CO$_2$ released by carbonate sediment production in some coastal areas may offset the benefits of seagrass "Blue Carbon" storage

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Abstract

Seagrass ecosystems have been identified as long-term carbon sinks whose conservation could serve as a tool to mitigate carbon emissions. Seagrasses alter landscapes in a way that stimulates carbon biosequestration, but discussions of their role in atmospheric CO$_2$ mitigation disregard the co-occurring inorganic carbon cycle, whose antagonist effect on CO$_2$ sequestration can buffer and potentially outweigh the effects of C$_{org}$ production on net carbon exchange with the atmosphere. This study examines the extent of both organic carbon (C$_{org}$) and inorganic carbon (C$_{inorg}$) stocks as proxies for long-term production and calcification in the poorly studied seagrass meadows of southeastern (SE) Brazil and compares values to Florida Bay (U.S.A.), a well-studied system known for both high autotrophy and calcification, representing extremes of CaCO$_3$ soil content. Seagrass soils in SE Brazil contain an average of 67.6 ± 14.7 Mg C$_{org}$ ha^{-1} in the top 1 m, compared to an average of 175.0 ± 20.4 Mg C$_{org}$ ha^{-1} for their counterparts in Florida Bay. C$_{inorg}$ as CaCO$_3$ in SE Brazil averaged 141.5 ± 60.0 Mg C$_{inorg}$ ha^{-1} in the top meter of soil while the warmer, calcification-promoting waters of Florida Bay had higher soil C$_{inorg}$ areal stock, averaging 754.6 ± 26.7 Mg C$_{inorg}$ ha^{-1}. When the CO$_2$ evasion related to CaCO$_3$ production is considered, seagrass ecosystems with high CaCO$_3$ content may have CO$_2$ sequestered via C$_{org}$ accumulation negated by CO$_2$ produced by calcification. These findings prompt the reconsideration of carbon inventory methods and encourage regionally- and community-specific assessments of CO$_2$ sequestration abilities of seagrass ecosystems.

Concerns of increasing greenhouse gas emissions and potential mitigation strategies have driven a renewed interest in carbon sequestration abilities in natural ecosystems (Mcleod et al. 2011). Seagrass meadows, along with mangrove forests and tidal marshes, are recognized amongst the most efficient natural carbon sinks as well as globally important carbon stocks that could significantly exacerbate global greenhouse gas emissions if compromised; these systems have become collectively known as "Blue Carbon" ecosystems (Duarte et al. 2010; Fourqurean et al. 2012a). These important ecosystem features have led to a push for carbon finance policies and frameworks to secure carbon stocks through the protection of existing seagrass ecosystems, as well as promotion of seagrass recolonization to increase CO$_2$ capture ("Blue Carbon" strategies; Ullman et al. 2012;

Hejnowicz et al. 2015). Before science can translate to effective policy, factors influencing long-term carbon storage and loss, and the related exchange of CO$_2$ with the atmosphere need to be understood. Gaps in knowledge regarding the link between organic carbon (C$_{org}$) soil stocks in seagrasses and CO$_2$ sequestration are actively being addressed, however the influence of calcification and carbonate dissolution, both of which directly affect CO$_2$ partial pressure (pCO$_2$) in the water column and thus CO$_2$ exchange with the atmosphere, have been largely overlooked.

Seagrass ecosystems are highly productive, and their functioning alters their environment and promotes C$_{org}$ storage (Smith 1981; Fourqurean et al. 2012a). Seagrass meadows contain limited living biomass compared to many terrestrial and marine plant communities, though through a combination of high primary production rates and low herbivory pressure, high quantities of organic matter enter the detrital pathway (Duarte et al. 2010). Considering that the vast majority of seagrass community metabolism estimates suggest net autotrophy and positive net ecosystem production

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(NEP), much of the primary production is likely buried or exported, rather than remineralized in situ (Mateo et al. 2006). Net autotrophic seagrasses meadows reduce pCO_2 in the water column during photosynthetically driven carbon fixation into biomass, thus causing disequilibria across the water–air interface that encourages atmospheric CO_2 invasion. Seagrasses also develop complex canopies that often decrease current velocity and alter the turbulence in a way that increases deposition and adds allochthonous and non-seagrass C_{org} to soil stocks (Fonseca and Fisher 1986; Kennedy et al. 2010). Similar mechanisms prevent sediment erosion, allowing for anoxia to develop just millimeters beneath the soil surface, thus promoting the preservation of soil organic matter (OM) (Holmer 2009). C_{org} preserved and stored in stable, anoxic soils beneath seagrass meadows is considered to have avoided the remineralization to CO_2 that would have otherwise occurred without seagrasses (Duarte et al. 2010; Fourqurean et al. 2012a). A major crux of Blue Carbon science is to understand the conditions in which accumulated seagrass soil C_{org} stocks could be remineralized to CO_2, thus increasing water column pCO_2 and the potential for CO_2 evasion to the atmosphere.

The seagrass soil C_{org} stock is often interpreted to represent net uptake of atmospheric CO_2, both representing an integrated, long-term record of NEP (thus historic CO_2 invasion) and the C_{org} stock that is at risk of remineralization during environmental change (thus potential for future CO_2 evasion). Some seagrasses exert a strong, direct effect on C_{org} content of underlying soils; these are typically species with high biomass that form peat-like mattes (Macreadie et al. 2015; Marbà et al. 2015; Serrano et al. 2015). However, some seagrass ecosystems lack a tight seagrass biomass—soil C_{org} correlation (e.g., Campbell et al. 2015), suggesting that there are multiple, sometimes interacting, drivers of C_{org} storage whose effects are difficult to isolate (Howard et al. 2016; Serrano et al. 2016). Seagrasses are a polyphyletic group that range greatly in morphology and environmental conditions, making their importance to soil C_{org} storage difficult to assess (Lavery et al. 2013). Published work and global databases are biased toward particular seagrass species, diversity hotspots and areas with active research programs (Fourqurean et al. 2012a; Johannessen and Macdonald 2016), and are lacking from southwestern coasts of the Atlantic Ocean (Fourqurean et al. 2012a). Overlooked and under-sampled regions must be evaluated for a more complete range in seagrass carbon content as well as regionally specific valuation.

Organic carbon metabolism and storage have been the foci of seagrass carbon sequestration discussions and ecosystem valuation, though water column pCO_2, and thus the air–sea CO_2 exchange potential, are complicated by calcification and carbonate dissolution. Through calcification, organisms utilize dissolved inorganic carbon (DIC) to produce solid $CaCO_3$ used in shells and skeletons, and the rate of calcification is influenced by the saturation state of seawater

with respect to solid $CaCO_3$ (Langdon et al. 2000; Orr et al. 2005). Carbonates produced in seagrass ecosystems are dominated by high-magnesium calcite and aragonite (Nelsen and Ginsburg 1986; Bosence 1989). Each carbonate mineral form has a different solubility in seawater (Stumm and Morgan 1996), hence the calculation of a "carbonate saturation state" would need to be done with respect to these mineral phases. However, factors that act to increase or decrease the solubility of carbonate mineral phases are the same, regardless of mineral form. While calcification decreases total alkalinity and DIC and in the water column, it produces CO_2 (Frankignoulle et al. 1995). In other words, calcification acts as a net sink for total DIC through the production of solid phase carbonates, though it is a net source for dissolved CO_2. A portion of produced CO_2 will likely be used in photosynthesis or consumed in the dissolution of carbonate minerals (Millero 2007; Smith 2013), though some fraction will alter the ΔpCO_2 across the water–air interface and thus influence the exchange of CO_2 with the atmosphere. Conversely, the dissolution of $CaCO_3$ consumes CO_2 from the surrounding water and produces DIC and alkalinity. The tendency for $CaCO_3$ to dissolve is thermodynamically linked to variables such as depth (i.e., pressure), pH, temperature, and salinity that affect the carbonate saturation state (Millero 2007). For example, sulfide oxidation and aerobic remineralization during sediment organic matter decomposition decrease pore-water pH, which then drives carbonate dissolution (Ku et al. 1999; Burdige and Zimmerman 2002). Carbonate saturation state and, thus, both net calcification and net $CaCO_3$ dissolution are thermodynamically driven by local environmental conditions and are augmented by biological production and respiration reactions, respectively. These organismal metabolic processes along with calcification reactions have been considered "reaction couplets," where the two reactions are independent yet mutually influential (Smith 2013).

Seagrasses provide substrate and habitat for calcifying epiphytes (Frankovich and Zieman 1994), macroalgae (Collado-Vides et al. 2007), and benthic invertebrates (van der Heide et al. 2012), while they promote the deposition of detrital $CaCO_3$ particles (Gacia et al. 2002). Seagrasses also precipitate $CaCO_3$ themselves, likely linked to high CO_2 demands and their alteration of internal pH (Enríquez and Schubert 2014). Seagrass ecosystem metabolism has also been linked to carbonate saturation state with productive systems promoting calcification due to their photosynthetic utilization of CO_2 that increases the availability of dissolved carbonate ions (Semesi et al. 2009; Hendriks et al. 2014). In fact, net autotrophy of the expansive seagrass meadows of the Florida Reef Tract has been hypothesized to act as an acidification refugia for calcifying organisms (Manzello et al. 2012; but *see* Muehllehner et al. 2016).

Many of the most expansive seagrass meadows (Mediterranean Sea, Florida Bay, coastal Australia) are found in soils

consisting primarily of carbonates and seagrass ecosystems have been identified as large reservoirs of inorganic carbon (C_{inorg}; Duarte et al. 1995; Mazarrasa et al. 2015). If the $CaCO_3$ in the soils underlying these seagrass meadows are autochthonous, then net calcification in these systems must produce more CO_2 through calcification than consumed by $CaCO_3$ dissolution. Such an occurrence would influence net exchange of CO_2 with the atmosphere and potentially offset CO_2 sink tendencies of autotrophic seagrass ecosystems. Further, if net $CaCO_3$ production is positively correlated with net primary production, then CO_2 sequestration capacity of seagrasses as well as any respiration related CO_2 from degraded seagrass meadows may be buffered by C_{inorg} reactions.

The ratio of organic carbon to inorganic carbon production has been considered when assessing net ecosystem exchange of CO_2 with the atmosphere and the pCO_2 in seawater (Suzuki 1998; Lerman and Mackenzie 2005). Net autotrophy and the net storage of C_{org} suggest seagrass ecosystems are long-term CO_2 sinks, a relationship key for Blue Carbon climate change mitigation strategies. However, these values should be considered in relation to C_{inorg} production and storage in underlying soils to evaluate the net exchange of CO_2 between seagrass meadows and the atmosphere. Here, we inventory C_{org} and C_{inorg} stocks in seagrass colonized soils as proxies for long-term production and calcification across southeastern Brazil, a region poorly studied for both soil C_{org} and C_{inorg} (Fourqurean et al. 2012a; Mazarrasa et al. 2015; Copertino et al. 2016). We emphasize the importance of C_{inorg} to net CO_2 sequestration in seagrass meadows by comparing C_{org} and C_{inorg} content of the Brazilian seagrass soils. We further compare the Brazilian soils to those from Florida Bay, a well-studied system acknowledged for Blue Carbon storage (Fourqurean et al. 2012b), high calcification rates (Stockman et al. 1967; Nelsen and Ginsburg 1986; Bosence 1989), and net autotrophic seagrass ecosystems (Zieman et al. 1989; Long et al. 2015). To better understand the state of seagrass communities and their potential role in C_{org} storage in SE Brazil, we also measure seagrass morphology (shoot density, above/belowground biomass, and leaf length) as they have been correlated with C_{org} storage previously (Serrano et al. 2015). We measure ratios of leaf carbon (C), nitrogen (N), and phosphorus (P) to infer nutrient limitation (see Fourqurean et al. 1992) as nutrient availability has been suggested to influence C_{org} storage via altered seagrass primary production, ecosystem respiration, and sedimentation/erosion regimes (Armitage and Fourqurean 2016; Howard et al. 2016). To understand the influence of seagrass compared to other potential C_{org} sources to underlying sediments, we also compare site-specific $\delta^{13}C$ values of sediment C_{org} to that of the overlying seagrasses (Kennedy et al. 2010).

Methods

Seagrass characteristics and underlying soil carbon stocks were measured between June and August 2015 at 14 sites along the southeastern Brazilian coastline (Supporting Information Online Resource 1, 2) including the states of Espírito Santo and Rio de Janeiro. This sampling covers much of the known geographical distribution of seagrass meadows within the region (Creed 1997, 1999, unpubl. data). Seagrasses in the region are found in shallow water (max depth 3 m) in primarily silicate sand with water temperatures ranging seasonally from approximately 15°C to 25°C (Creed 2003).

Data from SE Brazil were compared to existing data from Florida Bay, U.S.A. (Supporting Information Online Resource 3, 4; Armitage and Fourqurean 2016; Howard et al. 2016; Fourqurean unpubl.), a subtropical embayment hosting 1660 km² of seagrasses, typically *Thalassia testudinum*, *Halodule wrightii*, and *Syringodium filiforme* (Zieman et al. 1989). The bay is typically < 3 m deep, with temperatures fluctuating seasonally between 20°C and 28°C and regular periods of hypersalinity due to evaporation exceeding freshwater input (Fourqurean and Robblee 1999). Due to high N : P in freshwater runoff and low phosphorus mobility related to adsorption to carbonate sediments, seagrass production and biomass in Florida Bay is severely phosphorus limited (Fourqurean et al. 1992). Florida Bay has long been recognized for high calcification rates and for providing a source of carbonate sand and mud to the surrounding areas (Stockman et al. 1967; Bosence et al. 1985; Bosence 1989).

For seagrass characteristics, 15 cm diameter cores were collected at randomly chosen locations during low tide within each sampling site in triplicate. Seagrass biomass was separated from sediment using a coarse mesh bag. Seagrasses were separated by species and shoots were counted. Leaves were counted on each shoot, measured, and scraped of any epiphytes. Aboveground and belowground components were separated and dried at 50°C until a constant weight was achieved. Dry weight of above- and belowground components were recorded. The dried leaf samples were homogenized and ground to a fine powder using a motorized mortar and pestle. Powdered samples were analyzed for total carbon (C) and nitrogen (N) content using a CHN analyzer (Thermo Flash EA, 1112 series). Total phosphorus content was determined by a dry-oxidation, acid hydrolysis extraction followed by a colorimetric analysis of phosphate concentration of the extract (Fourqurean et al. 1992). Homogenized leaf samples were additionally analyzed for $\delta^{13}C$ using Elemental Analysis - Isotope Ratio Mass Spectrometry (EA-IRMS) techniques; high temperature catalytic combustion was used to combust the organic carbon to CO_2, which was then measured on a Finnigan MAT Delta C IRMS in a continuous flow mode. Isotopic ratios (R) were reported in the standard delta notation (‰) : δ (‰) = $[(R_{sample}/R_{standard}) - 1] \times 1000$. These results are presented with respect to the international standard Vienna Pee Dee Belemnite (V-PDB). Analytical reproducibility of the reported values, based on sample replicates, was better than ± 0.08‰.

Soil cores were collected at randomly selected locations within each site in duplicate by driving a manually operated piston core (6 cm diameter) into the soil until 1 m depth or the depth at which the piston core could no longer be inserted. A depth of one meter was chosen for straightforward comparison to existing soil carbon inventories and is not associated with a known period of accumulation. Cores were then subsampled at up to 10 cm intervals using predrilled sampling ports as described by Campbell et al. (2015). This method yielded samples of ~ 9 cm^3 along the depth profile, while minimizing compaction. Sediment samples of a known wet volume were dried and weighed to calculate dry bulk density (g dry soil mL wet soil^{-1}). Soil samples were homogenized using a motorized mortar and pestle then analyzed for C_{org} and C_{inorg} using previously described methods (Fourqurean et al. 2012*b*). Surface soil samples from each site were acid-fumed to remove carbonates and analyzed for δ^{13}C of C_{org}.

Data analysis

Stocks of inorganic and organic carbon were measured using methods reported by Campbell et al. (2015). C_{org} and C_{inorg} content data were converted from % of dry wt to stock (mol C mL soil^{-1}) by multiplying carbon content (% dry wt) by dry bulk density (g dry soil mL wet soil^{-1}) and the molecular mass of C. These values were used to calculate C_{org} and C_{inorg} areal stock in the top 1 m of soil, presented as Mg C hect^{-1} (*see* Campbell et al. 2015), which were then used to compute site specific $C_{org} : C_{inorg}$ areal stock ratios. Carbon stock values (in mol C mL soil^{-1}) were additionally used to estimate CO$_2$ net sequestration (CO$_2$ $_{net\ sequestered}$), defined as the total calculated flux of CO$_2$ from the atmosphere to seagrass soils during soil production, with the caveat that negative values of CO$_2$ $_{net\ sequestered}$ indicate evasion of CO$_2$ from seagrass soils to the atmosphere, using the equation:

$$C_{org\ stored} - \Psi * C_{inorg\ stored} = CO_{2\ net\ sequestered} \quad (1)$$

Where $C_{org\ stored}$ is the C_{org} density in mol mL soil^{-1}, Ψ is the gas exchange : reaction ratio of CO$_2$ and CaCO$_3$ proposed by Smith (2013; *see* Eq. 2), $C_{inorg\ stored}$ is the C_{inorg} density in mol mL soil^{-1}, and CO$_2$ $_{net\ sequestered}$ is the moles of CO$_2$ sequestered in mL of soil.

$$Ca^{2+} + (1+\Psi)\ HCO_3^- + (1-\Psi)\ OH^- = CaCO_3 + \Psi CO_2 + H_2O \quad (2)$$
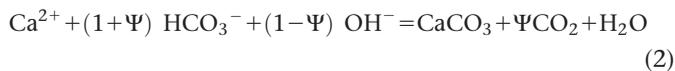
For the shallow, coastal sites of this study, we used $\Psi = 0.6$ as discussed by Smith (2013) and employed by Mazarrasa et al. (2015). Equation 1 implicitly assumes all soil carbon is autochthonous and remains in the system; it assumes that there is no export of carbon produced in the ecosystem or import of carbon from outside of the system. Nevertheless, allochthonous carbon in seagrass meadows is commonly

included in Blue Carbon stock assessments in the literature (Fourqurean et al. 2012*a*; Pendleton et al. 2012; Howard et al. 2014). While this condition is likely to not hold in many ecosystems, rarely has the net exchange between seagrasses and adjacent ecosystems been assessed. Equation 1 uses an 1 : 1 relationship between the net CO$_2$ uptake driven by NEP and C_{org} storage as used previously (Fourqurean et al. 2012*a*; Pendleton et al. 2012; Mazarrasa et al. 2015). Positive values of CO$_2$ $_{net\ sequestered}$ were interpreted to indicate net CO$_2$ sequestration while negative values indicate net CO$_2$ evasion, assuming sea–air CO$_2$ gas transfer is continued until equilibrium is reached.

Ordinary least squares model II linear regressions were used to compare C_{org} stock to seagrass biomass to test for the dependence of C_{org} stocks on seagrass density. δ^{13}C values of bulk seagrass leaf tissue and C_{org} component of soils were compared to previously reported data from Florida Bay (Howard et al. 2016) and globally (Kennedy et al. 2010). Differences in measured seagrass and soil parameters between sites were tested using analysis of variance (ANOVA) or Mann–Whitney–Wilcoxon procedures after data were checked for normality and equal variances. Additionally, C : N, C : P, and N : P molar ratios of leaf tissue were computed to evaluate nutrient availability. Values were compared between sites and previously reported data, including the ideal N : P "Seagrass Redfield Ratio" of 30 : 1 (Atkinson and Smith 1983; Duarte 1990; Campbell and Fourqurean 2009). All averages are accompanied by the standard error of the mean (SEM) with the exception of Table 3, which presents standard deviation (SD) to be faithful to the literature from which those data were extracted.

Results

The seagrass species found in the sampling regions of SE Brazil was typically *Halodule wrightii* with *Halophila decipiens* also found intertidally in Santa Cruz and <2 m depth in Urca, and *Halodule emarginata* found at sites near Vitória (*see* Supporting Information Online Resources 1, 2 for locations of sampling sites). Total seagrass biomass was low across the region, averaging 37.5 ± 7.2 g m^{-2} across sites with a maximum of 91.1 g m^{-2} for the sampling period (Table 1). Aboveground biomass was a small component of total biomass averaging $28.7\% \pm 4.5\%$ of total biomass, ranging from 4.5% to 60.4% of the total biomass. Leaves were short, averaging 4.1 ± 0.1 cm for *Halodule wrightii* and 3.8 ± 0.1 cm for *Halodule emarginata*, with a maximum leaf length of 5.4 cm and 3.9 cm, respectively. Seagrasses exhibited extremely high shoot density with an average of 4063 ± 853 shoots m^{-2} across sites. Seagrass nutrient content varied between sites (ANOVA, $F_{1,30}$, $p < 0.05$). Leaf tissue N : P ratios ranged from 18.8 to 38.9 between sites with an average ratio of 24.0 ± 1.3 (Table 2). Seagrasses leaf tissue N : P molar ratios fell below the "Seagrass Redfield Ratio" of 30 : 1 with the exception of

Table 1. Shoot densities and biomass of seagrasses inhabiting study sites in SE Brazil. Data are mean $\pm$ SEM ($n = 3$).

Map key	Site name	Seagrass species	Shoot density (plant m^{-2})	Average leaf length (cm)	Aboveground biomass (g m^{-2})	Belowground biomass (g m^{-2})	Total biomass (g m^{-2})	Ratio above : below-ground biomass
1	Bracui—site 1	Halodule wrightii	1886.3 $\pm$ 349.3	5.4 $\pm$ 0.4	1.1 $\pm$ 0.2	6.5 $\pm$ 1.3	7.7 $\pm$ 1.5	0.2 $\pm$ 0.1
2	Bracui—site 2	Halodule wrightii	1848.6 $\pm$ 105.0	3.7 $\pm$ 0.3	0.9 $\pm$ 0.1	4.4 $\pm$ 0.6	5.3 $\pm$ 0.7	0.2 $\pm$ 0.1
3	Ilha Grande—site 1	Halodule wrightii	2735.1 $\pm$ 690.2	3.9 $\pm$ 0.2	15.3 $\pm$ 2.3	10.0 $\pm$ 0.4	25.3 $\pm$ 2.5	1.5 $\pm$ 0.9
4	Ilha Grande—site 2	Halodule wrightii	1659.9 $\pm$ 132.0	5.2 $\pm$ 0.3	1.6 $\pm$ 0.0	16.8 $\pm$ 1.1	18.4 $\pm$ 1.1	0.1 $\pm$ 0.1
5	Urca	Halophila decipiens	-	-	14.1 $\pm$ 1.9	21.6 $\pm$ 1.0	35.7 $\pm$ 1.7	0.7 $\pm$ 0.4
6	Arraial do Cabo	Halodule wrightii	9450.3 $\pm$ 1428.2	4.4 $\pm$ 0.3	29.1 $\pm$ 0.4	62.1 $\pm$ 20.7	91.1 $\pm$ 21.1	0.6 $\pm$ 0.4
7	Ilha do Japones—site 1	Halodule wrightii	2489.9 $\pm$ 214.2	4.9 $\pm$ 0.3	28.9 $\pm$ 0.2	33.7 $\pm$ 3.0	62.6 $\pm$ 2.9	0.9 $\pm$ 0.5
8	Ilha do Japones—site 2	Halodule wrightii	1905.2 $\pm$ 207.5	4.0 $\pm$ 0.2	25.5 $\pm$ 0.6	30.8 $\pm$ 7.5	56.3 $\pm$ 8.1	1.0 $\pm$ 0.6
9	Manguinhos	Halodule wrightii	6677.4 $\pm$ 385.2	3.3 $\pm$ 0.1	4.6 $\pm$ 0.1	51.7 $\pm$ 5.7	56.3 $\pm$ 5.8	0.1 $\pm$ 0.1
10	Praia da Ferradura	Halodule wrightii	2093.8 $\pm$ 471.2	3.5 $\pm$ 0.1	24.7 $\pm$ 0.1	43.7 $\pm$ 4.4	68.4 $\pm$ 4.5	1.5 $\pm$ 0.9
11	Praia dos Ossos	Halodule wrightii	7054.7 $\pm$ 1700.3	4.8 $\pm$ 0.2	26.8 $\pm$ 0.1	42.8 $\pm$ 6.8	69.6 $\pm$ 6.8	0.7 $\pm$ 0.4
12	Vila Velha	Halodule emarginata	603.6 $\pm$ 68.0	3.9 $\pm$ 0.2	0.6 $\pm$ 0.1	7.6 $\pm$ 1.5	8.2 $\pm$ 1.5	0.1 $\pm$ 0.1
13	Vitoria	Halodule emarginata	2207.0 $\pm$ 598.9	3.8 $\pm$ 0.1	8.8 $\pm$ 5.8	13.4 $\pm$ 2.8	22.2 $\pm$ 8.6	0.6 $\pm$ 0.3
14	Santa Cruz	Halodule wrightii	10,468.9 $\pm$ 1044.0	2.0 $\pm$ 0.1	1.4 $\pm$ 0.2	29.1 $\pm$ 0.4	30.6 $\pm$ 0.6	0.1 $\pm$ 0.0
14	Santa Cruz	Halophila decipiens	5809.8 $\pm$ 796.5	-	1.6 $\pm$ 0.2	3.3 $\pm$ 0.4	4.8 $\pm$ 0.6	0.5 $\pm$ 0.3

the most northern site, Santa Cruz. Both C : N and C : P were low across sites, averaging 11.3 $\pm$ 0.3 and 271.2 $\pm$ 19.9, respectively. These values can be compared to average ratios of *Halodule wrightii* from south Florida (22.7 $\pm$ 0.4 for C : N, 1014.1 $\pm$ 51.8 for C : P; Campbell and Fourqurean 2009) and median ratios of aquatic plants in general (20 for C : N, 550 for C : P; Atkinson and Smith 1983).

Seagrass δ^{13}C values of leaf tissue from Brazilian sites ranged from $-13.4‰$ to $-7.7‰$ with an average of $-10.1 \pm 0.4‰$ (Table 2). The C_{org} component of surface soils collected beneath sampled seagrasses showed δ^{13}C values ranging between $-11.3‰$ and $-27.7‰$ averaging $-18.3 \pm 1.3‰$. These values, with the exception of one sample from Bracuí, fell within the global range of δ^{13}C seagrass surface sediment values ($-26.6‰$ to $-7.2‰$; Kennedy et al. 2010), though the majority of sites sampled in Brazil were depleted in δ^{13}C in comparison when adjusted for seagrass δ^{13}C values using the Kennedy et al. (2010) global model (Supporting Information Online Resource 5). Seagrass surface sediment C_{org} from SE Brazil was on average more depleted in δ^{13}C than Florida Bay ($-18.3 \pm 1.3‰$ compared to $-12.7 \pm 0.5‰$, ANOVA, $F_{1,24}$, $p < 0.05$).

Sediment density at Brazilian sites ranged between 0.61 g mL^{-1} and 1.60 g mL^{-1} with an average of 1.09 $\pm$ 0.02 g mL^{-1}. There was no relationship between C_{org} content and sediment density for surface sediments (ordinary least squares model II regression, $p > 0.05$, $n = 14$). C_{org} content of the surface soil samples (top 2 cm) averaged 0.78% $\pm$ 0.15% of dry wt. across all study sites in SE Brazil, ranging between 0.10% and 1.95% of dry weight (Fig. 1, Supporting Information Online Resource 6). The highest surface soil C_{org} content was found at Vila Velha while lowest was found at

Bracuí. There was a difference in C_{org} content of soil samples collected north and south of Cabo Frio (ANOVA, $F_{1,12}$, $p < 0.05$). Samples collected on the northern side of Cabo Frio averaged 1.2% $\pm$ 0.1% across sites and down the sampled depth profile, while sediments collected on the southern side of Cabo Frio averaged 0.6% $\pm$ 0.1%. The Brazilian samples were lower in soil C_{org} content than those from Florida Bay (which averaged 2.3% $\pm$ 0.1% of dry wt across sites and downcore; Fig. 1; Supporting Information Online Resource 7; ANOVA, $F_{1,16}$, $p < 0.05$). There was no clear relationship between seagrass living biomass and surface soil C_{org} content across the samples from SE Brazil (ordinary least squares model II regression, $p > 0.05$, $n = 14$), nor was there a relationship between surface soil δ^{13}C and C_{org} content (ordinary least squares model II regression, $p > 0.05$, $n = 14$).

The C_{inorg} content of the soil samples averaged 1.31% $\pm$ 0.60% of dry wt. across all samples collected in the top 1 m of SE Brazil sites, with a large range between 0.01% and 6.34% of dry wt. (Fig. 2, Supporting Information Online Resource 6). There was a difference in C_{inorg} content of soil samples collected north and south of Cabo Frio (ANOVA, $F_{1,12}$, $p < 0.05$). Only sites on the northern side of Cabo Frio had soils with appreciable C_{inorg} content, averaging 3.1% $\pm$ 0.3% across sites and down the sampled depth profile. Those sediments collected on the southern side of Cabo Frio averaged 0.12% $\pm$ 0.02%. Our southeastern Brazil study sites as a whole, as well as the northern subset alone were consistently lower in soil C_{inorg} content compared to Florida Bay (Fig. 2; Supporting Information Online Resource 7; ANOVA, $F_{1,16}$, $p < 0.05$), which averaged 9.45% $\pm$ 0.35% of dry wt.

The sites in southeastern Brazil had lower total C_{org} areal stock than those in Florida Bay in both living biomass and

Table 2. Elemental and stable isotope composition of seagrass leaves collected across sites in SE Brazil. Data are mean $\pm$ SEM ($n = 1$–3).

Map key	Site name	Seagrass species	C content (% dry wt.)	N content (% dry wt.)	P content (% dry wt.)	C : N	C : P	N : P	$\delta^{13}C$ (‰)
1	Bracui—site 1	*Halodule wrightii*	43.2 ± 0.75	5.0 ± 0.14	0.39	10.1 ± 0.1	290.1	29	-10.3 ± 0.0
2	Bracui—site 2	*Halodule wrightii*	42.7 ± 0.28	5.0 ± 0.15	0.43	10.0 ± 0.2	258.8	26.5	-10.6
3	Ilha Grande—site 1	*Halodule wrightii*	42.2 ± 0.11	3.7 ± 0.03	0.44 ± 0.01	13.3 ± 0.1	249.6 ± 3.7	18.8 ± 0.1	-9.9 ± 0.0
4	Ilha Grande—site 2	*Halodule wrightii*	41.5 ± 0.13	4.4 ± 0.05	0.45 ± 0.03	10.9 ± 0.2	237.7 ± 18.8	21.7 ± 1.4	-11.0 ± 0.1
5	Urca	*Halophila decipiens*	35.4 ± 0.42	3.8 ± 0.14	0.42 ± 0.01	10.9 ± 0.3	220.3 ± 5.6	20.3 ± 1.0	-9.7 ± 0.0
6	Arraial do Cabo	*Halodule wrightii*	40.0 ± 0.63	4.4 ± 0.04	0.45 ± 0.03	10.5 ± 0.2	232.0 ± 13.4	22.1 ± 1.0	-11.7
7	Ilha do Japones—site 1	*Halodule wrightii*	38.9 ± 0.12	3.5 ± 0.05	0.37 ± 0.01	12.9 ± 0.2	273.3 ± 4.3	21.1 ± 0.7	-8.1 ± 0.0
8	Ilha do Japones—site 2	*Halodule wrightii*	39.5 ± 0.60	3.8 ± 0.05	0.33 ± 0.01	12.1 ± 0.3	307.9 ± 13.6	25.4 ± 0.4	-7.7 ± 0.00
9	Manguinhos	*Halodule wrightii*	43.1 ± 0.28	4.4 ± 0.18	0.41 ± 0.01	11.6 ± 0.4	268.3 ± 3.4	22.5 ± 1.0	-11.5 ± 0.1
10	Praia da Ferradura	*Halodule wrightii*	41.0	4.8	0.48	9.9	222.2	22.5	-9.9
11	Praia dos Ossos	*Halodule wrightii*	41.6 ± 0.28	4.4 ± 0.03	0.42 ± 0	11.1 ± 0.1	254.7 ± 5.3	23.0 ± 0.4	-9.5 ± 0.1
12	Vila Velha	*Halodule emarginata*	42.9 ± 1.34	5.2 ± 0.22	0.52 ± 0.03	9.6 ± 0.3	215.4 ± 17.0	22.4 ± 1.7	-13.4 ± 0.1
13	Vitoria	*Halodule emarginata*	41.1 ± 0.51	4.20 ± 0.09	0.42 ± 0.01	11.5 ± 0.4	253.3 ± 3.2	22.1 ± 0.9	-9.9 ± 0.1
14	Santa Cruz	*Halodule wrightii*	42.8 ± 0.44	3.8 ± 0.07	0.22 ± 0.001	13.2 ± 0.1	513.2 ± 4.8	38.9 ± 0.7	-10.0 ± 0.0
14	Santa Cruz	*Halophila decipiens*	-	-	-	-	-	-	-8.7 ± 0.4

Table 3. Regional comparisons of C_{org} (Fourqurean et al. 2012*a*) and C_{inorg} areal stocks (Mazarrasa et al. 2015) in seagrass ecosystems with calculated CO_2 net sequestration.

Region	Soil C_{org} Mg C ha^{-1}		Soil C_{inorg} Mg C ha^{-1}		CO_2 net sequestration Mg C ha^{-1}
	n	Mean $\pm$ SD	n	Mean $\pm$ SD	Mean $\pm$ SD
North Atlantic	24	48.7 ± 36.2	35	204.9 ± 209.4	-74.24 ± 166.2
Tropical Western Atlantic	13	150.9 ± 48.4	60	869.5 ± 422.9	-370.8 ± 331.2
Mediterranean	29	372.4 ± 204.7	42	654.4 ± 462.1	-20.24 ± 412.3
South Atlantic	5	137 ± 64.8	-	-	-
Indopacific	8	23.6 ± 12.0	145	713.9 ± 566.0	-404.74 ± 438.5
South Australia	9	268.3 ± 155.7	121	603.9 ± 376.2	-94.04 ± 330.4
Southeastern Atlantic (this study)	14	67.6 ± 55.0	14	141.5 ± 224.3	-17.3 ± 182.3

top 1 m of soil (Fig. 3, ANOVA, $F_{1,16}$, $p < 0.05$). Soil C_{org} areal stocks averaged 67.6 ± 14.7 Mg C_{org} hect^{-1} for sites in SE Brazil while sites Florida Bay averaged 175.0 ± 20.4 Mg C_{org} hect^{-1}. Areal stocks of C_{org} in living biomass averaged 0.14 ± 0.03 Mg C_{org} hect^{-1} for sites in SE Brazil while site in Florida Bay averaged 1.22 ± 0.59 Mg C_{org} hect^{-1}. The sites in southeastern Brazil also had significantly less C_{inorg} areal stock than FL Bay (141.5 ± 60.0 Mg C_{inorg} hect^{-1} and 754.6 ± 26.7 Mg C_{inorg} hect^{-1}, respectively). When ratios of organic to inorganic carbon areal stock (as measured by Mg C hect^{-1}) were calculated, the sites in SE Brazil had significant higher values than their counterparts in Florida Bay (6.4 ± 3.7 compared to 0.2 ± 0.1, ANOVA, $F_{1,16}$, $p < 0.05$). When soil carbon stocks were used to compute $CO_{2\ net\ sequestered}$, values for Florida Bay

were consistently negative, suggesting Florida Bay seagrass soils were a CO_2 source during soil production, despite higher areal stock of C_{org} (Fig. 4). Values from Brazil on the other hand were positive at most sites, indicating net CO_2 sequestration during the production of soil. However, due to the higher $CaCO_3$ stocks in areas north of Cabo Frio, average $CO_{2\ net\ sequestered}$ in southeast Brazil was still slightly negative at -17.3 ± 182.3 Mg C hect^{-1} (mean $\pm$ SD) when computed using Eq. 1 (*see* Table 3).

Discussion

Seagrasses meadows are typically autotrophic ecosystems whose positive NEP acts as a sink for CO_2 while producing and storing C_{org} (Duarte et al. 2010; Fourqurean et al.
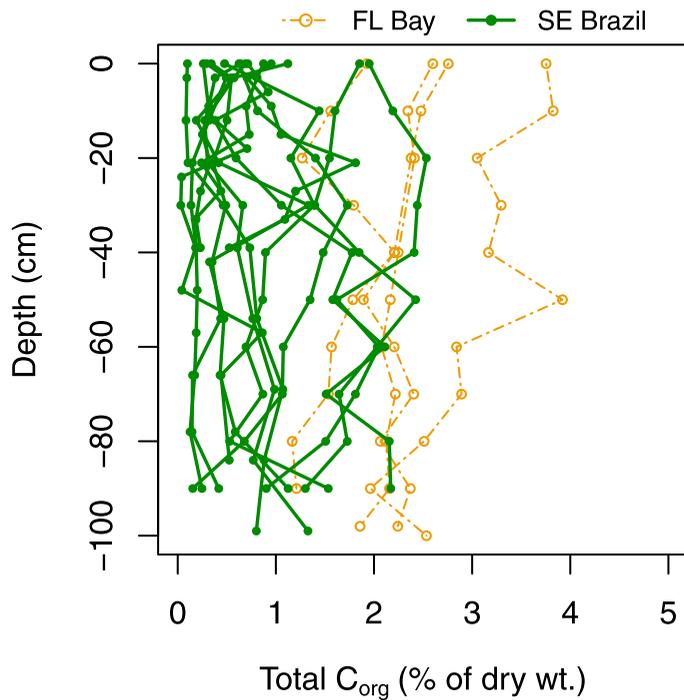
Fig. 1. Down core profiles of mean soil C_{org} content across all sites in SE Brazil and FL bay (mean, $n = 2$–3). Error associated with mean are displayed in the Supporting Information Material. [Color figure can be viewed at wileyonlinelibrary.com]
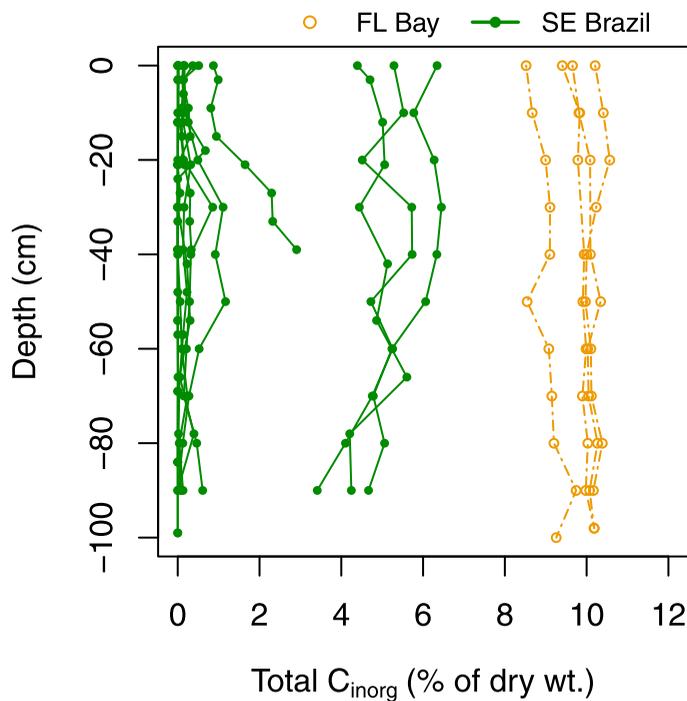
Fig. 2. Down core profiles of mean soil C_{inorg} content across all sites in SE Brazil and FL bay (mean, $n = 2$–3). Errors associated with mean are displayed in the Supporting Information Material. [Color figure can be viewed at wileyonlinelibrary.com]
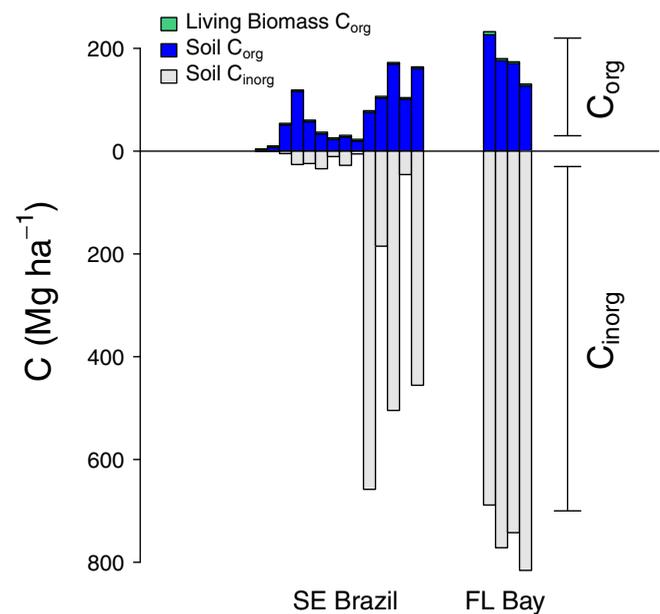
Fig. 3. Site specific carbon areal stocks including C_{org} and C_{inorg} associated with living biomass and soils. Sites are arranged from southernmost survey site on the left to northernmost site on the right. [Color figure can be viewed at wileyonlinelibrary.com]
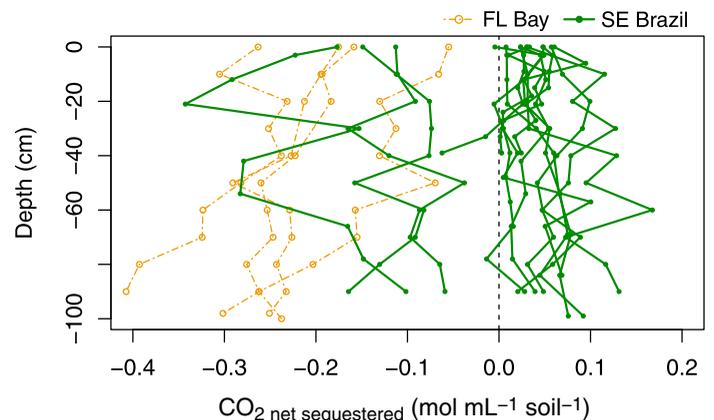
Fig. 4. Down core profiles of mean CO_2 net sequestration across survey sites. Positive values indicate that CO_2 is consumed during soil production while negative values indicate that the production of soil carbon resulted in net CO_2 production. Data derived from both C_{org} and C_{inorg}, assuming standard gas exchange : reaction ratios. [Color figure can be viewed at wileyonlinelibrary.com]

2012*a*). At the same time, seagrass meadows are hotspots for $CaCO_3$ storage, particularly in the tropics where $CaCO_3$ saturation state is high and calcifying organisms thrive (Mazarrasa et al. 2015). While the Blue Carbon community attempts to quantify and understand ecosystem organic carbon metabolism under environmental change, there has been little consideration of the concurrently, and perhaps synergistically, occurring calcification-$CaCO_3$ dissolution processes that buffer and potentially dominate CO_2

exchange related to NEP. The overwhelming effect of calcification on CO_2 production compared to NEP has been emphasized in coral reef and open ocean systems (Ware et al. 1992; Suzuki 1998; Lerman and Mackenzie 2005). For example, Gattuso et al. (1999*a*) note that coral reefs have a tendency to consume CO_2 due to net autotrophy, but to act as a net source of CO_2 due to higher calcification rates.

The relationship between C_{inorg} and CO_2 production in seagrass ecosystems has been pointed out previously; Mazarrasa et al. (2015) published the first assessment of the global carbonate stocks in seagrass sediments, underscoring the importance of calcification to CO_2 production. Even though sediment stocks of C_{inorg} outweigh C_{org} in every geographic region for which they could find data (Table 3) by five-fold on average, Mazarrasa et al. (2015) conclude that seagrass meadows are still strong CO_2 sinks due to higher C_{org} stocks in vegetated sediments compared to adjacent un-vegetated, carbonate sands. However, $CaCO_3$ production and storage, like C_{org} production and storage, is influenced by a combination of both regional factors and local seagrass ecology. The relative storage of C_{org} and C_{inorg}, and therefore the net CO_2 exchange, varies greatly depending on geomorphological context and seagrass species. Rather than generalized claims regarding seagrass CO_2 sink capabilities, seagrass-inhabited areas need to be assessed separately, taking into account local benthic community composition and environmental influence on production, deposition and storage of both C_{org} and C_{inorg} to determine the value of such systems as CO_2 sinks.

Soils from sites in SE Brazil consistently ranked in the bottom 25% of global values for C_{org} content and stocks (Fourqurean et al. 2012*a*) and were significantly lower than those measured in Florida Bay (Fourqurean et al. 2012*b*; Howard et al. 2016). Using $\delta^{13}C$ values of surface soils as indictors of C_{org} sources to surface soils, we identified that seagrasses contributed a large percentage of the C_{org} in surface soils despite the sparse nature and small stature of the seagrasses. Using the Kennedy et al. (2010) global model, over a third of sites sampled had surface soils consisting mostly of seagrass-derived C_{org} (Supporting Information Online Resource 5). Given the close proximity of these seagrasses to land and their low density, an even greater influence of terrestrial material to marine soil stocks might have been expected (Kennedy et al. 2004). Our finding may be explained by high relative turnover rates of the pioneering seagrasses found in Brazil (Marques 2010).

There was no significant linear relationship between sea-grass biomass and underlying soil C_{org} stocks, or between soil C_{org} source (as implied by $\delta^{13}C$ values) and soil C_{org} content, at our Brazilian study sites. Nutrient-limited primary production has been used to explain limited C_{org} storage in nutrient-poor Florida Bay (Armitage and Fourqurean 2016), though low C : N and C : P ratios of leaf tissue suggest that was not the case for our Brazilian seagrass meadows. C : N

and C : P ratios of Brazilian seagrasses are amongst the lowest recorded Duarte (1990), indicating N and P supplies were plentiful compared to carbon fixation rates. Sediments at most Brazilian sites were sandy (personal observation), suggesting a high energy environment that may promote erosion while limiting anoxia and C_{org} persistence (Magni et al. 2002; De Falco et al. 2004). Coarser grain size could also decrease the surface area of mineral sediments onto which OM adsorbs (Keil and Hedges 1993; Arndt et al. 2013). Low C_{org} stocks could also be explained by the general lack of local productivity and OM input; seagrasses were sparse and sites were separated from common terrestrial inputs by beaches. Soils in Florida Bay had higher C_{org} areal stock on average, though values varied widely with production and living biomass limited by P availability (Fig. 3; Armitage and Fourqurean 2016). While *Halodule wrightii* is common in Florida Bay, the morphology of the more common *T. testudinum* promotes deeper, more complex rhizome networks, a denser canopy, and thus a higher likelihood of increased soil C_{org} content (*see* Howard et al. 2016).

C_{inorg} in surface soils underlying seagrass in SE Brazil ranged from 0.10% to 6.34% of dry weight. Translated to areal stock, SE Brazil averaged 141.5 ± 59.9 Mg C_{inorg} ha^{-1}, putting it well below the global mean of 654 ± 24 Mg C_{inorg} ha^{-1} for seagrass ecosystems in a recent review of available data (Mazarrasa et al. 2015). There was no clear correlation between seagrass shoot density or biomass and soil C_{inorg} content in SE Brazil, similar to the analysis of global data (Mazarrasa et al. 2015), though there was a clear spatial pattern. Sediments on the southern side of Cabo Frio consistently had C_{inorg} values less than 0.6% of dry weight, placing them in the bottom 5% of seagrass ecosystems reported in Mazarrasa et al. (2015), while sediments north of the cape had a roughly fourfold higher C_{inorg} content on average. Cabo Frio marks a division between northern tropical waters provided by the Brazilian current and colder southern water provided by local upwelling and the Malvinas current (Summerhayes et al. 1976; Vicalvi and Milliman 1977). These drastically different thermal conditions not only define the degree of saturation of $CaCO_3$ in seawater (Millero 2007), that promotes calcification in the north and hinders it in the south, but also regulates the distribution of organisms that contribute to sediment C_{inorg} stocks (da Rocha et al. 1975; Melo et al. 1975). For example, the calcified green macroalgae *Halimeda*, bryozoans and coralline algae present north of Cabo Frio are markedly absent from the benthos to the south (Vicalvi and Milliman 1977). The warm waters of Florida Bay have long been regarded as a hotbed of biogenic carbonate production (Stockman et al. 1967; Bosence 1989). Warmer waters, like those in Florida Bay, are also more favorable to non-skeletal $CaCO_3$ precipitation where high temperature, salinity, and pH drive chemical precipitation (Robbins and Blackwelder 1992). Autochthonous precipitation in Florida Bay has been reported to be high enough to make the bay a net exporter of

carbonate sediment (thus C_{inorg}) to the surrounding environment (Bosence et al. 1985; Bosence 1989).

Buffering capacity of the C_{org}-C_{inorg} reaction couplet

Primary producers and calcifying organisms have previously been considered mutually beneficial. The high pH/low CO_2 conditions generated by autotrophic communities have been theorized to aid calcification by raising the $CaCO_3$ saturation state both internally within autotrophs and in overlying waters (Gattuso et al. 1999b) and there is some empirical evidence for such a mutualistic relationship (Semesi et al. 2009). Barrón et al. (2006) found high rates of net autotrophy in meadows of *Posidonia oceanica*, though half of the CO_2 uptake by NEP was negated by concurrent net $CaCO_3$ production. Applied to the Blue Carbon framework, this relationship could buffer the CO_2 sink capabilities of seagrasses and other autotrophic systems; net CO_2 consumption during periods of net autotrophy could be attenuated by CO_2 produced by concurrent calcification.

It has been argued that the real value of seagrasses in any climate change mitigation strategy derives from the large stock of C_{org} already present in seagrass sediments that could be rapidly remineralized if the seagrass beds were lost (Fourqurean et al. 2012a; Pendleton et al. 2012), though to date there is little evidence of how much of the stored C_{org} would be respired as CO_2 following habitat change. Some amount of CO_2 produced by remineralization of stored C_{org} could be consumed by the dissolution of $CaCO_3$ sediments. Ku et al. (1999) measured high rates of sediment $CaCO_3$ dissolution in Florida Bay correlated to sulfide oxidation in pore water beneath seagrasses. Yates and Halley (2006) found net dissolution of sediment $CaCO_3$ during the night, cloudy days, and other periods when respiration outweighed primary production. Local ecosystem respiration could re-dissolve signification portions of shallow water gross $CaCO_3$ production (Walter and Burton 1990; Ku et al. 1999; Yates and Halley 2006; Burdige et al. 2010). The ability of $CaCO_3$ dissolution to buffer the release of CO_2 from remineralized C_{org} is limited to areas where calcification commonly occurs and $CaCO_3$ is present. This "reaction couplet" could potentially be very important in Florida Bay where both calcification and primary production regularly occur at high rates. The lack of calcification and $CaCO_3$ stock in SE Brazil could mean that organic carbon metabolism could have a clearer, more direct effect on carbonate chemistry, pCO_2, and possibly net CO_2 exchange with the atmosphere.

There are other possible interactions between $CaCO_3$ and C_{org} that may complicate Blue Carbon assessments. Calcification and $CaCO_3$ deposition may enhance C_{org} preservation by accelerating its burial in anoxic layers of soil where remineralization is thought to be slower (Arndt et al. 2013). Further, C_{org} is more recalcitrant when formed into a matrix with mineral surfaces (Keil and Hedges 1993; Arndt et al. 2013); additional absorption sites provided via calcification could promote C_{org} preservation.

Long-term balance of net C_{org} and C_{inorg} production

The integrated effects of net calcification (calcification and $CaCO_3$ dissolution) and metabolism (photosynthesis and respiration) on carbonate chemistry have been measured previously (Barrón et al. 2006; Yates and Halley 2006; Yates et al. 2007; Anthony et al. 2011), but these methods are far from capturing the long-term, net CO_2 sequestration relevant to climate change mitigation discussions. First order approximations of integrated, long term net CO_2 invasion related to changes in water column pCO_2 can be made by taking inventory of the products of calcification and biological metabolism remaining in the sediment (i.e., particulate C_{org} and C_{inorg}). The C_{org} stored beneath seagrasses is assessed in terms of CO_2 (Fourqurean et al. 2012a) and the CO_2 mitigation potential is referenced as grounds for seagrass conservation (Howard et al. 2014; Hejnowicz et al. 2015). Mazarrasa et al. (2015) have compared molar $C_{org} : C_{inorg}$ content of seagrass sediments, indicating a slight trend toward C_{inorg} dominance, and C_{inorg} outweighs C_{org} in all recorded regions (Table 3); perhaps more emphasis needs to be placed on its importance to pCO_2 in water and exchange with the atmosphere.

Using sediment carbon content to infer historic CO_2 sequestration or potential CO_2 evasion during environmental change (both in Eq. 1 and previous studies) is, of course, not without methodological difficulties. Equation 1 assumes that soil carbon stocks and atmospheric CO_2 are quantitatively linked. The effects of marine NEP and net calcification on atmospheric CO_2 exchange have been previously discussed (Tokoro et al. 2014), though the quantity of carbon inventoried at a site does not necessarily reflect past or future atmospheric CO_2 exchange. Soil carbon imported laterally from adjacent systems would overestimate CO_2 invasion calculated by Eq. 1. Similarly, not all C_{org} and C_{inorg} remaining from NEP and calcification reactions remain in situ; Duarte and Krause-Jensen (2017) estimate that potential sequestration of seagrass carbon exported beyond the meadows may approach 30%.

More importantly to Blue Carbon mitigation strategies, CO_2 sequestered in seagrass soil is presupposed to be rereleased to the atmosphere during environmental change. This aspect of the soil carbon—atmospheric CO_2 relationship assumes high reactivity of C_{org}, despite various degrees of OM recalcitrance between compounds and their environmental settings (Arndt et al. 2013). Our discussions of $CaCO_3$ dissolution suffer from similar assumptions. For example, carbonate mineral forms vary in their solubility in seawater and therefore their saturation state (Stumm and Morgan 1996). The buffering capacity of seawater determines the air–sea CO_2 exchange potential as a result of biogeochemical reactions. This is addressed by $\Psi = 0.6$ for the

$CaCO_3$ reactions, while the equivalent value is 1 for the biological reactions (photosynthesis, respiration). The importance of these assumptions for determining the reliability of our flux calculations should be addressed in future research.

Conclusion

Seagrasses are highly valued for nutrient processing and providing habitat for commercially important species; carbon sequestration and storage could provide an additional ecosystem service to promote conservation of this threatened, globally declining ecosystem (Waycott et al. 2009; Hejnowicz et al. 2015). Our analyses show that net CO_2 sequestration by seagrasses cannot simply be calculated by measuring existing C_{org} stocks because of the relationships between net primary production and inorganic carbon reactions that also influence atmosphere-ecosystem CO_2 flux. Here, we document not only regional differences in C_{org} storage but also differences in C_{inorg} stocks related to regional ecology and abiotic features. Considered separately, an excess of carbonate production compared to biological production could suggest net production of CO_2, as is suggested for other carbonate-producing systems (Ware et al. 1992; Gattuso et al. 1999a). Considered a synergistic couplet, C_{org} and C_{inorg} processes could buffer one another's effect on CO_2 production, cushioning long-term changes in CO_2. Either way, C_{inorg} storage must be considered in Blue Carbon inventories just as inorganic carbon processes may be proven to be important in overall seagrass ecosystem CO_2 production.

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Conflict of Interest

None declared.

Submitted 19 December 2016
Revised 04 April 2017; 16 May 2017
Accepted 06 June 2017

Associate editor: Núria Marbà