Ecosystem Functions of Tidal Fresh, Brackish, and Salt Marshes on the Georgia Coast

Kazimierz Więski · Hongyu Guo ·
Christopher B. Craft · Steven C. Pennings

Abstract We examined patterns of habitat function (plant species richness), productivity (plant aboveground biomass and total C), and nutrient stocks (N and P in aboveground plant biomass and soil) in tidal marshes of the Satilla, Altamaha, and Ogeechee Estuaries in Georgia, USA. We worked at two sites within each salinity zone (fresh, brackish, and saline) in each estuary, sampling a transect from the creekbank to the marsh platform. In total, 110 plant species were found. Site-scale and plot-scale species richness decreased from fresh to saline sites. Standing crop biomass and total carbon stocks were greatest at brackish sites, followed by freshwater then saline sites. Nitrogen stocks in plants and soil decreased across sites as salinity increased, while phosphorus stocks did not differ between fresh and brackish sites but were lowest at salty sites. These results generally support past speculation about ecosystem change across the estuarine gradient, emphasizing that ecosystem function in tidal wetlands changes sharply across the relatively short horizontal distance of the estuary. Changes in plant distribution patterns driven by global changes such as sea level rise, changing climates, or fresh water withdrawal are likely to have strong impacts on a variety of wetland functions and services.

K. Więski · H. Guo · S. C. Pennings (✉)
Department of Biology and Biochemistry, University of Houston,
Houston, TX 77204, USA
e-mail: spennings@uh.edu

C. B. Craft
School of Public and Environmental Affairs, Indiana University,
Bloomington, IN 47405, USA

Introduction

Ecological communities differ in their structural attributes and hence in ecosystem functions. Since some of these functions provide in a direct or indirect way goods and services satisfying human needs (de Groot et al. 2002), there have been attempts to assess their value (Farber et al. 2002; Costanza et al. 2008). For example, tidal marshes are estimated to provide services to the society of about $10,000 $ha^{-1}year^{-1}$ (in 1994 dollars; Costanza et al. 1997) in the form of habitat (e.g., diversity), regulation (e.g., denitrification and nutrient retention), and productivity (e.g., biomass) functions. Given a total acreage of approximately 16,000 km^2 in North America (Greenberg et al. 2006), this translates into a total value of $16 billion yearly.

All tidal marshes, however, are not the same, and many do not provide the same levels of ecosystem functions. For example, within a riverine estuary, variation in salinity may lead to marked differences in the functioning of tidal marsh plant communities (Odum 1988). Odum argued that salinity-driven stress should reduce plant diversity in tidal salt marshes compared to tidal freshwater marshes, while the lower salinity stress in the tidal freshwater systems should increase decomposition rates, net primary production of vascular plants, and ultimately organic matter accumulation. Craft (2007) showed that soil organic matter content and accumulation differed markedly among tidal fresh, brackish, and salt marsh sites, but we are unaware of any studies that have compared plant community functions at replicated sites across the estuarine salinity gradient.

To test the hypothesis that the productivity and nutrient retention functions of tidal marshes would increase from salt to fresh marshes, we examined patterns of habitat (plant diversity), production (plant biomass and total C), and regulation (stocks of N and P in aboveground plant biomass and soil) functions in tidal salt, brackish, and freshwater marshes of the Satilla, Altamaha, and Ogeechee estuaries in Georgia.

Methods

Field and Laboratory Methods

Vascular plant diversity, biomass, and nutrient retention were measured at replicate sites along the salinity gradient. We studied two sites within each of three salinity zones (fresh, brackish, and saline) in each of three riverine estuaries along the Georgia coast (Fig. 1, Electronic Supporting Material, Appendix 1). Salinity zones were initially determined based on the dominant vegetation and position along the estuary. Down-estuary sites dominated by *Spartina alterniflora* were selected as saline; mid-estuary sites dominated by mixtures of *S. alterniflora*, *Spartina cynosuroides*, and *Juncus roemerianus* were selected as brackish; and up-estuary sites dominated by mixtures of *S. cynosuroides*, *Schoenoplectus tabernaemontani*, and *Zizaniopsis miliacea* were selected as fresh.

Salinity records from the water column near the Altamaha River sites during 2006 showed that we had identified three distinct salinity regions in this estuary (Fig. 2). Water column salinities increased from spring
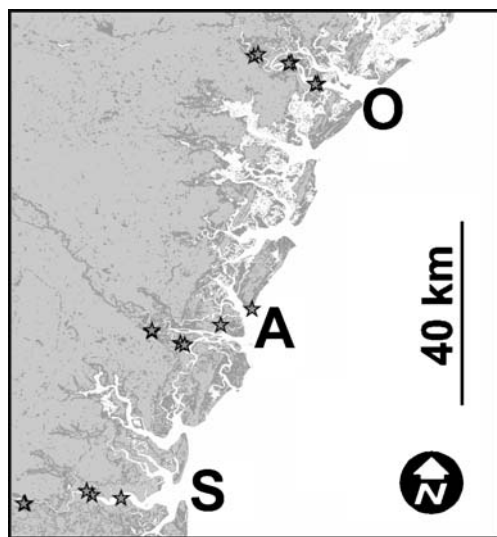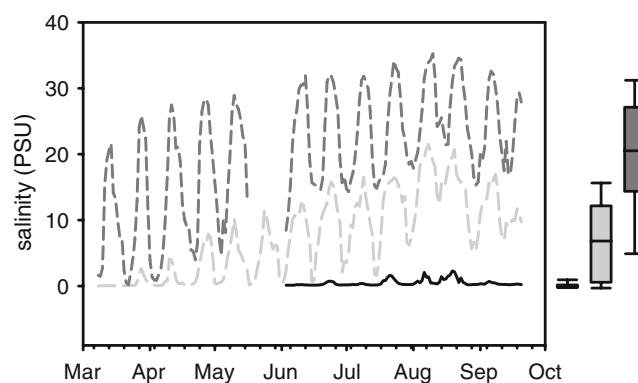

Fig. 2 Pattern of water column salinity near study sites on the Altamaha River in 2006 during the study period (freshwater zone, *solid line*; brackish zone, *gray dashed line*; saline zone, *black dashed line*). Data are derived from the GCE-LTER salinity monitoring program (datasets: gce7_hydro_daily_2006, gce8_hydro_daily_2006, gce9_hydro_daily_2006). *Box*: median, 25th and 75th percentile; *whisker*: tenth and 90th percentile

through the summer due to reduced river discharge and fluctuated due to the spring-neap tide cycle. The highest salinities (up to 35 PSU) were observed at saline sites, followed by brackish (up to 21 PSU) and fresh sites (usually less than 1 but occasionally up to 2 PSU). We measured water column salinities in the other two estuaries once a month in July, August, and October 2006 and in July 2008 when we visited the sites, and these limited values were broadly consistent with the more frequent records from the Altamaha River except that the fresh and brackish sites were somewhat saltier than on the Altamaha River (Satilla: fresh: 6.7 (1.5), brackish: 23.7 (1.3), saline: 30.8 (0.71); Ogeechee: fresh: 12.2 (1.4), brackish: 23.6 (1.9), saline: 28.9 (0.4); PSU (standard error)), in part because they represented summer and fall seasons when river discharge in Georgia is generally lower and salinities higher (e.g., Fig. 2). Although there appeared to be some variation among rivers in the exact salinity values, the sites represented a clear and strong salinity and vegetation gradient on each estuary, and can reasonably be treated as replicates of three broad categories of tidal marsh.

In July 2006, we located a transect, 100–150 m long, from the creekbank to the marsh platform at each site. Species richness was measured in 50 plots (1 m^2) spaced evenly along each transect. Based on our personal observations of plant phenology and literature reports, we re-sampled the same sites in October, when aboveground plant biomass was around its maximum (Gallagher et al. 1980; Schubauer and Hopkinson 1984). At this time, we located 12 plots, three at the creekbank, six along a creekbank–marsh platform transect, and the last three on the marsh platform. Species richness was measured in each plot (0.25 m^2). Following that, all the plant material (live and standing dead) was harvested, sorted by dominant

Fig. 1 Map of the Georgia coast showing study sites on the three river systems (*S* Satilla River, *A* Altamaha River, *O* Ogeechee River). Geographic coordinates for sites are provided in Electronic Supporting Material, Appendix 1

species, dried at 60° to constant biomass (3 days), and weighed.

In October, we also collected leaf and shoot samples for C, N, and P analysis from plants adjacent to the study plots. A single entire leaf (or shoot for *S. tabernaemontani*) was clipped from each of three separate plants. Collections were made from the five most dominant species occurring at our sites: *S. alterniflora*, *S. cynosuroides*, *J. roemerianus*, *Z. miliacea*, and *S. tabernaemontani*. For grasses, the intermediate-aged leaves (in between new and yellow) were collected; for *Juncus* and *Schoenoplectus*, fully green leaves or shoots were collected. Samples were stored on ice and frozen upon return to the laboratory. The samples were later freeze-dried (LABCONCO freeze drier, collector temperature −48°, 60 h per sample). Freeze-dried samples with a total area less than ca. 20 cm^2 were pulverized in toto, bigger samples were cut with scissors into pieces (ca. 2–3 cm^2), and a sub-sample was pulverized (SPEX mill, 5 min per each sample). Organic C and N were determined using a Perkin Elmer 2400 CHN analyzer. Total phosphorus was determined by colorimetric analysis after digestion in nitric-perchloric acid (Sommers and Nelson 1972).

Standing stocks of C, N, and P were calculated for each site by multiplying the C, N, or P composition of leaves of each species by that species' standing biomass at that site. "Other" species, whose C, N, and P composition were not measured, made up in sum a moderate proportion of the total biomass (Table 1) and were assumed to have the average nutrient composition (adjusted for biomass) of the dominant species at a given site. Simply ignoring species whose C, N, and P composition were not measured led to lower estimates of standing stocks but did not change statistical conclusions about how standing stocks varied along the estuary (data not shown).

In July of 2005, duplicate soil cores (8.5 cm diameter by 30 cm deep, one from the creekbank and one from the marsh platform) were collected from each site, for a total of 36 cores. Cores were sectioned in the field into 2-cm depth increments. Increments were dried at 70°C, weighed for bulk density, ground and sieved through a 2-mm mesh screen, and analyzed for organic carbon, total nitrogen, and total phosphorus as described above. Bulk density was calculated from the dry weight per unit volume for each depth increment after correcting for moisture content of a

Table 1 Species composition at study sites

Salinity zone	River	Site	SA	SC	JR	ZM	ST	SM	PC	SD	SR	TD	BM	DS	IF	Other
Fresh	Satilla	1	0.0	*73.9*	0.0	25.0	0.0	0.0	0.0	0.0	0.8	0.0	0.0	0.0	0.0	0.3
		2	0.0	*0.0*	0.0	37.9	0.0	0.0	0.0	0.0	4.2	0.0	0.0	0.0	0.0	57.9
	Altamaha	1	0.0	0.0	0.0	*87.9*	0.0	0.0	1.3	0.0	0.0	0.0	0.0	0.0	0.0	10.8
		2	0.0	0.0	0.0	*70.4*	0.0	0.0	0.4	0.0	0.4	0.0	0.0	0.0	0.0	28.8
	Ogeechee	1	9.2	*40.8*	0.0	0.0	40.0	0.0	0.0	0.0	0.0	0.0	0.0	5.8	0.0	4.2
		2	11.7	*41.5*	0.0	0.0	36.6	0.0	0.0	0.0	0.0	0.0	0.0	3.3	0.0	6.9
Brackish	Satilla	1	21.7	3.2	*55.8*	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	19.3
		2	25.0	20.0	*55.0*	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	Altamaha	1	16.7	14.2	*57.1*	0.0	0.0	9.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2.9
		2	*30.0*	15.4	23.3	0.0	0.0	17.9	0.0	0.0	0.0	0.0	0.0	5.4	0.0	7.9
	Ogeechee	1	*48.7*	0.0	47.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.4	3.4
		2	25.0	5.8	*35.4*	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.8	32.9
Saline	Satilla	1	*74.7*	0.0	24.9	0.0	0.0	0.0	0.0	0.4	0.0	0.0	0.0	0.0	0.0	0.0
		2	*75.0*	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	25.0
	Altamaha	1	*77.1*	0.0	0.0	0.0	0.0	0.0	0.0	5.0	0.0	5.8	11.3	0.0	0.0	0.8
		2	*76.7*	0.0	23.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	Ogeechee	1	*66.8*	0.0	32.4	0.0	0.0	0.0	0.0	0.8	0.0	0.0	0.0	0.0	0.0	0.0
		2	*68.3*	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	31.7

Data are percent biomass composition in 0.25 m^2 plots

Other-remaining 97 species

Dominant species for each salinity zone of each river are indicated in italics

SA Spartina alterniflora, *SC Spartina cynosuroides*, *JR Juncus roemerianus*, *ZM Zizaniopsis miliacea*, *ST Schoenoplectus tabernaemontani*, *SM Schoenoplectus americanus*, *PC Pontederia cordata*, *SD Salicornia depressa*, *SR Schoenoplectus robustus*, *TD Typha domingensis*, *BM Batis maritima*, *DS Distichlis spicata*, *IF Iva frutescens*

sub-sample that was dried at 105°C. Soil C, N, and P pools (0–30 cm) were calculated from bulk density and C, N, and P concentrations.

Statistical Analysis

Data were transformed when necessary to improve normality and homogeneity of variance and analyzed using two- or three-way analysis of variance (ANOVA) with salinity zone, estuary, and (when relevant) elevation (creekbank, transect, and platform) as main factors, and sites as replicates (elevation was nested within site). This approach allowed us to incorporate variation due to interactions between elevation within a marsh, estuary salinity zone, and estuary. In some cases, these interactions were statistically significant when the strength of the pattern with salinity differed among estuaries; however, these interactions did not change the fundamental nature of the estuarine salinity pattern but only its magnitude, which might have been driven in part by our ability to precisely match salinity zones among estuaries, which were not the focus of our study; thus, for clarity, we did not emphasize them here. Because our focus was on main effects of salinity, we present our results as grand averages for each salinity zone (for presentation, data were averaged over plots within a site, averaged over sites representing a salinity zone within each estuary, and finally averaged for each salinity zone over the three estuaries). Summary ANOVA tables reporting all effects and their interactions are presented in the Electronic Supporting Material (Appendices 2, 3, and 4).

Results

Salt marsh sites were dominated by *S. alterniflora*, with moderate amounts of *J. roemerianus*, brackish sites by mixtures of *S. alterniflora*, *S. cynosuroides*, and *J. roemerianus*, and fresh sites by mixtures of *S. cynosuroides*, *S. tabernaemontani*, and *Z. miliacea* (Table 1). Across all 18 sites, a total of 110 plant species were found; most of these individually contributed little to aboveground standing biomass although in sum, they could comprise a moderate proportion of the biomass at any one site (Table 1). Species richness at the site scale decreased by over five times across the salinity gradient from fresh to salt (Fig. 3b) and did not differ among estuaries (Satilla=11.3, Altamaha=13.0, and Ogeechee=12.2). Plot-scale richness was almost four times lower than site-scale richness, but the general pattern of decreasing richness with increasing salinity was identical with the site-scale pattern in both summer and fall (Fig. 3a). Consistent with the greater species richness of the fresh sites was greater variation among rivers in the dominant vegetation, with *Z. miliacea*
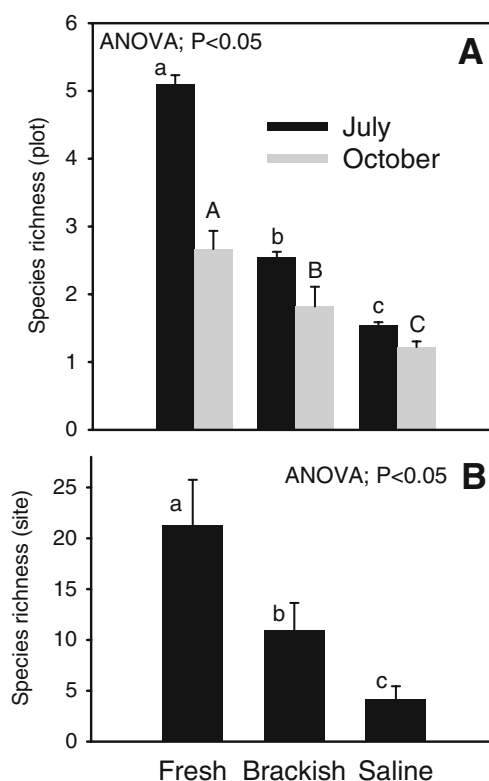

Fig. 3 Macrophyte species richness patterns at the plot scale in 2 months (**a**) and at the site scale (**b**) in three salinity zones. Note that the plot size in October (0.25 m²) differed from that in July (1 m²). Analysis of variance values were calculated separately for all three data sets. Differences among means within a data set (Tukey's test) are indicated by *letters above bars*

dominating the Altamaha and Satilla sites and *S. tabernaemontani* dominating the Ogeechee sites (Table 1).

Vegetation height decreased with increasing salinity, whereas aboveground biomass was greatest at brackish and lowest at saline sites (Fig. 4a, b). Aboveground carbon stocks paralleled patterns of biomass in that they were greatest at the brackish sites and lowest at the salt marsh sites (Fig. 4b).

The dominant plant species differed in carbon, nitrogen, and phosphorus composition (Fig. 5a–c). In particular, *J. roemerianus*, which was most abundant in the brackish marshes, had the highest carbon content and the lowest nitrogen and phosphorus content of the dominant species.

Soil organic carbon stocks (0–30 cm) were lower at the saline versus the brackish and fresh sites (Fig. 6a). Soil nitrogen stocks did not differ between fresh and brackish sites but were lowest at the saline sites (Fig. 6b). Plant nitrogen stocks paralleled the soil pattern (Fig. 7a). Soil phosphorus stocks were marginally ($P=0.06$) greater at the brackish versus the fresh and saline sites (Fig. 6b), whereas plant phosphorus stocks did not differ between fresh and brackish sites (although there was a slight trend towards a peak at the brackish sites) and were lowest at saline sites
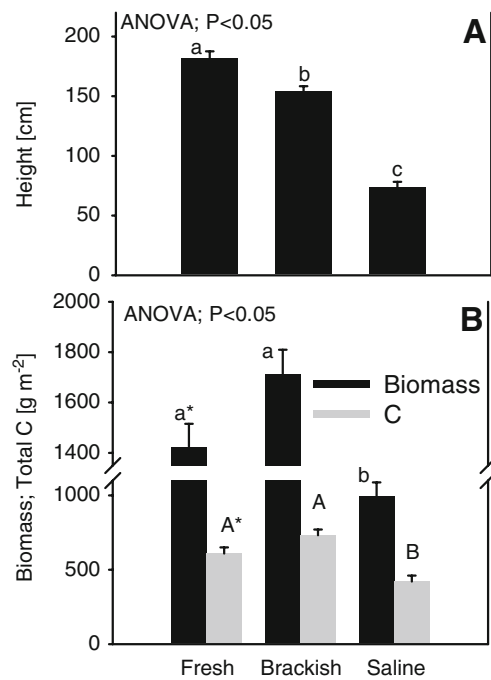
Fig. 4 Height (**a**) and aboveground biomass and total carbon stocks (**b**) of macrophytes in three salinity zones. Differences among means within a data set (Tukey's test) are indicated by *letters above bars*. *Asterisk* (*) denotes *P*=0.07 for the comparison for both biomass and carbon between the fresh and brackish sites

adapting to the harsh saline conditions (Baldwin and Mendelssohn 1998; Howard and Mendelssohn 1999, 2000). Nevertheless, throughout evolutionary time, a limited number of species have successfully crossed the salinity barrier and shifted their range of occurrence down the estuaries to became salt marsh plants, most of which are able not only to tolerate high salinities but also a wide range in salinity (Fig. 2). The ecological filter acts in the opposite direction: salt marsh plants perform better under low salinity stress (Naidoo and Kift 2006; Maricle et al. 2007) since their osmoregulation-related energy expenses are smaller. Usually, however, salt marsh plants are excluded from lower salinity regions of the estuary. In New England, transplant experiments showed that freshwater plants competitively displace salt marsh plants to the harsher environment of the salt marsh (Crain et al. 2004); we are currently conducting similar experiments in Georgia to see
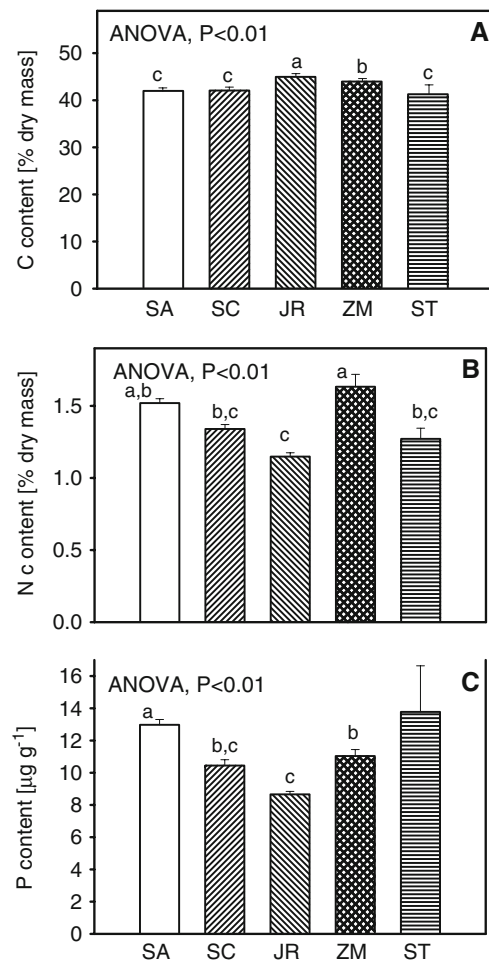
(Fig. 7b). Vegetation N:P ratios declined with increasing salinity (Fig. 8).

Discussion

In all three estuaries, an increase in plant species richness, height, and nitrogen content was associated with a decrease in salinity from salt to brackish to fresh tidal marsh sites. Aboveground plant biomass and total carbon, however, were highest at brackish sites, and total phosphorus was high in the freshwater and brackish sites and only declined at the saline sites. In general, these results support Odum et al. (1984) speculations about how ecosystem function should change along the estuarine gradient; however, the high levels of aboveground biomass, C and P stocks at the brackish sites were unexpected and deserve further attention.

The decline in plant species richness with salinity that we observed was consistent with past studies on the Atlantic Coast (Perry and Atkinson 1997; Crain et al. 2004). The high plant richness observed in freshwater marshes can be explained by salinity's role as an evolutionary and ecological filter in structuring estuarine plant communities. In evolutionary terms, high salinities present an almost insurmountable evolutionary barrier that prevents most of the numerous freshwater marsh species from

Fig. 5 Carbon (**a**), nitrogen (**b**) and phosphorus (**c**) content of dominant macrophyte species. *SA Spartina alterniflora, SC Spartina cynosuroides, JR Juncus roemerianus, ZM Zizaniopsis miliacea, ST Schoenoplectus tabernaemontani.* Differences among means within a data set (Tukey's test) are indicated by *letters above bars.* Data for *S. tabernaemontani* were not included in the analysis of variance analysis of P content (**b**) due to large intraspecific variation
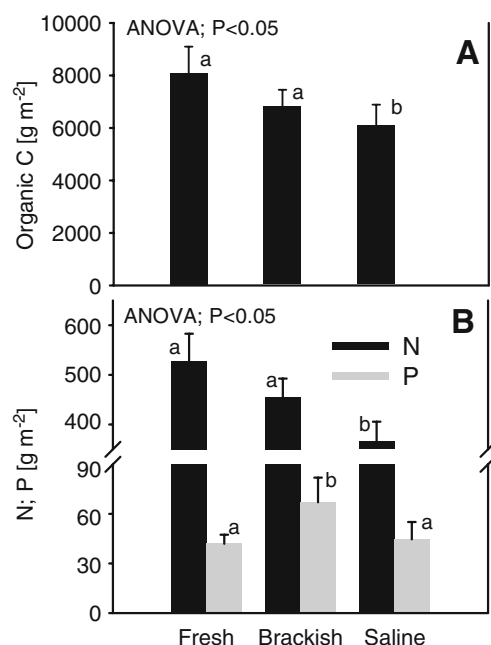
Fig. 6 Soil organic carbon (**a**) and nitrogen and phosphorus stocks (**b**; 0–30 cm) in three salinity zones. Differences among means within a data set (Tukey's test) are indicated by *letters above bars*

if the same mechanism operates in the southeast. Occasionally, however, individual "salt marsh" plants successfully colonize fresher habitats and in that way increase the species richness of fresher habitats (Guo unpublished data). Thus, the plant species richness of tidal fresh marshes is higher than that of salt marshes because (1) almost all the plants that could tolerate flooded soils are excluded from salt marshes by salt stress and (2) many of the plants common in salt marshes occasionally occur at low abundance in fresher regions of the estuary.

Finally, the decrease in species richness at the brackish sites might also be driven in part by increased competition. We speculate that the high aboveground biomass and plant height in the brackish marsh indicates higher levels of competition at brackish sites, leading to exclusion of less competitive plants, partially contributing to the drop in richness from the fresh to the brackish sites. The lowest levels of aboveground biomass at salt marsh sites were likely due almost completely to abiotic stress, because salt marsh soils contain high levels of salinity and sulfides (King et al. 1982). Therefore, the diversity–biomass relation along the estuarine gradient could be seen as resulting from the interplay of two separate forces: competition, increasing in strength from the fresh to brackish environment, and abiotic stress, increasing further down the estuary from brackish to saline environments. Preliminary experimental results support the hypothesis that competition in fact is stronger in brackish than fresh tidal marshes (Guo, unpublished data), and thus could partially

explain the drop in species richness from fresh to brackish sites.

Although studies from the Atlantic Coast agree that plant species richness declines with increasing salinity, studies from the Gulf Coast have not confirmed this pattern. Instead, studies at the Rio Grande Delta found a lack of variation in species richness along the salinity gradient (Judd and Lonard 2004). The relatively high richness (compared with Atlantic Coast salt marshes) found by Judd and Lonard (2004) in Gulf Coast salt marshes is consistent with other studies of Gulf Coast salt marshes (Judd and Lonard 2002; Kunza and Pennings 2008), but more studies are needed to determine why diversity patterns along the estuarine gradient might differ between the Atlantic and Gulf Coasts.

Frequent remarks in the literature about the high productivity of salt marshes might at first glance appear to contradict our result that brackish and tidal fresh marshes were even more productive. Nevertheless, other studies of tidal fresh and brackish marshes have also reported very high plant productivities (Birch and Cooley 1982; Schubauer and Hopkinson 1984). Many of the past salt marsh productivity studies focused on single species or a single marsh zone rather than considering the range of conditions along the estuary or across the elevational gradient of the marsh (Udell et al. 1969; White et al. 1978; Dame and Kenny 1986). In sum, although previous workers were correct to wax enthusiastic about the high productivity of salt marshes, they often were simply
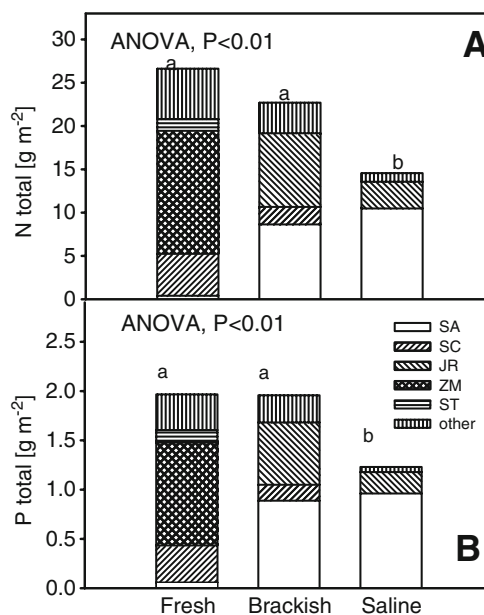

Fig. 7 Total nitrogen (**a**) and phosphorus (**b**) in aboveground macrophyte biomass in three salinity zones. Differences among overall means within a data set (Tukey's test) are indicated by *letters above bars*
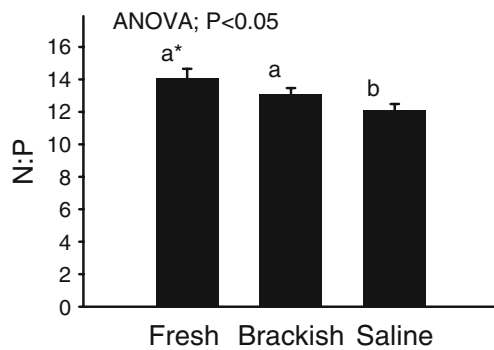
Fig. 8 N:P ratio of the plant community in three salinity zones. Differences among means within a data set (Tukey's test) are indicated by *letters above bars*

unaware that the tidal fresh and brackish marshes upstream were on average even more productive. The high productivity of lower salinity systems suggests that they might be particularly valuable in terms of supporting higher trophic levels or recycling nutrients, and we suggest that they merit more study than they have received to date.

Because salinity is a physiological stress for plants, one would expect that plant productivity would decline monotonically with increasing salinity. The unexpected finding that the brackish marshes supported the highest levels of aboveground plant biomass—mainly *Juncus*—might be related to higher bioavailability of nutrients at these sites. Loomis and Craft (in review) measured greater rates of sedimentation and P accumulation in soils of brackish marshes that they speculated was driven by their proximity to the estuary turbidity maximum. In addition, occasional saline water intrusions into freshwater marshes can increase nutrient release from sediments (Weston et al. 2006). Thus, it is possible that high aboveground plant biomass in the brackish marsh is driven by higher nutrient availability; if so, this might explain the trend towards higher plant P content at these sites. Alternatively, the accumulation of greater aboveground biomass in areas dominated by *Juncus* may be due to its phenology. In contrast to the relatively rapid biomass turnover of other salt marsh plants such as *S. alterniflora* (Dai and Wiegert 1996), *J. roemerianus* leaves are retained for several years (Eleuterius and Lanning 1987), leading to a higher standing biomass for the same amount of carbon fixed. This hypothesis is consistent with the fact that N stocks did not peak in the brackish marsh sites (suggesting that N was not more available at brackish sites), but instead decreased monotonically with increasing salinity.

Marsh nutrient retention capacity depends on the balance between the nutrient loss and retention within the system. One way nutrients can be stored within the system is by being taken up into plant tissues. Our data indicate that plant communities along the estuarine gradient vary in their capacity for nutrient storage and that this variation can be explained by the fact that the different plant species that dominate different salinity regions of the estuary vary in nutrient composition. Thus, the high aboveground nitrogen stocks of the freshwater marsh were driven by the high leaf N content of *Z. miliacea*. Although the brackish marsh dominant, *J. roemerianus*, had a low N content, the high aboveground biomass of *Juncus* led to brackish marshes having intermediate aboveground N stocks. This pattern was reversed in the salt marsh: although this region was dominated by *S. alterniflora*, which has a high N composition, the community aboveground N stocks were low due to comparatively low values of standing biomass. Nutrients can also be accumulated in soils: for nitrogen, we observed higher soil stocks in fresh and brackish marshes, a pattern that is consistent with results from other authors (Hatton et al. 1983; Craft 2007) Thus, both plant and soil N stocks are greatest in tidal fresh marshes and decrease downstream towards more saline marshes.

Interspecific variation in phosphorus composition generally followed the pattern of nitrogen, with the exception that the P content of *Z. miliacea* was not particularly high. As a result, P stocks in vegetation did not differ between fresh and brackish marshes, but decreased in saline marshes. Craft (2007) also observed no difference in soil P concentration between fresh and brackish marshes though both were significantly greater relative to salt marsh soils. In both studies, there was a marginal trend towards higher vegetation and soil P stocks at brackish sites.

Total stocks of N and P were far greater in the soil than in plants; however, the plant stocks should not for this reason be ignored. N and P stocks in marsh soils generally are recalcitrant, and only the more labile forms are available to microbes and soil macrofauna. As material becomes buried and soils more anoxic, processing of these pools decreases sharply, and they no longer are actively cycled by plants and microorganisms in the system. In contrast, aboveground plant material is readily available to herbivores, detritivores, and decomposer microbes and is important for sustaining a variety of marsh food webs. In short, the ecosystem functions of the two pools are markedly different.

The vegetation N: P ratios decreased across the increasing salinity gradient consistently with the hypothesized shift of nutrient limitation from P limitation in freshwater systems to N limitation in marine systems (Vitousek and Howarth 1991). According to theory, N:P ratios below 14 are typical of N limitation, ratios higher than 16 indicate P limitation, and values from 14 to 16 are inconclusive (Koerselman and Meuleman 1996). These results are consistent with a number of studies showing that salt marshes, which typically have N:P ratios <14, are limited by N rather than P. In addition, these results suggest

that our brackish and tidal freshwater marshes sites, which had N:P ratios approaching but still less than 14, might be limited by N also. This hypothesis is supported by Frost et al. (2009) who found that N additions stimulated above-ground biomass production of *Z. miliacea* in a tidal freshwater marsh of the Altamaha River but observed no response to P additions. Although the shift in N:P ratios that we documented is broadly consistent with theory, some studies have shown that N:P ratios have a limited ability to predict which nutrients are limiting in particular marsh systems (Morse et al. 2004, Crain 2007), and thus, these ratios should be used as predictive tools with some caution.

In sum, our results generally supported Odum's hypotheses that macrophyte diversity, biomass, and nutrient retention would decrease from tidal fresh to tidal salt marshes. Soil organic C and N stocks also were greater in tidal fresh and brackish marshes than in salt marshes. The high aboveground biomass levels that we found in brackish marshes, however, were unexpected and deserve further study to see if these results are general and what mechanisms drive this pattern. Our results, in combination with those of Craft (2007) and Loomis and Craft (in review), suggest that plant diversity, primary production, and nutrient recycling ecosystem functions of tidal fresh and brackish marshes exceed those of salt marshes. We emphasize that not all possible ecosystem functions were examined in these studies—in particular, we did not consider support of higher trophic levels. At the least, however, our combined results suggest that tidal fresh and brackish marshes should be considered at least as high a conservation priority as salt marshes, and possible higher, especially since tidal fresh marsh acreage is much less than salt marsh acreage, in part because it has been heavily impacted historically for agricultural purposes (Odum et al. 1984). Finally, any discussion of conservation priorities for these habitat types needs to take into account that their distributions will change with sea level rise, and that the losses (or gains) of acreage may not be equivalent across all three habitat types (Craft et al. 2009).

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