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Comparative Metabolism and Blue Carbon Sequestration of Two Wetland-Dominated Estuaries

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Coastal tidal wetlands and estuaries play important roles in the global carbon budget by contributing to the net withdrawal of CO_2 from the atmosphere. We quantified the linkages between terrestrial and oceanic systems, marsh-to-bay carbon exchange, and the uptake of CO_2 from the atmosphere in the wetland-dominated Plum Island Sound (MA, USA) and Duplin River (GA, USA) estuaries. The C budgets revealed that autotrophic marshes [primary production:ecosystem respiration (P:R) ~1.3:1] are tightly coupled to heterotrophic aquatic systems (P:R ~0.6:1). Levels of marsh gross primary production are similar in these systems (865 ± 39 and 768 ± 74 gC m^{-2} $year^{-1}$ in Plum Island and the Duplin, respectively) even though they are in different biogeographic provinces. In contrast to inputs from rivers and coastal oceans, tidal marshes are the dominant source of allochthonous matter that supports heterotrophy in aquatic systems. Dissolved inorganic carbon (DIC) exported from marshes to the coastal ocean was a major flux pathway in the Duplin River; however, there was no evidence of DIC export from Plum Island marshes and only minor export to the ocean. Burial was a sink for 53% of marsh net ecosystem production (NEP) on Plum Island, but only 19% of marsh NEP in the Duplin. Burial was the dominant blue carbon sequestration pathway at Plum Island, whereas in the Duplin, DIC and organic carbon export to the ocean were equally important. Regional- and continental-scale C budgets should better reflect wetland-dominated systems to more accurately characterize their contribution to global CO_2 sequestration.

Introduction

Salt marshes and other tidal wetland-dominated estuaries are among the most productive ecosystems on Earth because of the substantial loadings of inorganic and organic materials from land and the daily mixing of their waters by ocean tidal currents. The performance of these systems, including the rates of primary production and ecosystem respiration; exchange of materials with the land, atmosphere, and ocean; and the long-term accumulation of organic matter, can be assessed by quantifying the dynamics of inorganic and organic forms of carbon. With the increased awareness and understanding of the connection between atmospheric CO_2 levels and global warming over the past 20 years, several studies have quantified the exchange of CO_2 between the atmosphere and global ecosystems [1]. Many reports have documented the potential for carbon burial and sequestration of atmospheric CO_2 by blue carbon systems, those ecosystems at the land–sea interface that include salt marshes, mangroves, and seagrasses [2–4]. Indeed, even though the global area of coastal blue carbon ecosystems is several orders of magnitude lower than that of the open ocean, their global CO_2 sequestration rate through the burial of organic carbon (OC) is 0.08 to 0.22 Pg C $year^{-1}$ [1], nearly 10% of that for the entire open ocean [5–7].

In recent years, progress has been made at the regional and global scales in developing coastal zone carbon budgets to better define the impact of climate change and human activities in the coastal zone and to quantify the role of coastal systems as sources or sinks of atmospheric CO_2. These large-scale carbon budgets are based on limited in situ data from a limited number of studies at disparate sites, and therefore require novel empirical modeling and statistical approaches for budget creation and extrapolation [8–10]. Interestingly, many of these large regional-scale C budget syntheses rely heavily on only a few studies of key C processes, such as OC burial and dissolved inorganic carbon (DIC) exchange between tidal marshes and estuarine waters. The accuracy of these key processes was not tested until we examined them within the context of complete whole-ecosystem dynamic C assessments. For example, the burial of autochthonous OC within a system is constrained by net ecosystem production (NEP), the balance between gross primary production (GPP), and ecosystem respiration (R); however, there

are few direct measures of NEP for coastal ecosystems. Understanding the dynamic exchange of energy and material within and between ecosystems at the land–sea interface is critical for defining and testing our knowledge of how these systems regulate the Earth's climate through blue carbon sequestration. We need a greater number of detailed carbon budgets for all tidal wetland-dominated estuaries to better inform the development of models and extrapolations at regional and global scales.

In addition, we are witnessing a global trend of tidal wetland loss, either due to direct human actions such as dredging and filling or sea level rise (SLR) and sediment starvation, largely due to indirect human actions such as land management and river engineering, for example, dams [11–13] and climate change [14,15]. Wetland OC losses through erosion or gains through transgression have not yet been incorporated into global blue carbon budgets [6,7,16], which likely influences their overall contribution.

Here, we present detailed carbon budgets for 2 of the largest salt marsh-dominated estuaries in 2 contrasting biogeographic provinces along the US east coast. Our budgets detail C dynamics in the salt marsh and adjacent tidal waters using whole-system measures of GPP, R, and NEP, thus defining the autotrophic and heterotrophic nature of the component marsh and estuary subsystems, as well as the integrated whole. Our direct NEP measures enabled us to constrain the measures of blue carbon burial and question the reliability of using unconstrained values in large-scale regional or global syntheses. Finally, we note the evolution of blue carbon sequestration in wetland-dominated systems and consider the importance of additional carbon pathways in an expanded blue carbon budget, such as wetland area gain or loss, the deposition of allochthonous OC onto tidal marshes, and the export of inorganic and organic carbon to the continental shelf.

Materials and Methods

Site description

Metabolism and carbon flux were examined in salt marsh-dominated estuaries of the Plum Island Sound in northeastern Massachusetts, USA and the Duplin River in central Georgia, USA (Fig. 1). Both systems have been studied intensively since the 1990s as part of the National Science Foundation supported by the Long-term Ecological Research Program (LTER).

The Plum Island Sound estuary is in the cold water (mean 10 °C), Acadian biogeographic province of the northeastern United States at the point where the importance of tidal wetlands decreases relative to that of rocky intertidal and fjord systems further north. The Duplin River estuary is within the Sapelo Island National Estuarine Research Reserve in the warm water (mean 20 °C), Carolinean biogeographic province and is

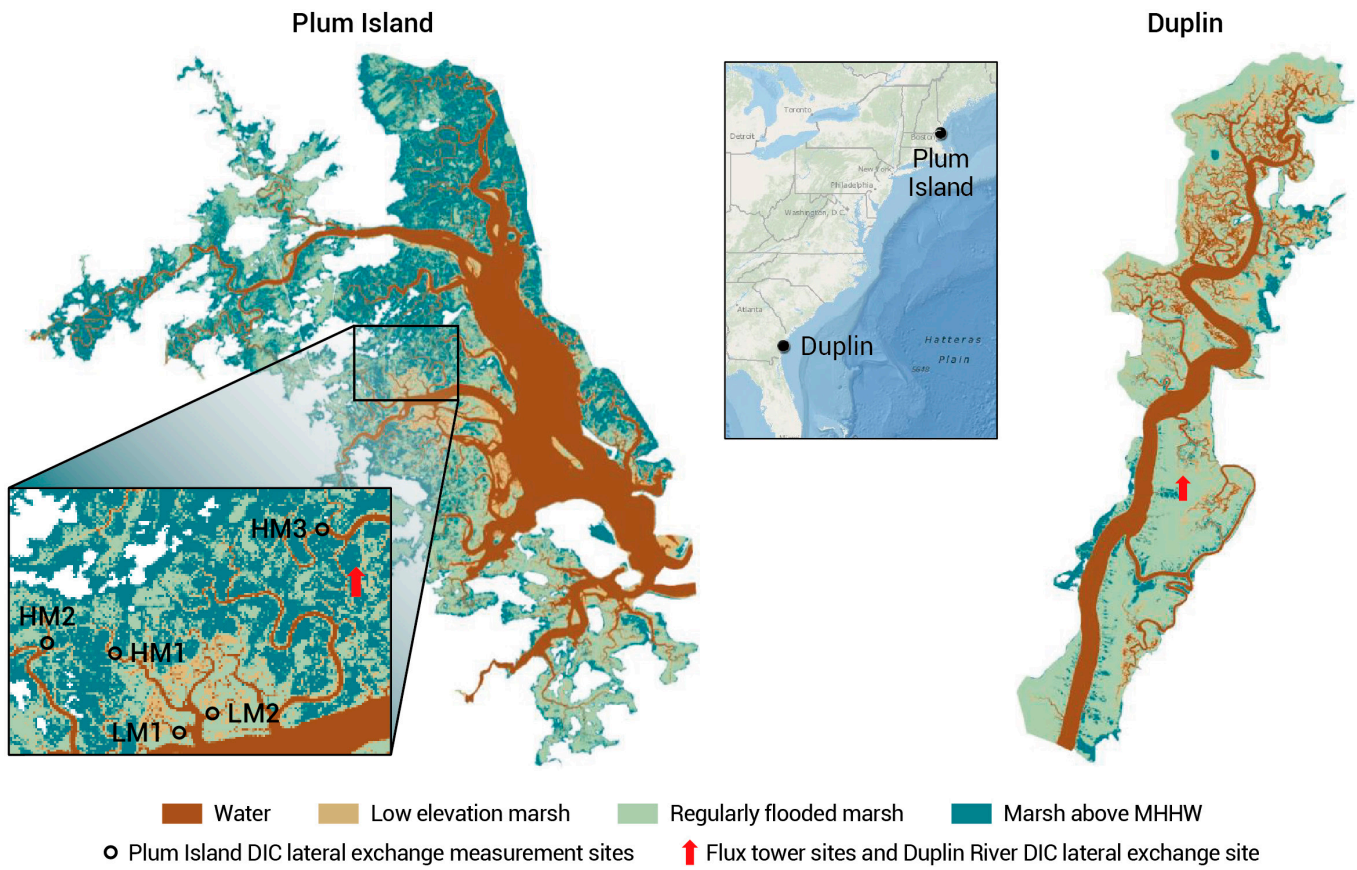

Fig. 1. Map of marsh and water distribution in the 2 study sites with an inset showing the locations of the Plum Island and Duplin estuaries along the US east coast. Colors in the site maps represent the distribution of tidal creeks and sounds (brown), and the relative distribution of salt marshes across an elevation gradient extending from where they start (mean sea level) along creekbanks, and across the low and high elevation portions of the marsh platform [light green for marshes less than mean higher high water (MHHW) and dark green for those above MHHW]. The length of the Plum Island system is 24 km (from northwestern most point to where the inlet to the Sounds meets the ocean). For the Duplin River, the length of the system from the tidal mouth at the south to the uppermost northern extent is 12.5 km. Absolute areas of marsh and water are shown in Figs. 4 and 5. The location of the lateral DIC exchange measurement sites in Plum Island is shown on the inset.

representative of the broad intertidal, wetland-dominated estuaries of the southeastern United States. Both estuarine ecosystems are relatively undeveloped but have a marked human presence in the terrestrial watersheds that drain into them (Table 1).

Sixteen hundred kilometers to the south, the bar-built Duplin River salt marsh-estuary ecosystem (Fig. 1) is approximately 12.5 km long with approximately 8 km^2 of intertidal marsh and 3.5 km^2 of estuarine and tidal creek waters (marsh:water area ~2.3:1). Freshwater input from the adjacent Sapelo Island is trivial compared to that from the tidal prism, and the salinity in this well-mixed estuary with Type 1B circulation [17] is controlled primarily by major river inputs (primarily the Altamaha River) to nearby Sounds and the coastal ocean. The water residence time increases from <1 d in the lower estuary where the tidal prism moves onto the continental shelf to 14 d at the head of the estuary [18,19]. The marsh platform is relatively flat and situated between approximately 0.8 and 1.2 m above mean sea level (MSL). In this mesotidal system (2.1 m mean tide), marsh floods had the highest tides (mean high water = 0.95 m). The marsh area in this sediment-rich system is relatively stable [20]. Marsh sediments have an average bulk density of approximately 0.55 g cm^{-3} and OC content of 4.4% [21]. *Spartina alterniflora* is the dominant vegetation in this system. The key site descriptors are listed in Table 1.

The bar-built Plum Island Sound salt marsh-estuary ecosystem (Fig. 1) is 24 km long with approximately 40 km^2 intertidal marsh and 20 km^2 of water body (marsh:water area ~2:1). Estuarine waters are well mixed with Type 1A circulation [17] with semi-diurnal tides of approximately 2.6 m. Estuarine salinity ranges seasonally and longitudinally from 0 to 32 largely in relation to freshwater runoff from the Parker and Ipswich Rivers (11.0 $m^3 s^{-1}$ average). OC loading from watersheds averages 53 kg ha^{-1}, with 95% contribution from dissolved organic carbon (DOC) (PIE LTER database; [22]). The estuarine water residence time ranges from <1 d in the Sound to >30 d during the summer low river flow in the upper estuary [22]. The marsh platform is relatively flat and situated mostly above the mean higher high water, indicating that marsh flooding occurs mainly during spring tides. The marsh area in this sediment-starved system is unstable, with significant marsh edge erosion and ponding on the marsh platforms [20,23,24]. Marsh sediments have an average bulk density of approximately 0.272 g cm^{-3} and organic matter content of 30% [24,25]. The dominant vegetation transitioned from fresh communities (Typha, Scirpus, and Carex) to brackish and saline communities (*S. alterniflora* and *Spartina patens*). The key site descriptors are listed in Table 1.

Methods

We estimated the carbon budget fluxes and stocks for the tidal marshes and estuarine waters of the Plum Island and Duplin River systems, focusing on OC (Fig. 2 and Table 2). We present all fluxes as positive values (as done in several regional coastal carbon budgets, e.g., [9]), which is contrary to many ecosystems or global budgets where net inputs of CO_2 from the atmosphere to the ecosystem are assigned negative values [26]. Our exception is in reporting NEP for either marsh or aquatic estuarine subsystems, where a negative value denotes a heterotrophic system in which respiration (R) exceeds GPP. We defined the C budget as consisting of 2 OC compartments for the marsh and tidal waters that either process or store matter: autotrophs and heterotrophs combined, and marsh soil or water column OC. External sources or sinks of OC include rivers that drain terrestrial watersheds and oceans. Rivers are also sources of

Table 1. Geographical, physical, and chemical characteristics of the Plum Island Sound and Duplin River salt marsh-dominated estuaries

Parameter	Plum Island	Duplin	Reference
Biogeographic province	Acadian	Carolinean	[97]
Annual temperature (°C)	9.5 (−3 to 22)	20 (11–28)	[66,98]
Salinity range	0–32	20–32	
Marsh area (km^2)	42.2	11.7	[24,27]
Aquatic area (km^2)	17.4	3.2	[24,27]
Marsh:water area	2.4:1	2.7:1	[24,27]
Marsh platform elevation (m above MSL)	1.4	0.8–1.1	[24,39,99]
Sediment availability	Low	High	[21,24]
Marsh stability	Edge erosion and ponding	Stable	[20,24];
Tidal range (m)	2.9	2.2	NOAA tidal datums
Sea level rise rate (mm $year^{-1}$)	2.9	3.3	NOAA tides and currents Ft Pulaski and Boston
Marsh sediment bulk density (mg cm^{-3})	0.272	0.55	[21,24,25,28]
Marsh sediment organic content (%)	30.0	8.8	[21,24,25,28]
Watershed OC loading (kg ha^{-1})	53	Indirect only	PIE and GCE LTER databases [22,100]
River runoff ($m^3 s^{-1}$)	11.0	Indirect only	USGS discharge; [71]
Water residence time (d)	<1–30	<1–14	[18,19,71]

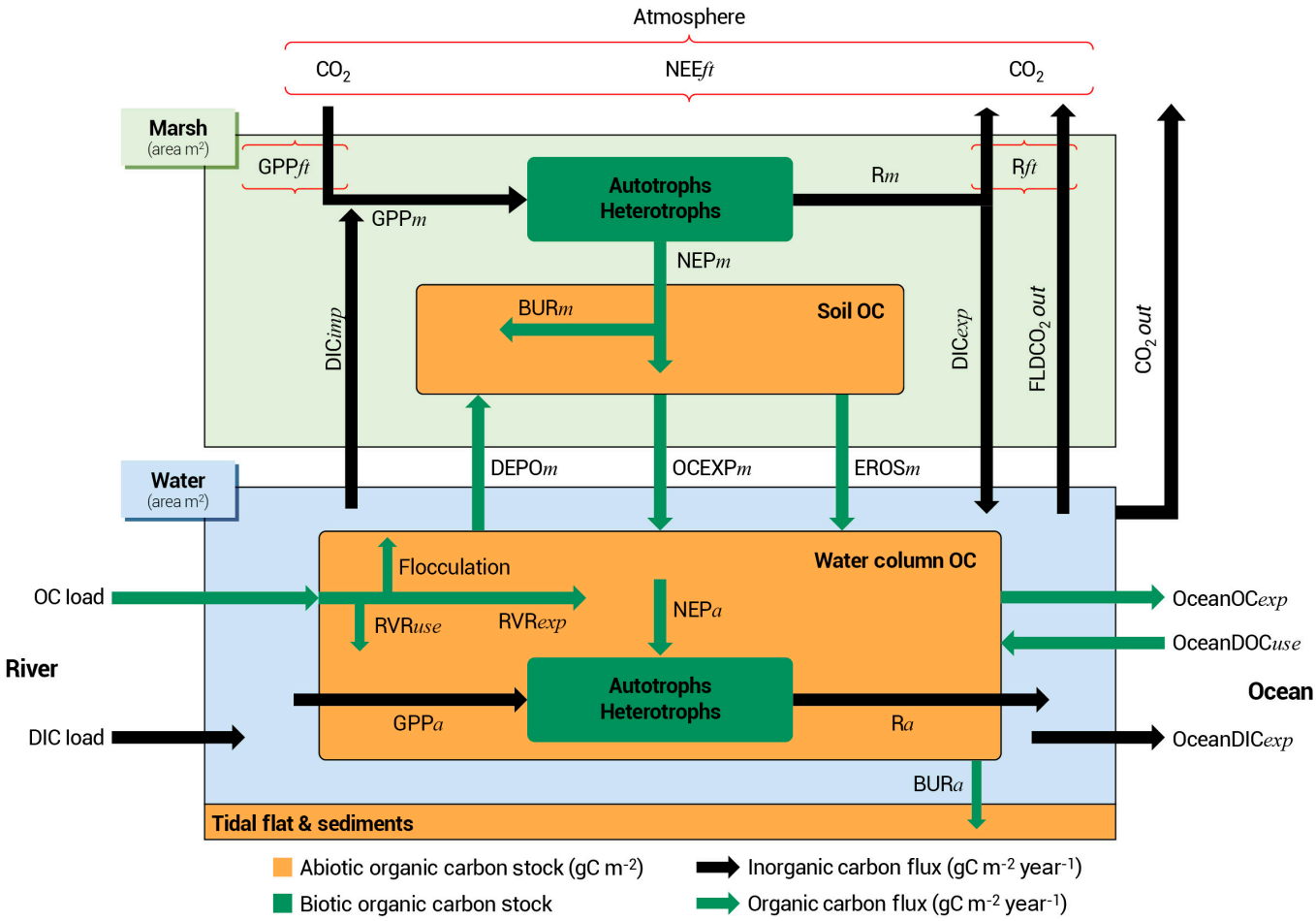

Fig. 2. Generalized diagram of carbon fluxes and stocks for a marsh-dominated estuarine system (marsh and aquatic subsystems) with connections to adjacent terrestrial (river) and oceanic systems. BUR*m&a*, OC burial; CO_2*out*, degassing of estuarine waters when within creekbanks; DEPO*m*, deposition of OC onto marsh; DIC, dissolved inorganic carbon; DIC*imp&exp*, DIC exchange between tidal creeks and marsh surface in conjunction with tidal flood/ebb; *EROSm*, OC erosion of marsh edges; FLDCO$_2$*out*, degassing of flood tide water, which is seen by flux towers; GPP*ft*, CO_2 exchange between marsh and atmosphere attributable to GPP; GPP*m&a*, corrected measures of GPP for marsh (*m*) and aquatic systems (*a*); NEE*ft*, Net ecosystem exchange of CO_2 over a marsh as measured by eddy covariance flux towers; NEP*m&a*, corrected measures of marsh and aquatic net ecosystem production; OC, total organic carbon; OC load and DIC load, allochthonous input of organic and inorganic carbon from watershed; OceanDOC*use*, use of oceanic DOC in estuary; OceanOC*exp* and OceanDIC*exp*, export of OC and DIC to ocean; Rft, CO_2 fluxes to the atmosphere as seen by the eddy covariance towers, which must be corrected to obtain Rm; R*m&a*, corrected measures of marsh and aquatic ecosystem respiration; RVR*use*, utilization of riverine OC during estuarine passage. Terms within red parentheses are fluxes measured at the flux towers. Fluxes are represented per unit marsh or aquatic area [m^2 marsh or water per year (gC m^{-2} year^{-1})]. Fluxes and their abbreviations are described in detail in Tables 2 and 3 and the text.

inorganic carbon; however, these fluxes are only partially considered in the Plum Island or Duplin budgets. Combined autotrophs and heterotrophs process OC through metabolism, with a concomitant exchange of CO_2 or DIC with tidal waters and/or the atmosphere. For marshes, we relied on published values of GPP and the net ecosystem exchange (NEE) of CO_2 derived from eddy covariance (EC) flux towers. As EC towers measure CO_2 exchange only with the atmosphere, primary production and respiration (autotrophic and heterotrophic combined) must be corrected for lateral exchange of DIC with tidal waters. CO_2 fluxes to the atmosphere must also be corrected for any CO_2 degassing or in-gassing from tidal waters when flooding the marsh, as we want to discriminate between the metabolism of the marsh and that of open-water sounds, bays, and tidal creeks. DIC export was added to the flux tower measure of respiration to determine total marsh respiration, and DIC import was added to the flux tower measure of GPP to determine total marsh production. CO_2 degassing from a flooded water column inflates the flux tower measure of respiration and deflates the tower measure of the GPP. NEP is the balance between the corrected EC flux tower (*ft*) measures of GPP and R.

$$Rm = Rft + DIC\,exp - FLDCO_2\,out \quad (1)$$

$$GPPm = GPPft + DICimp + FLDCO_2\,out \quad (2)$$

$$GPPm - Rm = NEPm \quad (3)$$

where R*m* is total marsh respiration, GPP*m* is total marsh GPP, R*ft* is respiration as measured by the flux tower, GPP*ft* is GPP as measured by the flux tower, DIC*exp* is the export of DIC from the marsh to tidal creek water, DIC*imp* is the import of DIC from tidal creek water to the marsh, FLDCO$_2$*out* is the degassing of CO_2 from supersaturated flood tide water covering

Table 2. Major methods employed in developing carbon budgets for the Plum Island Sound and Duplin River estuarine ecosystems

Flux or stock abbreviation	Description	Approach	References
Marshes			
GPP*m* and GPP*ft*	Marsh gross primary production—CO_2 uptake	Eddy covariance before and after correction	[28,35,36]
R*m* and R*ft*	Marsh respiration—TCO_2 production	Eddy covariance with and without correction	As above
NEE*ft*	Marsh net ecosystem exchange of CO_2	Eddy covariance without correction	As above
DIC*imp* or DIC*exp*	Import or export of DIC to or from marsh	Measurement of DIC and water flux on incoming and outgoing tides over full tidal cycles	[27,38]; this study
NEP*m*	Marsh net ecosystem production	Eddy covariance NEE corrected for lateral DIC and vertical CO_2 exchange (degas) from marsh tidal flood waters	This study
BUR*m*	Marsh OC burial	^{137}Cs and ^{210}Pb profiles, OC density profiles, bulk density	[21,28]
OCEXP*m*	Export of OC from marsh	Mass balance	This study
DEPO*m*	Deposition of OC onto marsh	Mineral input times organic:inorganic ratio of tidal water total suspended matter	[21,24]; GCE and PIE databases [101,102]
EROS*m*	Erosion of marsh edge OC	Change analysis of aerial photographs and LiDAR flights	[20,24]
Soil OC	OC stock in marsh soil	Loss on ignition or CN analyzer and bulk density	[21,25]
Aquatic			
GPP*a*	Aquatic gross primary production	Free-water diurnal changes in DO and/or DIC along estuarine continuum corrected for air–sea exchange and advection/dispersion	[27,71,72]
R*a*	Aquatic benthic and pelagic respiration	Free-water diurnal changes in DO and/or DIC along estuarine continuum corrected for air–sea exchange and advection/dispersion	[27,71,72]
NEP*a*	Aquatic net ecosystem production	Balance between GPP*a* and R*a* and/or net 24-h gas exchange with atmosphere	[27,72]
OceanDIC*exp*	DIC export to ocean	DIC flux from concentration gradients and advection and dispersion metrics Duplin. C isotopic biomarkers PIE	[27,38]
CO_2*out* and FLDCO_2*out*	Sea to air CO_2 flux from creeks and when flooding marsh	Gas exchange from water when in channel or over marsh determined from aqueous—atmosphere pCO_2 gradient, gas exchange coefficient, and wind speed (assumed 0 when over marsh). Measured in Duplin only	[27]
River OC load and DIC load	Input of organic and inorganic carbon to estuarine waters	Monthly monitoring by PIE LTER studies—flow-weighted TOC concentration and river flow (USGS). C isotopic biomarkers. Not available for Duplin	PIE LTER database—[22,38,103]
Flocculation	Flocculation of riverine DOC	10% riverine DOC load, Plum Island only	[104]
RVR*use*	Decomposition of riverine DOC, DOC flocculation, and POC	For Plum Island based on time series bioassays of riverine DOC, DIC production/O_2 consumption rates, and freshwater transit time over the year. For the Duplin system based on freshwater fraction, Altamaha River DOC concentration and decay rate, and freshwater residence time	[70,71,90,100,105]; SINERR salinity
OceanDOC*use*	Decomposition of marine DOC in estuary	Decomposition rates over time determined from bioassays of coastal DOC where bacterial growth, O_2 consumption, DIC production, and salt water residence time were measured	[29,71,72,105]

(Continued)

Table 2. (Continued)

Flux or stock abbreviation	Description	Approach	References
BUR*a*	Burial of OC in estuarine sediments	Accretion as on the marsh but using bottom sediment measures of bulk density and OC content	[106,107]; this study
RVR*exp*	Export of riverine OC	Mass balance of river OC loading versus POC settling, flocculation, and DOC decomposition (Plum Island only)	This study
OceanOC*exp*	Export of riverine and marsh/estuarine derived OC	Mass balance of all inputs and losses	This study

the marsh, and NEP*m* is the net marsh ecosystem production (not NEE, which is only a measure of the balance between CO_2 flux to and from the atmosphere, as seen by EC towers).

The lateral exchange of DIC for the Duplin was determined for a small tidal creek within an EC flux tower footprint by Wang et al. [27] and was measured at Plum Island for this study. Lateral exchange of DIC at Plum Island was measured during 35 complete low-tide to low-tide tidal cycles at 5 tidal creek sites draining small (<0.15 km^2) areas of tidal marsh (Fig. 1) between March and December in 2016 and 2017. These measurements captured the full neap-spring range of tides in the system (from 2.3 to 3.6 m). One of the small creeksheds overlapped the flux tower footprint described by Forbrich et al. [28]. The net DIC exchange was measured as the difference between the product of water discharge and DIC concentration during flood and ebb tides. Water discharge was determined by measuring flow velocity and creek cross-sectional area using a Teledyne StreamPro acoustic Doppler current profiler (4 replicate tows across the creek every 15 min). The DIC concentrations were measured using an Apollo SciTech DIC Analyzer on gas-tight samples obtained every 15 min and preserved in mercuric chloride. The flow-weighted average DIC concentrations were determined for each flood and ebb tide (Fig. 3B). The water balance between the incoming flood and outgoing ebb tides was close (2.5 ± 9.4%), and we used the average water exchange value for each ebb/flood tidal cycle and the flow-weighted DIC ebb and flood tide concentrations to remove any DIC flood/ebb imbalance due solely to water imbalance (as done by Ganju et al. [12] for sediment balances). The net DIC exchange was determined as the difference between the flood and ebb tides in the marsh drainage area of the tidal creek system. We did not correct the DIC exchange measures for the metabolism occurring in the floodtide water itself over the marsh. Floodtide water spreads out over an immense area of the salt marsh at high tide such that the surface area-to-volume ratio increases by over an order of magnitude relative to when water is confined within tidal creeks. Thus, metabolism in the floodtide water contributed minimally to the total change in DIC or O_2 per unit area.

The marsh NEP is partitioned into burial (from ^{137}Cs or ^{210}Pb studies) and lateral exchange of OC to adjacent tidal creeks. Burial was based on ^{137}Cs and ^{210}Pb profiles and measures of bulk density and organic content from 4 locations within the flux tower footprint on Plum Island and 6 locations in the vicinity of the Duplin River. The deposition of OC onto the marsh following tidal flooding and the erosion of marsh creekbank OC have been reported in the literature (Table 2).

$$\mathrm{OCEXP}m = \mathrm{NEP}m + \mathrm{DEPO}m - \mathrm{BUR}m \quad (4)$$

where OCEXP*m* is OC export from the marsh, DEPO*m* is the deposition of OC on the marsh surface during tidal flooding, and BUR*m* is the burial of OC in the marsh sediments.

For the carbon budget of estuarine water bodies, we balanced the published values of allochthonous inputs from rivers and marshes with measures of whole-system gross production, respiration, and NEP (based on O_2 for Plum Island and O_2 and CO_2 for Duplin; Table 2). Allochthonous OC loadings from the Parker and Ipswich River watersheds were obtained from the Plum Island Ecosystems Long-Term Ecological Research Database (http://dx.doi.org/10.6073/pasta/25150e120c52bf62f1b1c7e7d7c5e274). Constituent concentrations determined from monthly grab samples were multiplied by the cumulative discharge [measured by US Geological Survey (USGS) gauging stations] during the interval between the preceding and following grab sample dates and then summed for the water year. For the Duplin River, there is a trivial direct input of carbon from the Sapelo Island watershed; however, there is an indirect input of OC from nearby rivers, as evidenced by the overall lowering of the salinity of estuarine and nearshore shelf waters. Utilization of this OC in the Duplin was calculated from the average age of the estuarine water, the terrestrial fraction of coastal DOC [average salinity in Duplin relative to 35 practical salinity units (psu) oceanic water], the average concentration of coastal DOC, and published values of the decomposition rate [29]. The utilization of terrestrial OC in the Plum Island estuary was determined from DOC decomposition rates determined from bioassays and freshwater transit time through the estuary. We further assume in Plum Island that all particulate OC (POC) and the portion of DOC that flocculates (10%) remain in the system, where it either contributes to marsh accretion, is metabolized, or is exported to the ocean (Table 2). We estimated the decomposition of oceanic DOC in the estuary using published measures of ocean end-member DOC concentration, DOC lability, and average seawater age in the estuary. The input of OC from the marsh to the estuarine waters was calculated as the mass balance of the marsh C budget (Fig. 2). Estimates of OC burial in creek bottoms assume that accretion rates are similar to those of the marsh but use bottom sediment measures of bulk density and organic content. Net C exchange with the ocean is required to balance the overall aquatic C budget.

$$\mathrm{OceanOC}exp = \mathrm{GPP}a + \mathrm{RVR}use + \mathrm{OceanDOC}use + \mathrm{EROS}m + \mathrm{OCEXP}m - \mathrm{R}a - \mathrm{BUR}a - \mathrm{DEPO}m \quad (5)$$

where OceanOC*exp* is the mass balance-calculated export of OC to the ocean, not including riverine DOC not decomposed during estuarine transport; GPP*a* is aquatic GPP; RVR*use* is POC, DOC floc, and decomposed DOC in Plum Island or just decomposed DOC in the Duplin; OceanDOC*use* is the decomposition of oceanic DOC in the estuary; EROS*m* is OC eroded from marsh shorelines; OCEXP*m* is as above; R*a* is aquatic respiration; BUR*a* is OC burial in estuarine sediments; and DEPO*m* is OC deposited in the marsh during tidal flooding (Table 2).

An estimate of the riverine OC export from Plum Island to the ocean was determined by the mass balance of terrestrial inputs and their consumption, RVR*use* (DOC decomposition and POC and DOC flocculation) in the estuary. The DIC export to the ocean was measured directly in the Duplin and from ^{13}C and ^{14}C natural isotope measurements in Plum Island Sound.

We lacked sufficient information to estimate the gross input and net output of riverine C sources in the Duplin River.

Similar to marshes, aquatic NEP is a fundamental ecosystem property of estuarine waters, indicating the degree to which metabolism cannot be supported entirely by autochthonous production (GPP*a*).

$$\mathrm{NEP}a = \mathrm{GPP}a - \mathrm{R}a \tag{6}$$

For heterotrophic systems, where R is greater than GPP, we identified the magnitude of all potential food sources meeting R based on the relative magnitude of their inputs to the systems.

$$\begin{aligned}\mathrm{R}a = {} & \alpha(\mathrm{OCEXP}m) + \beta(\mathrm{EROS}m) + \gamma(\mathrm{GPP}a) \\ & + \mathrm{RVR}use + \mathrm{OceanDOC}use\end{aligned} \tag{7}$$

where α, β, and γ are the fractional amounts of an input respired and the sum of the fractions is 1.

$$\alpha + \beta + \gamma = 1 \tag{8}$$

$$\alpha = OCEXPm / (OCEXPm + EROSm + GPPa) \tag{9}$$

$$\beta = EROSm / (OCEXPm + EROSm + GPPa) \tag{10}$$

$$\gamma = GPPa / (OCEXPm + EROSm + GPPa) \tag{11}$$

As RVR*use* and OceanDOC*use* were used in their entirety (directly measured respiration), we subtracted their magnitudes directly from R*a*, leaving the portion

$$\begin{aligned}\alpha(\mathrm{OCEXP}m) + \beta(\mathrm{EROS}m) + \gamma(\mathrm{GPP}a) = \\ \mathrm{R}a - \mathrm{RVR}use + \mathrm{OceanDOC}use\end{aligned} \tag{12}$$

Salt marsh blue carbon sequestration was calculated based on the rate of OC burial [3–7,16] and then adjusted for carbon pathways that either augmented or detracted from that [30–32]. Burial was adjusted for the deposition of allochthonous OC (e.g., algal or riverine material) onto the marsh surface in conjunction with sediment deposition occurring during tidal inundation [24]. The redeposition of salt marsh peat eroded from the marsh edges is considered autochthonous and, thus, was not included in the adjustment. The erosion of marsh peat that was not redeposited on the marsh surface was used to adjust the burial.

DIC and OC export to the ocean and OC burial in estuarine sediments are additional forms of blue carbon sequestration if they are of salt marsh OC origin and are not released as CO_2 gas into the atmosphere prior to entering the oceanic pool. The argument for including these pathways is that many continental shelves are typically undersaturated with respect to CO_2 and thus are sinks for atmospheric CO_2, and that the DIC entering the ocean will mix with the large oceanic pool of DIC, which has a residence time of millennia. The extent to which continental shelves are sources or sinks of CO_2 remains an active study area; therefore, the results obtained here may not be applicable worldwide [33,34]. OC entering the ocean may be buried or decomposed into DIC, again entering a pool with a long turnover. Estuarine burial and the export of OC to the ocean were calculated based on the magnitude of salt marsh OC entering estuarine waters relative to all combined OC inputs (see Eqs. 7 to 12). For the Plum Island and Duplin estuaries, the combined inputs of OC to estuarine waters included exports from salt marshes, erosion of salt marsh soils, riverine inputs metabolized during estuarine transport, oceanic inputs metabolized while residing in the estuary, and primary production within the estuary. The sum of salt marsh export and marsh erosion (excluding that redeposited onto the marsh) as a percentage of all combined inputs was multiplied by the estuarine OC mass balance to determine the export of salt marsh-derived OC.

The DIC of salt marsh origin (directly or indirectly via the decomposition of marsh carbon in estuarine waters) was calculated differently for each estuarine system. For the Duplin, we summed the DIC input from marsh drainage and calculated the DIC produced in conjunction with estuarine respiration of OC of marsh origin (again as the percentage of OC input from marshes relative to all other inputs). As net CO_2 evasion from estuarine waterbodies is known for the Duplin, the quantity of DIC produced but not released to the atmosphere is that which exits the ocean and is therefore directly calculated. For Plum Island, previous ^{14}C and ^{13}C natural abundance studies have quantified riverine DIC inputs and outputs to the ocean, and the production internal to estuarine waters exported to the ocean (Table 2). The DIC produced internally from the salt marsh was calculated from the percentage of estuarine respiration attributable to the input of salt marsh OC (as for the Duplin). DIC produced from respiration that was not taken up by phytoplankton or the salt marsh during tidal inundation or exported to the ocean was assumed to be lost to the atmosphere (which has not been quantified at Plum Island). The calculated CO_2 evasion was similar in magnitude to that measured in the Duplin estuary, supporting this approach.

Measures of variability for all fluxes that comprise the Plum Island and Duplin OC budgets were calculated and reported as standard deviations. We used rates published in the literature (Table 2), where possible, for example, with rates of OC burial in the marsh [21,28]. Standard deviations were calculated de novo for rates not previously published, for example, OC deposition in the marsh and DIC exchange between the marsh and the estuary on Plum Island. The magnitudes of some values reflect the cumulative nature of error propagation when fluxes are calculated from multiple terms, each with their individual errors, for example, the consumption of oceanic DOC in the Duplin system calculated from the product of OC concentration, saltwater content of the estuary, residence time of saltwater in the estuary, labile percentage of DOC, and decay rate of the labile fraction of DOC.

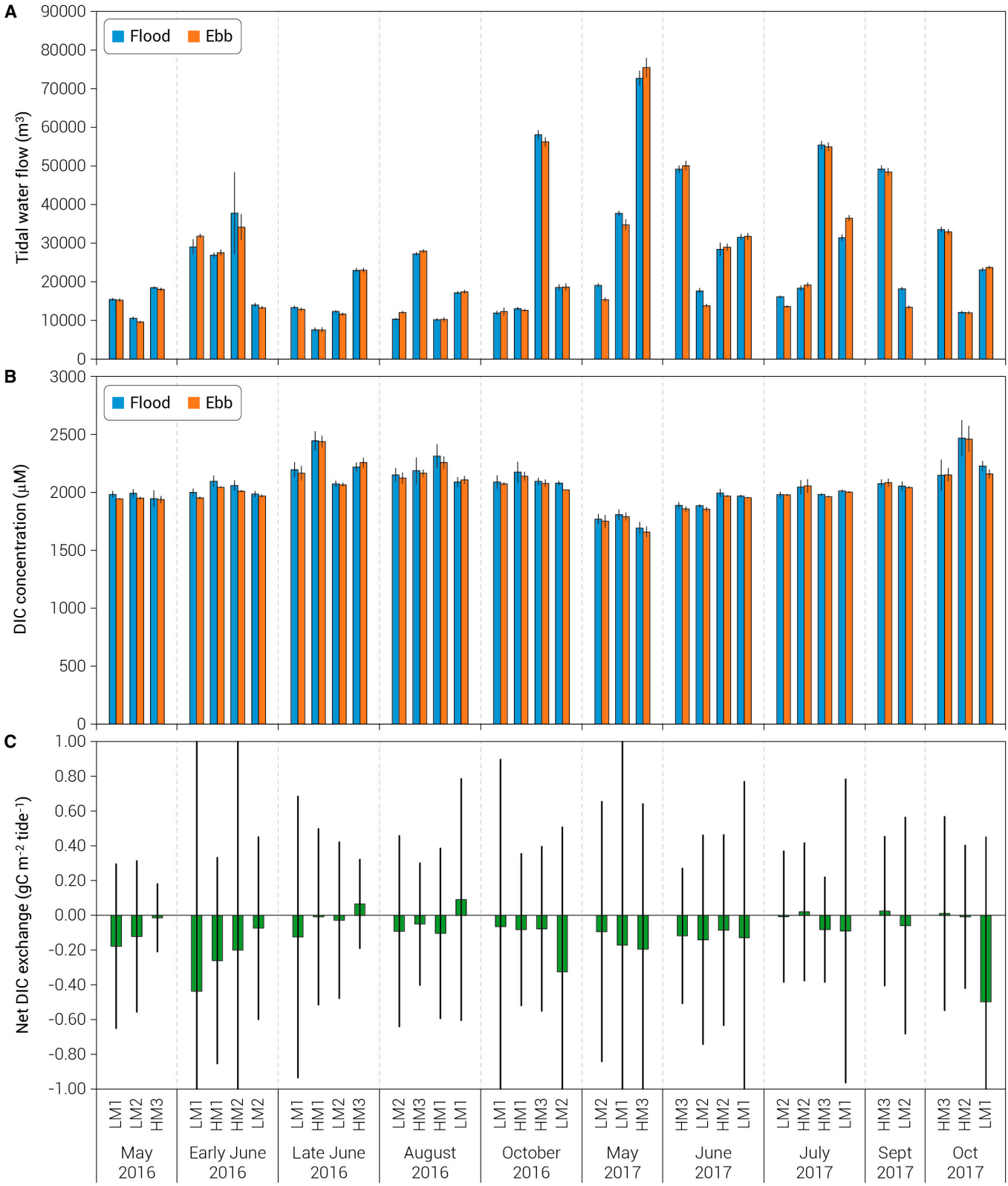

Fig. 3. (A) Average (± SD) water exchange during flood and ebb tides measured every 15 min during 35 separate tidal cycles at marsh/estuary sites on Plum Island, (B) flow-weighted average (± SD) DIC concentrations taken every 15 min during each tidal cycle, and (C) the calculated net exchange of DIC based on water mass and DIC concentration. The calculated annual average exchange of DIC is -23 ± 30 gC m^{-2} $year^{-1}$, denoting net retention of DIC during tidal exchange.

Results

Lateral exchange of inorganic C between marsh and estuary

We found contrasting patterns of DIC exchange between the marsh and tidal creeks for the Duplin and Plum Island systems. Over 2 years and across various total water exchange volumes on Plum Island (Fig. 3A), there was little difference between the flow-weighted average DIC concentrations during the flood and ebb tides (Fig. 3B). When the water discharge (Fig. 3A) and DIC concentrations (Fig. 3B) were combined to determine the net exchange of DIC during each tidal cycle for the marsh drainage area of the tidal creek system (Fig. 3C), the average net DIC exchange was −0.103 (± 0.135) gC m^{-2} per tide, indicating an import of DIC to the marsh. Only 5 of the 35 measurements indicated net DIC export. Scaled to tidal creekshed size, the average annual input of DIC to the marsh was 23 ± 30 gC m^{-2} (Fig. 4 and Table 3).

For the Duplin (Fig. 5), we saw an export of DIC from the marsh to tidal creek [27], averaging an export of 65 ± 36 gC m^{-2} of marsh $year^{-1}$. This is equivalent to a DIC input of 151 ± 83 gC m^{-2} water $year^{-1}$ for the estuary. Wang et al. [27] also reported CO_2 degassing of tidal water when flooding the marsh at an average rate of 74 ± 11 gC m^{-2} $year^{-1}$ (Fig. 5 and Table 3).

Marsh

Plum Island (Fig. 4 and Table 3)

The GPP of the marsh ecosystem at Plum Island estimated by the EC approach averaged 842 ± 26 gC m^{-2} $year^{-1}$ over a 5-year period [28]. It was higher during wet summer years (807 to 900 gC m^{-2}) than during years with less late spring rainfall (737 to 759 gC m^{-2} $year^{-1}$). The total marsh ecosystem respiration averaged 655 ± 24 gC m^{-2} $year^{-1}$ over the same 5-year period without systematic annual variability (532 to 643 gC m^{-2} $year^{-1}$). The net CO_2 exchange (NEE) averaged −187 ± 16 gC m^{-2} $year^{-1}$. A net import of DIC to the marsh during tidal flooding (−23 ± 30 gC m^{-2} $year^{-1}$) led to an underestimation of GPP by the flux tower. After correcting for the lateral DIC influx, GPP and NEP averaged 865 ± 39 and 210 ± 34 gC m^{-2} $year^{-1}$, respectively.

Plum Island marshes increase in elevation by approximately 3 mm $year^{-1}$ [28] through the accumulation of marsh grass-derived peat and surface deposition of mineral and organic matter during tidal flooding. The organic contribution to deposition from tidal flooding amounts to an average of 42 ± 9 gC m^{-2} $year^{-1}$ [24]. Elevation gain from the burial of undecomposed marsh grass root and rhizome production and deposition during tidal flooding is 111 ± 8 gC m^{-2} $year^{-1}$. Although the overall elevation gain of the marsh platform was roughly in balance with the SLR, there was a net erosion of the shoreline. The input of OC to tidal waters from edge erosion is 32 ± 7 gC m^{-2} $year^{-1}$ (calculated as total erosion divided by total marsh area). The net OC balance for the marsh is 172 ± 35 gC m^{-2} $year^{-1}$, 32 ± 7 gC m^{-2} $year^{-1}$ from erosion and 140 ± 34 gC m^{-2} $year^{-1}$ as determined using mass balance.

Duplin (Fig. 5 and Table 3)

The GPP of the marsh system in the Duplin estimated by EC averaged −768 ± 74 gC m^{-2} $year^{-1}$ over a 2-year period [35,36]. Total marsh respiration was 627 ± 102 gC m^{-2} $year^{-1}$ as determined from the flux tower measure of respiration (594 ± 95 gC m^{-2} $year^{-1}$) corrected for the efflux of CO_2 from estuarine waters when flooding the marsh (32 ± 5 gC m^{-2} $year^{-1}$) and the export of DIC from the marsh during ebb flux of tidal waters draining the marsh (65 ± 36 gC m^{-2} $year^{-1}$). Thus, the total marsh respiration was split between CO_2 flux to the atmosphere (562 ± 95 gC m^{-2} $year^{-1}$) and DIC drainage (65 ± 36 gC m^{-2} $year^{-1}$). The accumulation and burial of undecomposed marsh grass roots and rhizomes and flood tide-deposited OC averaged 27 ± 14 gC m^{-2} $year^{-1}$ over the past 50 to 100 years (^{137}Cs and ^{210}Pb time frames). Tidal floodwaters that supply mineral matter that supports marsh accretion introduce 12 ± 17 gC m^{-2} $year^{-1}$ of OC. The net C balance for the marsh suggests an export of 127 ± 128 g OC m^{-2} $year^{-1}$ to the tidal waters of the estuary. The relative contribution of OC deposition to marsh surface elevation gain is minor, as the sediment organic matter content is <5% C. Elevation gain is supported primarily by the deposition of mineral matter during tidal flooding [37]. The Duplin marshes do not appear to be gaining or losing land on a net basis [20] and are therefore contributing a trivial erosional input of OC to tidal waters (0.02 ± 0.07 gC m^{-2} $year^{-1}$).

Net marsh/water exchange of organic C

The areal inputs of marsh-derived C to each square meter of the estuarine water body were scaled from marsh outputs, accounting for the relative difference in the areas of marsh and water for each system (marsh:water 2.33:1 and 2.39:1 for Duplin and Plum Island, respectively).

There are 3 flows of OC between the marsh and estuarine water bodies in the Plum Island Sound estuary: deposition of aquatic POC onto the marsh surface, erosion of peat from shoreline edges, and excess NEP, as determined by the mass balance. These amount to 99 ± 21 gC m^{-2} $year^{-1}$ transferred to the marsh, 76 ± 18 gC m^{-2} $year^{-1}$ entering water via marsh edge erosion, and 334 ± 81 gC m^{-2} $year^{-1}$ entering the aquatic system from excess OC produced on the marsh.

For the Duplin (Fig. 5), the 127 gC m^{-2} $year^{-1}$ that mass balance suggests must be exported from each square meter of marsh represents an input of 295 ± 298 gC m^{-2} of water $year^{-1}$.

Estuary

Plum Island

Over a 10-year period, the GPP of the Plum Island aquatic portion of the estuary averaged 297 ± 45 gC m^{-2} $year^{-1}$ (Fig. 4), and the rate of ecosystem respiration was 518 ± 67 gC m^{-2} $year^{-1}$. The negative NEP of −221 ± 22 gC m^{-2} $year^{-1}$ indicates a strongly heterotrophic system dependent on allochthonous OC inputs. The average annual riverine input of POC and DOC over a 10-year period averaged 185 ± 58 gC m^{-2} $year^{-1}$, with >90% being DOC. We assume that all the POC and 10% of the DOC that flocculates upon entering the estuary accumulate in the aquatic system, where they are either metabolized or deposited on the marsh surface. We estimate that only 8 ± 3 g DOC was metabolized per square meter estuary. The mass balance of riverine inputs and internal losses suggests that 148 ± 58 gC m^{-2} $year^{-1}$ passes through the estuary into the ocean. The utilization of oceanic DOC is calculated to be 52 ± 71 gC m^{-2} $year^{-1}$. The combined inputs of autochthonous and allochthonous OC were greatly in excess of the −221 gC m^{-2} $year^{-1}$ net heterotrophy. Therefore, mass balance suggests the export of 324 ± 121 gC m^{-2} $year^{-1}$, of which 148 ± 58 gC m^{-2} $year^{-1}$ is terrestrially derived riverine OC and the

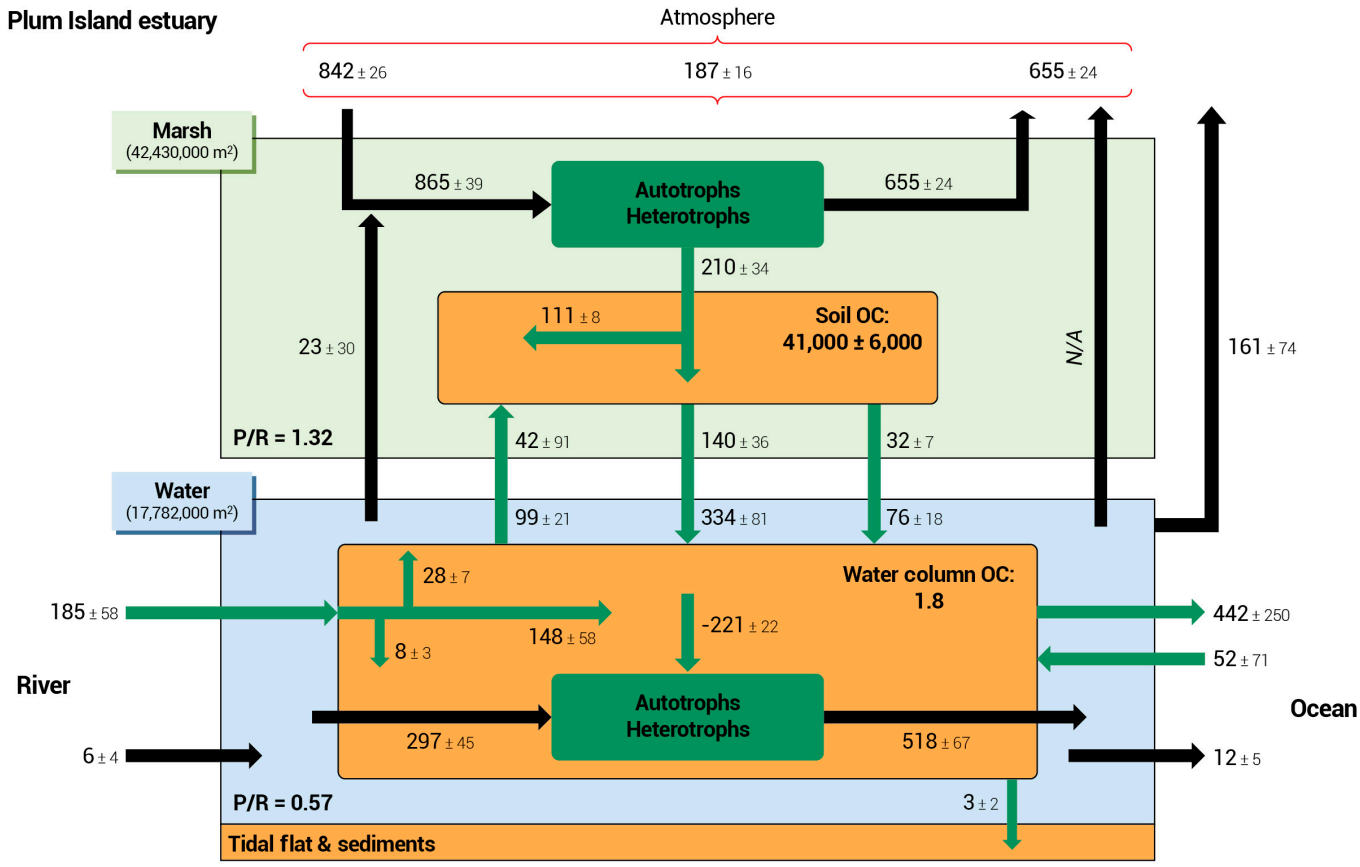

Fig. 4. Carbon budget for the saltmarsh-dominated Plum Island Sound estuary, following the compartment and flux design presented in Fig. 2 and Tables 2 and 3. Units are expressed in gC per unit area of either marsh or water ± 1 SD. Because the marshes are flooded infrequently in this system, we assume that the degassing of CO_2 from water when it is flooding the marsh is extremely minor and we assign a zero (0) value to this unmeasured flux. If this assumption is incorrect, then estimates of *Ra* and NEP on the marsh would be lowered and increased in direct proportion, accordingly.

remainder a combination of marsh and in situ algal production (176 ± 117 gC m^{-2} $year^{-1}$). C isotope biomarkers indicated a fluvial DIC input and export to the ocean of 6.08 ± 4.1 gC m^{-2} $year^{-1}$ and an export of estuarine-derived DIC of 5.59 ± 2.9 gC m^{-2} $year^{-1}$. Because estuarine NEP was 221 ± 22 gC m^{-2} $year^{-1}$ and the marsh takes up 23 ± 73 gC m^{-2} marsh $year^{-1}$ CO_2, degassing is calculated to be 161 ± 74 gC m^{-2} $year^{-1}$ [38].

Duplin

GPP in the water column and benthos of the Duplin River was 407 ± 61 gC m^{-2} $year^{-1}$ in 2014 ([27]; Fig. 5). Respiration was 618 ± 80 gC m^{-2} $year^{-1}$, indicating net heterotrophy of −211 ± 21 gC m^{-2} $year^{-1}$. We estimate that this heterotrophy was met by a combination of riverine (17 ± 6), oceanic (44 ± 64), and marsh exports (295 ± 298 gC m^{-2} $year^{-1}$). The overall net organic C balance suggests that 114 ± 308 gC m^{-2} $year^{-1}$ is exported to the ocean from each square meter of estuarine water body annually. The DIC balance for the system does not include contributions from local rivers because we assume that most is exported directly to the open ocean. CO_2 degassing to the atmosphere was calculated to be 260 ± 39 gC m^{-2} $year^{-1}$, with 72% coming from open water bodies within creekbanks. The remainder is exchanged for water when it is over the marshes at high tide. There is an export of DIC from the Duplin to the ocean at 102 ± 76 gC m^{-2} $year^{-1}$. Notably, we measured a greater export of DIC to the ocean than could be explained by DIC production within the aquatic system, and assumed that the imbalance came from underestimated marsh drainage. We measured an export of DIC from the marsh of 15 gC m^{-2} $year^{-1}$; however, mass balance showed it to be 65 ± 36 gC m^{-2} $year^{-1}$. We likely underestimated DIC drainage over a 24-h period, because we previously [27] focused on the daytime when there was undoubtedly DIC uptake by the marsh algal community.

Discussion

In this study, NEP was directly measured as the net balance between the whole-system measures of GPP and R. Most studies estimate NEP as the balance between the sum of the component levels of GPP and R, which are typically measured at a small spatial scale (e.g., plots, chambers, and bottles). However, NEP was measured directly as the daily balance between O_2 or CO_2 production/consumption for large areas that directly encompass the spatial variability in plant, microbial, and animal communities. Aquatic metabolism was measured along the 12.5- and 24-km continuums of the Duplin and Plum Island estuaries, respectively. Marsh metabolism was measured using EC flux towers, which have ~1-km^2 creekshed footprints covering a broad range of spatial variability in plant, microbial, and animal communities. NEP is a fundamental metric for ecosystem performance. It defines the upper limit to which OC can either be stored or exported to adjacent ecosystems when

Table 3. Annual C fluxes for the Plum Island and Duplin River systems. Italicized "m" refer to fluxes to or from the marsh, whereas italicized "a" refers to fluxes in estuarine waters. NA indicates that fluxes have not been quantified or included in the budgets reported here.

		Duplin estuary		Plum Island estuary	
C flux pathway	Abbreviation	Flux (gC m^{-2} $year^{-1}$)	SD	Flux (gC m^{-2} $year^{-1}$)	SD
Marsh system		m^{-2} marsh		m^{-2} marsh	
EC tower CO_2 uptake	GPP*ft*	768	74	842	26
EC tower CO_2 release	R*ft*	594	95	655	24
EC tower NEE	NEE*ft*	–159	52	–187	16
Gross primary production	GPP*m*	768	74	865	39
Respiration	R*m*	627	102	655	24
Net ecosystem production	NEP*m*	141	126	210	34
Burial	BUR*m*	27	14	111	8
Deposition	DEPO*m*	12	17	42	9
OC export	OCEXP*m*	127	128	140	36
Edge erosion	EROS*m*	0.02	0.07	32	7
Marsh-water DIC import or export	DIC*imp* DIC*exp*	65	36	–23	30
CO_2 degas of floodwater	FLDCO$_2$*out*	32	5	NA	-
Aquatic system		m^{-2} water		m^{-2} water	
Gross primary production	GPP*a*	407	61	297	45
Respiration	R*a*	618	80	518	67
Net ecosystem production	NEP*a*	–211	21	–221	22
River OC load	OC load	NA	-	185	58
River POC and flocculation	Flocculation	NA	-	28	7
River DOC consumption	RVR*use*	17	6	8	3
River OC export to ocean	RVR*exp*	NA	-	148	58
River IC load	DIC load	NA	-	6	4
Burial	BUR*a*	3	2	3	0.2
Deposition onto marsh	DEPO*m*	28	41	99	21
OC export from marsh	OCEXP*m*	295	298	334	81
Edge erosion	EROS*m*	0.05	0.16	76	18
Ocean DOC consumption	OceanDOC*use*	44	64	52	71
Marsh-water DIC import or export	DIC*exp* DIC*imp*	151	83	–54	71
CO_2 floodwater degas	FLDCO$_2$*out*	74	11	NA	-
CO_2 degas over creek	CO$_2$*out*	186	28	161	74
DIC export to ocean	OceanDIC*exp*	102	76	12	5
OC export to ocean	OceanOC*exp*	114	308	176	117

positive and the extent to which stored capital (OC) is consumed or brought in from adjacent systems when negative.

Role and directionality of DIC flux between marsh and water

We assessed the vertical (exchange with the atmosphere) and horizontal (lateral exchange) inorganic carbon fluxes in both systems to accurately measure marsh and estuarine metabolism. The lateral fluxes of DIC in the Duplin and Plum Island tidal marshes influenced the GPP, R, and NEP calculations. The export of DIC from the marsh to the estuary represents the respiration of fixed C in the marsh system not captured by the EC tower, and must be considered in estimates of marsh respiration (Eq. 1). Conversely, the import of DIC to the marsh system indicates a higher GPP than that captured by tower measurements and must be considered in the estimates of marsh GPP (Eq. 2). The net export of OC from the marsh to the water column would not affect the NEP attributable to the marsh, although it would alter the C balance of the marsh system. For the Duplin salt marshes, we observed a loss of CO_2 to the atmosphere from tidal waters during marsh flooding and the export of DIC when the water receded into the tidal creeks (Fig. 5). These fluxes increased marsh R and decreased marsh NEP relative to the flux tower measurements alone. For the Plum Island marshes (Fig. 4), our measurements suggest a net retention of DIC (Fig. 3), although the net exchange

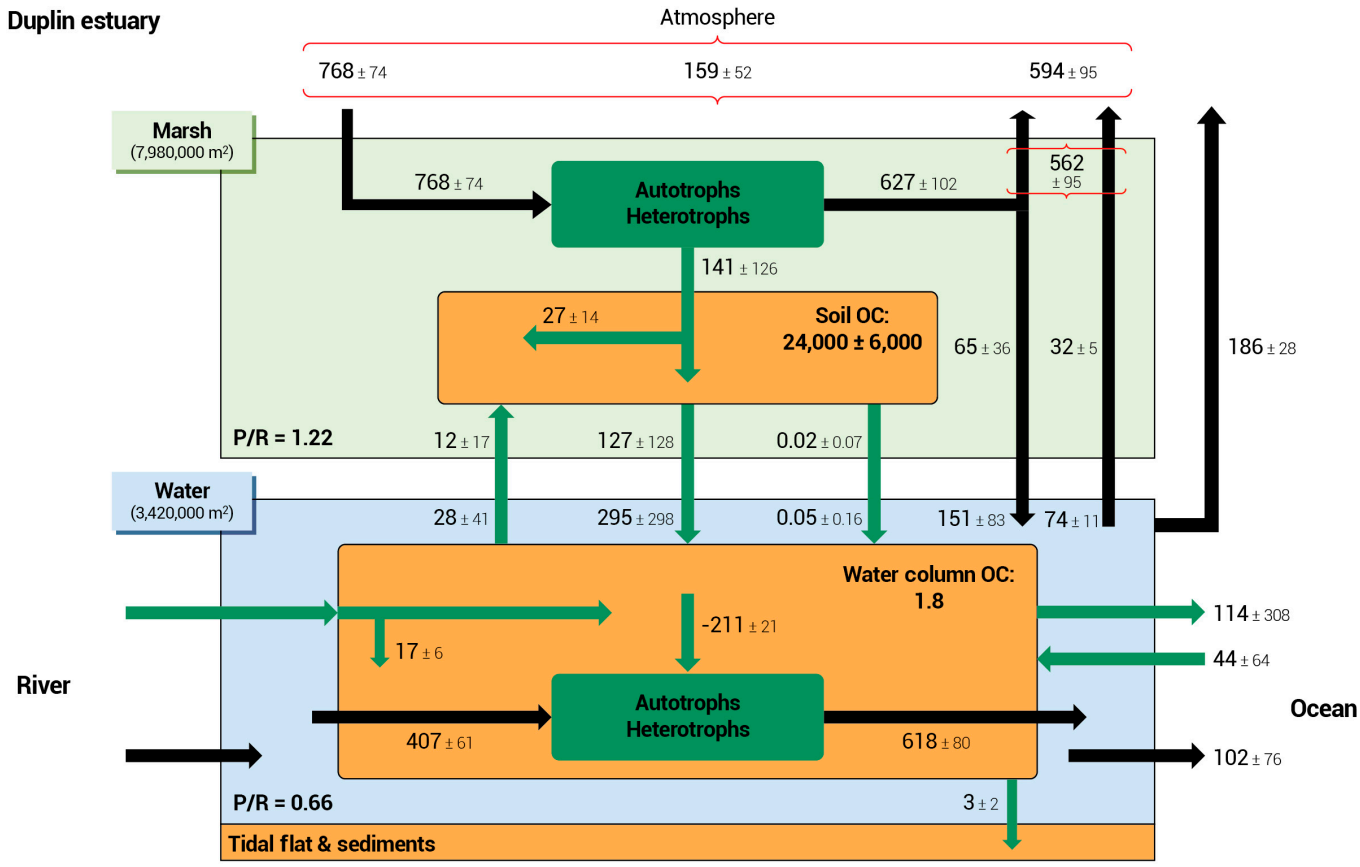

Fig. 5. Carbon budget for the salt marshes and adjacent tidal waters of the Duplin River estuary. Design follows Figs. 2 and 4 and Tables 2 and 3. Riverine inputs of organic and inorganic carbon are not quantified because they do not pass through the Duplin estuary during flow to the ocean. The utilization of riverine DOC is calculated based on lability, residence time, and fraction of freshwater within the estuary. Units are expressed in gC per unit area of either marsh or water ± 1 SD.

measurements were not significantly different from zero. Therefore, the EC flux tower measurements of the NEE were underestimated. Thus, the GPP and NEP were greater than those measured by the tower. Marsh ponds and pannes have been increasing in areal extent over the past 50 years in the Plum Island system, presumably because of declining drainage networks, sea-level rise, and sediment starvation [23,24,39]. These areas have high rates of metabolism, primary production: ecosystem respiration (P:R) ratios of up to 3:1, and have limited inorganic carbon (51) because of a combination of submerged aquatic vegetation, benthic microalgae, and autotrophic bacteria. Presumably, DIC imports to the marsh partially satisfy the carbon debt associated with the high levels of pond autotrophy.

The lack of DIC export from marshes to the water column on Plum Island is contrary to the literature, which shows the export of DIC from salt marshes to estuarine systems (for example 43). Wang et al. [27] found 15 gC m^{-2} marsh $year^{-1}$ of DIC export in Duplin marshes, and other published estimates range from 150 to 250 gC m^{-2} $year^{-1}$ [40–42]. In contrast, Wang et al. [43] and Tamborski et al. [44] reported large (>4 gC m^{-2} $year^{-1}$) surface and subsurface exports of DIC from marshes in Waquoit Bay, MA, to coastal waters, which may indicate deep peat decomposition and possible marsh collapse, subsidence, and permanent inundation. Wang and Cai [40] suggested that most of the DIC exported from the Duplin River to the ocean originated from DIC drainage from marshes to tidal waters. Our results for the Duplin confirm the importance of marsh inputs, as we found that 42% came from marshes (Fig. 5; 151 gC m^{-2} DIC exported from marsh to estuary and 211 gC m^{-2} DIC produced via net heterotrophy in the estuary). Our results for the Duplin also agree with Wang and Cai's [40] estimate of DIC export to the ocean (102 versus 109 gC m^{-2} $year^{-1}$). We found that lateral and vertical exchanges of DIC and CO_2 with tidal waters greatly biased estimates of marsh metabolism based solely on NEE and that measures of NEE must be corrected to determine the NEP of the marsh system. Although DIC export from marshes was not observed in the Plum Island estuary, previous studies have reported an accumulation of DIC within the estuary, evasion of CO_2 from open waters, and its export to the coastal ocean [38]. C isotopes indicated that the DIC source originated from the watershed and within the estuary itself. Because the marsh was not a source of DIC in the estuary, we conclude that DIC export resulted from the decomposition of OC exported from the marsh and decomposed within the water column and benthos. The highly heterotrophic nature of these estuarine subsystems agrees with the general conclusion of Smith and Hollibaugh [45] that bays and estuaries are among the most heterotrophic systems in the biosphere. Moreover, Odum [46] concluded that salt marshes donate an excess of organic matter to adjacent tidal waters, thereby contributing to secondary production in excess of that supported directly by allochthonous production.

Marsh productivity comparison

The Plum Island and Duplin marshes are strongly autotrophic, with GPP levels approximately 30% higher than respiration (Figs. 4 and 5 and Table 3). Having nearly the same levels of GPP at the more northerly Plum Island was unexpected, as previous studies have found a consistent decline in marsh production with increasing latitude along the east coast of North America [47,48]. At Plum Island, there is a single growth period from May to September, whereas in the Duplin, warmer temperatures and a lack of ice promote year-round growth. Turner [47] attributed the geographic gradient to parallel patterns of solar energy inputs; others have suggested the significant influence of tidal amplitude [49]. Although the tidal amplitude was higher at Plum Island (Table 1), the marshes were markedly higher in the tidal frame and therefore flooded only during spring tides. Nearly the same or only slightly higher levels of GPP in the Plum Island marshes may indicate that the dominant *S. patens* is inherently more productive than *S. alterniflora*, which dominates in the Duplin marshes. In coastal Louisiana, Hopkinson et al. [50] found that *S. patens* was the most productive wetland species among the 6 species studied, including *S. alterniflora*. The high levels of GPP on Plum Island may also reflect the contribution of marsh ponds, which can be highly autotrophic [51]. The Duplin marshes have no ponds, and bare areas devoid of marsh grass become salt flats and pannes, with minimal evidence of benthic primary producers.

Fate of marsh autotrophy

There are large amounts of excess OC produced (NEP) in the Plum Island (210 ± 34 gC m^{-2} $year^{-1}$) and Duplin (141 ± 126 gC m^{-2} $year^{-1}$) marsh systems, with fates that differ markedly between the 2 systems (Figs. 4 and 5). In the Plum Island marshes, 53% of this net production is buried and stored in the sediments, with 47% likely exported to adjacent tidal waters. However, in the Duplin marshes, only 19% of net production is stored in sediments, and 81% of the carbon is likely exported. On Plum Island, the accumulation of soil OC contributes substantially to marsh elevation gain [24], whereas in the Duplin, OC accumulation is negligible and not a major component of marsh elevation gain [21]. Najjar et al. [9] also found that a relatively low percentage of marsh NEP was buried in tidal wetlands of the US east coast and that the percentage buried decreased to the south. Ouyang and Lee [52] showed that burial rates decreased at lower latitudes as well. Several factors might explain these patterns and decoupling from NEP, which we illustrate in Fig. 6.

In a recent synthesis of factors controlling sediment organic matter decomposition or accumulation, Spivak et al. [53] dispensed traditional models that suggest that OC is preserved because of generally recalcitrant macromolecules (e.g., lignin) in an anoxic environment lacking energetically favorable electron acceptors. Rather, several factors, including mineral protection, redox zonation, water content and movement, and plant–microbe interactions, were cited as likely significant controls on OC preservation that require better integration into mechanistic decomposition models [53]. Temperature is often identified as a key factor controlling geographic patterns, and the higher net burial of OC in cooler Plum Island soils suggests that temperature controls carbon burial in this study (Fig. 6). However, other studies have shown abundant OC burial and accumulation in subtropical and tropical environments (such as Okefenokee Swamp in nearby coastal GA and mangroves in Belize; [54]). The mineral content of sediments is considered a predictor of low rates of OC lability [55]; however, the Duplin sediments with much greater mineral content [25] have greater levels of belowground OC decomposition and less burial. Plum Island and Duplin marshes share characteristics, such as minimal pore water movement, reducing conditions in the soil, and similar soil lignin content. Many models of marsh response to SLR predict that accumulation and elevation gain are directly related to plant lignin, the production of which varies in direct proportion to plant production. According to these models, as long as the flooding depth is below the optimum depth for plant production, marshes will maintain their elevation [56–58]. Our results agree with those of Spivak et al. [53], who concluded that the link between rising sea levels, higher plant production, and greater lignin accumulation in soils that lead to marsh accretion is less straightforward than these models suggest; we observed no relationship between levels of GPP and relative OC burial in our comparison of the Plum Island and Duplin systems.

The Duplin and Plum Island marshes also differed in the extent to which excess OC from NEP was exported to tidal waters, with 81% exported in the Duplin marshes compared with 47% in Plum Island (Figs. 4 and 5). The GPP was relatively similar in these 2 systems, suggesting that differences in exports were not directly related to production levels. If export is related to tidal energy, marsh flooding, and drainage, we would expect higher C export from the Plum Island marshes, as the tidal range at Plum Island is higher than that in the Duplin (Table 1 and Fig. 6). However, the marsh platform is substantially higher in the tidal window at Plum Island than in the Duplin, and consequently, floods and drains only occur fortnightly during the highest spring tides (Table 1). In addition to marsh flooding frequency, rainfall is another factor that might contribute to greater exports in the Duplin marshes. Substantial erosion of marsh surface sediments and organic matter can occur during intense thunderstorm rainfall and low tides [59–61]. Although similar storms are likely to occur on Plum Island, the extremely dense nature of the *S. patens* plant canopy likely reduces the erosional force of raindrops (Fig. 6).

In the Duplin River marshes, standing dead stems of *S. alterniflora* undergo substantial fragmentation due to grazing by the marsh periwinkle *Littoraria irrorate* [62], which are lacking in the Plum Island marshes. The breakdown of macrophytes into small POC may promote particle exchange in tidal waters. The burrowing activity of marsh fiddler crabs (*Uca sp.*), which is common only in the Duplin River marshes, also promotes the oxidation of soils, belowground organic matter decomposition, and exchange of marsh porewaters with tidal creeks [63]. The relative lack of grazing, plant breakdown, and burrowing in the Plum Island marshes likely allowed a dense marsh canopy to develop over several years, which likely retarded the decomposition and exchange of OC with tidal waters (Fig. 6).

A greater amount of NEP is buried at Plum Island, resulting in less C being available for export from the marsh than from the Duplin. However, this creates a circular argument: Does higher burial require less export, or does less export lead to greater burial? We lack data to partition P, R, and NEP between the aboveground and belowground zones in the marsh; however, most organic matter stored in sediments is root and rhizome material [64]. Belowground organic matter can only be exported as porewater drainage of DIC or DOC following decomposition, except at the creekbank where erosion mobilizes

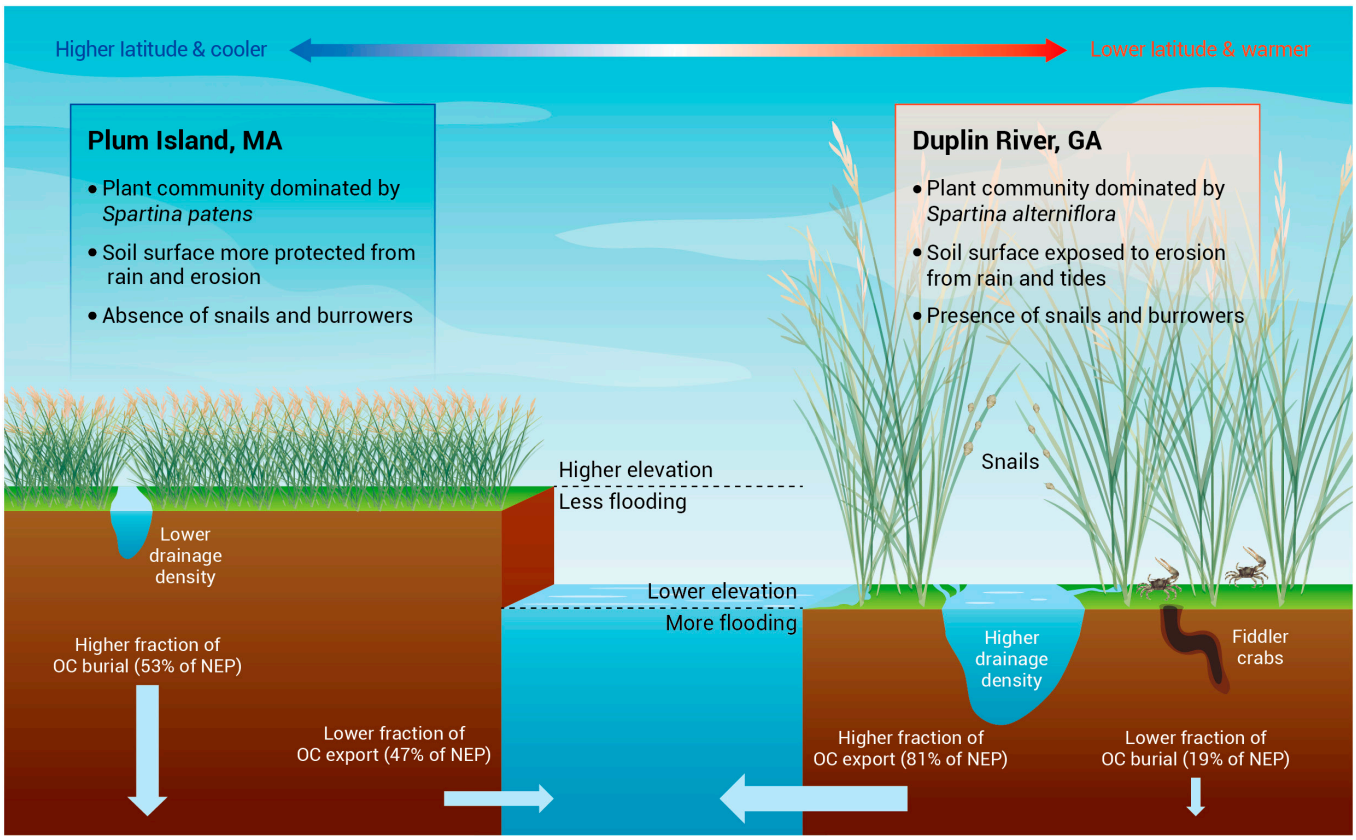

Fig. 6. Conceptual diagram of major factors controlling differences in the fate of marsh autotrophy between the Plum Island and Duplin River tidal marshes.

belowground particulates. As porewater drainage is mostly confined to the creekbank zone (typically up to 20 m inland from the creek edge), the differences between the Duplin and Plum Island may be related to drainage density ([65]; Fig. 6). Unfortunately, the drainage densities of the 2 systems were not compared. Drainage densities have been decreasing on Plum Island over the past century, as mosquito drainage ditches created during colonial times and during the economic depression of the 1930s have not been actively maintained and, in some cases, have been filled and recolonized by marsh plants. A combination of slower belowground decomposition rates and lower drainage densities throughout the Plum Island system may lead to less OC export from the marsh, whereas greater fragmentation of aboveground plant tissues by snails, more intense rains, and higher drainage densities result in higher levels of OC export in the Duplin system. A variable level of OC decomposition is the most likely explanation for the greater export in the Duplin marshes; however, we lack a complete understanding of why decomposition differs between sites.

Aquatic C budget

The GPP of tidal waters is higher in the Duplin River than in Plum Island Sound (407 ± 61 versus 297 ± 45 gC m^{-2} $year^{-1}$); however, tidal water respiration is higher (618 ± 80 versus 518 ± 67 gC m^{-2} $year^{-1}$, respectively; Figs. 4 and 5 and Table 3). Consequently, both systems are strongly heterotrophic with P:R ratios of 0.66 and 0.57, respectively, with similar NEP rates (−211 ± 21 and −221 ± 22 gC m^{-2} $year^{-1}$, respectively). Sustaining such heterotrophy in systems lacking abundant organic reserves (1.8 gC m^{-2} $year^{-1}$ standing stock of suspended OC in each system) requires the input of OC from adjacent systems. Aquatic GPP was sufficient to fuel only 66% and 57% of aquatic respiration in the Duplin and Plum Island systems, respectively. This conclusion is in agreement with previous budgets for the Duplin [66,67]. Estimates of water column P and R for the Duplin are higher than those previously reported (326 and 528 gC m^{-2} $year^{-1}$, respectively; [67]), which may reflect the difficulties of estimating metabolism by scaling up discrete measures in bottles and chambers. Hopkinson and Smith [68] reported that whole-system measures of respiration were almost always higher than chamber/bottle measures. Greater increases in respiration than in production indicated that the system was more heterotrophic than previously estimated. We are confident that DIC export from the Duplin system to the ocean is supported by the decomposition of wetland-derived OC in heterotrophic tidal waters and DIC export directly from tidal marshes. DIC was not exported from the Plum Island marshes. It is unclear why carbon is exported from the Duplin marshes as both DIC and OC and only as DOC from the Plum Island marshes.

Sources of allochthonous OC

There are 3 potential sources of OC fueling the heterotrophic aquatic systems on Plum Island and the Duplin: terrestrial organic matter entering via rivers; oceanic DOC entering through tidal mixing; and export of organic matter from the adjacent salt marshes through pore water drainage, edge erosion, and inputs from the marsh surface during tidal exchange. Watershed groundwater inputs of terrestrial organic matter are trivial in the Duplin [69] and Plum Island estuaries. The riverine input of

terrestrial OC in the Plum Island system is 185 ± 58 gC m^{-2} $year^{-1}$ (Fig. 4), although the contribution of this OC to metabolism is minor. We assume that all POC and 10% of the DOC flocculates and is decomposed in the system; however, this only amounts to 28 ± 7 gC m^{-2} $year^{-1}$ of potential aquatic respiration (some of this POC is deposited on the marsh surface, which would contribute to total marsh respiration; [24]). DOC is the largest component of riverine OC inputs to Plum Island; however, because of a relatively low lability (<20% per month; [70]) and relatively short transit times through the estuary (days to several weeks; [71]), only 8 ± 3 gC m^{-2} $year^{-1}$ is decomposed. Thus, terrestrial OC can sustain only 7% of aquatic respiration or 16% of aquatic heterotrophy. For the Duplin River system, river water does not enter the system directly, but rather via exchange with the adjacent coastal ocean, into which freshwater inputs have been mixed (Fig. 5). Based on the average salinity in the Duplin, the concentration of riverine DOC above the head of tides in the system, the DOC lability, and measures of freshwater residence time (5.5 d), we estimate that the utilization of terrestrial OC is only 17 ± 6 gC m^{-2} $year^{-1}$ (Fig. 5). Terrestrially derived organic matter thus supports only 3% of aquatic respiration and 8% of aquatic heterotrophy in the Duplin system.

Utilization of oceanic inputs of OC is greater than utilization of terrestrial DOC inputs in both systems (44 ± 64 and 52 ± 71 gC m^{-2} $year^{-1}$ in the Duplin and Plum Island systems, respectively; Figs. 4 and 5). Nevertheless, these inputs of organic matter are minor relative to the overall level of heterotrophy, sustaining 7% of respiration and 21% of NEP for the Duplin, and 10% of respiration and 24% of NEP for Plum Island. The relative importance of oceanic DOC on Plum Island was similar to that estimated by Vallino et al. [72] during summer.

The major source of allochthonous OC in the aquatic systems of both estuaries was the adjacent salt marsh (Figs. 4 and 5). The mass balance of marsh OC indicated that 140 gC m^{-2} $year^{-1}$ was exported to the tidal waters on Plum Island and 127 gC m^{-2} $year^{-1}$ from the Duplin marshes. Along with edge erosion in both systems, the total input of marsh OC relative to the areal extent of tidal waters was 410 and 295 gC m^{-2} of water surface $year^{-1}$. Thus, the input of OC from Plum Island marshes is almost twice that required to sustain aquatic net heterotrophy (−221 ± 22 gC m^{-2} $year^{-1}$) and greatly exceeds terrigenous inputs. For the Duplin River, marsh inputs exceeded aquatic NEP (−211 gC m^{-2} $year^{-1}$) by approximately 40%. Even if the maximum estimated inputs from river and ocean are assumed (i.e., the average plus the standard deviation), only 62% of aquatic system heterotrophy can be supported by these inputs, indicating that marsh OC inputs must provide at least 38% of the observed aquatic heterotrophy in the Duplin.

Several whole-system analyses of estuarine metabolism have established the importance of allochthonous and autochthonous sources of organic matter, similar to what we present here. This contrasts with small mesotrophic lake systems, which, because of their subsidence by terrestrial allochthonous inputs, can be net sinks for C in their sediments, net sources of CO_2 to the atmosphere, and net sources of OC to downstream systems [73]. Smith and Hollibaugh [45] conducted a whole-system metabolic analysis of the Tomales Bay estuary and determined that the heterotrophic bay was dependent on allochthonous inputs from oceanic exchange and terrestrial runoff. Lacking tidal marshes, as in the systems studied here, the relative importance of terrestrial and oceanic sources is much greater in Tomales Bay. Terrigenous OC loading accounted for approximately half of the observed mean heterotrophy, whereas marine DOC inputs during upwelling events accounted for the other half. POC was the most important terrestrial component, and Smith and Hollibaugh [45] concluded that the turnover time of this POC was in the order of decades, supporting our assumption for the Plum Island system that all terrigenous POC is consumed within the estuary because it settles out. The utilization of terrigenous DOC was considerably lower than that of oceanic DOC in Tomales Bay, indicating a nearly conservative mixing behavior. In the Hudson River tidal freshwater estuary, the aquatic system is markedly heterotrophic, with a P:R of 0.57 [74], similar to that observed in this study. Primary production by phytoplankton and fringing marshes can provide a maximum of 56% of the heterotrophic respiration, implying that terrestrial allochthonous OC inputs provide at least 34% of the OC required to support heterotrophy in the freshwater tidal region of the Hudson River [74]. Chesapeake Bay is another system driven by allochthonous inputs from the watershed; however, inputs of inorganic (sediment and nutrients) and organic matter in the large estuarine system result in a heterotrophic upper bay owing to low primary production (too turbid) and decomposition of labile organic matter [75]. The lower portion of the Chesapeake Bay is autotrophic because its primary production is supported by inorganic nutrient inputs. Overall, the Chesapeake Bay system exports OC to the ocean, reflecting whole-system autotrophy.

Linkages with the coastal ocean

In this study, we quantified the utilization of oceanic DOC in the Plum Island and Duplin estuaries. Despite the offshore input of OC, our mass balance shows a net export of OC from estuaries to the ocean, supported by other allochthonous and autochthonous sources of OC (Figs. 4 and 5). For the Plum Island estuary, of the 185 ± 58 gC m^{-2} $year^{-1}$ terrigenous inputs, only 36 ± 8 gC m^{-2} $year^{-1}$ is consumed internally, indicating that 148 ± 58 gC m^{-2} $year^{-1}$ passes through the ocean. The mass balance indicates that an additional 176 ± 117 gC m^{-2} $year^{-1}$ is exported from the marsh/aquatic system to the coastal ocean. At this point, we cannot determine how much of this export was of marsh or aquatic origin. The Plum Island estuary also exports small quantities of DIC to the coastal ocean from fluvial (6.1 ± 4.1) and marsh/estuarine origin (5.59 ± 2.9 g DIC m^{-2} $year^{-1}$).

The Duplin River estuary exports organic and inorganic forms of C to the ocean. The net export of DIC to the ocean (102 ± 76 gC m^{-2} $year^{-1}$) includes a large contribution (42%) from the tidal marshes (65 gC m^{-2} marsh $year^{-1}$ or 151 gC m^{-2} water $year^{-1}$). These results agree with the conclusions of Wang and Cai [40] that DIC is exported from estuaries and has a large marsh contribution. According to mass balance calculations, the Duplin estuary exports 114 ± 308 gC m^{-2} $year^{-1}$ of autochthonous organic matter to the ocean. This quantity does not include terrigenous OC, which may be mixed with estuarine water without utilization. The exported organic matter represents an undetermined mix of marsh- and estuarine-derived materials.

A pattern of net export of autochthonous organic matter from estuaries to oceans is common in the east and Gulf of Mexico coasts of the United States [67,75], particularly for salt marsh-dominated estuaries and drowned river valley estuaries that experience high inorganic N loading. Drowned river valley

estuaries (e.g., Narragansett Bay and Chesapeake Bay) export autochthonous OC to the coastal ocean; however, unlike salt marsh-dominated systems (e.g., Sippewissett, Flax Pond, North Inlet, and Barataria Bay), algae are the dominant source of exported organic matter. For most river-dominated systems with significant terrestrial sources of OC, most terrestrial OC passes through unmetabolized [74,75]. Ittekkot and Laane [76] estimated that on average globally, 35% of terrestrial carbon is metabolized during estuarine transport.

Comparison to regional- and continental-scale coastal C budgets

In the past 10 years, several organic and inorganic C budgets have been developed for coupled watersheds, tidal wetlands, estuaries, and shelf systems at regional and continental scales [8–10]. Such C budget syntheses enable us to better define the contribution of coastal systems to global C budgets, illustrate the processing of C inputs from terrestrial systems and the combined export of C from coastal systems to the open ocean, and will lead us to a better understanding of environmental changes, such as coastal hypoxia and tidal wetland loss caused by human activities. These synthetic budgets were not created from detailed measures of all the major fluxes in all estuaries in specific regions, as we did for the Duplin and Plum Island systems here. Rather, fluxes were determined in these syntheses from a combination of models relating fluxes to more easily observed measures (e.g., using the ratio of dissolved inorganic N relative to total OC loading from rivers entering estuaries to estimate estuarine aquatic NEP; [8]) and from the literature at unspecific locations across regions, such as dissolved inorganic flux from tidal wetlands to adjacent estuarine waters [9] and OC burial in marshes [9,10,52].

Comprehensive C budgets for tidal wetland-dominated estuarine systems, such as those presented here for the Duplin and Plum Island systems, are rare [77] but critical to fully understand individual flux pathways. Our comprehensive budget enabled us to confirm a portion of the export of OC from tidal wetlands, which is often calculated using the mass balance. The Plum Island and Duplin River C budgets generally agree with many of the broad conclusions reached in these 3 regional- and continental-scale C budgets [8–10]. For instance, there is agreement that tidal wetlands are autotrophic, estuarine waters are heterotrophic, tidal wetlands are a net sink for atmospheric CO_2 with OC burial decreasing from north to south, and marshes are a major source of allochthonous organic C to estuaries. There is further agreement that the burial of OC in estuarine sediments is not a major flux in overall coastal C cycling and that some riverine OC is processed within estuaries; however, for the most part, this OC is exported to the continental shelf.

With closer inspection of the regional scale C budgets, differences emerge between the "average" estuary of the US east coast and the highly salt marsh-dominated estuaries of the Duplin and Plum Island estuaries. The parameters used in formulating the elegant models in Herrmann et al. [8], which serve as the foundation for much of the Windham-Myers et al. [10] and Najjar et al. [9] budgets, best describe open water and drowned river valley estuaries (for example, MERL mesocosms at the University of Rhode Island, Narragansett Bay, and Chesapeake Bay). For example, the OC loading from tidal wetlands and terrestrial watersheds was determined using the SPARROW model, and the estuarine NEP was determined as a function of the DIN:TOC (dissolved inorganic nitrogen:total organic carbon) ratio of the watershed loading. The ratio of saline tidal wetland area to estuarine area averages 0.23:1 for the Atlantic coast, approaches 0.5:1 in the South Atlantic Bight (SAB; [10]), and is approximately 2.4 for the salt marsh-dominated Duplin and Plum Island systems (Figs. 4 and 5). The residence time of estuarine water in Herrmann et al. [8] was 15 and 5 months for the Gulf of Maine (GOM) and SAB, whereas it was between 0.1 and 0.2 months in Plum Island and the Duplin. The DIN:TOC ratio averages 0.03 and 0.015 for GOM and SAB, respectively, and <0.00003 for Plum Island. Variations in parameterization affect the predicted C dynamics. These differences warrant highlighting because these salt marsh-dominated systems (as well as other wetland- and submerged aquatic vegetation-dominated systems) are major blue carbon hotspots, and scaling from regional assessments to global blue carbon budgets may be misleading.

Unsurprisingly, some aspects of the C dynamics of the highly salt marsh-dominated Duplin and Plum Island estuaries differ substantially from those of an average estuary of the SAB, Mid-Atlantic Bight, and GOM regions of the US east coast included in Herrmann et al. [8]. Herrmann et al. [8] reported that tidal wetlands contributed 15% and 40% of the total allochthonous OC input to the GOM and SAB estuaries, respectively, whereas we found them to contribute 70% and 83% to Plum Island and the Duplin, respectively. Herrmann et al. [8] reported burial in estuarine sediments at 6% and 2% of total OC inputs for the GOM and SAB, respectively, whereas we found it to be 0.4% and 0.3% for the Duplin and Plum Island, respectively. Herrmann et al. [8] found that estuarine NEP averaged −48 and −85 gC m^{-2} $year^{-1}$ for the GOM and SAB, respectively; however, we found it to be −221 and −211 for the Duplin and Plum Island, respectively (Figs. 4 and 5). Indeed, tidal wetland loading, burial, and NEP for the Plum Island and Duplin systems were outside the 95% confidence limit of Herrmann et al. [8]. To better model the NEP relation in wetland-dominated systems in an approach similar to that of Herrmann et al. [8], perhaps it should be modified to include a measure of residence time, a parameter important in predicting longitudinal and overall patterns of estuarine metabolism [78] and processing N import from rivers [79].

Blue carbon budget for the Duplin and Plum Island estuaries

Our consideration of the coastal blue carbon sequestration of atmospheric CO_2 has evolved since the foundational blue carbon inventories of Chmura et al. [2], Nellemann et al. [3], Laffoley and Grimsditch [80], and Mcleod et al. [4]. In addition to OC burial in sediments, recent budgets have accounted for the burial of allochthonous organic material [31]), changes in tidal wetland areas [15,81], CH_4 and N_2O emissions to the atmosphere [32,82,83], and DIC and OC export to the coastal ocean [9,10,30,84]. Our detailed C budgeting of the Plum Island and Duplin systems enables us to balance previous estimates of burial with allochthonous OC inputs and erosion and constrain estimates of the other blue carbon fluxes. The evolution of thinking about blue carbon has shifted our focus beyond the tidal wetlands themselves, realizing that they are one component of the larger land–sea interface system, the region on Earth that transforms, stores, and transports OC between the terrestrial and ocean realms [7,85].

The burial of OC (Fig. 7) must be corrected for allochthonous inputs to be classified as blue carbon [86]. Deposition of OC onto the marsh platform at flood tide at Plum Island

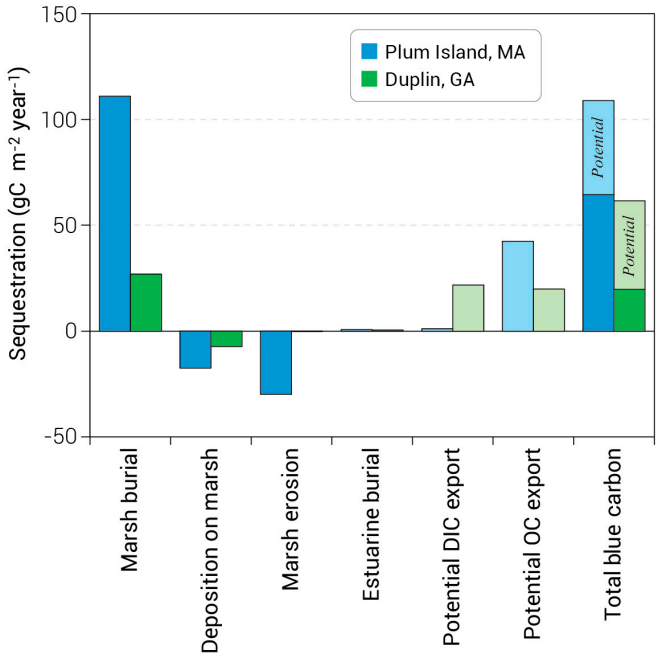

Fig. 7. Detailed assessment of CO_2 sequestration pathways and magnitudes for the Plum Island and Duplin estuaries in addition to the commonly used burial metric. OC and DIC exported to the ocean are categorized as potential blue carbon sinks as the extent of OC decomposition and DIC degassing while on the continental shelf has not yet been rigorously quantified. The total blue carbon column represents the sum of directly estimated and potential sequestration values. Units: gC m^{-2} marsh $year^{-1}$. The potentially important counteractive fluxes of radiatively active methane and nitrogenous gas fluxes are not quantified.

amounted to 42 gC m^{-2} marsh $year^{-1}$, whereas it was 12 gC m^{-2} marsh $year^{-1}$ in the Duplin, but only 17.4 and 7.3 gC m^{-2} $year^{-1}$ of this was allochthonous (estuarine primary production). At both sites, a large fraction of the OC deposited on the marsh surface originated as marsh OC exported to tidal waters or eroded from the marsh edges (Fig. 7), which would thus be included in accounting for blue carbon. Although small, the inputs of allochthonous reduce the sequestration value of OC burial by 16% to 27%. We are unaware of similar calculations for other salt marshes, but for seagrass blue carbon systems, it can amount to 50% of total OC burial [31].

Another correction that should be considered in traditional blue carbon budgets based solely on burial is the areal loss (or gain) of the ecosystem area through direct and indirect human actions, such as clearing and filling for land-use change, restoration, logging of mangroves, and erosion from SLR [3,4] or from natural marsh erosion and progradation processes. The observed marsh edge erosion in the Plum Island system is directly related to increasing estuarine sediment deficits coupled with SLR [14,24], amounting to 29.8 gC m^{-2} marsh $year^{-1}$ in the Plum Island estuary (Fig. 7). The erosion of the salt marshes in the Duplin River marshes was trivial. The transgression of salt marshes into the uplands as SLRs can counteract erosion [15,81,87]; however, it is trivial in both systems studied here [37].

Marsh-derived OC burial in estuarine sediments, along with OC and DIC export to the ocean, are potentially additional forms of blue carbon sequestration [30], depending on the duration of sequestration. We labeled these potential fluxes because we lacked sufficient information to calculate the magnitude to which DIC was lost as CO_2 to the atmosphere prior to leaving either the GOM (Plum Island) or the SAB (Duplin). The inner shelf waters (0 to 20 km) of both systems are seasonally supersaturated with respect to CO_2 and on annual bases net emitters of CO_2 [88,89]. However, based on the magnitude of DIC inputs relative to DIC standing stocks of these systems (inputs = 1.5% of stock in SAB), the magnitude of net CO_2 degassing (5.4% of pool degassed per year), and the residence times of water on the inner or total shelves (5 to 80 d), we estimated that <6% of marsh DIC inputs were degassed [88,90,91]. For those not lost as CO_2 once in continental shelf waters, the DIC mixes with oceanic water with a long residence time [6,7,92] and is thus removed from the active carbon cycle. Similarly, marsh-derived OC is exported to the ocean, where it escapes decomposition or is decomposed into DIC. Likewise, it is largely sequestered in the long term and contributes to blue carbon. DOC decomposition rate coefficients (k) between approximately 0.0023 and 0.004 d^{-1} [29,90] and residence times of 5 to 80 d resulted in a small portion of DOC being converted to DIC (between 1.2% and 27% would be converted to DIC depending on residence time and k). This input was smaller than the direct DIC input from marshes. In the Duplin and Plum Island systems, the salt marsh-derived OC buried in estuarine sediments amounts to 0.5 and 0.7 gC, respectively. The salt marsh-derived OC that further escapes into the ocean is greater in magnitude (20 gC and 43 gC m^{-2} marsh $year^{-1}$ for the Duplin and Plum Island systems, respectively). This is a fraction of the total OC exported to the ocean from both systems, owing to the export of terrestrial- and estuarine-derived OC (Figs. 4 and 5). DIC is exported to the ocean in both systems, although the marsh is only a partial sink for DIC on Plum Island. For Plum Island, approximately 6.1 gC m^{-2} $year^{-1}$ of DIC enters from the Ipswich and Parker Rivers and exits to the ocean [38], and an additional 5.59 gC m^{-2} $year^{-1}$ is produced internally to the estuary and exits to the ocean. The marsh-derived portion of the 5.59 gC was blue carbon. We calculate this portion of the total DIC export as the percentage of estuarine respiration (518 gC m^{-2} $year^{-1}$) supported by marsh erosion and marsh OC export [(203+46)/518) * 5.59 = 3 gC m^{-2} water $year^{-1}$ or 1.13 gC-DIC m^{-2} marsh $year^{-1}$]. For the Duplin system, the DIC of marsh origin exported to the ocean is considerably larger than that for Plum Island (21.86 gC m^{-2} $year^{-1}$) and includes DIC from direct marsh drainage and decomposition of marsh-derived organic matter in the estuary. This value is small compared with levels of DIC entering or produced in the Duplin estuarine waters, as most is degassed to the atmosphere (34%) or taken up by primary production (53%). The same was true for the Plum Island system, where 31% was degassed and 54% was taken up by primary production (Figs. 4 and 5). In the Plum Island system, the marsh is a sink for estuarine DIC and thus a negative term in the blue carbon budget (Fig. 6).

Estuarine respiration indicates a net production of 221 gDIC m^{-2} $year^{-1}$ internally (Fig. 4). Accounting for the internally produced DIC export to the ocean of 5.59 gDIC m^{-2} $year^{-1}$ and the DIC retained by the marsh (Fig. 4), we calculated a net atmospheric release of 161 g CO_2 m^{-2} $year^{-1}$.

OC exported from the Plum Island and Duplin salt marshes is one of 5 OC sources to estuarine waters (export, marsh erosion, aquatic primary production, river DOC utilization, and oceanic DOC utilization), whose fate is either deposited back onto the marsh surface, estuarine burial, respiration, or export to the ocean. To be included in the salt marsh blue carbon budget, OC exports must be derived solely from the marsh. For

the Plum Island system, after correcting for alternate fates and weighting for the relative marsh contribution to tidal waters, we estimated that 25% of marsh inputs to the estuary are exported to the ocean. For the Duplin system, we estimated that 16% of marsh inputs to the estuary pass through the ocean (Fig. 6). Thus, OC export increased blue carbon sequestration in the Duplin and Plum Island systems by 76% and 39%, respectively, relative to burial sequestration alone.

Inorganic and organic carbon exchange between tidal salt marshes and their adjacent terrestrial and oceanic systems can greatly alter coupled marsh/estuarine C dynamics and salt marsh blue carbon sequestration. For the Duplin estuary, processes other than OC burial in marsh soils increased the overall sequestration rate due to burial by a factor of 2.3, from 27 gC m^{-2} marsh $year^{-1}$ of direct burial to 62 gC m^{-2} marsh $year^{-1}$ when accounting for other fates of blue carbon. In contrast, Plum Island blue carbon sequestration decreased by 3%, from 111 gC m^{-2} marsh $year^{-1}$ to 108 gC m^{-2} marsh $year^{-1}$. Interestingly, the direct measure of OC burial in marsh soils suggests that blue carbon burial is approximately 4 times higher in Plum Island than in the Duplin, accounting for the various fates of C, resulting in total blue carbon sequestration in these systems being within a factor of 2 of each other. Clearly, an accurate assessment of blue carbon sequestration requires a full analysis of salt marsh and estuary C dynamics, well beyond those measured solely by analyses of total OC burial rates in marsh soils.

We did not include the release of CH_4 and N_2O to the atmosphere resulting from anaerobic metabolism (methanogenesis and denitrification), nitrification, or other biogeochemical pathways in salt marsh sediments in our corrected blue carbon budget. The release of these radiatively critical gases can offset net CO_2 sequestration [32,93] because the greenhouse warming potential of these gases is 32 to 45 times higher than that of CO_2 for CH_4 and 310 times higher for N_2O [94]. We did not quantify these potential flux pathways at Plum Island or the Duplin (Fig. 6); however, with the median CH_4 fluxes from salt marshes amounting to 1 gC m^{-2} $year^{-1}$ [32], we may have missed an important component of the blue carbon budget. Saline marshes in coastal Louisiana, USA release 11 gCH_4-C m^{-2} $year^{-1}$, which counteracts over 300 gCO_2-C m^{-2} $year^{-1}$ [95].

Conclusion

With the acceleration of global climate change and the ever-increasing levels of atmospheric CO_2, it is important to understand the responses of ecosystems that provide critical services that ameliorate anthropogenic activities, such as land-use change, nutrient enrichment, and climate change. However, our understanding of the control of blue carbon burial in coastal wetland-estuary systems remains limited, and simple models of marsh survival and OC accumulation are wrongly assuming that lignin content and the increased magnitude of its production can predict blue carbon storage. This study shows no correlation between marsh production (OC or lignin) and burial. Taking the advice of Spivak et al. [53], we need to better integrate decomposition mechanisms and dominant marsh macrophyte types into blue carbon models to improve predictions of soil OC storage in a changing world. Further, predictions that *S. patens* in marshes that sit relatively high in the tidal frame (such as Plum Island and other northern marshes) may transition to *S. alterniflora* in response to accelerating sea-level rise [96] may have important implications for C cycling and storage given the apparently strong dependence of these processes on plant type.

On the other hand, wetland-dominated estuaries like Plum Island and the Duplin are contributing to CO_2 sequestration in marsh soils and through the export of OC and DIC to the coastal ocean. Exported DIC and OC metabolized elsewhere contributes to oceanic DIC and alkalinity inventories, which have a millennial time frame, and can thus be included in marsh blue carbon inventories. We find that a full accounting of the fate of blue carbon can result in substantial changes from blue carbon estimates based solely on OC burial in marsh soils. Our work here has generated some of the most complete OC budgets for 2 tidal wetland systems and makes clear that there remains substantial uncertainty around the rates of processes controlling carbon sequestration in coastal systems. As suggested by Regnier et al. [7], there is a critical need for additional observation-based evidence to better constrain flux rates of critical sequestration calculations. We need to focus on vegetated coastal ecosystems, especially lateral fluxes of both inorganic and organic forms of C between vegetated and adjacent estuarine and coastal ocean systems. It is clear that modification of earth system models to factor in passage of water and processing of materials through the dynamic estuarine environment will greatly contribute to our overall understanding of the importance of ecosystems at the land–margin interface in regard to atmospheric C budgets and global climate change. We hope that the results here show how the importance of examining C budgets at the local scale to better constrain budgets and models at greater hierarchical scales.

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Competing interests: The authors declare that they have no competing interests.

Data Availability

Most underlying data can be found in the data repositories of the NSF-funded GCE and PIE LTER studies, as mentioned here in text and tables.

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