

Comparison of nitrogen cycling in salt marsh zones related to sea-level rise

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ABSTRACT: Zones in salt marshes can be distinguished by different community and ecosystem properties. As marshes respond to changes in sea level, one might expect alterations in the relative proportions of these zones and, hence, alterations in overall functioning. We used ecological network analysis to assess potential changes in 1 ecosystem function, nitrogen cycling. We constructed nitrogen cycle networks of zones (creekbank, low marsh, and high marsh) for 3 salt marshes on the East Coast of the USA; Great Sippewissett in Massachusetts, Upper Phillips Creek in Virginia, and Sapelo Island in Georgia. The same network structure was applied to all zones, largely using data derived from the literature on the 3 marshes. The factors used to analyze how nitrogen flowed through each zone included how nitrogen imported into the marsh was exported, how imports were related to primary productivity, and how much nitrogen was cycled within the system. Emphasis was placed on identifying patterns across zones that were consistent for all 3 marshes. When precipitation and tidal particulate nitrogen (PN) were the imports, export from active cycling via burial and denitrification significantly increased in importance moving across the marsh from the creekbank to the high marsh. Relative nitrogen cycling also significantly increased from creekbank to high marsh. As the area of the marsh zones decrease or increase in response to sea-level rise, nitrogen dynamics will change as a consequence. If the landscape slope is low allowing the marsh to migrate overland, the high marsh zone will increase in area. Nitrogen cycling as a percentage of total system throughput will increase per unit area averaged over the total marsh. If, however, the marsh stalls because of a steep slope at the upland margin, cycling will decrease on a per unit area basis. If the supply of sediment is great and the marsh progrades toward the sea, nitrogen cycling within the marsh may decrease. Therefore, as relative sea-level rises, the response of a salt marsh's nitrogen cycle will depend on the slope and sediment supply available to the marsh.

KEY WORDS: Salt marsh · Nitrogen cycle · Network analysis · Sea-level rise

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INTRODUCTION

Salt marshes located along the East Coast of the USA can be divided into zones that reflect different communities and environmental conditions; i.e., creekbank, low marsh, and high marsh. These zones may experience increased inundation and move horizontally in the landscape as relative sea-level rises. The way these zones respond to increased inundation depends on their position in the landscape, slope, and sedimentary regime (Redfield 1972, Stevenson et al.

1985, Bertness 1992, Brinson et al. 1995, Christian et al. 2000). The creekbank either may prograde seaward or erode depending on sediment supply. The high marsh may either transgress overland or have its landward movement stalled at the upland's edge depending on the slope of the landscape (Brinson et al. 1995). Thus, the area of each zone may change as these processes continue over decades.

Although these zones are recognized by their plant communities, they also have different ecosystem functions (Christian et al. 2000). Some of these functions include primary production (Kruczynski et al. 1978, Gallagher et al. 1980), sedimentation and peat accu-

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mulation (Bricker-Urso et al. 1989, Kastler & Wiberg 1996), and biogeochemical cycling (Howarth & Hobbie 1982, Osgood et al. 1995). The cycling of nitrogen is particularly important, complex, and well studied (Valiela et al. 1975, 1976, Chalmers 1979, Valiela 1983, Hopkinson & Schubauer 1984, Howes et al. 1986). Nitrogen is often the limiting nutrient to primary production and plays significant roles in electron transfers within salt marsh soils. Some nitrogen cycle processes strictly related to microbes include nitrogen fixation, the process by which molecular nitrogen in the atmosphere is reduced by bacteria and cyanobacteria to NH_4^+ ; nitrification, the aerobic process where NH_4^+ is oxidized first to NO_2^- , and is then further oxidized to NO_3^- ; and denitrification, the process used by facultatively anaerobic bacteria to oxidize organic material using NO_3^- as a terminal electron acceptor with a byproduct of dinitrogen gas. Although various aspects of nitrogen cycling have been assessed within marsh zones (e.g., Hanson 1977, Anderson et al. 1997), there has been little attention to how rising sea level may affect the individual processes or nitrogen cycling as a whole.

Integrative tools are needed to assess ecosystem-level functioning. Ecological network analysis is such a tool (Wulff et al. 1989). It is a collection of algorithms of model analysis to evaluate flow and cycling of energy and material through ecosystem networks and index the 'structure' of the networks, i.e., the interconnectedness of the compartments. A network is a system of interconnected 'nodes.' In most ecological networks, the nodes are model compartments for matter or energy (e.g., nitrogen in marsh plants or sediment organic carbon). The interconnections are the flows of that matter or energy between nodes (e.g., ammonium uptake by plants or resuspension of sediment organic carbon) or between nodes and outside system boundaries (i.e., imports, exports and dissimilations like denitrification). The algorithms in ecological network analysis provide information in 3 particularly useful ways: (1) quantification of direct and indirect relationships among compartments; (2) description of flow structure and characteristics of cycling; and (3) indexing of systems-level attributes or emergent properties of the ecosystem. Overviews of ecological network analysis and its applications are in Ulanowicz (1986) and Wulff et al. (1989).

Although ecological network analysis has been used mostly on networks of food webs (Baird & Ulanowicz 1989, Christensen & Pauley 1993), it has had limited application to biogeochemical cycling. Finn (1980), in an early study, examined cycling of different elements within the Hubbard Brook forest ecosystem. However, most recent studies of biogeochemical cycling have focused on nutrient cycling in coastal aquatic eco-

systems. For example, Christian et al. (1992) found that recycling of nitrogen dominated loading in the maintenance of primary productivity within the Neuse River Estuary, North Carolina, USA. Primary producer growth form (i.e., phytoplankton, macroalgae, and phanogram) and temporal growth and decay patterns were strong controls over nitrogen cycling across several coastal ecosystems (Fores & Christian 1993, Fores et al. 1994, Christian et al. 1996). More recently, Ulanowicz & Baird (1999) examined the interaction of nitrogen, carbon and phosphorus in regulating different components of food webs in the Chesapeake Bay. Network analyses such as these require considerable information about elemental processing within ecosystems and, therefore, are limited to systems that have been extensively studied.

Three salt marshes along the Atlantic coast of the United States have been well studied with system's level assessment of nitrogen cycling: Great Sippewissett Marsh, Massachusetts (Valiela & Teal 1979a,b); Upper Phillips Creek Marsh, Virginia (Anderson et al. 1997); and Sapelo Island Marshes, Georgia (Whitney et al. 1981, Hopkinson & Schubauer 1984). Some measurements were made in the mid to late 1970s, while other measurements of the same process were made in the late 1990s utilizing more sophisticated techniques. Therefore, it is difficult to address trends from marsh to marsh because of the differences in methods among the marshes. However, measurements within the zones of each marsh have often been made with comparable methods. All 3 marshes have creekbank, low marsh and high marsh zones but with some different characteristics such as climate and plant species. We used the 3 well-studied sites as representatives of Atlantic coast salt marshes with which to construct and analyze networks. The main goals of this research were to compare the nitrogen cycles of 3 different salt-marsh zones and determine how relative sea-level rise may affect nitrogen cycling. An inter-marsh comparison was not attempted given the methodology issue mentioned above. We focused on specific aspects of cycling capable of being assessed through network analysis and determined if patterns existed among zones consistent for all marshes. Specifically, we addressed how imports of nitrogen are exported from a zone and how flows within a zone relate to primary production. Using the outcome from these analyses, we postulated how nitrogen cycling across a marsh may be affected by rising relative sea level.

MATERIAL AND METHODS

Study sites. Great Sippewissett Marsh is located in Falmouth, MA, near Woods Hole (41.35' N, 70.38' W)

and is approximately 48 ha (Finn & Leschine 1980) (Table 1). It is tidally fed by Buzzards Bay through a single entrance, Sippewissett Creek (Howes et al. 1986). The marsh is bounded on 3 sides by glacial moraine and sand dunes on the fourth side. The low and high marshes are accreting at 1 mm yr⁻¹ and the creekbank as much as 14 mm yr⁻¹ (Valiela 1983).

Upper Phillips Creek Marsh is located near Nasawadox, VA, on the southern end of the Delmarva Peninsula (37.26° 38' N, 75.52° 05' W) (Blum 1993), and is estimated to be approximately 58 ha. It is tidally fed by Phillips Creek, a tributary of Hog Island Bay. The marsh originated from a Pleistocene sand ridge that was breached by sea-level rise within the last 200 yr (Chambers et al. 1992). It is surrounded by farmland to the south and pine forests to the north and west (Blum 1993, Hmieleski 1994). The marsh has increased in size by 8% in the last 50 yr due to the transgression of upland areas by high marsh (Kastler 1993). Sediment is accreting at approximately 2 mm yr⁻¹ in the low marsh (Kastler & Wiberg 1996) and as much as 15 mm yr⁻¹ on the creekbank (Christiansen 1998).

Sapelo Island marshes are located on Sapelo Island, GA (31° 19' N, 81° 18' W) (Schubauer & Hopkinson 1984). The marshes' total area is approximately 1140 ha (Kuenzler 1961). The marshes are fed by the Duplin River, which empties into Doboy Sound (Imberger et al. 1983). The barrier island was believed to have been formed as the result of beach ridges being intersected by sea-level rise, which submerged the area landward of the ridges during the late Holocene, forming lagoons and islands (Hoyt 1967).

Sources of information for network analysis. Most data were obtained from the literature. Great Sippewissett Marsh and Sapelo Island marshes were selected specifically because of the extensive literature available regarding nitrogen processes in these marshes. For Great Sippewissett, we used 27 papers published between 1974 and 1994. For Sapelo Island marshes, we used 42 articles published between

1959 and 1997. Much of the data for Upper Phillips Creek Marsh were also obtained from literature. However, because this marsh has been studied for a shorter period of time, fewer articles have been published. We used 4 articles from 1992 to 1998. Student theses, the Virginia Coast Reserve/Long-Term Ecological Research database (<http://www.vcrlter.virginia.edu>), and field measurements were used to supplement published data for Upper Phillips Creek Marsh. Details concerning the sources of information, conversions, reliability factors (RF) attributed to the strength of a data point, and final network flows and standing stocks can be found in Thomas (1998) and at the web site (available at: www.vcrlter.virginia.edu/thesis/Thomas98/thomas98.pdf). Values came from approximately 40 yr of studies utilizing a wide variety of methods. Although details for all 60 fluxes and 17 standing stocks are given in Thomas 1998, Table 2 highlights 4 of the 60 fluxes and the methods for their study. Aboveground and belowground primary production estimates were often determined from harvesting, but other methods were also applied in support. The microbial processes of mineralization and denitrification were different for each site. The RFs for each data point are given to demonstrate criteria for their assignment. RFs ranged from 0 to 4, with 4 being the most reliable; details of which are described later.

To supplement published data on Upper Phillips Creek Marsh, field samples were taken from May through December 1997. Aboveground biomass was harvested from replicate 0.0625 m² quadrants in the creekbank and low marsh in May and September. Samples were separated into live and dead biomass based on the presence of green on the stems and leaves, dried to a constant weight at 85°C. Samples were ground in a Wiley mill through a 40-mesh screen, and percent nitrogen was determined using Leeman Labs Control Equipment 440 Elemental Analyzer. These results were then used as estimates of primary

Table 1. Site descriptions

	Great Sippewissett	Phillips Creek	Sapelo Island
Age (yr)	2000 ^a	200 ^b	15 000 ^c
Geomorphic setting	Mainland	Mainland	Barrier Island
Tidal Range (mean m)	1.6 ^d	1.9 ^e	2.4 ^f
Surface water salinity (ppt)	32 ^g	9–33 ^h	15–28 ⁱ
Interstitial salinity (ppt)	28–38 ^j	9–26 ^e	35–40 ^k
Dominant plants	<i>Spartina alterniflora</i> , <i>Distichlis spicata</i> , <i>Spartina patens</i>	<i>S. alterniflora</i> , <i>D. spicata</i> , <i>S. patens</i> , <i>Juncus roemerianus</i>	<i>S. alterniflora</i> , <i>J. roemerianus</i>
Freshwater sources	Groundwater, precipitation	Precipitation	Precipitation

^aValiela (1983); ^bChambers et al. (1992); ^cHoyt (1967); ^dValiela et al. (1978); ^eAnderson et al. (1997); ^fSchubauer & Hopkinson (1984); ^gCarpenter et al. (1978); ^hHmieleski (1994); ⁱPomeroy et al. (1972); ^jHowes et al. (1986); ^kNestler (1977)

Table 2. Sample of data used for model construction. RL: reliability factor

Marsh	Process	Data	Methodology	Source	RF
Great Sippewissett	Aboveground primary production	630 g dry wt m ⁻² × yr ⁻¹	Sequential harvest	Valiela et al. (1975)	3
Phillips Creek	Aboveground primary production	846.9 g dry wt m ⁻² × yr ⁻¹	Harvest/tagging	Tolley (1996)	3
Sapelo Island	Aboveground primary production	1350–2840 g dry wt m ⁻² × yr ⁻¹	Harvest	Schubauer & Hopkinson (1984)	3
		1489 g C m ⁻² × yr ⁻¹	Canopy productivity model	Dai & Wiegert (1996)	4
Great Sippewissett	Belowground primary production	3500 g m ⁻² × yr ⁻¹	Sequential harvest	Valiela et al. (1976)	3
		18.6–20.4 g N m ⁻² × yr ⁻¹	¹⁵ NH ₄ ⁻ tracer/harvest	White & Howes (1994b)	4
Phillips Creek	Belowground	676–2143 g N m ⁻² × yr ⁻¹	Litter bag/harvest	Blum (1993)	4
Sapelo Island	Belowground primary production	2100 g m ⁻² × yr ⁻¹	Sequential harvest	Gallagher & Plumley (1979)	3
		4780 g m ⁻² × yr ⁻¹	Sequential harvest	Schubauer & Hopkins (1984)	3
Great Sippewissett	Belowground mineralization	14.9–16.3 (net) g N m ⁻² × yr ⁻¹	¹⁵ N labeled litter bag	White & Howes (1994b)	4
Phillips Creek	Belowground mineralization	84 (gross) g N m ⁻² × yr ⁻¹	¹⁵ NH ₄ ⁻ isotope pool dilution	Anderson et al. (1997)	4
Sapelo Island	Belowground mineralization	19.7 (net) g N m ⁻² × yr ⁻¹	Harvest	Hopkinson & Schubauer (1984)	4
Great Sippewissett	Denitrification	6.85–20.32 g N m ⁻² × yr ⁻¹	Bell jar/gas partition	Kaplan et al. (1979)	4
		4.1–5.6 g N m ⁻² × yr ⁻¹	¹⁵ N loss	White & Howes (1994a)	4
Phillips Creek	Denitrification	0.6 g N m ⁻² × yr ⁻¹	¹⁵ N ₂ O isotope pool dilution	Anderson et al. (1997)	4
Sapelo Island	Denitrification	12 g N m ⁻² × yr ⁻¹	N ₂ diffusion/concentration	Haines et al. (1977)	4

production. Belowground (root/rhizome) biomass was estimated in May, September, and December using a 3.5 cm diameter aluminum corer to depths of up to 28 cm. Both macroorganic matter (MOM) (Gallagher 1974) and bulk densities (Chalmers 1979) were measured. MOM was determined by cutting the core into 2 sections, 0 to 10 and 10 to 28 cm. Some samples were used to determine the ratio of live:dead root matter. Separation was based on color and turgidity (Schubauer & Hopkinson 1984). The samples were dried to constant weight at 85°C, and ground using a Wiley mill through a 40-mesh screen. Percent nitrogen was determined as above and used for estimates of belowground production. The mussel *Gukensia demissa* and snail *Littorina irrorata* populations were counted within 0.0625 m² quadrants in September to estimate the biomass of the mussel and grazer compartments respectively. These samples were used either in addition to available data or to make estimates where little to no data were available.

Network construction. For the purposes of network construction, the marshes were divided into 3 zones that represented various flooding regimes and plant communities (Table 1). The flooding regime of each zone was standardized but was similar to published values (Kuenzler 1961, Meany et al. 1976, Jordon & Valiela 1982, Valiela et al. 1985, Kneib 1991, Blum 1993, Hmielecki 1994, Anderson et al. 1997). The 'Creekbank' zone was assumed to be flooded by all

high tides and dominated by the tall form of *Spartina alterniflora*. 'Low marsh' was assumed to be flooded by 50% of all high tides, i.e., 50% of high tide events reached and covered the low marsh. The low marsh was assumed to be dominated by the short form of *S. alterniflora*. And 'high marsh' was assumed to be flooded by 10% of all high tides and dominated by plants locally found in high marsh areas. These include *Spartina patens*, *Distichlis spicata*, and *Juncus* spp. depending on geographical location.

Networks were constructed for each zone of each marsh. The networks were constructed by estimating values for all compartments and flows in the general box and arrow diagram shown in Fig. 1. The general structure reflects the type of data available in the literature and the potential for flow importance, and therefore does not contain all possible flows. We emphasized the importance of sources of nitrogen to the marsh zones by explicitly identifying imports as precipitation, tidal creek, and groundwater. The surface water compartments represent the different species of nitrogen found in surface water (Fig. 1). Surface particulate nitrogen (PN) includes bacteria, algae, zooplankton, detritus, and nitrogen associated with suspended sediment. Fungi and bacteria associated with leaf decay are part of the Standing Dead compartment. Benthic filter feeders are predominately represented by *Gukensia demissa*, the Atlantic ribbed mussel, but theoretically represent all filter feeders in the marsh.

The Grazer/Nekton compartment is a compilation of many different types of animals. It includes primarily crabs (e.g., *Uca pugilator*), snails (e.g., *Littorina irrorata*), insects (e.g., *Orchelimum fidicinium*), and birds (e.g., *Branta canadensis*). The pore water compartments, like the surface water compartments, represent the different nitrogen species found in pore water. Soil organic N (SON), however, is an aggregation of many things including decaying roots and rhizomes, decaying leaf litter, biodeposition, and nitrogen associated with soil particles.

Each flow or standing stock estimate was assigned a reliability factor (RF), reflecting the perceived reliability of the original data. A RF of 4 meant the value was given in a peer-reviewed journal reference or other reliable references (e.g., web site of VCR-LTER) as a direct measure of standing stock or flux with little regard for the methodology used. A RF of 3 meant the value was given in a reference, but we needed to manipulate it into the standard units of the network. A RF of 2 meant that the data point was an estimate or had to be heavily manipulated by conversions or extrapolation. A RF of 1 meant the data point was a very rough estimate. And, a RF of 0 meant it was derived by mass balancing the inputs and outputs of the compartment. On many occasions, more than 1 source was used to estimate a flow or standing stock value. Both data points and their associated RFs used for a value were averaged.

The resulting averaged RF values were used to balance the model's flows. Each compartment's surplus (excess input) or deficit (excess output) nitrogen flow was determined by adding all inputs to a compartment and subtracting all exports from that compartment. To achieve steady state, each compartment's inputs must equal its outputs. The following rules involving RFs were used as guidelines to help balance each compartment. If a data point had a RF of 4, it was changed no more than 10% in either direction to help balance the compartment. A RF of 3 was changed no more than 20%, 2 was changed up to 30%, 1 was changed up to 40%, and 0 was changed as needed to balance the compartment. For example, if the value of a flow was unknown (i.e., a RF of 0), the flow value was assumed to be the balance of all other inputs and exports of the compartment. These percentage guidelines were arbitrarily chosen to help retain the integrity of the data during the balancing process; at times they could not be strictly followed.

The reliability of the networks was evaluated as follows. An average RF was calculated for each flow based on the individual RF values of data used to compute that flow when more than one reference source was used. Each network contained a total of 60 flows; the RFs of these were used to compute a grand mean

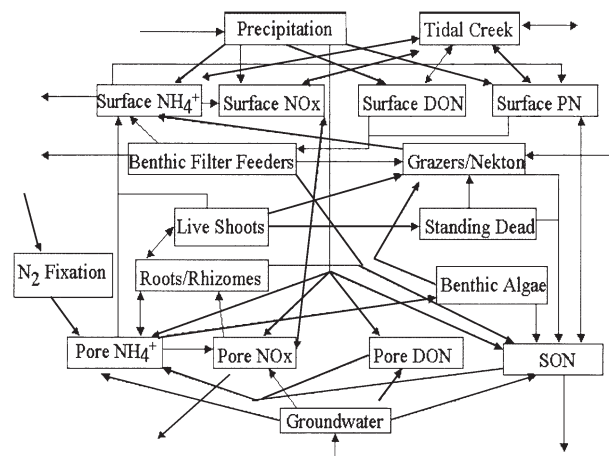


Fig. 1. Nitrogen cycle

RF. The grand mean RFs and the distributions of average RF values were used to estimate the degree to which each network was based on established information.

Network analysis. Ecological network analysis was used to evaluate the structure of the 9 networks (3 zones in 3 marshes). The software package was NETWRK4 (Ulanowicz 1987, available at://www.cbl.cees.edu/~ulan/ntwk/network.html). The package contains several subroutines in FORTRAN for network analysis. We used the subroutines for Input Environs Analysis, matrices of Total Contribution and Total Dependency, and the subroutine for Biogeochemical Cycle to calculate Finn Cycling Index (FCI). Below we provide a conceptual description of each analysis. Detailed descriptions of the mathematics can be found in Kay et al. (1989) and other cited references.

Input Environs Analysis computes exchange matrices and export vectors of fractional flows that result from the exogenous input of one unit of flow into a compartment. The coefficients in each vector and matrix represent the relative amounts of internal flows and outputs (or probabilities of flow) resulting from 1 unit of input (Kay et al. 1989). We used this analysis to determine how inputs to the systems were exported, and compared the distributions of exports between marsh zones relative to different sources of nitrogen.

The total contribution matrix evaluates the fraction of a compartment's throughput (total input or output) that contributes to another compartment's throughput both directly and indirectly (Kay et al. 1989). For example, the matrix can determine the fraction of nitrogen that flows through the benthic filter feeder compartment that will travel directly and indirectly to above-ground primary production. In this case, there is no

known direct flow from benthic filter feeders to above-ground production, but a possible indirect flow would be from benthic filter feeders to SON by way of bio-deposition (Fig. 1). The SON is then mineralized to Pore NH_4^+ that is taken up by plant roots and translocated aboveground.

The total dependency matrix evaluates the fraction of a compartment's total throughput that resided at some point in another compartment (Hannon 1973). Again, the connections may be direct or indirect. For example, this matrix can determine the fraction of aboveground production's nitrogen throughput that came indirectly from benthic filter feeders. The diagonals of both total dependency and total contribution matrices can be used to determine the amount of material that is cycled from a compartment, through the system, and back to a compartment. These matrices were used to evaluate how important certain sources of imported nitrogen are to various compartments, such as how important nitrogen from precipitation is to root/rhizome production.

Flows may be divided into those passing through the system and those associated with internal cycling (Finn 1976). Internal cycling involves the tracing of nitrogen as it leaves a compartment, passes through 1 or more compartments and returns to the original. The nitrogen involved in the internal cycling, the Finn Cycling Index (FCI), is the fraction of the sum of all flows through the system (total system throughput, TST) (Finn 1976). Cycled Throughput (CT), the quantity of material cycled, is the FCI multiplied by TST. These 2 indices were used to determine the amount of recycling within each marsh zone. Average Path Length (APL) is another way of measuring cycling (Finn 1980). It is calculated with the following formula: $(\text{TST-Inputs})/\text{Inputs}$ (Kay et al. 1989) and increases with increased cycling.

To determine what the fraction of nitrogen mineralization was of total processing of nitrogen, the flows from SON and Pore DON to Pore NH_4^+ were summed and divided by TST. There has been very little study of Pore DON mineralization. Therefore, most flow was considered to come from SON. The methods used for measuring mineralization were different for each marsh, resulting in measurements of both gross and net mineralization (Table 2). The measurements were used as initial conditions when balancing the compartments. Net measurements worked better than gross for our model with most balancing changes being less than 40% of measurement (see Thomas 1998). To determine if primary production's uptake and/or requirements could be met by mineralization, the sum was divided by 'belowground production' represented by the uptake of Pore NH_4^+ and Pore NO_x by Roots/Rhizomes. 'Belowground production' was used

because it contained the total flow of nitrogen into the plant that then was distributed both above- and below-ground. Mineralization was also divided by CT to determine the fraction of cycling associated with mineralization.

Evaluation of patterns. The non-parametric Friedman test was used to determine if patterns across marsh zones were statistically significant (Potvin & Roff 1993). The Friedman test analyzes within-subject effects based on rank. Given the limited number of samples ($n = 9$), all 3 marshes had to have the same rank order for significance at $p = 0.05$. If one rank pair was reversed, the p-value was raised to at least 0.097. The statistical software used was Systat 7.01. Therefore, we highlighted those patterns that were common to all marshes and indicated where patterns may have been similar for 2 of the 3 marshes. Little emphasis was placed on inter-marsh comparisons. Methodologies differed considerably among marshes. Thus, although values for the networks within a marsh were internally consistent, we did not consider that strong, quantitative inter-marsh inferences were warranted.

RESULTS

Distribution of important flows

Overall, the 3 marshes showed consistent patterns among zones in some flows and TST, but not in other flows. TST, tidal imports, and tidal exports decreased moving from creekbank to high marsh (Table 3). This was mainly the result of reduced tidal flushing as it was assumed that the creekbank was inundated by 100% of high tides, low marsh by 50%, and high marsh by only 10%. Tidal flow was 8 to 44% of TST. The largest internal flows were associated with primary production and mineralization and did not show consistent patterns across marsh zones.

Fate of imported nitrogen

We evaluated how nitrogen from major import routes was exported from each marsh zone and focused on patterns that were found for all 3 marshes. Precipitation and tidal imports of each nitrogen species were considered for analysis. Possible export routes included tidal export of each nitrogen species, denitrification, burial, harvest of mussels, and volatilization of ammonia. The output data from Input Environs Analysis were placed in stacked bar graphs in Figs 2, 3, 4 & 5. Each bar section represents the fraction of total import that was exported by each potential route.

In all marshes, burial of the import precipitation became a more important export route moving from the creekbank to high marsh zone (Fig. 2). In the creekbank zone, more than half of the precipitation was exported from the marsh by tide. Tidal export of precipitation steadily decreased and denitrification of precipitation increased in importance moving across the marsh from creekbank to high marsh, except for Sapelo Island. At Sapelo Island, denitrification of precipitation was highest and tidal export of precipitation was lowest in the low marsh.

Imported Surface PN would have been processed within the marsh in many different ways because of the diversity of constituents (e.g. bacteria, algae, zooplankton, etc.). There were, however, consistent patterns of export routes for all marshes (Fig. 3). Tidal export of all forms decreased significantly in importance from creekbank to high marsh. Burial and denitrification increased in importance as export routes along the same gradient. Interestingly, the dominant export trends associated with Surface PN were all statistically significant, but none for the other tidal imports were.

Each marsh processed the NH₄⁺ differently as can be seen in the patterns of different nitrogen species exported tidally by each marsh (Fig. 4). The importance of tidal export or denitrification across zones had no significant trend. Burial increased in importance as an export route moving from creekbank to high marsh in Great Sippewissett and Upper Phillips Creek, but not Sapelo Island where it was greatest in the low marsh. The patterns of NO_x processing across each marsh also differed (Fig. 5). Tidal flushing and burial showed no significant patterns among marsh zones for all marshes. Burial is essentially nonexistent as an export route for Surface NO_x in

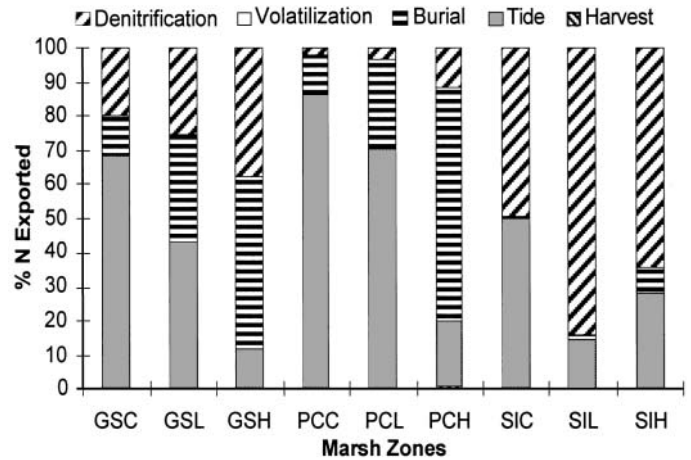


Fig. 2. How precipitation is exported. GS: Great Sippewissett; PC: Phillips Creek; SI: Sapelo Island; C: Creekbank; L: lowmarsh; H: high marsh

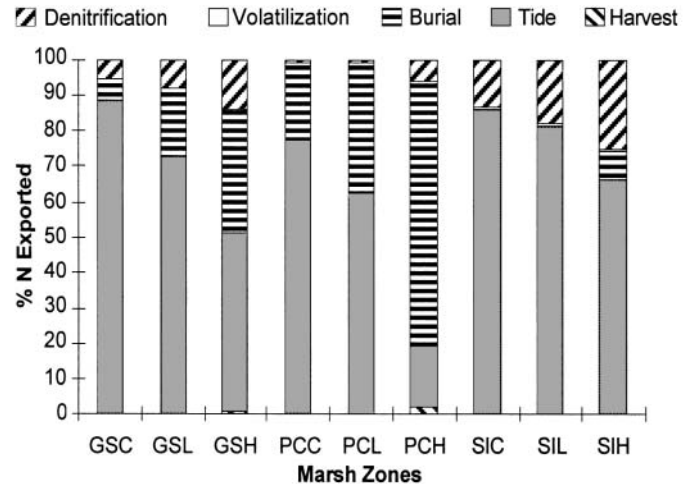


Fig. 3. How tidal PN is exported. GS: Great Sippewissett; PC: Phillips Creek; SI: Sapelo Island; C: Creekbank; L: low marsh; H: high marsh

Table 3. Important network flows (g N m⁻² yr⁻¹). TST: total system throughput

	Great Sippewissett			Upper Phillips Creek			Sapelo Island		
	Creekbank	Low	High	Creekbank	Low	High	Creekbank	Low	High
Tidal import	81.1	44.6	8.77	65.8	34.7	8.11	165	87.5	16.3
Precipitation	0.56	0.56	0.56	0.45	0.45	0.45	0.3	0.3	0.3
Groundwater	13.3	13.3	13.3	0.04	0.04	0.04	0.04	0.04	0.04
Nitrogen fixation	5.03	2.75	5.87	1	1	1	39.8	23.7	4.5
Tidal export	87.9	45.6	8.83	63.1	30.5	5.6	162	74.5	16.1
Burial	6.13	9.51	11.4	3.6	5.16	3.53	1.44	1.35	1.2
Denitrification	9.58	7.54	8.58	0.6	0.6	0.6	41.6	35.7	3.91
Primary production	30.2	27	29	21.1	27.7	15.8	51.6	38.3	53.5
Translocation	1.4	1.26	1.26	7	7	7	16.2	14.8	13.3
Detritus formation	25.3	21.8	24.2	18.4	26.8	14.5	44.4	31.5	46.7
Mineralization	27.2	30.1	30	27.8	31.1	11.7	92.5	79.3	80.9
Nitrification	10	11.9	14.8	3.6	4	3.55	41.5	28.7	3.77
All other flows	114	107	63.4	78.8	72.5	26.1	246	211	162
TST	412	323	220	290	242	98	902	627	403

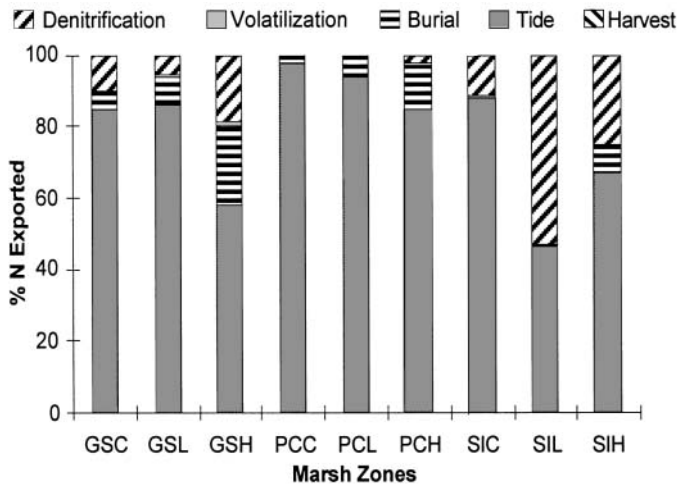


Fig. 4. How tidal NH_4^+ is exported. GS: Great Sippewissett; PC: Phillips Creek; SI: Sapelo Island; C: Creekbank; L: low marsh; H: high marsh

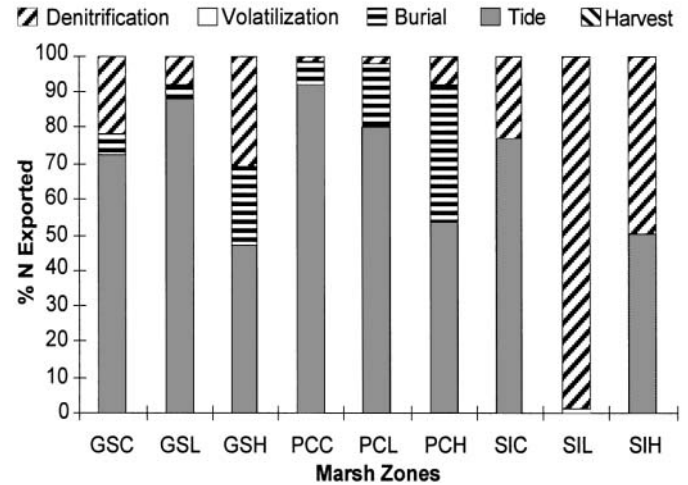


Fig. 5. How tidal NO_x is exported. GS: Great Sippewissett; PC: Phillips Creek; SI: Sapelo Island; C: Creekbank; L: lowmarsh; H: high marsh

Sapelo Island. Denitrification was a dominant export route in Sapelo, but much less so in the other marshes, and there was no significantly consistent pattern across marsh zones.

Import contribution to primary production

The total contribution matrix was used to determine the fraction of precipitation, tidal inputs, and groundwater that went to primary production, as most major nitrogen flows were associated with primary production (Table 3). The analysis is from the contributing compartment's perspective. Uptake by root/rhizome biomass represented plant primary production, as it reflected production for both below- and aboveground production. In all 3 marshes and in all 3 zones, precipitation had a higher fraction of its throughput go to primary production than did tidal import (Table 4). The fraction increased significantly moving from creekbank to high marsh. In Upper Phillips Creek high marsh almost 90% of nitrogen from precipitation went to primary production.

Total tidal contributions to primary production tended to increase from creekbank to high marsh but with notable exceptions (Table 4). For example, the percent of Surface NH_4^+ throughput contributing to primary production showed this pattern for Upper Phillips Creek, but for Great Sippewissett and Sapelo Island, it was least in the low marsh. Surface NO_x behaved very differently in each marsh. For Great Sippewissett and Upper Phillips Creek it followed the Surface NH_4^+ trend, but in Sapelo Island there was no fraction of Surface NO_x that contributed to primary production. Surface DON is seen to contribute little if any of its throughput to primary production, except in Phillips Creek. However, we did not ascribe biological activity to this chemical species because of the lack of information to the contrary. Surface PN significantly increased its percent contribution moving from creekbank to high marsh at all sites.

In Great Sippewissett, much of the groundwater nitrogen import contributed to primary production. In the creekbank zone, groundwater contributed 68.3% of its throughput to primary production, in the low marsh zone it contributed 70.2%, and in the high

Table 4. Total contribution of tide, precipitation, and groundwater to primary production. Fraction of total input that contributes to primary production

	Great Sippewissett			Upper Phillips Creek			Sapelo Island		
	Creekbank	Low	High	Creekbank	Low	High	Creekbank	Low	High
Precipitation	0.386	0.545	0.668	0.412	0.630	0.891	0.167	0.250	0.506
Tidal NH_4^+	0.119	0.092	0.242	0.040	0.102	0.164	0.075	0.044	0.489
Tidal NO_x	0.221	0.087	0.338	0.248	0.431	0.513	0.000	0.000	0.001
Tidal DON	0.001	0.003	0.002	0.193	0.257	0.274	0.000	0.071	0.001
Tidal PN	0.098	0.176	0.263	0.380	0.534	0.698	0.088	0.095	0.499
Groundwater	0.683	0.702	0.694						

marsh it contributed 69.4%. No analyses were done on this pattern's significance because of the lack of information on groundwater flow in the other 2 marshes.

Primary production's dependence on imports

The total dependency matrix was used to determine the fraction of primary production that originated from precipitation, tidal imports, and groundwater. The analysis is thus from the receiving compartment's perspective. A larger percentage of primary production's throughput originated from tidal import than precipitation in all marsh zones (Table 5). For example, precipitation only accounted for 0.1 to 9.5% of primary production's throughput, but Surface NH_4^+ accounted for 3.1 to 41.5%.

Precipitation significantly increased in importance moving from creekbank to high marsh. For example, in Sapelo Island, precipitation was a negligible fraction of primary production's throughput in the creekbank, but in the high marsh it was 2.4%. In contrast, tidal imports varied in importance across marsh zones. For example, Surface NH_4^+ decreased in importance to primary production from creekbank to high marsh in Great Sippewissett, increased in Sapelo Island, but was highest in the low marsh at Upper Phillips Creek. Surface NO_x also varied greatly in its importance to primary production. In Great Sippewissett, it was least important in the low marsh and most important in the creekbank marsh. In Upper Phillips Creek, it decreased in importance moving across the marsh from creekbank to high marsh. And in Sapelo Island, primary production did not depend on Surface NO_x . Primary production depended very little on Surface DON, and no patterns across zones were found. Surface PN played a relatively important role in primary production in all marshes but not in a consistent way. It ranged from 4.3 to 59.2% of primary production's throughput.

Primary production in Great Sippewissett was also very dependent on groundwater. In the creekbank zone, 62.8% of primary production's throughput came

from groundwater. In the low zone, it was 68.1%, and in the high zone, it was 62.6%.

Cycling

With the exception of the dependencies of primary production on Surface NO_x in Upper Phillips Creek, Surface PN in Sapelo Island's high marsh, and groundwater in Great Sippewissett; dependencies on individual imports were less than 50%. We inferred that recycling must contribute significantly to primary production of marsh plants. Several indices were used to examine this inference. First, it was evaluated by the diagonal coefficients for root/rhizome biomass (i.e., roots) within the total dependency matrix, a measure of how much nitrogen enters, leaves and reenters root/rhizome biomass. These values were among the highest coefficients in every case (Table 5). In each marsh, recycling associated with primary production significantly increased in importance moving from creekbank to high marsh (Table 5). Recycling for other compartments was determined from appropriate diagonal coefficients of the total dependency matrix (Table 6). Recycling of the soil nutrients (Pore NO_x , PN and NH_4^+) consistently increased from creekbank to high marsh. The other compartments, such as shoots, mussels, grazers, and benthic algae, did not show any significant trends in their patterns of recycling.

Overall total system cycling, as determined by FCI and APL, increased from creekbank to high marsh in every marsh (Table 6). FCI varied from 30% in the creekbank of Great Sippewissett to 80% in the high marsh at Sapelo Island. Thus, 30 to 80% of all flows of nitrogen were involved in internal cycling. Increased cycling corresponds to an increase in the number of path lengths (i.e., the number of processes as represented as connections between compartments) the average atom of nitrogen undergoes between entering and leaving the system (APL). APL ranged from 3 to 18.

Mineralization within marsh soils was evaluated because of its importance to internal cycling and to primary production (Table 3). In general, the mineral-

Table 5. Total dependency of primary production on precipitation, tide, and groundwater. Fraction of primary production's inputs

	Great Sippewissett			Upper Phillips Creek			Sapelo Island		
	Creekbank	Low	High	Creekbank	Low	High	Creekbank	Low	High
Precipitation	0.014	0.024	0.028	0.017	0.026	0.096	0.002	0.004	0.024
Tidal NH_4^+	0.113	0.078	0.054	0.125	0.180	0.156	0.043	0.031	0.415
Tidal NO_x	0.135	0.039	0.043	0.791	0.783	0.631	0.000	0.000	0.000
Tidal DON	0.004	0.006	0.001	0.000	0.000	0.002	0.000	0.198	0.001
Tidal PN	0.125	0.175	0.052	0.1790	0.196	0.043	0.220	0.162	0.592
Groundwater	0.576	0.716	0.674						
Recycling	0.417	0.464	0.504	0.596	0.667	0.807	0.600	0.615	0.889

Table 6. Indicators of cycling within systems and compartments (based on Total Dependency Matrix). Numbers for compartments are the fractions of throughput recycled. TST: total flow through the system; CT: amount of flow involved in cycling; APL: average number of compartments unit of flow passes through. p-value reflects significance of trends across zones

	Great Sippewissett			Upper Phillips Creek			Sapelo Island			p-value = 0.05
	Creekbank	Low	High	Creekbank	Low	High	Creekbank	Low	High	
TST	413	323	221	290	242	98	903	628	404	
CT	122	118	104	105	121	52	369	261	323	
FCI	0.297	0.365	0.471	0.361	0.5	0.532	0.408	0.415	0.801	0.05
APL	2.98	4.16	6.65	3.31	5.67	9.1	3.40	4.63	18	0.05
Mussels	0.19	0.218	0.068	0.029	0.069	0.000	0.01	0.039	0.524	0.368
Grazers	0.11	0.162	0.11	0.028	0.053	0.049	0.021	0.014	0.298	0.558
Shoots	0.108	0.18	0.229	0.483	0.456	0.712	0.489	0.495	0.788	0.097
Roots/rhizomes	0.417	0.464	0.504	0.596	0.667	0.807	0.600	0.615	0.889	0.05
Benthic algae	0.111	0.196	0.194	0.267	0.275	0.004	0.429	0.496	0.776	0.264
Pore NOx	0.152	0.197	0.257	0.252	0.344	0.400	0.000	0.001	0.002	0.05
SON	0.447	0.509	0.529	0.543	0.65	0.71	0.622	0.65	0.906	0.05
Pore NH ₄ ⁺	0.421	0.504	0.533	0.549	0.65	0.71	0.623	0.65	0.906	0.05

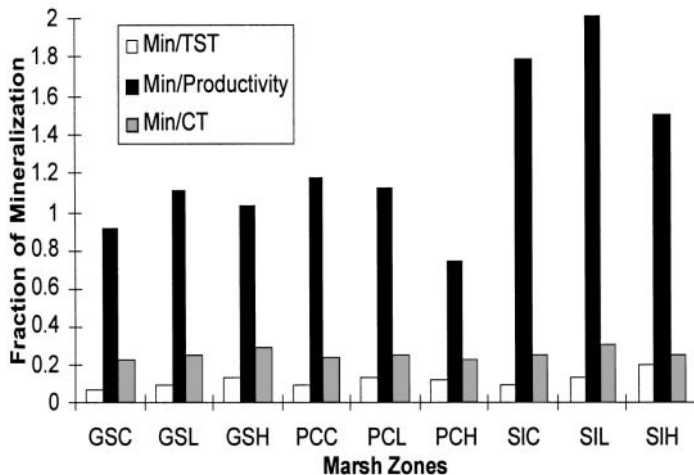


Fig. 6. Relative mineralization. GS: Great Sippewissett; PC: Phillips Creek; SI: Sapelo Island; C: Creekbank; L: low marsh; H: high marsh

ization rates used in the model varied little across marsh zones because of a lack of data for different zones. To determine the relative contribution of mineralization rate to each marsh zone in a comparable way, mineralization rate was divided by 3 factors; TST, primary production, and CT. Mineralization as a percentage of TST was 20% or less (Fig. 6). In both Great Sippewissett and Sapelo Island, the highest percentage was in the high marsh, whereas in Upper Phillips Creek, the highest percentage was in the low marsh. It was lowest in the creekbank zone for each marsh.

Mineralization was divided by primary production to determine if mineralization could provide primary producers with enough nitrogen to meet their need. In most cases, mineralization/production was near or above 1.0, meaning that mineralization could meet the full demand of primary producers (Fig. 6). In Great Sippewissett and Sapelo Island marshes, mineraliza-

Table 7. (a) Flow grand mean reliability factor (RF) for marsh zones. (b) % of total system throughput (TST) associated with RFs

(a)										
	Creekbank	Low	High	Overall						
Great Sippewissett	3.06	2.75	3.02	2.94						
Upper Phillips Creek	2.95	3.08	2.79	2.94						
Sapelo Island	2.73	2.86	2.71	2.76						
(b)										
RF	Great Sippewissett			Upper Phillips Creek			Sapelo Island			
	Creekbank	Low	High	Creekbank	Low	High	Creekbank	Low	High	
4	52.81	44.38	31.85	28.23	39.98	50.24	46.41	41.78	46.40	
3	26.43	32.87	39.77	55.13	48.61	17.90	38.88	37.42	28.41	
2	6.77	7.86	12.51	0.12	0.12	9.80	0	0	0	
1	2.20	3.41	1.35	4.04	2.22	11.49	0	0	0	
0	11.80	11.47	14.52	12.49	9.08	10.57	14.71	20.79	25.19	

tion/production was highest in the low marsh. In both Upper Phillips Creek and Sapelo Island mineralization/production was lowest in the high marsh; but in Great Sippewissett, it was lowest in the creekbank marsh.

The mineralization rate was divided by CT to determine the percent of cycled throughput that resulted from mineralization. In all cases, mineralization was 30% or less of CT (Fig. 6). In both Upper Phillips Creek and Sapelo Island, the low marsh showed the greatest amount of mineralization/CT. Great Sippewissett's mineralization/CT was highest in the high marsh.

Reliability of information

Grand mean RF values were always above 2.7 and ranged to 3.1 out of a possible maximum of 4 (Table 7a). Great Sippewissett and Sapelo Island marsh zones had a higher percentage of flows associated with higher RFs than Upper Phillips Creek. However, for both marshes, the data were generally either RF = 4 or were obtained by balancing the compartments inputs and outputs, RF = 0. Very few flows had RFs of 2 or 3. When the weighting of average RFs was done by amount of flow and compared to the percentage of TST, a better picture regarding reliability emerged (Table 7b). In all 3 marshes, the greatest percentage of TST was associated with RFs of 3 and 4. Sapelo Island had the greatest amount of flow associated with an average RF of 0. Twenty-one and 25% of flows in Sapelo Island's low and high marsh zones respectively were associated with an RF of 0. The rest of the marsh zones were less than 15%.

DISCUSSION

The literature is replete with differences found between marsh zones for particular nitrogen flows and in individual marshes. For example, Hanson (1977) found that nitrogen fixation occurred at a higher rate in the creekbank zone than the low marsh in Georgia. Many have studied above- and below-ground primary production across marsh zones (Valiela et al. 1975, Gallagher & Plumley 1979, Schubauer & Hopkinson 1984, Blum 1993, White & Howes 1994, Dai & Weigert 1996). The general conclusion is that aboveground production is higher in the creekbank zone than the low marsh (Gallagher & Plumley 1979, Dai & Weigert 1996), but belowground production may be just the opposite (Valiela et al. 1976). High marsh production depends on the dominant plant species (Valiela et al. 1975, 1976). There is also evidence that the N mineralization rates may be

faster in the creekbank than the low marsh due to tidal flushing (Howarth & Hobbie 1982). Again, mineralization rates in the high marsh may depend on the dominant plant species (Good et al. 1982). Denitrification, although difficult to measure, was found to be highest in the creekbank zone and lowest in the high marsh zone associated with differences in tidal flushing (Kaplan et al. 1979).

Network analysis was used to integrate the various flows within the zones of salt marshes and assess the integrated nitrogen cycles of these zones. We constructed and analyzed the networks of 3 well-studied marshes. These marshes span 10° latitude, have different climates, tidal regimes, water qualities and plant community characteristics. We have considered them representative of Atlantic coastal marshes and as replicates to strengthen inferences regarding the existence of patterns across marsh zones. These patterns are placed into the context of rising sea level and horizontal migration of marshes.

All consistent patterns for the 3 marshes either increased or decreased from creekbank to high marsh. Tidal import and export of nitrogen followed this trend and constituted approximately 40% of TST in the creekbank and only 10% of TST in the high marsh. Simultaneously, TST decreased from creekbank to high marsh. Thus, at first glance, one might expect that (1) metrics linked to imports would decrease inward from the creek and (2) metrics divided by TST would increase inward from the creek. Although these trends are found for some attributes, the complexity of the networks prevents this simplistic outcome as a rule. For example, the contribution of Tidal NH_4^+ to primary production has a different trend for each marsh (Table 4).

Marsh zone trends

The only import/export patterns that were consistent for all marshes were associated with precipitation and Surface PN import. Burial and denitrification significantly increased in relative importance across the marsh from creekbank to high marsh when the import route was either of these. The pattern for denitrification does not conflict with Kaplan et al.'s (1979) findings that denitrification rates are faster in the creekbank zone. They were measuring absolute rates, whereas our findings consider relative rates as percent of throughput within a marsh zone. Patterns associated with the increased burial and denitrification of precipitation with distance into the marsh are not surprising. Decreased frequency of flooding in the high marsh zone allows more opportunity for marsh/surface water interaction and incorporation into soil processes. In the

creebank and low marsh zones, flooding is more frequent, and there is greater opportunity for the precipitation to be flushed out by tide before there is contact with the marsh surface. We also found that the tidal export of Surface PN import significantly decreases in importance moving across the marsh from creebank to high marsh. Patterns related to Surface PN may reflect the decrease in inundation frequency and sedimentation/resuspension cycle (Kastler & Wiberg 1996, Christiansen & Wiberg 2000).

Primary production's need for nitrogen may be supplied by imported and internally recycled sources. Often a significant fraction of nitrogen from precipitation was taken up by plants. However, because precipitation contributes only a small amount of nitrogen to the system (Table 3), the absolute amount remained below $0.5 \text{ g N m}^{-2} \text{ yr}^{-1}$. Contributions relative to compartment throughput from almost all import sources were highest in the high marshes (Table 4). This is consistent with the recognition that the hydrodynamics of high marshes may be more bog-like than intertidal (Stasavich 1998, Christian et al. 2000). Contributions to production from precipitation not only were highest in all high marshes but also lowest in all creebanks. This is similar to the trends for exports and relates to the time of contact with the marsh surface and potential for removal on ebb tides. The recycling of nitrogen within primary producers, defined as the fraction of nitrogen that originated in the root/rhizome compartment that returned to that compartment, showed a significant pattern across marsh zones. It increased in importance moving across the marsh from creebank to high marsh. It accounted for between 41.7 and 88.9% of primary production's throughput (Table 5). This high degree of recycling is consistent with the findings of Anderson et al. (1997), who conducted one of the most complete and up-to-date analyses of nitrogen cycling within salt marshes.

The importance and patterns of cycling within the marsh zones were evaluated in several ways. Both FCI and APL significantly increased moving across the marsh from creebank to high marsh, indicating that larger proportions of nitrogen flows were involved in cycling as one moves into the marsh from its seaward edge. Relative cycling (FCI and APL) increased as one moved toward the high marsh from the creebank, although absolute amounts of cycling did not (CT). Total systems throughput decreased from creebank to high marsh (Table 6). Much of TST at the creebank was as tidal import and export that diminish with distance inward. In contrast, 2 of the processes most responsible for cycling, primary production and mineralization, did not decrease or increase consistently across the marshes. Thus, the changes in relative cycling were more associated with

decreased tidal flushing than internal biological processing. However, the total amount of nitrogen involved in cycling does not show any consistent pattern (Table 6).

FCI ranged from 30% in Great Sippewissett creebank zone to 80% in Sapelo Island high marsh zone, but all but the latter were less than 55%. Thus, generally a third to a half of the flows of nitrogen for most marsh zone networks were involved in some kind of recycling. This broad range has been found for nitrogen cycles from other coastal, but more open water, ecosystems (Baird et al. 1995, Christian et al. 1996). Generally, the FCI values tended to be higher in the open water systems than reported here, however. APL ranged from 3.0 in Great Sippewissett creebank zone to 18.0 in Sapelo Island high marsh. All but the latter was less than 10 lengths. Thus, an average nitrogen atom entering a marsh zone was transferred at least 3 times between compartments or between a compartment and the environment before leaving. As the number of transfers increase, one may infer that more are involved with internal cycling. Thus, APL correlates with FCI and is an index of that cycling. Again the range of APL values is within that of others reported for nitrogen cycling (Baird et al. 1995, Christian et al. 1996).

Recycling within the soil compartments showed similar trends. Besides roots/rhizomes, only Pore NO_x , NH_4^+ , and SON increased recycling within each compartment from creebank to high marsh. Recycling fractions were very similar between Pore NH_4^+ and SON reflecting their role in the primary production/mineralization cycle. These 2 processes were seen to drive nitrogen recycling within the salt marsh in almost all cases (Table 3). As all of these components were within the marsh sediments, one may also infer that most recycling was at or below the marsh surface.

Mineralization within soils is a very important part of total nitrogen cycling within the marsh (Anderson et al. 1997). It provides the much needed Pore NH_4^+ for primary production. Mineralization rates were measured at each marsh (Valiela & Teal 1979b, White & Howes 1994a,b, Neirkirk 1996, Anderson et al. 1997), but not necessarily in each zone. Therefore, the rates within a marsh used in the networks tended to be similar among zones (Table 3). The similarity of mineralization or decomposition rates among zones has not been fully examined. Blum (1993) did not find the decomposition of marsh plant roots/rhizomes to be significantly different between creebank and low marsh at Upper Phillips Creek, but others have reported differences among zones for various measures of decomposition or microbial heterotrophy (Howarth & Hobbie 1982, King 1988).

Reliability of information and networks

A major concern about integrative studies such as this is the reliability of the information used. The data used for our analyses were derived from a wide variety of sources spanning four decades. Sources of uncertainty included (1) systematic differences in methodology, (2) availability of information, and (3) statistical variation. Different methodologies were used to measure rates of various processes. For example, White & Howes (1994) used ^{15}N labeled litterbags to measure the net rate of mineralization in Great Sippewissett, and Anderson et al. (1997) used a $^{15}\text{NH}_4$ isotope pool dilution to measure the gross rate of mineralization in Upper Phillips Creek (Table 2). The marshes were also not studied equally in all areas of interest. Sometimes a single value had to be used for all 3 zones of a marsh (e.g., mineralization in Sapelo Island marshes). Both Great Sippewissett and Sapelo Island have been very well studied for several decades, while Upper Phillips Creek only has been studied for approximately 10 yr. Studies for each marsh have emphasized different aspects of the nitrogen cycle. For example, total nitrogen budgets were emphasized for Great Sippewissett (Valiela & Teal 1979a,b), while Sapelo Island studies emphasized individual processes within the nitrogen budget (Hanson 1977, White & Howes 1994, Dai & Weigert 1996). Furthermore, earlier studies may not have involved techniques as accurate as later studies. Anderson et al. (1997) used the most up-to-date methods on several processes in Upper Phillips Creek, compared to earlier measures in the other 2 systems (e.g., Kaplan et al. 1979, Whitney et al. 1981). Information on statistical error was generally not available in the literature. Therefore, the data obtained from the literature was of varying but unknown degrees of reliability.

We developed a ranking system to assess reliability. Each datum was assigned a reliability factor 0 to 4, 4 being the most reliable. Assignment of a particular RF was based on methodology, length of study, and the amount of manipulation required to get it into the unit $\text{g N m}^{-2} \text{yr}^{-1}$. The reliability of the networks could then be assessed. The flow-weighted grand mean RFs for the 9 networks were between 2.71 and 3.06 out of 4. A value of 3 for an individual estimate indicated good confidence in the original data, largely from literature, but need for manipulation to obtain proper units. We infer from the averages that most of the significant flows associated with each network were from reasonable literature estimates. In fact over 70% of the total system throughput was at the level of 3 or 4 for all but 1 network. Although the networks appear to reflect the state of knowledge of these marshes, as knowledge improves, our conclusions may need to be revisited.

This need may be greater than for assessments of individual processes, but this does represent the first attempt at synthesizing information at the ecosystem level from these 3 well-studied marshes.

Network analysis models are generally static, steady state models representing a time averaged 'snapshot' of each system. The assumption for this approach is that the flows into and out of a compartment balance within the specified time unit. We used averaged cycling over a year. In fact, data were not available for any 1 yr, and we represented a hypothetical year that linked the various individual measurements. Thus, results could not assess either intra- or interannual variation. Also, network analysis requires that all flows within the model have values. In many cases, not all flow amounts are known, and estimates from mass balance are necessary to finalize the model. The effects of this are unknown. Evaluation of the strength of knowledge is the impetus for developing RFs for each flow.

Another limitation of network analysis for model comparison is that the models have the same topology. This means that the models have similar numbers of compartments with similar amounts of aggregation within each compartment and that compartments represent similar ecological players. This was not an issue for our models as the same model was used for each marsh and zone.

Relation to sea-level rise

Coastal salt marshes respond to rising sea level in a variety of ways. During transgression and over the long-term, a georeferenced point within a high marsh will become low marsh. Low marsh will become creekbank, and then creekbank will become intertidal and subtidal mudflats (Brinson et al. 1995). If the marsh is prograding at the seaward edge, mudflat can become creekbank and then low marsh. It is unlikely, however, that low marsh will become infrequently flooded high marsh in the context of rising sea level (Christian et al. 2000). As these landscape changes take place, there are changes in ecosystem characteristics. These include shifts in dominant plant species, amount and distribution of plant production and biomass, soil structure, and, as we have shown, the ways in which nitrogen is processed.

Recall that each marsh zone had different levels of relative recycling. Averaged over the 3 marshes, the FCI for the creekbank was 35.6%, low marsh was 42.7% and the high marsh was 60.1%. The APL followed the same pattern with the creekbank averaging 3.23, the low marsh averaging 4.82, and the high marsh averaging 11.25. Both of these indices had significant trends across the marsh. Other significant

trends were the increase in importance of burial and denitrification as removal mechanisms moving toward the high marsh when precipitation and Tidal PN are the import routes.

The following responses to sea-level rise are based on our network analyses of nitrogen cycles. We make predictions in the context of 4 scenarios for whole marshes similar to those used by Brinson et al. (1995) and Christian et al. (2000). They focused on the sustainability of coastal marshes with respect to the slope at their upland edge and availability of sediments. To assess marsh wide response, we take into account (1) consistent trends in network analyses across marsh zones and (2) the potential for change in relative area of each zone. As an example of a trend, when a zone is transformed to one with more frequent flooding, it will probably experience a decrease in the importance of burial and denitrification as export routes, and a decrease in relative recycling. But this does not mean that the total marsh is experiencing these patterns. Four scenarios for whole marshes are as follows:

(1) If the marsh is migrating overland and maintaining its total area by eroding at water's edge to the same degree keeping similar areas of each zone, there will be little change in its overall cycling characteristics.

(2) The marsh may migrate overland, erode excessively at the water's edge, and lose low marsh while gaining high marsh. This marsh will experience increased recycling per average squared meter of the total marsh. For example, using the average FCI numbers given above, if a marsh is composed of 10 m² creekbank, 100 m² low marsh, and 100 m² high marsh, the average recycling would be 50.6%. If the marsh were to lose 50 m² low marsh and gain 40 m² high marsh, average recycling would increase to 54.5%. Also, the importance of precipitation to cycling will increase, as high marsh area increases and low marsh area decreases. This scenario is similar to what is found at Upper Phillips Creek (Kastler & Wiberg 1996).

(3) If, as is the case in Great Sippewissett (Valiela 1983) and Sapelo Island (Pomeroy & Weigert 1981), the marsh is migrating overland and prograding toward the sea, the overall change in the characteristic of the nitrogen cycle will depend on the rate at which each geomorphic process occurs. If prograding occurs more rapidly than overland migration and relative area of low marsh increases, the marsh will experience an overall decrease in nitrogen cycling per unit area. If, however, the marsh is migrating overland faster than it is prograding, then there will be an increase in cycling.

(4) If the marsh is stalling at a steep slope, the marsh will cycle less nitrogen per average squared meter, independent of what occurs at the water's edge. The high marsh will decrease in size relative to low marsh. Depending on the steepness of the slope and sediment

supply, the marsh may ultimately be replaced with open water.

In conclusion, the nitrogen cycle of salt marshes experiencing rising relative sea level will generally change. The degree and direction of change will depend on the landscape setting of the marsh and the ability of the marsh to sustain itself. Slope and degree of sediment supply will play key roles in determining how the nitrogen cycle of a salt marsh will be affected by rising sea level.

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