alterniflora*. In general, nutrient enrichment studies in macrophyte-based systems show reduced plant species richness under nitrogen enrichment (Tilman 1984, 1987; Goldberg and Miller 1990).

On the other hand, recent research suggests that the loss of high marsh dominants *S. patens* and *J. gerardii* in northeast salt marshes may be influenced by apparent sea-level rise (Warren and Niering 1993; Donnelly and Bertness 2001). Greater frequency and duration of flooding, increased salinity and sulfides due to sea-level rise have resulted in displacement of *S. patens* by *S. alterniflora* and forbs (Warren and Niering 1993; Donnelly and Bertness 2001). Although marshes in some New England estuaries are being adversely affected by rising sea level, it appears that Narragansett Bay salt marshes are keeping up with the rise in sea level by various sediment accretion mechanisms (Bricker-Urso et al. 1989; Donnelly and Bertness 2001). Since sea-level rise causes a similar decline in high marsh-dominant plants as caused by eutrophication, increased nitrogen loads to salt marshes may exacerbate the adverse effects of sea level rise. We also recognize that additional factors that were not directly examined in this study such as changes in sediment supply and human impacts of ditching on the marsh landscape will also have varying degrees of influence on marsh vegetation patterns.

On a large spatial scale, Valiela et al. (2000b) described the salt marsh as a subcomponent of the entire coastal landscape and the role the marsh system plays in intercepting land-derived nitrogen. In this field survey of Rhode Island fringe salt marshes, we examined the relationships of some possible anthropogenic stressors, percent residential development and N-loading, as well as some physical characteristics with marsh vegetation patterns. Tidal flooding, marsh width, or slope related significantly with species richness and the distribution of Spartina species on the landscape, and these results are supported by a number of reports that have described the stressful sediment conditions (e.g., low redox; oxygen deficiency; high sulfides) for plants associated with flooded marsh soils (e.g., Howes et al. 1981; Mendelssohn et al. 1981). Interspecific plant interactions have been described to influence the New England marsh landscape (Bertness and Ellison 1987; Levine et al. 1998; Bertness and Pennings 2000; Emery et al. 2001), and the significant relationships of N-load with plant structure in this survey cannot be discounted as also possibly influencing the marsh landscape due to interspecific competition. Regardless of the cause, changes in the plant structure (i.e., species richness; extent, density, and height of dominant species) could result in a reduction of the available niches for other biota (i.e., plants and animals), and, therefore, a reduction in the overall marsh biodiversity and capacity to support nekton (Weinstein and Balletto 1999; Deegan 2002).

This survey suggests that the reduction of plant species richness and *S. patens* and the increase of tall *S. alterniflora* could in part be a response to elevated nitrogen loads due to residential development in adjoining watersheds to the marshes. It is clear that physical characteristics such as tidal flooding, marsh slope, and width also influence plant structure in Narragansett Bay. Nevertheless, along with previously reported marsh fertilization studies in New England (Levine et al. 1998; Emery et al. 2001), this field survey supports the hypothesis of competitive displacement of dominant marsh plant species under elevated nitrogen, but

Acknowledgments

structure.

We thank Al Beck, Roger Green, and Kenny Raposa of the Prudence Island National Estuarine Research Reserve for helping us select sites on the island for the survey, Mohamed Abdelrhman for conducting the marsh elevation surveys, John Kiddon and Steve Ryba for field support, and Hal Walker and Dan Campbell for insightful discussions and critical review of our study. We are grateful for the guidance and the assistance that Jim Heltshe provided on the statistical analyses in the manuscript. Mention of trade names or commercial products does not constitute endorsement or recommendation for use by the U.S. Environmental Protection Agency (EPA). This report, contribution number AED-01-099, has been technically reviewed by the EPA's Office of Research and Development, National Health and Environmental Effects Research Laboratory, Atlantic Ecology Division, Narragansett, Rhode Island, and approved for publication. Approval does not signify that the contents necessarily reflect the views and policies of the Agency.

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Received for consideration, February 13, 2002 Revised, December 13, 2002 Accepted for publication, January 14, 2003