NITROGEN, PHOSPHORUS, AND SULFUR DYNAMICS IN A LOW SALINITY MARSH SYSTEM DOMINATED BY *SPARTINA ALTERNIFLORA*

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Abstract: In the upper reaches of estuaries, the pulsing of nutrient inputs and salinity occurs on fine temporal and spatial scales. We investigated the supply and exchanges of N, P, and S along a salinity gradient in a Chesapeake Bay subestuary. Interactions among nutrients in surface water, sediment porewater, and shoots of the dominant marsh macrophyte *Spartina alterniflora* were also examined. The system was characterized by a spatial gradient in nutrient availability, with the low salinity region representing abundant allochthonous nitrogen and phosphorus inputs and minimal sulfur availability. Autochthonous production and consumption of nutrients were most important at the midpoint of the salinity gradient. These patterns were reflected in the N, P, and S content of *S. alterniflora* over one growing season. This brackish tidal creek system also had a gradient of temporal variability in levels of inorganic nitrogen, phosphorus, and sulfur. The higher salinity portion experienced the damping effect of waters of more constant nutrient composition, whereas the upper portion of the system was characterized by highly pulsed nutrient availability. Interchanges between nutrient pools were apparent throughout the system. Sediment, and even surface-water, concentrations of nutrients seemed to respond to plant root zone oxidation and uptake and release of nutrients. Porewater biogeochemical processes were linked to surface-water nutrient dynamics as well.

Key Words: wetland biogeochemistry, porewater, *Spartina alterniflora*, sulfur, oligohaline marsh, salinity gradient, spatial variability

INTRODUCTION

The importance of physical pulses in tidal marshes has been well-demonstrated for freshwater and high salinity systems (cf. Odum et al. 1995). However, the relatively less-studied oligohaline and mesohaline marsh ecosystems experience nutrient and salinity pulses that are potentially far more dynamic.

Temporal scaling of nutrient variability in low salinity marshes may range from event-scale pulses to seasonal time scales of decomposition of organic matter and of assimilation, immobilization, and biogeochemical transformation of nutrients. Interannual climatic variability may also have a large impact in low salinity systems on plant species composition, primary production, and sediment biogeochemical processes. Spatially, because of their positioning in the landscape, low salinity wetlands in the upper reaches of estuaries are subject to physical variability over relatively fine scales. Rainfall and wind-generated tidal fluxes are superimposed on upland point- and diffuse-source loading, generating variability in surface-water nutrient concentrations. This variability may be reflected in sediment porewater composition and in marsh macrophyte nutrient pools, and the latter, in turn, may impact surface-water levels via export.

Phosphate is usually abundant in salt marsh sediments; however, low salinity portions of Chesapeake Bay have shown phosphorus limitation, especially in winter and spring (D'Elia et al. 1986, Fisher et al. 1992, Wigand and Stevenson 1994). Interactions between sediment iron, sulfide, and phosphate produce marked seasonal changes in dissolved phosphate in surface waters and in sediments (Krom and Berner 1981, Froelich 1988, Roden and Edmonds 1997). A common pattern in estuarine systems is the occurrence
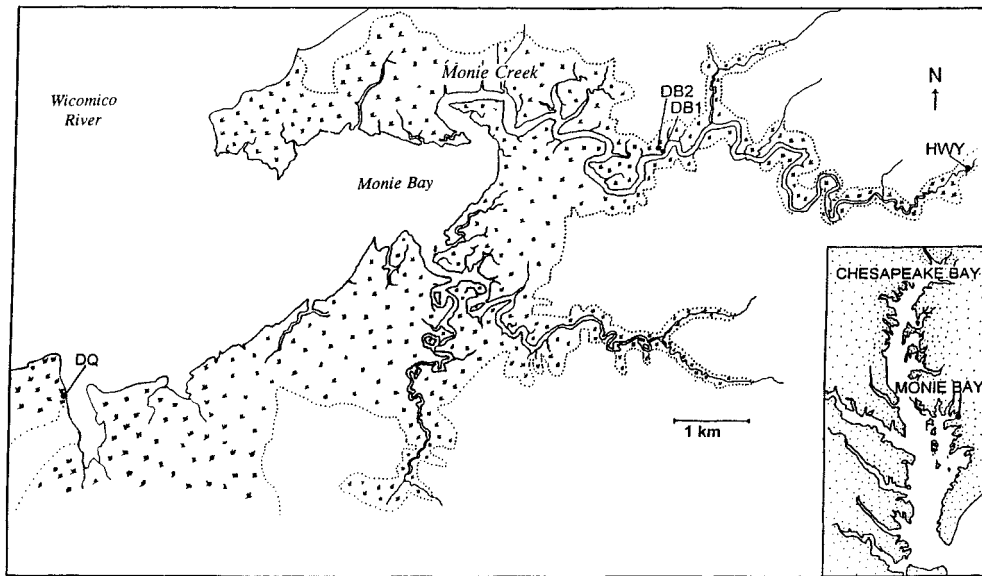
Figure 1.   Location of Monie Bay; map of study sites.

of a late summer phosphate maximum in the water column (e.g., Martin 1965, Taft and Taylor 1976). Such seasonal phosphate release has been documented in other brackish Chesapeake Bay marshes (Stevenson et al. 1977).

As with phosphate, seasonal variations in nitrogen availability to marshes may be substantial in upper estuarine systems (Rizzo and Christian 1996). Nitrate is lost to ground water from soils of mid-Atlantic agricultural fields in winter (Staver and Brinsfield 1990), often generating strong nitrogen pulses in nearby surface waters. In summer and fall, surface-water nitrogen is enhanced by the decomposition of organic matter (Wolaver et al. 1983, Jordan and Correll 1985). Event-scale pulses are also important; delivery of nitrate to stream waters was at a maximum in a Chesapeake Bay tributary watershed during heavy storms (Prestegaard and O'Connell 1995). Processes of uptake and transformation result in strongly biochemically-driven nitrogen fluxes in marsh sediments (Scudlark and Church 1989, Vorosmarty and Loder 1994, White and Howes 1994).

The supply of the essential element sulfur may be limited in low salinity systems remote from sources of atmospheric sulfur. Although sulfur is usually abundant in salt marshes and is potentially harmful to vegetation when reduced (Linthurst 1979, Morris 1980, DeLaune et al. 1983, Koch et al. 1990), its role as a plant nutrient is also important in oligohaline wetlands, where sulfate availability may vary widely. In the marsh cordgrass *Spartina alterniflora* Loisel., tissue sulfur concentrations and ratios of sulfur to other nutrients are much higher than in most plant species (Ornes and Kaplan 1989), and sulfate may limit the

growth of *S. alterniflora* at very low salinities (Stribling 1997).

This study examined variability, sources, and interchanges of nitrogen, phosphorus, and sulfur within surface water, porewater, and *S. alterniflora* shoot tissue in a brackish tidal creek system on the eastern shore of Chesapeake Bay. We investigated the extent to which *S. alterniflora* shoots reflected pulsed surface-water inputs and variations in porewater nitrogen, phosphorus, and sulfur. We also examined the response of porewater pools of N, P, and S to the seasonal dynamics of the vegetation and the response of surface-water concentrations to changes in porewater levels.

METHODS

Study Site

The study was conducted in Monie Bay (38°13'N, 75°51'W), an embayment on the Wicomico River on the lower eastern shore of Chesapeake Bay, Maryland, USA (Figure 1). Agricultural activities (crop farming and livestock and poultry operations) in the Monie Bay watershed result in substantial inputs of nitrate and phosphate (Cornwell et al. 1994). We sampled four marsh sites (Figure 1) encompassing a salinity gradient, including three on Monie Creek, the largest creek feeding Monie Bay, and a fourth near Monie Bay itself. The first site, designated ''HWY,'' is at the uppermost navigable portion of the creek. Above this location, a highway culvert dams the creek. This location receives much particulate and dissolved organic input from upland runoff (Cornwell et al. 1994). Approxi-

mately midway downstream, we sampled two marsh sites, a well-drained creek bank levee (DB1) and the low interior marsh behind it (DB2). The fourth site (DQ), at Dames Quarter on the southwestern end of Monie Bay, represented the high salinity end point of the system. Annual mean salinity ranged from 1.3 ppt at HWY to 16 ppt at DQ. *Spartina alterniflora* was a dominant species at all four of these sites.

To measure upstream inputs, we sampled a fifth location (HEAD) for surface-water nutrients, sulfate, and chloride in March of 1991 and from March to November of 1992. This site, several km above the HWY site, is at the nontidal headwaters of Monie Creek, where the forested stream crosses a roadway. Finally, we also sampled surface water from a small tributary that drains the DB2 marsh and empties into Monie Creek (DBCr) to represent the surface water associated with the DB2 site. Sediment and hydrodynamic characteristics of the sites are described in Stribling et al. (1998).

Sample Collection and Analysis

Porewater, surface water, and *S. alterniflora* shoots were sampled monthly. Plants were clipped 2 cm above the marsh surface. We measured total standing crop by sampling from three 0.25 m² quadrats per sampling site. Additionally, six individual live shoots were pooled for each plant nutrient sample (three replicate samples per site). Plants were washed free of debris, rinsed with deionized water, dried at 65° C to constant weight, and ground in a Wiley Mill (40 mesh). Plant tissue analyses were conducted at the Soil Testing Service, University of Maryland and included total shoot carbon, hydrogen, nitrogen, sulfur, and phosphorus concentrations. Shoot total phosphorus concentration was measured with a nitric and perchloric acid digestion using a Technicon Autoanalyzer. Infrared gas analysis was used for carbon and hydrogen determination; nitrogen concentration was determined according to Campbell (1992). Sulfur was measured by infrared detection after combustion to sulfur dioxide. We sampled porewater from each marsh site from January through November 1992 for sulfide, iron, ammonium, phosphate, sulfate, and chloride analyses. Porewater samples were collected using modified Hesslein (1976) diffusion equilibrators. The equilibrators were of plexiglas, 30 cm long, with five round chambers of 4-cm diameter and 12-mL volume. Porewater sampling was thus integrated from five 4-cm-deep sections centered at depths of 3, 8, 13, 18, and 23 cm. Each equilibrator was initially filled with de-oxygenated water, which was adjusted to the approximate salinity of the sampling site with NaCl. The holes were covered with 0.2-μm polycarbonate membrane and with 120-μm Nytex

mesh to protect the membrane. The equilibrators were submerged overnight in de-oxygenated water that was bubbled with N_2 then deployed for 10 to 14 days. One equilibrator was installed at each marsh site.

For dissolved free sulfide determination, water was drawn directly from the equilibrator chamber through a Whatman GFF filter into diamine sulfide reagent (Cline 1969) for colorimetric analysis (Lambert and Oviatt 1986). The remainder of the sample was divided into filtered aliquots for subsequent ammonium, phosphate, iron, sulfate, and chloride analyses. The latter samples were stored frozen prior to analysis. Sulfate and chloride concentrations were determined using a Dionex ion chromatograph; phosphate was measured using the ascorbic acid method and ammonium using the indophenol method (Parsons et al. 1984). Concentrations of dissolved Fe were determined according to Gibbs (1979).

Coincident with retrieval of the equilibrators, we collected nutrient samples from the surface water adjacent to each marsh site. Filtered (Whatman GFF) samples were stored frozen and were analyzed using a Technicon Autoanalyzer for ammonium, orthophosphate, nitrate, and nitrite, and with ion chromatography used for sulfate and chloride analysis.

Replicated data for *S. alterniflora* shoot nutrient concentrations were analyzed using a two-way analysis of variance and Tukey's HSD test for post-hoc comparisons (Statistical Analysis System 1999). Porewater and surface-water nutrient concentrations were measured on single samples in order to maximize the representation from different sampling dates and locations.

RESULTS

Surface-Water Nitrate, Ammonium, and Phosphate

Throughout the Monie Bay system, surface-water concentrations of phosphate and ammonium generally peaked in summer and nitrate in winter (Figure 2). Mean annual N and P concentrations decreased overall with distance downstream (Table 1). Elevated mean annual phosphate levels at the uppermost, nontidal HEAD site reflected its proximity to fields receiving routine applications of fertilizer (including low N:P poultry manure) in spring. At most sites, month-to-month variability in surface-water nitrate (Figure 2) coincided with characteristic late winter/early spring peaks in overland and ground-water flows. Variability on much shorter time scales was associated with events such as the August 1992 storm, which delivered a 12-cm rainfall in four days. This resulted in surface-water peaks in nitrate and phosphate at the HEAD site and in a sharp decrease in ammonium and phosphate
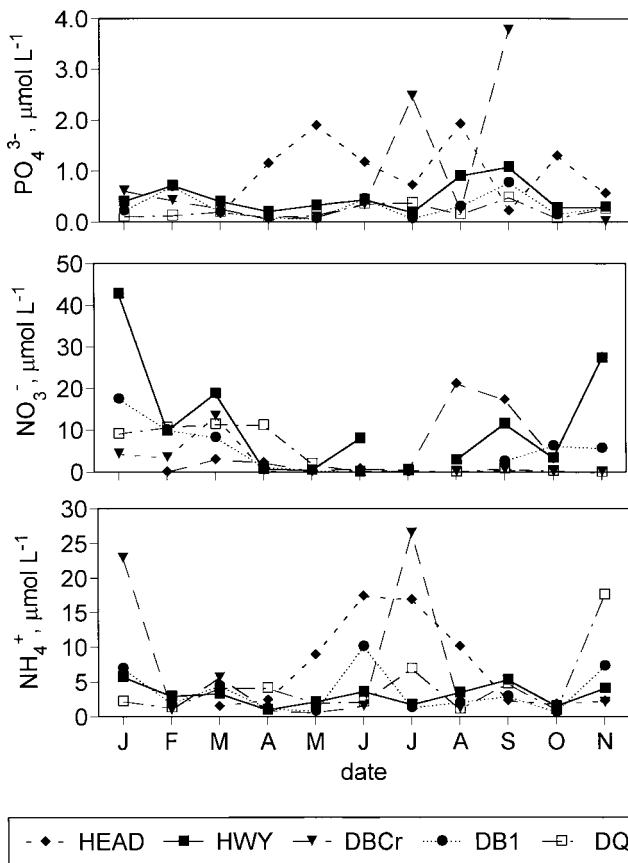
Figure 2. Surface-water dissolved phosphate, nitrate, and ammonium concentrations.

at DBCr. In contrast to the strong event-scale variability at the upstream (HEAD, HWY) sites and at DBCr, surface-water N and P levels were relatively constant at the higher salinity DQ site (Figure 2).

Porewater Ammonium and Phosphate

Mean annual porewater ammonium and phosphate concentrations were highest among the marsh sites in the interior DB2 sediments (the subtidal DBCr porewater ammonium was highest overall). The more well-drained marshes DB1 and DQ had the lowest mean values for ammonium and phosphate, respectively (Table 2). Porewater concentrations of both nutrients increased with depth except in July, when elevated levels were found from 8–13 cm, especially at DB2 (Figure 3). These data suggest that an adsorbed reservoir of phosphate at intermediate depths was released as sediment anoxia moved upward with increasing temperature.

Porewater concentrations of ammonium and phosphate were usually lowest in winter and highest in summer (Figure 3), paralleling the seasonal increase in sediment anoxia. (Ammonium may also have been re-

Table 1. Mean annual concentrations of nitrate, phosphate, and ammonium (μmol L^{-1}) and of sulfate (mmol L^{-1}) in surface water. Sulfate values are derived from 3-cm depth porewater, except at HEAD. Means at HEAD represent March–November only.

Location	NO$_3^-$	PO$_4^{-3}$	NH$_4^+$	SO$_4^=$
HEAD	8.4	1.01	7.0	0.05
HWY	12.5	0.47	3.1	0.72
DBCr	2.2	0.82	6.9	5.64
DB1	5.8	0.30	3.6	5.56
DQ	5.7	0.21	4.3	10.69

leased via desorption with increasing salinity.) However, at the DB1 site, concentrations of ammonium and phosphate in the root zone were relatively low during the peak growing season, increasing only in September or October at senescence. Brief, sharp decreases in porewater levels at DB2 followed the August rainfall event (Figure 4).

Surface-Water Sulfate

Because sampling was not timed with tide stage, surface-water sulfate concentrations reflected more the variability of tidal stages than more long-term changes. We therefore used porewater values at 3-cm depth to represent an integration of surface-water concentrations (Figure 5a). Although sulfate concentrations at 3 cm are slightly reduced relative to surface water, they seem to better integrate the fluctuations over the tidal cycle and thus provide a more accurate representation of the changes in availability of sulfate to the sediments. Mean annual sulfate concentrations at 3-cm depth (Table 1) ranged from 0.05 mmol L^{-1} at HEAD to 8.76 mmol L^{-1} at DQ. Seasonal pulsing of sulfate was evident upstream in the strong July peaks, whereas the high salinity DQ site showed little change over the year. Event-scale fluctuations were reflected in a sharp drop in sulfate concentration after the August rainstorm at all sites except DQ (Figure 5a). Sulfate concentrations at the low salinity HWY site were near zero at the outset of the growing season and never exceeded 3 mmol L^{-1}.

Molar sulfate:chloride ratios in surface water varied

Table 2. Mean annual porewater phosphate and ammonium concentrations (μmol L^{-1}) from 3–23 cm depths.

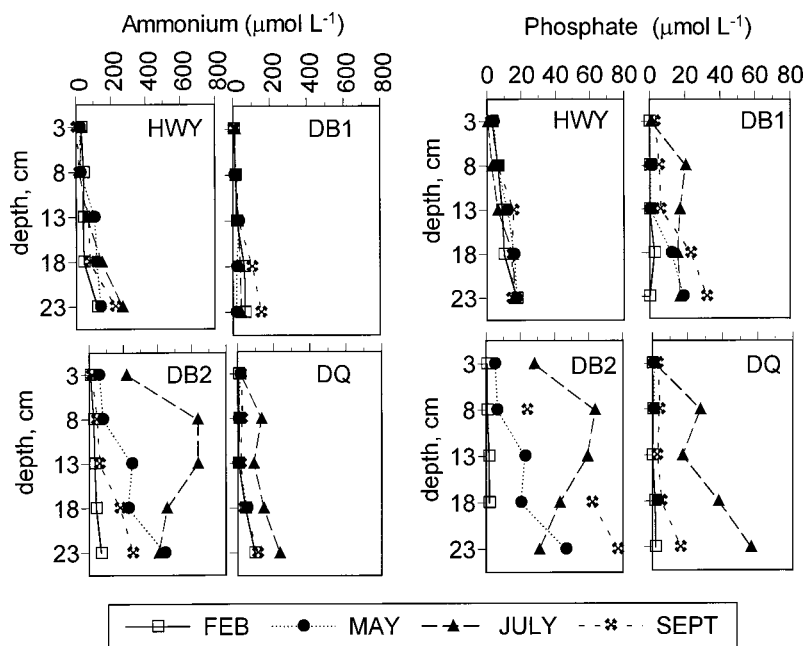| Location	PO$_4^{-3}$	NH$_4^+$
HWY	9.55	59.69
DBCr	12.43	147.38
DB1	19.40	31.41
DB2	22.33	125.10
DQ	8.78	46.57

Figure 3. Depth profiles of porewater ammonium and phosphate for months encompassing the growing season.

strongly with season in the Monie Bay system (Figure 5b), reflecting seasonal variability in sediment biogeochemical processes of sulfate production and consumption. The standard seawater ratio of 0.0517 was exceeded at most sites in February and at all sites in May, whereas strong sulfate depletion was apparent everywhere by July or August. The elevated winter/spring ratios probably reflect oxidation of stored sulfide minerals; the minimal ratios are consistent with high rates of sediment sulfate reduction.

Porewater Sulfur

Although surface-water sulfate concentrations increased over the summer, with most peaking in July, only at the HWY site did the porewater levels follow this pattern. Elsewhere, porewater sulfate was most strongly influenced by biogeochemical processes, and sulfate reduction below 3-cm depth led to minimal values in July or September. Sulfate:chloride ratios indicated extreme sulfate depletion at the HWY site by May; however, there was a brief increase in the ratio in July. Most other sites showed later, more steady sulfate depletion; at the DQ site, sulfate:chloride ratios remained relatively high except for a sharp drop in July (Figure 6).

Porewater sulfide concentrations were very low at most sites until late summer. However, at the interior DB2 site, sulfide was abundant below 3 cm from late spring through summer, with the exception of August (Figure 4).

Spartina Nitrogen, Phosphorus, and Sulfur Content

Shoot concentrations of total phosphorus, nitrogen and sulfur over the 1992 growing season (Table 3) differed significantly (p < 0.001 for all) by date, site, and date*site interaction (DF = 3 for site and date, 9 for site*date interaction; F = 12.40, 12.02, and 27.41 for P, N, and S site effect, respectively; F = 75.73, 123.32, and 54.37 for P, N, and S date effect, respectively; and F = 11.57, 7.73, and 15.03 for P, N, and S site*date interaction, respectively; error DF = 28 for N, 31 for P and 29 for S). Shoot nitrogen and phosphorus concentrations, elevated in winter, decreased significantly (Tukey's HSD, p < 0.05) over the growing season, with the exception of phosphorus at the DB1 site. Peak *S. alterniflora* biomass was reached between June (DB2) and August (HWY); senescence at all sites began in September. The greatest seasonal variation and by far the highest early shoot nitrogen and phosphorus concentrations were found at the HWY site, where early spring growth was relatively slow. The N:P ratio of *S. alterniflora* at this site increased to more than 50 by September, suggesting late season phosphorus limitation.

Shoot sulfur concentrations for the three higher salinity sites also decreased from February to May (Table 3), indicating that this element behaves similarly to other macronutrients as the plant accumulates structural carbon. However, the decrease over the growing season continued only at the low salinity HWY site. Elsewhere, shoot sulfur increased again in July and
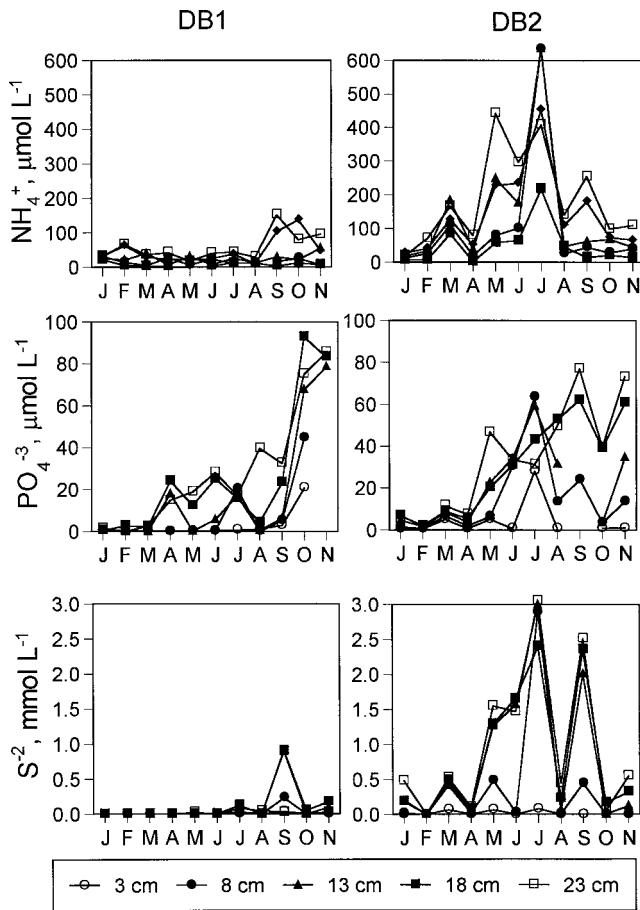
Figure 4. Porewater ammonium, phosphate, and sulfide concentrations at DB1 and DB2 for all sampling months. Plant roots were concentrated at 8-, 13-, and 18-cm depths (solid symbols).
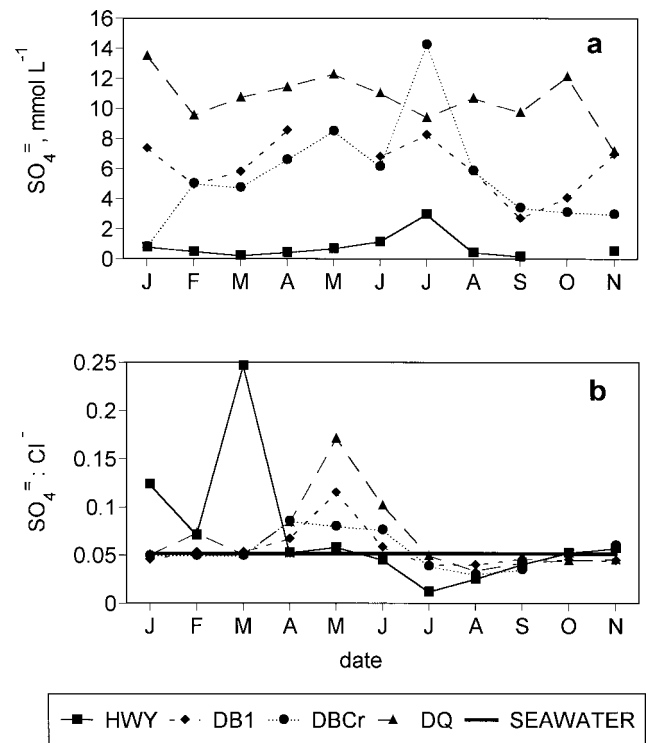

Figure 5. a. Porewater sulfate concentrations at 3-cm depth used as an indicator of surface-water sulfate concentrations independent of tide stage. b. Surface-water sulfate:chloride ratios.

continued to rise at the DQ and DB1 sites into September. The July shoot sulfur content at the DB2 site exceeded that for February (Tukey's HSD, $p < 0.05$).

Interannual comparisons of shoot phosphorus and nitrogen concentrations showed no significant differ-
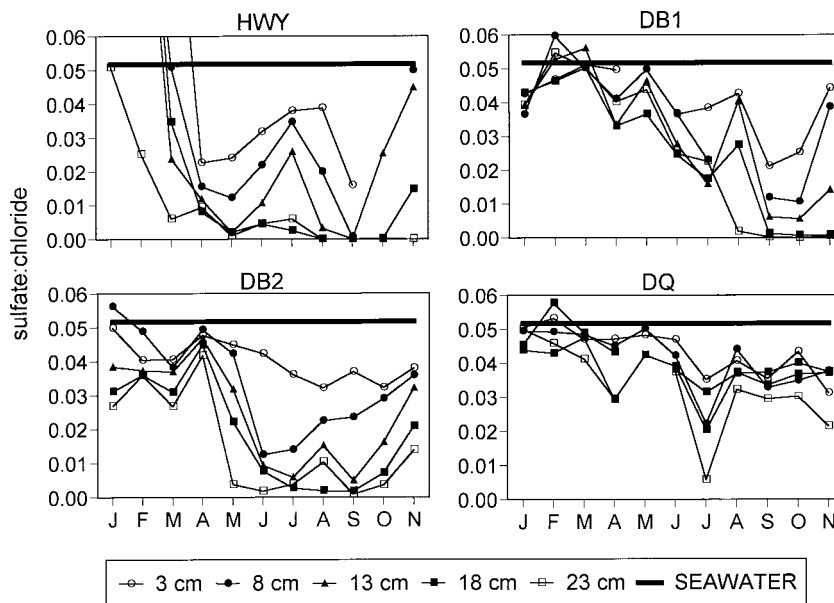

Figure 6. Porewater molar sulfate:chloride ratios. Thick lines denote the seawater ratio of 0.0517.

Table 3. 1992 *Spartina alterniflora* shoot elemental concentrations (%), ±1 S.D. February values are means of 2 samples.

Phosphorus	HWY	DB1	DB2	DQ
Feb	0.38	0.17 ± 0.02	0.18 ± 0.04	0.2 ± 0.02
May	0.27 ± 0.03	0.16 ± 0.05	0.11 ± 0.02	0.12 ± 0.01
July	0.09 ± 0.01	0.13 ± 0.00	0.07 ± 0.02	0.08 ± 0.01
Aug	0.03 ± 0.01	0.12 ± 0.01	0.06 ± 0.02	0.05 ± 0.03
Nitrogen	HWY	DB1	DB2	DQ
Feb	3.07	1.93 ± 0.26	2.17 ± 0.36	2.00 ± 0.21
May	2.01 ± 0.02	1.66 ± 0.12	1.60 ± 0.17	1.49 ± 0.08
July	1.02 ± 0.04	1.27 ± 0.13	1.04 ± 0.03	1.03 ± 0.09
Aug	0.75 ± 0.06	1.17 ± 0.07	0.69 ± 0.52	0.80 ± 0.09
Sulfur	HWY	DB1	DB2	DQ
Feb	0.53	0.57 ± 0.03	0.6 ± 0.03	0.69 ± 0.13
May	0.41 ± 0.03	0.3 ± 0.03	0.38 ± 0.03	0.24 ± 0.02
July	0.39 ± 0.04	0.39 ± 0.04	0.78 ± 0.05	0.44 ± 0.05
Aug	0.33 ± 0.02	0.44 ± 0.05	0.49 ± 0.08	0.52 ± 0.03

ences except by site; however, shoot sulfur differed significantly over the three year period by date (p < 0.005, DF = 2, F = 7.62), site (p < 0.005, DF = 3, F = 6.86), and date*site interaction (p < 0.0005, DF = 6, F = 7.61; error DF = 24). Analysis of variance by site showed that the only significant interannual variation in shoot sulfur concentration was at DB2, where high levels in July 1992 coincided with a three-year downward trend in spring rainfall.

DISCUSSION

Spatial and Temporal Variability

Spatial patterns of nutrient availability along a salinity gradient often reflect a shift from allochthonous inputs to autochthonous production (Rizzo and Christian 1996, Deegan and Garritt 1997). In Monie Creek, external sources (especially fertilizer) were abundant

and were important in supplying nitrate and phosphate upstream. Further downstream, sediment biogeochemical nutrient regeneration and consumption had a greater influence on the fluctuations of surface-water N and P. At the higher salinity end of the system, concentrations of N and P were both lower and more stable.

Sulfur supply also varied along the salinity gradient. Its proximity to Chesapeake Bay gave the downstream DQ site a fairly continuous input of seawater sulfate. Upstream, tidal sulfate supply was far more irregular. At the HWY site, sediment regeneration of sulfate via oxidation of stored sulfide minerals seemed to occur in spring, when sulfate:chloride ratios were extremely high even in surface water. There is, of course, the alternative possibility of allochthonous sulfur inputs from rainfall or from fertilizer runoff at the low salinity end. However, the concentrations of sulfate at the

Table 4. Interannual comparisons of *Spartina alterniflora* shoot elemental concentrations (%), ±1 S.D.

Phosphorus	HWY	DB1	DB2	DQ
7/90	0.09 ± 0.01	0.16 ± 0.06	0.05 ± 0.01	0.06 ± 0.02
7/91	0.14 ± 0.03	0.14 ± 0.03	0.08 ± 0.02	0.07 ± 0.02
7/92	0.09 ± 0.01	0.13 ± 0.00	0.07 ± 0.02	0.08 ± 0.01
Nitrogen	HWY	DB1	DB2	DQ
7/90	1.06 ± 0.08	1.06 ± 0.03	0.99 ± 0.04	1.00 ± 0.03
7/91	1.24 ± 0.26	1.22 ± 0.15	0.94 ± 0.05	1.03 ± 0.10
7/92	1.02 ± 0.04	1.27 ± 0.13	1.04 ± 0.03	1.03 ± 0.09
Sulfur	HWY	DB1	DB2	DQ
7/90	0.40 ± 0.04	0.31 ± 0.04	0.38 ± 0.22	0.50 ± 0.07
7/91	0.45 ± 0.04	0.33 ± 0.02	0.47 ± 0.11	0.47 ± 0.08
7/92	0.39 ± 0.04	0.39 ± 0.04	0.78 ± 0.05	0.44 ± 0.05

HEAD site were extremely low (mean 0.05 mmol L^{-1}), and levels upstream did not increase with precipitation. Porewater sulfate concentrations at HWY in January and February were also higher in the root zone than at the surface, implicating sediment as the sulfate source at this time.

The magnitude and relative importance of allochthonous and autochthonous nutrient inputs varies temporally as well as spatially in small creek systems (Prestegaard and O'Connell 1995, Rizzo and Christian 1996). In this study, nutrient pools were very dynamic, with evidence of event-scale and seasonal variability.

The August storm generated the strongest event-scale fluctuation in nutrient supply, increasing nitrate and phosphate and reducing sulfate in upstream surface water. Porewater concentrations of sulfide, phosphate, and ammonium also fell, especially at the DB2 site. An influx of fresh water can chemically, via oxidation, and physically, via advection, remove dissolved sulfides (Howarth et al. 1983) and ammonium from marsh porewater. As sediments become more oxidized, oxidized iron minerals, and thus adsorption of phosphate, also increase. Effects of the storm were not detected at the high salinity DQ site, which was relatively isolated from both event-scale and seasonal fluctuations by the damping influence of waters closer to Chesapeake Bay.

Seasonal variability in Monie Creek upstream nutrient dynamics was consistent with the characteristic sequence of biogeochemical processes in marshes. Winter and early spring conditions of low temperatures and more oxidized sediments result in the production of sulfate from sulfide minerals (Matson and Brinson 1985). The expected seasonal variability in sulfate supply and consumption was augmented by low salinity in Monie Creek, as limited tidal water sulfate inputs in winter and spring elevated the importance of sulfate derived from stored sulfides. Porewater phosphate and ammonium levels were also predictably low in winter and early spring, when decomposition is slow and phosphate binds to oxidized iron minerals (Scudlark and Church 1989). Conversely, seasonal temperature maxima and the associated consumption of sediment oxygen coincide with sharp drops in porewater sulfate, increases in sulfide, and release of phosphate and ammonium (Hines et al. 1989, Scudlark and Church 1989). These biogeochemical processes were especially evident in this study in the frequently flooded DB2 marsh. At DB1, where sediments were more oxidized, seasonal nutrient dynamics were more closely associated with the timing of plant growth and senescence (see below). Most of the spatial variability in porewater nutrient dynamics seemed to be linked to hydrology of the sampling site. The more frequently flooded DB2 site had consistently higher ammonium, phosphate, and sulfide concentrations during the growing season than were present in porewater at DB1.

Low year-to-year fluctuations in *S. alterniflora* shoot nitrogen concentrations at the DQ site contrasted markedly with high interannual variability at the uppermost HWY site. As was frequently the case for the other nutrient pools, seasonal variability in nutrient content of *S. alterniflora* shoots was also greatest upstream.

Interchanges

Marsh systems are very fluid with respect to interchanges between different nutrient pools (e.g., Childers et al. 1993). Exchanges between porewater and surface water were apparent in the DB2 marsh—DBCr creek system. The tributary has a relatively small volume, and water exchanged with the DB2 marsh sediments was not strongly diluted until it reached Monie Creek itself. High surface-water ammonium and phosphate concentrations at DBCr in July suggest export from sediments at DB2, where near-surface porewater levels of both nutrients also peaked in July. Conversely, sediment consumption of nitrate via denitrification or reduction to ammonium was reflected in the exceptionally low mean nitrate concentrations of the water at DBCr, largely independent of season. At the HWY site also, near-surface porewater phosphate increased in spring coincident with the upstream surface-water peak in May.

Extremely high winter and spring sulfate:chloride ratios in porewater at the HWY site were mirrored in the surface-water values. Sulfate enrichment in mesohaline North Carolina estuarine waters between spring and early summer was attributed to biogeochemical oxidation of reduced sulfur species in upper sediments (Matson and Brinson 1985), and Luther et al. (1982a) found that re-oxidation of sulfide minerals in a New Jersey marsh generated an excess of sulfate in March to April in waters flooding the marsh. Plant roots also aid in the oxidation of sulfide minerals stored in the root zone (Howarth and Teal 1979, Jordan and Correll 1985); the early growing season timing of the spring sulfate enrichment for Monie Creek suggests that this mechanism may also have been important at this time when temperatures were not yet optimum for high rates of sulfate reduction.

Sulfate reduction produced sulfate depletion not only in porewater but also in surface water of the Monie Bay system throughout the summer. At the upstream HWY site, however, when surface-water salinity peaked in July, sulfate:chloride ratios in the porewater also increased. Irregular sulfate:chloride ratios that increase

with salinity are indicative of sulfate limitation of microbial sulfate reduction (Howarth and Teal 1979).

Marsh macrophytes have been shown to influence porewater N, P, and S chemistry (Howarth and Teal 1979, Luther et al. 1982b, Lord and Church 1983, Giblin and Howarth 1984, Hines et al. 1989). At the DB1 site, increases in porewater ammonium and phosphate timed with plant senescence may have resulted from processes of both root nutrient uptake and sediment oxidation. In well-drained sediments such as these, plant roots substantially enhance oxidation of sediments (Howes et al. 1986), which would reduce dissolved phosphate and ammonium concentrations coincident with maximal root uptake rates. At senescence, nutrient uptake and root oxygen production decrease while decomposition and leaching release nutrients into porewater. Sediment oxidation by plant roots would explain the very low growing season porewater sulfide concentrations at the DB1 and DQ sites when sulfate:chloride ratios indicated ample rates of sulfate reduction. The September peaks in porewater sulfide at these sites may reflect cessation of root oxidation at the time of flowering (Hines et al. 1989), as well as the stimulation of sulfate reduction by the release of organic matter from dying plant material as *S. alterniflora* senescence begins (Howarth and Teal 1979).

The nutrient content of Monie Bay *S. alterniflora* also seemed linked to porewater and surface-water concentrations. At the HWY site, exceptionally high tissue levels of N and P early in the season, and very low P concentrations by September, reflected similar patterns for these nutrients in surface water at the upstream HEAD site, where most allochthonous nutrients entered the system. Indirectly, porewater dissolved sulfide concentrations may control shoot nitrogen levels; streamside *S. alterniflora* contains higher nitrogen concentrations than inland plants (Buresh et al. 1980) as sulfide interferes with nitrogen uptake in *S. alterniflora* (DeLaune et al. 1983, Koch et al. 1990). High nitrogen concentrations in the creekbank DB1 *S. alterniflora* and low values at DB2 were coupled with far more abundant sulfide at DB2.

Plant tissue sulfur has been shown to respond to porewater sulfur concentrations in salt marshes; a late season increase in the sulfur content of *S. alterniflora* shoots (Carlson 1980, Ornes and Kaplan 1989) may result from direct uptake of sulfide as a sulfur source by *S. alterniflora* (Carlson and Forrest 1982). High sulfur values in July in shoots at DB2 were associated with elevated summer porewater sulfide levels, and low porewater sulfide concentrations may explain the lack of a late season increase in plant sulfur at HWY, as well as the overall low plant sulfur concentrations at DB1. The availability of sulfate was also very low

at the HWY site; porewater concentrations were low enough to limit growth of the plant during the early growing season, and early spring biomass was far lower than at the other sites (Stribling 1997). In such low salinity marshes, macrophyte uptake and dissimilatory sulfate reduction may compete for limiting amounts of sulfate.

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