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PATTERNS OF CARBON METABOLISM, STORAGE, AND REMINERALIZATION IN SEAGRASS ECOSYSTEMS

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FLORIDA INTERNATIONAL UNIVERSITY

Miami, Florida

PATTERNS OF CARBON METABOLISM, STORAGE, AND REMINERALIZATION
IN SEAGRASS ECOSYSTEMS

A dissertation submitted in partial fulfillment of the

requirements for the degree of

DOCTOR OF PHILOSOPHY

in

BIOLOGY

by

Jason Lee Howard

2018

To: Dean Michael R. Heithaus
College of Arts, Sciences and Education

This dissertation, written by Jason Lee Howard, and entitled Patterns of Carbon Metabolism, Storage, and Remineralization in Seagrass Ecosystems, having been approved in respect to style and intellectual content, is referred to you for judgment.

We have read this dissertation and recommend that it be approved.

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The dissertation of Jason Lee Howard is approved.

Dean Michael R. Heithaus
College of Arts, Sciences and Education

Andrés G. Gil
Vice President for Research and Economic Development
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Florida International University, 2018

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CHAPTER I

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ABSTRACT OF THE DISSERTATION
PATTERNS OF CARBON METABOLISM, STORAGE, AND REMINERALIZATION
IN SEAGRASS ECOSYSTEMS

by

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Florida International University, 2018

Miami, Florida

Professor James W. Fourqurean, Major Professor

Coastal marine sediments have recently been identified as globally important stocks of organic carbon (C_{org}) that, if compromised, could significantly exacerbate global greenhouse gas emissions. While resource managers and policy makers are eager to incorporate this ecosystem service into seagrass ecosystem valuation frameworks, similar to those already in existence for terrestrial forests, there has been insufficient information regarding how environmental conditions and seagrass ecology control carbon storage. These include the influence of the seagrass to the production and preservation of soil organic matter, the fate of stored carbon following conversion of coastal wetlands, and the interactions between organic and inorganic carbon cycling. This dissertation intends to understand the drivers of C_{org} storage and preservation to better prioritize and evaluate the worth of seagrasses to large scale carbon cycles and greenhouse gas mitigation planning.

Long-term experiments and thorough field surveys reveal that seagrasses are not categorically necessary nor sufficient for long-term C_{org} storage. Soil C_{org} stocks as well as their recalcitrance and breakdown rates are all correlated with sediment grain size, where muddy, fine sediments have higher C_{org} stocks that are less likely to breakdown. Sediment grain size can be influenced by the presence of seagrasses at some sites, likely where the leaf canopy can modify local hydrology enough to create a depositional environment that wouldn't otherwise exist. However, similar depositional environments that collect and

store C_{org} can be obtained through local geomorphological features and natural hydrology, independent of benthic flora. This distinction has important implications on how soil C is managed to continue its preservation.

The relation between seagrass C_{org} and CO_2 can be blurred by calcification and carbonate dissolution processes that occur concurrently, and have direct but antagonistic effects on CO_2 . Carbonate processes are dependent on local environmental factors, though augmented by biological processes, thus the ability of carbonate processes to interfere with seagrass C_{org} storage and loss is limited to geographic areas where processes can occur. Warm, shallow waters, like those in Florida Bay, encourage calcification, though the magnitude of soil inorganic and organic carbon interaction can vary locally as well.

Seagrasses are declining globally thus additional ecosystem value via greenhouse gas mitigation could greatly benefit conservation efforts. To make conservation efforts worthwhile to greenhouse gas mitigation, these findings help to consider and prioritize sites where risk and impact of C_{org} lost is more severe.

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CHAPTER 1

INTRODUCTION

Current atmospheric concentrations of CO₂ are the highest in the last 800,000 years (Lüthi et al., 2008), and there is consensus that recent increases are a result of human activity (Solomon, 2007). Roughly 50% of the anthropogenic CO₂ released in recent times has been absorbed by the biosphere and the ocean (Le Quéré et al. 2009), leaving the remaining fraction in the atmosphere to increase the greenhouse effect and alter the climate (Solomon, 2007). Though the ocean acts as a buffer against rising atmospheric CO₂, the consequence is a decrease in oceanic water pH deemed “ocean acidification” (Raven et al., 2005; Orr et al., 2005) that negatively affects a wide range of organisms (Kroeker et al., 2013). Coordinated global efforts are being made to mitigate CO₂ emissions, which have led to a renewed interest in evaluating the carbon storage and flux in the biosphere (Canadell and Raupach, 2008; Mcleod et al., 2011). Terrestrial ecosystems, primarily forests, are responsible for absorbing an estimated 30% of fossil fuel-related CO₂ emissions through photosynthesis and net growth (Canadell et al., 2007), and currently store the equivalent of twice the atmospheric carbon in their biomass (Canadell and Raupach, 2008). The alteration of terrestrial ecosystems through land use and land-cover change, accounts approximately 12.5% of total CO₂ emissions released into the atmosphere (Houghton et al., 2012). The reduction of ecosystem degradation and destruction via land use change is an important component of global strategies to curb atmospheric CO₂ emissions, thus obligatory and voluntary carbon credit markets have been developed to add economic incentive to forest conservation (Rizvi et al., 2015).

Seagrass ecosystems, as well as other coastal wetlands (mangroves and tidal marshes), have also been recognized for their ability to sequester CO₂ and preserve it in biomass and underlying soil (Mcleod et al., 2011; Pendleton et al., 2012) and have been recommended to be integrated into national greenhouse gas inventories and climate mitigation strategies by

the IPCC (Hiraishi et al., 2014). Carbon stocks bound in vegetated coastal habitats (deemed “Blue Carbon”) can surpass in density those in terrestrial ecosystems already integrated into CO₂ mitigation frameworks and markets (Pendleton et al., 2012; Fourqurean et al., 2012), thus analogs of terrestrial carbon mitigation strategies for vegetated coastal habitats (deemed “Blue Carbon strategies”) could be valuable tools for both mitigating greenhouse gas emissions while conserving coastal wetland ecosystems (Hejnowicz et al., 2015). However, there is a fundamental difference in how terrestrial and marine ecosystems sequester and preserve carbon that complicates carbon stock assessments and valuation: Blue Carbon is primarily stored in underlying sediments rather than the biomass itself (Fourqurean et al., 2012; Howard et al., 2014). Terrestrial C stocks are primarily stored in biomass, thus gains (primary production) and losses (rapid oxidation via fires and decomposition) of stored carbon are direct and clear. Carbon stocks associated with seagrasses and other Blue Carbon habitats are significant in magnitude, though their controls require understanding of interacting ecological and biogeochemical processes that influence soil organic carbon (C_{org}) storage (Lovelock et al., 2017a).

Seagrasses can turn sandy sediments into C_{org}-rich sandy muds through the production of detritus and their particle-trapping efficiency, through there are mechanisms by which accumulated carbon stocks could be lost (Duarte et al., 2010, 2011; Arndt et al., 2013). Seagrass meadows can develop a complex matrix of leaves that can decrease current velocity and alter the turbulence in a way that increases deposition (Fonseca and Fisher, 1986; Hendriks et al., 2008). The muted water movement through the canopy allows for higher retention of allochthonous production but also the increased deposition of allochthonous C_{org} and non-seagrass detritus (Duarte et al., 2010; Kennedy et al., 2010). The modified hydrology due to seagrass canopy can reduce average sediment grain size by allowing for the accumulation of fine grained particles that would not otherwise occur (Miyajima et al., 2017). Finer sediments promote O₂ consumption at the sediment surface

through enhanced microbial activity (Hargrave, 1972; DeFlaun and Mayer, 1983) while limiting the diffusive ability of solutes through to porewaters (Cook et al., 2007; Silburn et al., 2017). As a result, anoxia has been shown to develop millimeters beneath the sediment surface (Borum et al., 2005) and the density of seagrasses reduces the oxygen input via pore-water advective transport (Burdige and Zimmerman, 2002). The resulting stable, anoxic environment is thought to enhance the longterm preservation of buried C_{org} (Duarte et al., 2010; Fourqurean et al., 2012).

There is fear seagrass ecosystem loss could result in environmental changes conducive to C_{org} stock loss and remineralization. The loss of leaf canopy could prompt erosion, exposing buried C_{org} to the oxic water column (Lovelock et al., 2017b). The enhanced remineralization of C_{org} in oxic environments is expected to exacerbate and hasten CO_2 emissions from seagrass ecosystems and other coastal vegetated habitats (Lovelock et al., 2017b), though the empirical evidence is limited. Moodley et al. (2005) and Dauwe et al. (2001) suggest that remineralization rates of OM in marine sediments are suppressed under anoxic conditions, while other work suggests that anoxic conditions may even accelerate OM breakdown (Harrison, 1989). More nuanced theories suggest that the sensitivity of OM remineralization rates to oxygen availability is dependent upon the recalcitrance of the OM, where decomposition rates of fresh, labile OM are independent of O_2 availability and breakdown of “aged”, recalcitrant OM is accelerated with oxygen (Burdige, 2007; Kristensen et al., 1995; Hulthe et al., 1998; Kristensen and Holmer, 2001). The importance of burial to the preservation of C_{org} is essential to developing appropriate Blue Carbon strategies.

Seagrass degradation and loss is commonly associated with environmental changes related to coastal development, particularly eutrophication and declines in water quality (McGlathery et al., 2007; Waycott et al., 2009). Increased nutrient loading related to human activity shifts production from benthic seagrasses to short-lived, phytoplankton in

the water column. Increased algal standing stocks decrease the light available for benthic production, causing seagrass loss (McGlathery et al., 2007). Increased nutrient supply is also suspected to modify C_{org} stocks (Macreadie et al., 2017a). Sediment microbes responsible for C_{org} remineralization may be nutrient limited by the high C:N and C:P of seagrass detritus (Lopez et al., 1995, 1998), thus increases in nutrient availability, particularly in combination with an erosional environment may spur the loss of C_{org} stocks.

A substantial body of work has accumulated in soil science suggesting that the addition of fresh organic material to soil increases the rate and extent of decomposition, though this phenomena but has only recently been considered for marine sediments (Guenet et al., 2010; Bianchi, 2011). The ‘priming effect’ is used to describe modified metabolism of refractory organic material after the input of labile organic carbon (Guenet et al., 2010). Organic carbon buried in the soils beneath seagrasses are considered aged and recalcitrant compared to fresh detritus and exudates found in the water column. The proximity of coastal habitats to labile C_{org} sources (both autochthonous and via run-off) and the potential for buried, recalcitrant C_{org} to be exposed during disturbance create an ideal conditions for microbial priming (Trevathan-Tackett et al., 2018).

Along with C_{org} production, seagrass ecosystems in many areas are though to promote calcification and carbonate production. 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), and have be documented to calcify themselves (Enríquez and Schubert, 2014). Seagrass ecosystem metabolism has also been linked to carbonate saturation state with productive systems promoting calcification (Semese et al., 2009; Hendriks et al., 2014). Calcification is a net producer of CO_2 , thus acting as a carbon source and offsetting carbon sequestration by autotrophic seagrass ecosystems (Millero, 2007). At the same time, the sediments produced via

calcification can increase sediment accretion rates, augment seagrass productivity and increase sorption sites for C_{org} to bind (Brandano et al., 2017; Macreadie et al., 2017b). In environments and periods of high CO_2 and low pH, carbonate dissolution acts as an important buffer to increasing $p\text{CO}_2$ (Walter and Burton, 1990; Yates and Halley, 2006). It is unclear the net effect of C_{inorg} processes on long-term CO_2 sequestration in seagrasses and how local environmental and ecological variation may play a role.

Seagrasses can and do modify their environment in ways that promote C_{org} storage (Mateo et al., 2006; Duarte et al., 2011), though the crux of Blue Carbon science is the mechanistic connection between the ecosystem and carbon storage. Unique characteristics of seagrass meadows may facilitate C_{org} storage compared to unvegetated sites (Orth, 1977; Macreadie et al., 2015) but it is difficult to isolate the direct effects of seagrasses from a slew of confounding environmental factors that shape C_{org} storage and persistence (Lavery et al., 2013). Seagrasses are a polyphyletic group that inhabit a range of environmental conditions, thus species-specific characteristics, environmental contexts, and their interactions may be important to understanding drivers of C stocks on local or regional scales.

More important to Blue Carbon strategies is understanding when and how much C_{org} is likely to be remineralized to CO_2 and lost to the atmosphere following habitat degradation or destruction (Johannessen and Macdonald, 2016; Lovelock et al., 2017a). Projects that focus on the preservation of soil C_{org} through ecosystem conservation and management assumes that C_{org} are vulnerable to remineralization. Currently, the majority of C_{org} stock in Blue Carbon ecosystems is assumed to be vulnerable to decomposition and thus a potential source of CO_2 emissions (Fourqurean et al., 2012; Lovelock et al., 2017a). This may be premature given the wide range in lability for seagrasses and other sources of C_{org} , as well as the variability in disturbances the potential responses of soil processes (Johannessen and Macdonald, 2016; Belshe et al., 2017).

The recognition of carbon sequestration in seagrass ecosystems provides a strong argument, along side other ecosystem services (Costanza et al., 2014), for their protection and restoration. For the service to be utilized through climate change mitigation frameworks it is necessary to improve scientific understanding of the underlying mechanisms that control C_{org} storage, its preservation and its likelihood to be lost to the atmosphere following disturbance. These are also the foci of this dissertation.

Chapter II and III examine the importance of seagrass ecosystems to soil C_{org} stocks. Chapter II examines the isolated effect of fertilization and seagrasses community on C_{org} stocks while controlling for differences in geomorphological and local hydrological factors that could directly influence C_{org} storage. We revisited seagrass meadows experimentally altered by 30 years of consistent nutrient fertilization provided by roosting birds. Differences in soil C_{org} between experimental blocks were clear, though differences related to seagrass community and density were undetectable.

Chapter III further explores drivers of C_{org} soil content by measuring 45 seagrass-inhabited sites across the South Florida seascape for soil carbon stock across a range of potential environmental and biological drivers of their variation. Chapter III also considers the role seagrass species composition, seagrass density, and soil type play in C_{org} preservation. Breakdown rates of OM were determined across sites using a deployed standard substrate. As oxygen exposure and erosion have been discussed as primary drivers of decomposition and a likely fate of seagrass soil C_{org} following ecosystem loss, we also investigate the effect of OM burial on breakdown rates. Seagrass community characteristics had little ability to explain variation in C_{org} stocks and no relation to soil C_{org} preservation. Sediment grain size, somewhat influenced by seagrass density, was determined a primary driver of C_{org} stocks and the effectiveness of C_{org} preservation via burial.

Chapter IV introduces the role of the inorganic carbon cycle to the traditional Blue Carbon framework. Calcification is augmented in seagrass ecosystems, particularly in shallow tropical areas, though its production of CO₂ acts antagonistically to carbon sequestered via seagrass production and OM entrapment. When the CO₂ evasion related to CaCO₃ production is considered, seagrass ecosystems with high CaCO₃ content may have CO₂ sequestered via C_{org} accumulation negated by CO₂ produced by calcification.

Chapter V investigates the type of C stored in seagrass soil to better understand its vulnerability to remineralization and potential interactions with carbonate that may buffer CO₂ flux. Soil C_{org} was ranked using a recalcitrance index, where a stepwise stepwise, thermo-oxidation analysis of soil carbon was used to categorize C_{org} depending on its ability to be oxidized. Soil C_{org} components vary in their recalcitrance and the relative fractions of recalcitrant C_{org} vary between sites. Values of δ¹³C of seagrasses, soil C_{org}, and soil C_{inorg} suggest that there may be a buffering of remineralized CO₂ by dissolving carbonates, though the intensity is related to site-specific factors.

In conclusion, this dissertation examines the ecological and environmental factors that drive storage and preservation of C_{org} stored in seagrass soils. In south Florida, C_{org} storage and preservation are shaped by hydrology, carbon input and sediment characteristics. Seagrasses may augment soils in some locations, but more broadly, they are not necessary nor sufficient for high soil C_{org} storage. Further complicating our assessment and valuation of seagrass C_{org} stocks are the co-occurring calcification-carbonate processes that buffer the sequestration of CO₂ during primary production, but also may buffer CO₂ emissions during remineralization. Like C_{org}, the importance of C_{inorg} processes varies geographically, depending on local conditions. We have already identified seagrasses, marshes and mangrove ecosystems as more important for Blue Carbon strategies. Perhaps we should further prioritize sites for conservation and management, taking into account

local ecological and environmental characteristics that may influence C_{org} stocks and their likelihood to exacerbate greenhouse gas emissions.

Work Cited

- Arndt, S., Jørgensen, B. B., LaRowe, D. E., Middelburg, J., Pancost, R. D., and Regnier, P. (2013). Quantifying the degradation of organic matter in marine sediments: A review and synthesis. *Earth-Science Reviews*, 123:53–86.
- Belshe, E. F., Mateo, M. Á., Gillis, L., Zimmer, M., and Teichberg, M. (2017). Muddy Waters: Unintentional Consequences of Blue Carbon Research Obscure Our Understanding of Organic Carbon Dynamics in Seagrass Ecosystems. *Frontiers in Marine Science*, 4:522.
- Bianchi, T. S. (2011). The role of terrestrially derived organic carbon in the coastal ocean: A changing paradigm and the priming effect. *Proceedings of the National Academy of Sciences*, 108(49):19473–19481.
- Borum, J., Pederson, O., Greve, T. M., Frankovich, T. A., Zieman, J., Fourqurean, J. W., and Madden, C. J. (2005). The potential role of plant oxygen and sulphide dynamics in die-off events of the tropical seagrass, *Thalassia testudinum*. *Journal of ecology*, 93(1):148–158.
- Brandano, M., Pomar, L., Mateu-Vicens, G., Cuffaro, M., Gaglianone, G., Petricca, P., and Stagno, V. (2017). Response: Commentary: Evaluating the role of seagrass in cenozoic CO₂ variations. *Frontiers in Environmental Science*, 5:74.
- Burdige, D. J. (2007). Preservation of Organic Matter in Marine Sediments: Controls, Mechanisms, and an Imbalance in Sediment Organic Carbon Budgets? *Chemical Reviews*, 107(2):467–485.
- Burdige, D. J. and Zimmerman, R. C. (2002). Impact of sea grass density on carbonate dissolution in Bahamian sediments. *Limnology and Oceanography*, 47(6):1751–1763.
- Canadell, J. G., Le Quéré, C., Raupach, M. R., Field, C. B., Buitenhuis, E. T., Ciais, P., Conway, T. J., Gillett, N. P., Houghton, R. A., and Marland, G. (2007). Contributions to accelerating atmospheric CO₂ growth from economic activity, carbon intensity, and efficiency of natural sinks. *Proceedings of the National Academy of Sciences of the United States of America*, 104(47):18866–18870.
- Canadell, J. G. and Raupach, M. R. (2008). Managing forests for climate change mitigation. *Science*, 320(5882):1456–1457.
- Collado-Vides, L., Caccia, V. G., Boyer, J. N., and Fourqurean, J. W. (2007). Tropical seagrass-associated macroalgae distributions and trends relative to water quality. *Estuarine, Coastal and Shelf Science*, 73:680–694.
- Cook, P. L., Wenzhöfer, F., Glud, R. N., Janssen, F., and Huettel, M. (2007). Benthic solute exchange and carbon mineralization in two shallow subtidal sandy sediments: Effect of advective pore-water exchange. *Limnology and Oceanography*, 52(5):1943–1963.

- Costanza, R., de Groot, R., Sutton, P., van der Ploeg, S., Anderson, S. J., Kubiszewski, I., Farber, S., and Turner, R. K. (2014). Changes in the global value of ecosystem services. *Global Environmental Change*, 26:152–158.
- Dauwe, B., Middelburg, J., and Herman, P. (2001). Effect of oxygen on the degradability of organic matter in subtidal and intertidal sediments of the North Sea area. *Marine Ecology Progress Series*, 31.
- DeFlaun, M. F. and Mayer, L. M. (1983). Relationships between bacteria and grain surfaces in intertidal sediments. *Limnology and Oceanography*, 28(5):873–881.
- Duarte, C. M., Kennedy, H., Marbà, N., and Hendriks, I. (2011). Assessing the capacity of seagrass meadows for carbon burial: Current limitations and future strategies. *Ocean and Coastal Management*, 83:32–38.
- Duarte, C. M., Marbà, N., Gacia, E., Fourqurean, J. W., Beggins, J., Barrón, C., and Apostolaki, E. T. (2010). Seagrass community metabolism: Assessing the carbon sink capacity of seagrass meadows. *Global Biogeochemical Cycles*, 24(4):GB4032.
- Enríquez, S. and Schubert, N. (2014). Direct contribution of the seagrass *Thalassia testudinum* to lime mud production. *Nature Communications*, 5.
- Fonseca, M. S. and Fisher, J. S. (1986). A comparison of canopy friction and sediment movement between four species of seagrass with reference to their ecology and restoration. *Marine Ecology Progress Series*, 29(1):15–22.
- Fourqurean, J. W., Duarte, C. M., Kennedy, H., Marbà, N., Holmer, M., Mateo, M. A., Apostolaki, E. T., Kendrick, G. A., Krause-Jensen, D., McGlathery, K. J., and Serano, O. (2012). Seagrass ecosystems as a globally significant carbon stock. *Nature Geoscience*, 5(7):505–509.
- Frankovich, T. A. and Zieman, J. C. (1994). Total epiphyte and epiphytic carbonate production on *Thalassia testudinum* across Florida Bay. *Bulletin of Marine Science*, 54(3):679–695.
- Guenet, B., Danger, M., Abbadie, L., and Lacroix, G. (2010). Priming effect: bridging the gap between terrestrial and aquatic ecology. *Ecology*, 91(10):2850–2861.
- Hargrave, B. T. (1972). Aerobic decomposition of sediment and detritus as a function of particle surface area and organic content. *Limnology and Oceanography*, pages 583–596.
- Harrison, P. G. (1989). Detrital processing in seagrass systems: a review of factors affecting decay rates, remineralization and detritivory. *Aquatic Botany*, 35(3-4):263–288.
- Hejnowicz, A. P., Kennedy, H., Rudd, M. A., and Huxham, M. R. (2015). Harnessing the climate mitigation, conservation and poverty alleviation potential of seagrasses: prospects for developing blue carbon initiatives and payment for ecosystem service programmes. *Frontiers in Marine Science*, 2:32.

- Hendriks, I. E., Olsen, Y. S., Ramajo, L., Basso, L., Steckbauer, A., Moore, T. S., Howard, J., and Duarte, C. M. (2014). Photosynthetic activity buffers ocean acidification in seagrass meadows. *BG*, 11(2):333–346.
- Hendriks, I. E., Sintes, T., Bouma, T. J., and Duarte, C. M. (2008). Experimental assessment and modeling evaluation of the effects of the seagrass *Posidonia oceanica* on flow and particle trapping. *Marine Ecology Progress Series*, 356:163–173.
- Hiraishi, T., Krug, T., Watanabe, K., Srivastava, N., Baasansuren, J., Fukuda, M., and Troxler, T. (2014). 2013 Supplement to the 2006 IPCC guidelines for national greenhouse gas inventories: wetlands . IPCC, Switzerland.
- Houghton, R. A., House, J., Pongratz, J., Van Der Werf, G., DeFries, R., Hansen, M., Quéré, C. L., and Ramankutty, N. (2012). Carbon emissions from land use and land-cover change. *Biogeosciences*, 9(12):5125–5142.
- Howard, J., Hoyt, S., Isensee, K., Telszewski, M., Pidgeon, E., et al. (2014). *Coastal blue carbon: methods for assessing carbon stocks and emissions factors in mangroves, tidal salt marshes, and seagrasses*. Conservation International, Intergovernmental Oceanographic Commission of UNESCO, International Union for Conservation of Nature, Arlington, Va, USA.
- Hulthe, G., Hulth, S., and Hall, P. O. (1998). Effect of oxygen on degradation rate of refractory and labile organic matter in continental margin sediments. *Geochimica et Cosmochimica Acta*, 62(8):1319–1328.
- Johannessen, S. C. and Macdonald, R. W. (2016). Geoengineering with seagrasses: is credit due where credit is given? *Environmental Research Letters*, 11(11):1–10.
- Kennedy, H., Beggins, J., Duarte, C. M., Fourqurean, J. W., Holmer, M., Marbà, N., and Middelburg, J. J. (2010). Seagrass sediments as a global carbon sink: Isotopic constraints. *Global Biogeochemical Cycles*, 24(4):GB4026.
- Kristensen, E., Ahmed, S. I., and Devol, A. H. (1995). Aerobic and anaerobic decomposition of organic matter in marine sediment: Which is fastest? *Limnology and Oceanography*, pages 1430–1437.
- Kristensen, E. and Holmer, M. (2001). Decomposition of plant materials in marine sediment exposed to different electron acceptors O₂, NO₃, and SO₄²⁻, with emphasis on substrate origin, degradation kinetics, and the role of bioturbation. *Geochimica et Cosmochimica Acta*, 65(3):419–433.
- Kroeker, K. J., Kordas, R. L., Crim, R., Hendriks, I. E., Ramajo, L., Singh, G. S., Duarte, C. M., and Gattuso, J.-P. (2013). Impacts of ocean acidification on marine organisms: quantifying sensitivities and interaction with warming. *Global Change Biology*, 19(6):1884–1896.
- Lavery, P. S., Mateo, M. A., Serrano, O., and Rozaimi, M. (2013). Variability in the Carbon Storage of Seagrass Habitats and Its Implications for Global Estimates of Blue Carbon Ecosystem Service. *PLoS ONE*, 8(9):e73748.

- Lopez, N., Duarte, C., Vallespinos, F., Romero, J., and Alcoverro, T. (1995). Bacterial activity in NW Mediterranean seagrass (*Posidonia oceanica*) sediments. *Journal of Experimental Marine Biology and Ecology*, 187:39–49.
- Lopez, N., Duarte, C. M., Vallespinos, F., Romero, J., and Alcoverro, T. (1998). The effect of nutrient additions on bacterial activity in seagrass (*Posidonia oceanica*) sediments. *Journal of Experimental Marine Biology and Ecology*, 224:155–166.
- Lovelock, C. E., Atwood, T., Baldock, J., Duarte, C. M., Hickey, S., Lavery, P. S., Masqué, P., Macreadie, P. I., Ricart, A. M., Serrano, O., and Steven, A. (2017a). Assessing the risk of carbon dioxide emissions from blue carbon ecosystems. *Frontiers in Ecology and the Environment*, 15(5):257–265.
- Lovelock, C. E., Fourqurean, J. W., and Morris, J. T. (2017b). Modeled CO₂ Emissions from Coastal Wetland Transitions to Other Land Uses: Tidal Marshes, Mangrove Forests, and Seagrass Beds. *Frontiers in Marine Science*, 4:143.
- Lüthi, D., Le Floch, M., Bereiter, B., Blunier, T., Barnola, J.-M., Siegenthaler, U., Raynaud, D., Jouzel, J., Fischer, H., and Kawamura, K. (2008). High-resolution carbon dioxide concentration record 650,000–800,000 years before present. *Nature*, 453(7193):379.
- Macreadie, P. I., Nielsen, D. A., Kelleway, J. J., Atwood, T. B., Seymour, J. R., Petrou, K., Connolly, R. M., Thomson, A. C., Trevathan-Tackett, S. M., and Ralph, P. J. (2017a). Can we manage coastal ecosystems to sequester more blue carbon? *Frontiers in Ecology and the Environment*, 57:1492.
- Macreadie, P. I., Serrano, O., Maher, D. T., Duarte, C. M., and Beardall, J. (2017b). Addressing calcium carbonate cycling in blue carbon accounting. *Limnol. Oceanogr.*, 31:513.
- Macreadie, P. I., Trevathan-Tackett, S. M., Skilbeck, C. G., Sanderman, J., Curlevski, N., Jacobsen, G., and Seymour, J. R. (2015). Losses and recovery of organic carbon from a seagrass ecosystem following disturbance. *Proceedings of the Royal Society B: Biological Sciences*, 282(1817):20151537.
- Mateo, M., Cebrián, J., Dunton, K., and Mutchler, T. (2006). Carbon flux in seagrass ecosystems. In *Seagrasses: Biology, Ecology and Conservation*, pages 159–192. Springer.
- McGlathery, K. J., Sundbäck, K., and Anderson, I. C. (2007). Eutrophication in shallow coastal bays and lagoons: the role of plants in the coastal filter. *Marine Ecology Progress Series*, 348:1–18.
- McLeod, E., Chmura, G. L., Bouillon, S., Salm, R., Björk, M., Duarte, C. M., Lovelock, C. E., Schlesinger, W. H., and Silliman, B. R. (2011). A blueprint for blue carbon: toward an improved understanding of the role of vegetated coastal habitats in sequestering CO₂. *Frontiers in Ecology and the Environment*, 9(10):552–560.
- Millero, F. J. (2007). The Marine Inorganic Carbon Cycle. *Chemical Reviews*, 107(2):308–341.

- Miyajima, T., Hori, M., Hamaguchi, M., Shimabukuro, H., and Yoshida, G. (2017). Geophysical constraints for organic carbon sequestration capacity of *Zostera marina* seagrass meadows and surrounding habitats. *Limnology and Oceanography*, 62(3):954–972.
- Moodley, L., Middelburg, J. J., Herman, P. M. J., Soetaert, K., and de Lange, G. J. (2005). Oxygenation and organic-matter preservation in marine sediments: Direct experimental evidence from ancient organic carbon-rich deposits. *Geology*, 33(11):889.
- Orr, J. C., Fabry, V. J., Aumont, O., Bopp, L., Doney, S. C., Feely, R. A., Gnanadesikan, A., Gruber, N., Ishida, A., Joos, F., Key, R. M., Lindsay, K., Maier-Reimer, E., Matear, R., Monfray, P., Mouchet, A., Najjar, R. G., Plattner, G.-K., Rodgers, K. B., Sabine, C. L., Sarmiento, J. L., Schlitzer, R., Slater, R. D., Totterdell, I. J., Weirig, M.-F., Yamanaka, Y., and Yool, A. (2005). Anthropogenic ocean acidification over the twenty-first century and its impact on calcifying organisms. *Nature*, 437(7059):681–686.
- Orth, R. J. (1977). The importance of sediment stability in seagrass communities. pages 281–300.
- Pendleton, L., Donato, D. C., Murray, B. C., Crooks, S., Jenkins, W. A., Sifleet, S., Craft, C., Fourqurean, J. W., Kauffman, J. B., Marbà, N., Magonigal, P., Pidgeon, E., Herr, D., Gordon, D., and Baldera, A. (2012). Estimating Global “Blue Carbon” Emissions from Conversion and Degradation of Vegetated Coastal Ecosystems. *PLoS ONE*, 7(9):e43542.
- Raven, J., Caldeira, K., Elderfield, H., Hoegh-Guldberg, O., Liss, P., Riebesell, U., Shepherd, J., Turley, C., and Watson, A. (2005). *Ocean acidification due to increasing atmospheric carbon dioxide*. The Royal Society.
- Rizvi, A. R., Baig, S., and Verdone, M. (2015). Ecosystems based adaptation: knowledge gaps in making an economic case for investing in nature based solutions for climate change. *Gland, Switzerland: IUCN*, 48.
- Semesi, I. S., Beer, S., and Björk, M. (2009). Seagrass photosynthesis controls rates of calcification and photosynthesis of calcareous macroalgae in a tropical seagrass meadow. *Marine Ecology Progress Series*, 382:41–48.
- Silburn, B., Kröger, S., Parker, E. R., Sivyer, D. B., Hicks, N., Powell, C. F., Johnson, M., and Greenwood, N. (2017). Benthic pH gradients across a range of shelf sea sediment types linked to sediment characteristics and seasonal variability. *Biogeochemistry*, 135(1):69–88.
- Solomon, S. (2007). *Climate change 2007-the physical science basis: Working group I contribution to the fourth assessment report of the IPCC*, volume 4. Cambridge university press.
- Trevathan-Tackett, S. M., Thomson, A. C. G., Ralph, P. J., and Macreadie, P. I. (2018). Science of the Total Environment. *Science of the Total Environment*, 621:1–7.
- van der Heide, T., Govers, L. L., de Fouw, J., Olf, H., van der Geest, M., van Katwijk, M. M., Piersma, T., van de Koppel, J., Silliman, B. R., Smolders, A. J. P., and van Gils, J. A. (2012). A Three-Stage Symbiosis Forms the Foundation of Seagrass Ecosystems. *Science*, 336(6087):1432–1434.

- Walter, L. M. and Burton, E. A. (1990). Dissolution of recent platform carbonate sediments in marine pore fluids. *American Journal of Science*, 290(6):601–643.
- Waycott, M., Duarte, C. M., Carruthers, T. J. B., Orth, R. J., Dennison, W. C., Olyarnik, S., Calladine, A., Fourqurean, J. W., Heck, K. L., Hughes, A. R., Kendrick, G. A., Kenworthy, W. J., Short, F. T., and Williams, S. L. (2009). Accelerating loss of seagrasses across the globe threatens coastal ecosystems. *Proceedings of the National Academy of Sciences*, 106(30):12377–12381.
- Yates, K. K. and Halley, R. B. (2006). Diurnal variation in rates of calcification and carbonate sediment dissolution in Florida Bay. *Estuaries and Coasts*, 29(1):24–39.

CHAPTER 2
FERTILIZATION CHANGES SEAGRASS COMMUNITY STRUCTURE BUT
NOT BLUE CARBON STORAGE: RESULTS FROM A 30-YEAR FIELD
EXPERIMENT

Abstract

Seagrass ecosystems are attracting attention as potentially important tools for carbon (C) sequestration, comparable to those terrestrial and aquatic ecosystems already incorporated into climate change mitigation frameworks. Despite the relatively low C stocks in living biomass, the soil organic carbon pools beneath seagrass meadows can be substantial. We tested the relationship between soil C storage and seagrass community biomass, productivity, and species composition by revisiting meadows experimentally altered by 30 years of consistent nutrient fertilization provided by roosting birds. While the benthos beneath experimental perches has maintained dense, *Halodule wrightii*-dominated communities compared to the sparse *Thalassia testudinum*-dominated communities at control sites, there were no significant differences in soil organic carbon stocks in the top 15 cm. Although there were differences in $\delta^{13}\text{C}$ of the dominant seagrass species at control and treatment sites, there was no difference in soil $\delta^{13}\text{C}$ between treatments. Averages for soil organic carbon content ($2.57 \pm 0.08\%$) and $\delta^{13}\text{C}$ ($-12.0 \pm 0.3\text{‰}$) were comparable to global averages for seagrass ecosystems, however our findings question the relevance of local-scale seagrass species composition or density to soil organic carbon pools in some environmental contexts.

Introduction

Organic carbon (C_{org}) storage and flux in coastal ecosystems has been of academic interest for over two decades (Smith, 1981) but has recently undergone a revival in light of climate change mitigation efforts. Seagrass ecosystems have been identified as globally significant C_{org} sinks (Duarte et al., 2005; Mcleod et al., 2011) with stocks comparable to terrestrial ecosystems already acknowledged for their carbon storage abilities (Fourqurean et al., 2012a). Understanding the environmental and ecological controls of C_{org} stocks, particularly during environmental change, is crucial for both global carbon budgeting, and more pragmatically, mitigating greenhouse gas emissions (Macreadie et al., 2014). It is clear that seagrasses can and do modify their environment in ways that promote C_{org} storage (Mateo et al., 2006; Duarte et al., 2011), however very seldom have these mechanisms been empirically shown to function at magnitudes and timescales that are applicable to localized disturbance regimes, climate change and global carbon cycles.

The majority of C_{org} bound in seagrass ecosystems is stored in the soils below the seagrass meadows rather than the biomass itself (Fourqurean et al., 2012a). Optimal conditions for C_{org} storage include high inputs of C_{org} along with low or infrequent disturbance, a depositional environment and anoxic soils (Duarte et al., 2011; Fourqurean et al., 2012a). High C_{org} input from seagrass is fueled by high productivity of seagrass meadows and typically low grazing pressure (Westlake 1963; Zieman and Wetzel 1980; Enriquez et al. 1993; Duarte and Cebrian 1996; but see Heck and Valentine 2006). This direct contribution of seagrass C_{org} to soil stock is evident from enriched soil ^{13}C values which reflect those of seagrasses, though large portions of stored C_{org} can be sourced to other, cohabiting marine primary producers (e.g. macroalgae and seagrass epiphytes) as well as imported (allochthonous) organic matter from other terrestrial and aquatic systems (Kennedy et al., 2010).

The seagrass canopy, comprised of a complex matrix of seagrass leaves, often decreases current velocity and alters the turbulence in a way that increases deposition and adds allochthonous C_{org} to soil stocks (Ward et al., 1984; Fonseca and Fisher, 1986; Hendriks et al., 2008). The relative contribution of non-seagrass sources of C_{org} to soil stocks varies greatly and can be estimated by the C isotopic composition of the soil relative to its sources (Kennedy et al., 2010). Generally, high ratios of $^{13}C/^{12}C$ suggest greater seagrass input while lower ratios are indicative of non-seagrass sources like autochthonous algae or allochthonous C_{org} from non-seagrass sources (Gacia et al., 2002). Once buried, the stable, anoxic conditions of seagrass soils are thought to lead to enhanced C_{org} preservation (Duarte et al., 2011). In some cases, buried organic matter can persist for millennia (Mateo and Romero, 1997; López-Sáez et al., 2009), as is the case for parts of Florida Bay (Fourqurean et al. 2012b).

These characteristics may facilitate carbon storage in seagrass ecosystems compared to unvegetated sites but it is difficult to assess their effect on long-term C_{org} storage. In some systems, higher C_{org} content has been found in soils underlying seagrasses compared to nearby unvegetated sediment (Greiner et al., 2013; Marbà et al., 2015; Ricart et al., 2015), while in other locations there is no clear relationship between seagrass biomass and soil C_{org} stocks (Campbell et al., 2014). Further, seagrass meadows of different species composition have been shown to vary 18-fold in C_{org} stocks, ostensibly because of interspecific differences in rates of production, effects on sediment stabilization and environmental context (Lavery et al., 2013). A common hurdle for understanding the effect of seagrasses on net C_{org} storage is separating the effect of the seagrass community from those direct effects of the environment. In Florida Bay, Armitage and Fourqurean (2016) noted a 300% difference in regional soil C_{org} storage across a naturally occurring productivity gradient (driven by nutrient availability) but saw no difference in soil C_{org} content when local productivity was increased by nutrient fertilization. Differences in

geomorphological and hydrological factors that control sedimentation and erosion can differ across the seascape and between patches of seagrass. Thus, simple correlations among seagrass species composition, biomass and soil C_{org} would be confounded by such spatial variability in the sedimentary environment linked to local hydrodynamics. These environmental effects can be both confounding as well as act synergistically with seagrass communities (Folmer et al., 2012).

Seagrass communities themselves could control the long-term storage of sediment C_{org} , and thus be important to greenhouse gas mitigation efforts and global carbon budgets, if 1) seagrasses enhance the input of C_{org} into the long-term soil carbon pool or 2) seagrasses prevent the erosion, decomposition and remineralization of the sediment C_{org} pool that would otherwise occur. Both propositions would support the importance of seagrasses in augmenting long-term C_{org} storage, though the latter would additionally support the importance of seagrasses to secure the globally significant soil C_{org} stocks already in existence. Published C_{org} burial estimates for seagrass meadows are strikingly high, however they are largely based on net primary production (NPP), short term sediment accretion studies, or a few species noted for their peat-like sediment mattes (Duarte et al., 2005, 2010). These indicators of long-term C_{org} storage may not be generalizable to all seagrass species and locations, particularly for a large, diverse, polyphyletic group like the seagrasses.

Decomposition, in contrast to burial, is thought to occur at low rates in seagrass meadows because of stable, anoxic soils that prevent aerobic metabolism (Duarte et al., 2010; Fourqurean et al., 2012a). Decomposing microbes may also be limited by high C:N and C:P ratios of sediment organic matter and perhaps by nutrient competition with seagrasses (Enriquez et al., 1993; Lopez et al., 1995, 1998). While issues of decomposition have been addressed in seagrass ecosystems (Harrison, 1989; Mateo et al., 2006), most

studies have focused on early decomposition, rather than the altered decomposition of aged, buried C_{org} that would be of interest to long-term carbon storage.

The aim of this study was to investigate controls of sediment C_{org} storage over a three decade period, specifically addressing 1) whether seagrass species composition and biomass, and 2) nutrient enrichment influence sediment C_{org} storage. To control for confounding differences in geomorphological and local hydrological factors that could directly influence C_{org} storage, we took advantage of an experiment that has been running continuously for 31 years. The original experiment altered nutrient input, seagrass and animal community composition, rates of net primary production, and biomass within experimental blocks. We hypothesized that higher seagrass biomass would result in greater trapping and preservation of C_{org} in sediment, but also that fertilization of seagrass meadows could relieve nutrient limitation of decomposers, resulting in decreased sediment C_{org} . We also predicted that organic matter with higher C:N and C:P ratios would be less likely to decompose, and thus more likely to persist in sediments. This hypothesis could be supported if soil ^{13}C signatures are more similar to those of local seagrass, particularly the carbon-rich *T. testudinum*, compared with those of *H. wrightii* and algae. This study addresses the controls of long-term C_{org} storage in seagrass ecosystems, an understanding of which is vital for determining the causal relationship between seagrass ecosystems and their associated organic carbon stocks.

Materials and Methods

This study was conducted on Cross Bank (Figure 2.1), a shallow (<50 cm deep) carbonate mud bank in east-central Florida Bay spanning east-west from 25°00.25' N 80°33.5' W to 25°00.6' N 80°36.6' W. Cross Bank, like most of the inner regions of Florida Bay, is severely phosphorus limited because of high N:P in freshwater runoff and low mobility

of P across the landscape owing to the adsorption of P onto carbonate sediments (Powell et al., 1989, 1991; Fourqurean et al., 1992, 1995; Herbert and Fourqurean, 2008). At this site, the benthos is dominated by the seagrass species *T. testudinum* interspersed with *H. wrightii* along with macroalgae *Penicillus capitatus*, *Halimeda monile*, and *Laurencia* sp., with sparse presence of *Batophora* sp., and *Dictyota* sp. In 1981, Cross Bank was the site of a study investigating the feeding behavior of wading birds nesting on the nearby mangrove islands (Powell et al., 1985). Markers were installed at 100 m intervals along the bank to serve as location references for behavioral studies, and these markers became bird perches frequented by piscivorous seabirds. Halos of dense seagrass approximately 1 - 2 m in diameter formed around the bird perches, hypothesized to be a result of nutrient input from the feces of the roosting seabirds. In 1983, this hypothesis was tested when five of the perch locations (600 m, 1200 m, 1800 m, 2400 m and 3100 m from the eastern end of Cross Bank) were selected as experimental sites (Powell et al., 1989). At each of these sites, the original perch was removed. Then, two additional stakes were installed five meters from the discontinued bird perch; a new perch consisting of a wooden block (5 cm x 10 cm x 10 cm) on top of PVC pipe (1.2 cm dia.) along with a control stake consisting of PVC sharpened to a point to prevent roosting. The resulting experimental design consisted of five sites, each with a fertilization treatment and control that has persisted for 31 years. Further site descriptions can be found in Powell et al. (1989), Fourqurean et al. (1995) and Ferguson (2008).

Sample Collection

In February and March 2014, we collected three replicate sediment samples from experimental bird perches and their associated controls from each of the five sites. Samples were taken haphazardly from the area extending 20 cm from the PVC bird perches and control stakes. Surface soils were collected using 60 mL plastic syringes that had been

modified into small piston cores (1 cm diameter, 3.0 cm depth). Deeper soil fractions were collected using a Russian Peat Borer (Aquatic Research Instruments Inc.) that produced soil cores 50 cm long by 5 cm in diameter. The extracted cores were subsampled at 10 cm (10 - 13 cm beneath surface) and 15 cm (15 - 18 cm beneath surface) by removing 3 cm core segments. The combination of methods resulted in samples from three depth fractions: 0 - 3 cm, 10 - 13 cm and 15 - 18 cm. Due to the nature of the sampling methods, soil compaction was minimized. Soils samples of known volumes were picked free of living plant tissue and stored in 18 oz pre-weighed bags (Whirlpak, Nasco), and transported to the lab for further preparation and analysis.

Surveys of seagrass standing crop (aboveground biomass) were completed in November 2014 to remain consistent and comparable with historical data. As sampling has been consistently conducted in November throughout the experiment's 31 years, seasonal variation in seagrass biomass and well as any related ecological function is lost. Small quadrats ($n = 3$, 10 cm \times 10 cm) were randomly placed within 30 cm of experimentally installed PVC stakes, from which all living, aboveground seagrass biomass was harvested. Seagrass leaves were separated by species, scraped of all epiphytes using a razor blade, rinsed and dried at 65 °C until a constant weight. We saw no sign of herbivory (bite or grazing marks) in the collected samples. Dried seagrass material was weighed, reported for individual species and total seagrass biomass, and compared to historic data (Powell et al., 1989, 1991; Fourqurean et al., 1995; Herbert and Fourqurean, 2008). Seagrass and soil samples were collected in different seasons though our interests in long-term C_{org} storage imply that temporary, seasonal differences in soil composition can be disregarded. Dry samples of each species were pooled within each replicate, homogenized and ground to a fine powder using a motorized mortar and pestle in preparation for stable isotope analysis.

Soil Analyses

Soil samples were analyzed for dry bulk density, organic and elemental content (C, N, P) as well as C_{org} content and $\delta^{13}\text{C}$. Soil samples of known volumes were stored on ice in pre-weighed sample collection bags until they were dried at 65 °C for a minimum of 48 hours to obtain a dry weight. Dry bulk density (DBD) was calculated as the dry weight of the soil divided by the volume of the original soil sample and expressed as gram dry weight per cubic centimeter.

The dried soil samples were homogenized and ground to a fine powder using a motorized mortar and pestle. Powdered samples were analyzed for total carbon (TC) and nitrogen content using a CHN analyzer (Fisons NA1500). Given the high calcium carbonate content of Florida Bay soils (Bosence, 1989a), it was necessary to account for the inorganic carbon (C_{inorg}) in the soil samples in order to measure C_{org} . Subsamples of dried material were weighed, ashed at 500 °C for five hours and reweighed, enabling organic content to be calculated as loss on ignition (LOI). To measure the C_{org} content of the soil samples, we used the instrumental analyzer-dry oxidation procedures described by Fourqurean et al. (2012b). In brief, ashed soil samples remaining after the LOI technique were reanalyzed using a CHN analyzer to quantify the C_{inorg} . The C_{inorg} content of the ash was used to calculate the C_{org} as $\text{TC} - C_{\text{inorg}}$ after scaling C_{inorg} back to the original soil weight using LOI. Though there is a correlation between LOI values and % C_{org} (Fourqurean et al., 2012a), only values of C_{org} are presented here. 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). Elemental content of phosphorus in soil samples was calculated on a dry weight basis.

Stable Isotope Analysis

Dry, homogenized samples of seagrasses and soil (0 and 15 cm depth fractions only) from each replicate were fumed with HCl for >7 days prior to isotopic analyses to remove associated carbonates. Samples were then redried and analyzed for $\delta^{13}\text{C}$ using standard elemental analyzer isotope ratio mass spectrometer (EA-IRMS) procedures. The elemental analyzer was used to combust the organic matter and to subsequently reduce the formed carbon-containing gases to CO_2 , which was then measured on a Finnigan MAT Delta C IRMS in a continuous flow mode. These results are presented with respect to the international standards of Vienna Pee Dee belemnite (V-PDB) for carbon using the secondary standards IAEA CH-6 for $\delta^{13}\text{C}$. Analytical reproducibility of the reported δ values was better than ± 0.08 for $\delta^{13}\text{C}$, based on sample replicates.

Data Analysis

The average aboveground biomass values of the three quadrats at each experimental replicate were used in statistical analyses. The effect of bird perch on total aboveground biomass as well as seagrass species specific weight contributions were assessed using a repeated measures analysis of variance with treatment (bird perch vs control) as the within-subject factor. Each site (consisting of one experimental set of stakes) constituted a subject in these analyses. The procedure was run separately for total biomass and species-specific contributions to total biomass $\delta^{13}\text{C}$ values of *T. testudinum* and *H. wrightii* leaf tissue were analyzed for treatment effects using a similar ANOVA. Data containing unequal variances were tested using Friedman's or Mann-Whitney-Wilcoxon tests depending if subjects were included.

Sediment cores from each PVC stake ($n = 3$) were averaged for each replicate prior to statistical investigation. Differences in soil characteristics as a function of both treatment and depth were assessed using mixed-model univariate repeated measures analysis of

variance with treatment and depth fraction as within-subject factors. Each site (consisting of one experimental set of stakes) constituted a subject in these analyses. Four of these ANOVAs were run; one for each nitrogen, phosphorus, $\delta^{13}\text{C}$ and C_{org} content of the soil. If data for any analysis did not meet one of the test's distribution-based assumptions, a Friedman's test for a randomized complete block design was used, classifying each subject as an experimental block. Treatment effect was then tested for each depth fraction.

Soil C_{org} content data was then compared to seagrass standing crop for each replicate for the two dominant seagrasses, *H. wrightii* and *T. testudinum*, as well as total seagrass standing crop using a Model II Linear Regression due to the error associated with both variables. This test was performed three times, once for each seagrass species as well as total aboveground biomass. A similar Model II Regression was used to test for a relationship between soil carbon density ($\text{mg C}_{\text{org}} \text{cm}^{-3}$) and the measured benthic community variables. Differences in soil $\delta^{13}\text{C}$ between depth fractions and treatments were tested using ANOVA or Mann–Whitney–Wilcoxon procedures after data were checked for normality and equal variances.

Results

Differences in aboveground seagrass biomass at treatment and control plots were similar to those previously reported (Powell et al., 1991; Fourqurean et al., 1995; Herbert and Fourqurean, 2008) with aboveground biomass from *H. wrightii* significantly higher at bird perch treatments compared to control sites (Figure 2.2; ANOVA, $p < 0.05$) with a mean difference of $92.0 \pm 15.5 \text{ g m}^{-2}$. Bird perches and controls did not show a significant difference in *T. testudinum* aboveground biomass ($p > 0.05$), likely due to a single leverage point (Figure 2.2). However there were significantly lower contributions of *T. testudinum* to total aboveground biomass from the bird perch treatments compared to control treatments

with a mean difference of 79.0 ± 12.6 %. Despite the documented effect of bird perches on aboveground biomass for individual species, differences between total aboveground seagrass biomass have not been consistent over the history of the experimental plots. Our sampling did not show a statistical difference between total aboveground biomass at the bird perch treatment and control sites when we sampled (ANOVA, $p > 0.05$).

Soil Characteristics

Dry bulk density (DBD) on Cross Bank was 0.59 ± 0.02 g mL⁻¹ and remained indistinguishable between bird perch and control sites with a mean difference of 0.00 ± 0.04 g mL⁻¹ (ANOVA, $p > 0.95$). There were, however, differences in DBD between five experimental blocks (ANCOVA, $p < 0.05$) with an average DBD ranging between 0.48 and 0.69 g mL⁻¹ for sites with the most extreme soil densities (Figure 2.3). DBD on average was lowest in surface soils, increasing down core by 0.01 g mL⁻¹ per cm of core depth. DBD was negatively correlated with C_{org} and N across the sites (Figure 2.4, linear regression, $p < 0.05$). There was a positive correlation between soil C_{org} and N content (Figure 2.5) though no correlation between soil P content and C_{org} content. DBD in surface soils showed a positive correlation with proximity to inhabited land (linear regression, $p < 0.05$).

The fertilization effect from roosting birds can be seen throughout the first 15 cm of soil with an average soil phosphorus content of 992 ± 341 µg P g⁻¹ at experimental bird perch plots compared to control plots of 64 ± 25 µg P g⁻¹ and the Florida Bay average of 99.5 ± 20.0 µg g⁻¹ (Fourqurean et al., 2012b). Sediment phosphorus was significantly different between bird perches and controls for all depth fractions (Friedman's test, $p < 0.05$). Within the bird perch treatments, there was no significant correlation between soil depth and phosphorus concentration (ANOVA, $p > 0.05$), and soil phosphorus concentrations for bird perch treatments exhibited different down-core patterns between sites (Figure 2.6)

ranging from consistently low P concentrations at Site 1, to differences in down-core soil P concentrations that range over two orders of magnitude (Sites 4 and Site 5).

Soil nitrogen content was slightly higher at bird perch treatments than controls (0.27 ± 0.01 % of dry weight and 0.25 ± 0.01 %, respectively; Figure 2.7; ANOVA, $p < 0.05$), but this slight difference was negligible. We also noted a varying N content of soils between the five sites; N content increased with proximity to inhabited land (linear regression, $p < 0.05$), ranging from an average of 0.29 % N at site 1 to an average of 0.23 % at site 5 but was also decreased with soil DBD (linear regression, $p < 0.05$). There was no effect of soil depth on N content (ANOVA, $p > 0.05$).

C_{org} content of the soil samples averaged 2.57 ± 0.08 % of dry weight across all samples collected, ranging between 1.12 to 4.64 % of dry weight. These values fall near the global mean of 2.5 ± 0.1 % and the more commonly used median of 1.8 % (Fourqurean et al., 2012a), as well as the average value reported for Florida Bay of 2.1 ± 0.3 % (Fourqurean et al., 2012b).

Long-term fertilization changed the nature of the seagrass community in our study site from *T. testudinum*-dominated to *H. wrightii*-dominated however, there were no significant differences in soil C_{org} content between these two benthic community types (Figure 2.8; ANOVA, $p > 0.05$). Similarly, there were no significant differences in C_{org} density (measured as $\text{g } C_{\text{org}} \text{ mL}^{-1}$) between controls and experimental plots. There were, however, significant differences in C_{org} content between the study sites (Figure 2.9, ANOVA between subject, $p < 0.05$). Site 1 had the highest average C_{org} content (2.95 ± 0.06 % of dry weight), while Site 5 had on average the lowest C_{org} content (2.12 ± 0.17 % of dry weight) throughout the core. A significant depth effect was not observed (ANOVA, $p > 0.05$). These trends correlate with soil DBD across the five sites.

Densities of both *H. wrightii* and *T. testudinum* varied within both perch and control sites. Ignoring the experimental setup, linear models were constructed between seagrass

densities and their respective surface soil C_{org} content including data from both experimental and control plots (Figure 2.10). There was no evidence for a correlation between *H. wrightii*, *T. testudinum*, or total seagrass aboveground biomass with C_{org} content in surface soils (Model II Linear Regression, $P > 0.1$). Similarly, there was no correlation between soil C_{org} stock in the first 3 cm and any of the measured benthic community variables (Model II Linear Regression, $P > 0.1$).

Carbon Stable Isotope values of seagrasses and soil C_{org}

T. testudinum leaves ($\delta^{13}\text{C} = -8.4 \pm 0.3 \text{‰}$) were more enriched in ^{13}C than *H. wrightii* ($-9.8 \pm 0.4 \text{‰}$; ANOVA, $p < 0.05$, Figure 2.11). Seagrass $\delta^{13}\text{C}$ was not affected by fertilization or site for either species (ANOVA, $p > 0.05$). The $\delta^{13}\text{C}$ of soil C_{org} averaged $-12.0 \pm 0.3 \text{‰}$, and ranged between -10.7‰ and -15.4‰ . There was no effect of treatment nor site on the soil $\delta^{13}\text{C}$ (ANOVA, $p > 0.05$). There was however a difference in $\delta^{13}\text{C}$ between surface soil and the 15 cm depth fraction (Figure 2.10; Mann–Whitney–Wilcoxon, $p < 0.05$) with surface soil being on average 1.5‰ more depleted. Variance was also lower in surface soils compared to 15 cm fraction (Levene’s test, $p < 0.05$).

Discussion

Over the 30 years since experimental bird perches were installed on Cross Bank, they have provided insight on the feeding behavior of seabirds (Powell et al., 1985), nutrient limitation and the nature of competition in seagrasses (Powell et al., 1989, 1991; Fourqurean et al., 1995), the effect of eutrophication on mollusk diversity in seagrass beds (Ferguson, 2008), and long-term ecosystem effects of short and long-term nutrient enrichment (Herbert and Fourqurean, 2008). After the three decades, the experimental plots also provided a novel setting for investigating the relationship between seagrass communities and long-term soil storage of C_{org} . Despite extreme, consistent differences in nutrient

availability, net primary production and seagrass community structure between bird perch treatments and control (herein called *Halodule*-dominated and *Thalassia*-dominated, respectively) sites over three decades, there was no difference in C_{org} storage in the top 15 cm of underlying soil. Varying morphologies, elemental stoichiometry, metabolism and wave attenuation capabilities exist between fertilized and control plots and between the dominant species, yet there were no differences in the content or density of C_{org} in the soils. There were, however, differences in the C_{org} soil storage between experimental blocks over the 3.6 km environmental gradient that they span.

The Seagrass – Soil C_{org} Link

The most direct way that seagrasses contribute to soil C_{org} storage is through the burial and preservation of its biomass in the underlying soil (see Holmer and Perillo 2009). Seagrass biomass itself contributes a global average of 50 % of the total stored soil C_{org} , though the tendency for a plant, or portion of the plant, to be stored can vary greatly due to environmental factors (Kennedy et al., 2010). For example, seagrass leaves can contribute more to local C_{org} carbon stores than rhizomes (Kennedy et al., 2010) yet are more likely to move laterally from its origin due to water currents and the buoyancy of leaves (Zieman et al., 1979). A significant fraction of seagrass biomass and production is positioned in belowground structures, accelerating the process of burial of seagrass-derived C_{org} . While this belowground plant material can be eroded out of the soil after death, its alternative fates are in situ decomposition or preservation. The quantity and molecular composition of buried organic material as well as its environmental setting all affect its preservation (Harrison, 1989; Arndt et al., 2013); all of these factors vary between *Thalassia*-dominated and *Halodule*-dominated sites.

While total aboveground biomass was indistinguishable between *Thalassia*-dominated plots and *Halodule*-dominated plots for the majority of the years sampled, belowground

morphology varies between the species. *H. wrightii* belowground biomass at Cross Bank consists of only 44 - 60 % of total plant mass compared to over 70 % for *T. testudinum* (Powell et al., 1989). Further, the ratio of thick, structurally complex rhizome to root biomass is almost twice as much for *T. testudinum* (Duarte et al., 1998). This difference in belowground allocation among species could help explain the lack of differences in soil C_{org} stores between dense, *Halodule*-dominated and more sparse *Thalassia*-dominated seagrasses on Cross Bank.

When seagrasses are relieved from nutrient limitation, they allocate less of their production to building belowground biomass (Gleeson, 1993; Lee and Dunton, 2000). Exemplifying this trend, Powell et al. (1989) noted that those *T. testudinum* plants that remain at the *Halodule*-dominated plots have less belowground biomass compared to those at *Thalassia*-dominated plots (74 – 88 % and 80 – 98 % total biomass, respectively). There is less belowground biomass at *Halodule*-dominated plots, with both inter- and intra-species differences that can alter soil C_{org} influx.

The rate and extent of decomposition for seagrass-derived organic matter is considered to be greatest in an oxidized water column and surface sediments where aerobic respiration can yield higher bacterial production rates (Harrison, 1989; Arndt et al., 2013). In Florida Bay, sediments inhabited by seagrasses are depleted of oxygen within the upper 5 mm of the sediment with decreasing concentrations along the depth profile (Borum et al., 2005). Though seagrasses can release oxygen into soil from their roots through advective exchange, bulk soil oxygen concentrations beneath seagrasses is zero compared to measurable concentrations in bare sediments (Burdige and Zimmerman, 2002; Holmer and Perillo, 2009), and any microzones of oxygen release around the roots are so small as to be indistinguishable using a 500 µm microelectrode (Borum et al., 2005). *T. testudinum* roots and horizontal rhizomes are on average deeper (approximately 15 cm) than those of *H. wrightii* which penetrate only a few centimeters (Duarte et al., 1998). These trends also

hold true at Cross Bank (personal observation) with horizontal rhizomes of *H. wrightii* (typically considered belowground biomass) observed to extend 20 - 30 cm up into the water column (Fourqurean et al., 1995).

The nutrient content of plant-derived organic matter can influence the rate of decomposition, with higher N and P content resulting in more rapid decomposition rates (Enriquez et al., 1993). The fertilization experiments utilized in this study altered the elemental stoichiometry of seagrasses, lowering the C:P ratio of both leaf and rhizome biomass (Herbert and Fourqurean, 2008; Powell et al., 1989), and by adding P to a severely P-limited ecosystem (Fourqurean et al., 1992). There is some evidence that heterotrophic soil-inhabiting bacteria that remineralize detritus can be P-limited in carbonate sediments (Lopez et al., 1995, 1998), thus relieving bacteria from limitation via enriched detritus and loaded phosphate could increase bacteria production and decomposition rates; yet we found no differences in soil C_{org} between fertilized and non-fertilized, P-poor plots.

All of the aforementioned trends would suggest greater decomposition and remineralization rates in *Halodule*-dominated sites. Herbert and Fourqurean (2008) noted ecosystem respiration rates 1.6 times higher for the *Halodule*-dominated plots, though measured net ecosystem production was shown to be five times greater on average at *Halodule*-dominated sites compared to the *Thalassia*-dominated sites. Net autotrophy could lead to the accumulation of organic matter, but differences in accumulated soil C_{org} are limited to between depth fractions and sites rather than between seagrass community types on Cross Bank. There was no consistent difference in total aboveground biomass between benthic community types at our sites, and based on species-specific morphology, there is likely more belowground biomass at *Thalassia*-dominated plots. Seagrasses are known to exude large portions of their primary production as DOC (Ziegler and Benner, 1999). This may account for some of the differences in net production however this exudate is likely too labile to be relevant in soil C_{org} storage. There are other factors on Cross Bank, primarily

export, that could account for the discrepancy between community-specific net ecosystem production and accumulated C_{org} .

Globally, approximately 50 % of the C_{org} contained in seagrass soil pools is not of seagrass origin (Gacia et al., 2002; Kennedy et al., 2010). Rather, it is a combination of imported, non-seagrass material (both terrestrial and aquatic) and autochthonous algal C_{org} that accumulates in seagrass meadows due to the altered hydrodynamic environment and additional substrate provided by seagrasses. *Zostera marina* (structurally comparable to *T. testudium*) seagrass canopies have been shown to reduce near-bottom mean velocities by 70 to 90 %, while wave heights were reduced 45 to 70 % compared to adjacent unvegetated regions (Hansen and Reidenbach, 2012). The fraction of the suspended particles deposited in the benthos is dependent on the settling speed of the suspended particles in relation to the upward force caused by water currents. It is the absolute water velocity (often decreased by the seagrass canopy) combined with the particle size and type that controls sedimentation (Boer, 2007).

Altered flow is generally thought to cause net deposition of C_{org} in seagrass meadows, contributing to underlying soil C_{org} pools (Kennedy et al., 2010; Fourqurean et al., 2012a), however this phenomena only occurs when the attenuation effects of seagrass decrease local water velocity below the threshold for deposition. While the canopies of *Thalassia*- vs *Halodule*- dominated plots have different soil capturing abilities due to differing above-ground structure (Mellors et al., 2002; Boer, 2007), these factors may have little influence if the local regional water velocity is too fast to allow for sedimentation, even when the current attenuation effects of seagrass canopies are considered. For example, Hansen and Reidenbach (2013) found that the current threshold required to induce soil suspension in *Zostera* meadows was surpassed 80 – 85 % of their sampling period in the winter and 55 % of the time in the summer. This can be compared to an unvegetated site, where this threshold was surpassed 90 % of the time across all seasons. While there is often more sed-

imentation and less soil suspension in seagrass meadows, local water velocity ultimately controls these factors. Our biomass measurements for Cross Bank are limited the autumn, so comments regarding site-specific seasonally would be unsupported. However, fall and winter have the lowest leaf emergence rates, standing stocks and productivity in Florida Bay (Zieman et al., 1999; Peterson and Fourqurean, 2001). The potential hydrodynamic effects of seagrasses are likely to be more pronounced during other seasons. Neither water velocity, wave frequency, nor shear stress were measured during this study, though we could use dry bulk dry density as an indicator of hydrologic stress on the sea bottom with lighter, less dense sediments indicative of low bottom stress. There was no difference in soil dry bulk density between the *Thalassia*- and *Halodule*-dominated plots, possibly due to similar hydrologic regimes. This could explain the similar soil C_{org} stocks between treatments. Rather than increased sedimentation and C_{org} storage in *Thalassia*-dominated plots, we could expect sedimentation and suspension to correlate more with local hydrological patterns than the benthic community density or assemblage. As further support, we noted differences in bulk densities between our five sites, hinting at differences in local depositional environments. As dry bulk density correlates negatively with C_{org} in Florida Bay, there is a tendency for higher C_{org} content at sites with lower dry bulk densities.

If the input of seagrass tissue itself is driving the C_{org} storage in seagrass soils, it is expected that there would be a correlation between seagrass community and soil $\delta^{13}C$. Surface soil C_{org} on Cross Bank was between 1.42 ‰ and 3.18 ‰ more enriched in ^{13}C than values predicted using global models (Kennedy et al., 2010). This enrichment suggests that there is a greater contribution of seagrass-derived C_{org} to the soils of Florida Bay than the global average. This high seagrass C_{org} in the soil may be related to exceptionally high quantities of seagrass C_{org} input on Cross Bank influencing soil C_{org} stocks proportionally greater than other seagrass meadows. Alternatively, and more likely, it is due to the isolation of the bank from allochthonous inputs like terrestrial plants and anthropogenic

sources that can be found closer to inhabited islands and mainland Florida. Cross Bank is located in an oligotrophic region of Florida Bay, 2.5 km from the nearest inhabitable island, thus algal contributions to soil C_{org} are likely low as well. *T. testudinum* and *H. wrightii* have different $\delta^{13}\text{C}$ values on Cross Bank, confirming species-specific values across Florida Bay (Campbell and Fourqurean, 2009). If seagrasses are important C_{org} sources to their localized underlying soils, then we would predict that the $\delta^{13}\text{C}$ of surface soils would reflect that of the dominant species inhabiting the area. We found that the $\delta^{13}\text{C} - C_{\text{org}}$ of surface soils were indistinguishable between *Thalassia*- and *Halodule*-dominated plots, despite the clear differences in $\delta^{13}\text{C}$ of their dominant seagrass species. We interpret this as a homogenization of soil organic matter (dead plant material, detritus, soil) within the region of Cross Bank. Rather than C_{org} remaining in situ, we hypothesize that repeated resuspension and transport allows mixing to occur within the spatial scale of our sites. This could also explain the similarities in soil C_{org} content between the two seagrass community types. Morphology and sediment characteristics of banks are shaped by water movement and direction in Florida Bay and given the courser grain size found on banks compared to basins we can infer periods of greater sediment suspension (Bosence, 1989b). Once buried, C_{org} undergoes diagenetic alteration that suggests a persistence of seagrass-derived C_{org} relative to other sources, as indicated by the higher $\delta^{13}\text{C}$ values of the organic matter at 15 cm compared to surficial samples.

Implications for Conservation and Blue Carbon Policies

The amount of C_{org} stored in soils under seagrass meadows is large enough to be factored into global carbon budgets (Fourqurean et al., 2012a) and while efforts are underway to integrate seagrass soil C_{org} into climate change mitigation efforts (Duarte et al., 2010, 2011; Mcleod et al., 2011), a thorough understanding of soil C_{org} storage is admittedly lacking (Pendleton et al., 2012; Macreadie et al., 2014). Seagrass coverage

and production have been linked causally to the long-term soil C_{org} stores in the literature (Duarte et al., 2010, 2011), and researchers postulate that seagrass expansion will lead to increased C_{org} stores (Duarte et al., 2013) and meadow destruction will lead to increased remineralization (Pendleton et al., 2012; Fourqurean et al., 2012a). These claims, however, have limited empirical support.

There have been case studies where seagrass recolonization and expansion have increased local soil C_{org} stores (Greiner et al., 2013; Marbà et al., 2015) but this is not always the case (Pedersen et al., 1997). Lavery et al. (2013) have shown geographic variability in seagrass soil C_{org} stores in coastal Australia but they have methodologically linked the variation to seagrass species. While morphological and physiological differences between species can account for some of the difference in C_{org} stores, Lavery et al. (2013) point out that environmental differences like hydrology and temperature have direct influences on both the species present as well as net C_{org} storage. Serrano et al. (2014) found that water column depth decreases seagrass soil C_{org} storage likely due to the negative effects of decreased light availability on seagrasses and cohabiting primary producers. However, they also suggest that environmental factors like soil accretion and depositional environment are drivers of C_{org} storage. Armitage and Fourqurean (2016) found that soil C_{org} content is positively related to long-term, landscape-wide trends in nutrient availability and productivity but short-term fertilization within regions of Florida Bay did not influence soil C_{org} content, despite its effects on production and seagrass standing stock. These points of environmental context, while generally overlooked in Blue Carbon literature, may have important implications for understanding soil C_{org} dynamics in vegetated coastal areas. Also, putting our results in the context of the work of Armitage and Fourqurean (2016), we may lack the large spatial scale changes required to alter soil C_{org} stores. If soil C_{org} is homogenized with the Cross Bank region of Florida Bank as suggested, then small scale increases in C_{org} at *Halodule*-dominated sites would be diluted across the larger,

less-productive area and bulk changes in C_{org} storage would be undetectable. On the other hand, regional increases in productivity could translate in to notable differences in soil C_{org} storage. Our work also confirms that there are drivers beyond the density, productivity, and species composition of seagrass meadows controlling C_{org} storage. Minor differences in geographic location can lead to differences in sedimentary environments across seagrass landscapes, interacting with and possibility overriding the effects of the seagrass meadow itself on C_{org} storage.

Conservation of seagrasses is important for established reasons such as nutrient cycling and providing nursery grounds for a variety of animals (Costanza et al., 2014; Hejnowicz et al., 2015), but the relationship between Blue Carbon stores and seagrasses is a complicated issue that includes species-specific characteristics and environmental contexts. Beyond the academic understanding of C_{org} storage and preservation, the current methods for assessing the Blue Carbon value of seagrass ecosystems are inadequate. On Cross Bank, the typical Blue Carbon accounting method of sediment coring would miss the differences in net ecosystem production (thus differences of CO_2 consumption) that have been reported between our experimental treatments. Organic carbon inputs in Florida Bay are dominated by seagrass-derived material, however the location and extent of preservation can be decoupled from its source, owing its storage and persistence to a combination of biological and environmental factors. Understanding these interactions and how to properly quantify seagrass contribution to carbon sequestration will prioritize and evaluate the worth of seagrass C_{org} stocks, both ecologically and economically.

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Work Cited

- Armitage, A. R. and Fourqurean, J. W. (2016). Carbon storage in seagrass soils: long-term nutrient history exceeds the effects of near-term nutrient enrichment. *Biogeosciences*, 13(1):313–321.
- Arndt, S., Jørgensen, B. B., LaRowe, D. E., Middelburg, J., Pancost, R. D., and Regnier, P. (2013). Quantifying the degradation of organic matter in marine sediments: A review and synthesis. *Earth-Science Reviews*, 123:53–86.
- Boer, W. F. (2007). Seagrass–sediment interactions, positive feedbacks and critical thresholds for occurrence: a review. *Hydrobiologia*, 591(1):5–24.
- Borum, J., Pedersen, O., Greve, T., Frankovich, T., Zieman, J., Fourqurean, J. W., and Madden, C. (2005). The potential role of plant oxygen and sulphide dynamics in die-off events of the tropical seagrass, *Thalassia testudinum*. *Journal of Ecology*, 93(1):148–158.
- Bosence, D. (1989a). Biogenic carbonate production in Florida Bay. *Bulletin of Marine Science*, 44(1):419–433.
- Bosence, D. (1989b). Surface sublittoral sediments of Florida Bay. *Bulletin of Marine Science*, 44(1):434–453.
- Burdige, D. J. and Zimmerman, R. C. (2002). Impact of sea grass density on carbonate dissolution in Bahamian sediments. *Limnology and Oceanography*, 47(6):1751–1763.
- Campbell, J. E. and Fourqurean, J. W. (2009). Interspecific variation in the elemental and stable isotope content of seagrasses in South Florida. *Marine Ecology Progress Series*, 387:109–123.
- Campbell, J. E., Lacey, E. A., Decker, R. A., Crooks, S., and Fourqurean, J. W. (2014). Carbon Storage in Seagrass Beds of Abu Dhabi, United Arab Emirates. *Estuaries and Coasts*, 38(1):242–251.

- Costanza, R., de Groot, R., Sutton, P., van der Ploeg, S., Anderson, S. J., Kubiszewski, I., Farber, S., and Turner, R. K. (2014). Changes in the global value of ecosystem services. *Global Environmental Change*, 26:152–158.
- Duarte, C. M. and Cebrian, J. (1996). The fate of marine autotrophic production. *Limnology and Oceanography*, 41:1758–1766.
- Duarte, C. M., Kennedy, H., Marbà, N., and Hendriks, I. (2011). Assessing the capacity of seagrass meadows for carbon burial: Current limitations and future strategies. *Ocean and Coastal Management*, 83:32–38.
- Duarte, C. M., Marbà, N., Gacia, E., Fourqurean, J. W., Beggins, J., Barrón, C., and Apostolaki, E. T. (2010). Seagrass community metabolism: Assessing the carbon sink capacity of seagrass meadows. *Global Biogeochemical Cycles*, 24(4):GB4032.
- Duarte, C. M., Merino, M., Agawin, N. S. R., Uri, J., Fortes, M. D., Gallegos, M. E., Marba, N., and Hemminga, M. A. (1998). Root production and belowground seagrass biomass. *Marine Ecology Progress Series*, 171:97–108.
- Duarte, C. M., Middelburg, J., and Caraco, N. (2005). Major role of marine vegetation on the oceanic carbon cycle. *Biogeosciences*, 2(2):1–8.
- Duarte, C. M., Sintes, T., and Marbà, N. (2013). Assessing the CO₂ capture potential of seagrass restoration projects. *Journal of Applied Ecology*, 50(6):1341–1349.
- Enriquez, S., Duarte, C. M., and Sand-Jensen, K. (1993). Patterns in decomposition rates among photosynthetic organisms: the importance of detritus C:N:P content. *Oecologia*, 94(4):457–471.
- Ferguson, C. A. (2008). Nutrient Pollution and the Molluscan Death Record: Use of Mollusc Shells to Diagnose Environmental Change. *Journal of Coastal Research*, 1:250–259.
- Folmer, E. O., van der Geest, M., Jansen, E., Olf, H., Anderson, T. M., Piersma, T., and van Gils, J. A. (2012). Seagrass–sediment feedback: an exploration using a non-recursive structural equation model. *Ecosystems*, 15(8):1380–1393.
- Fonseca, M. S. and Fisher, J. S. (1986). A comparison of canopy friction and sediment movement between four species of seagrass with reference to their ecology and restoration. *Marine Ecology Progress Series*, 29(1):15–22.
- Fourqurean, J. W., Duarte, C. M., Kennedy, H., Marbà, N., Holmer, M., Mateo, M. A., Apostolaki, E. T., Kendrick, G. A., Krause-Jensen, D., McGlathery, K. J., and Serano, O. (2012a). Seagrass ecosystems as a globally significant carbon stock. *Nature Geoscience*, 5(7):505–509.
- Fourqurean, J. W., Kendrick, G. A., Collins, L. S., Chambers, R. M., and Vanderklift, M. A. (2012b). Carbon, nitrogen and phosphorus storage in subtropical seagrass meadows: examples from Florida Bay and Shark Bay. *Marine and Freshwater Research*, 63(11):967.

- Fourqurean, J. W., Powell, G. V., Kenworthy, W. J., and Zieman, J. C. (1995). The effects of long-term manipulation of nutrient supply on competition between the seagrasses *Thalassia testudinum* and *Halodule wrightii* in Florida Bay. *Oikos*, 72(3):349–358.
- Fourqurean, J. W., Zieman, J., and Powell, G. V. (1992). Phosphorus limitation of primary production in Florida Bay: Evidence from C:N:P ratios of the dominant seagrass *Thalassia testudinum*. *Limnology and Oceanography*, 37(1):162–171.
- Gacia, E., Duarte, C. M., and Middelburg, J. (2002). Carbon and nutrient deposition in a Mediterranean seagrass (*Posidonia oceanica*) meadow. *Limnology and Oceanography*, 47(1):23–32.
- Gleeson, S. K. (1993). Optimization of tissue nitrogen and root-shoot allocation. *Annals of Botany*, 71:23–31.
- Greiner, J. T., McGlathery, K. J., Gunnell, J., and McKee, B. A. (2013). Seagrass restoration enhances “blue carbon” sequestration in coastal waters. *PLoS ONE*, 8(8):e72469.
- Hansen, J. C. R. and Reidenbach, M. A. (2012). Wave and tidally driven flows in eelgrass beds and their effect on sediment suspension. *Marine Ecology Progress Series*, 448:271–287.
- Hansen, J. C. R. and Reidenbach, M. A. (2013). Seasonal Growth and Senescence of a *Zostera marina* Seagrass Meadow Alters Wave-Dominated Flow and Sediment Suspension Within a Coastal Bay. *Estuaries and Coasts*, 36(6):1099–1114.
- Harrison, P. G. (1989). Detrital processing in seagrass systems: a review of factors affecting decay rates, remineralization and detritivory. *Aquatic Botany*, 23:263–288.
- Heck, Jr., K. L. and Valentine, J. F. (2006). Plant–herbivore interactions in seagrass meadows. *Journal of Experimental Marine Biology and Ecology*, 330(1):420–436.
- Hejnowicz, A. P., Kennedy, H., Huxham, M. R., and Rudd, M. A. (2015). Harnessing the climate mitigation, conservation and poverty alleviation potential of seagrasses: prospects for developing blue carbon initiatives and payment for ecosystem service programmes. *Frontiers in Marine Science*, page 32.
- Hendriks, I. E., Sintes, T., Bouma, T. J., and Duarte, C. M. (2008). Experimental assessment and modeling evaluation of the effects of the seagrass *Posidonia oceanica* on flow and particle trapping. *Marine Ecology Progress Series*, 356:163–173.
- Herbert, D. A. and Fourqurean, J. W. (2008). Ecosystem Structure and Function Still Altered Two Decades After Short-Term Fertilization of a Seagrass Meadow. *Ecosystems*, 11(5):688–700.
- Holmer, M. and Perillo, G. (2009). Productivity and biogeochemical cycling in seagrass ecosystems. *Coastal Wetlands: An Integrated Ecosystem Approach*. Elsevier Science, Amsterdam, pages 377–402.
- Kennedy, H., Beggins, J., Duarte, C. M., Fourqurean, J. W., Holmer, M., Marbà, N., and Middelburg, J. J. (2010). Seagrass sediments as a global carbon sink: Isotopic constraints. *Global Biogeochemical Cycles*, 24(4):GB4026.

- Lavery, P. S., Mateo, M. A., Serrano, O., and Rozaimi, M. (2013). Variability in the Carbon Storage of Seagrass Habitats and Its Implications for Global Estimates of Blue Carbon Ecosystem Service. *PLoS ONE*, 8(9):e73748.
- Lee, K. S. and Dunton, K. H. (2000). Effects of nitrogen enrichment on biomass allocation, growth, and leaf morphology of the seagrass *Thalassia testudinum*. *Marine Ecology Progress Series*, 196:39–48.
- Lopez, N., Duarte, C., Vallespinos, F., Romero, J., and Alcoverro, T. (1995). Bacterial activity in NW Mediterranean seagrass (*Posidonia oceanica*) sediments. *Journal of Experimental Marine Biology and Ecology*, 187:39–49.
- Lopez, N., Duarte, C. M., Vallespinos, F., Romero, J., and Alcoverro, T. (1998). The effect of nutrient additions on bacterial activity in seagrass (*Posidonia oceanica*) sediments. *Journal of Experimental Marine Biology and Ecology*, 224:155–166.
- López-Sáez, J. A., López-Merino, L., Mateo, M. Á., Serrano, O., Pérez-Díaz, S., and Serrano, L. (2009). Palaeoecological potential of the marine organic deposits of *Posidonia oceanica*: A case study in the NE Iberian Peninsula. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 271(3-4):215–224.
- Macreadie, P. I., Baird, M. E., Trevathan-Tackett, S. M., Larkum, A. W. D., and Ralph, P. J. (2014). Quantifying and modelling the carbon sequestration capacity of seagrass meadows – A critical assessment. *Marine Pollution Bulletin*, 83(2):430–439.
- Marbà, N., Arias-Ortiz, A., Masqué, P., Kendrick, G. A., Mazarrasa, I., Bastyan, G. R., Garcia-Orellana, J., and Duarte, C. M. (2015). Impact of seagrass loss and subsequent revegetation on carbon sequestration and stocks. *Journal of Ecology*, 103:296–302.
- Mateo, M., Cebrián, J., Dunton, K., and Mutchler, T. (2006). Carbon flux in seagrass ecosystems. In *Seagrasses: Biology, Ecology and Conservation*, pages 159–192. Springer.
- Mateo, M. A. and Romero, J. (1997). Detritus dynamics in the seagrass *Posidonia oceanica*: elements for an ecosystem carbon and nutrient budget. *Marine Ecology Progress Series*, 151(1):43–53.
- McLeod, E., Chmura, G. L., Bouillon, S., Salm, R., Björk, M., Duarte, C. M., Lovelock, C. E., Schlesinger, W. H., and Silliman, B. R. (2011). A blueprint for blue carbon: toward an improved understanding of the role of vegetated coastal habitats in sequestering CO₂. *Frontiers in Ecology and the Environment*, 9(10):552–560.
- Mellors, J., Marsh, H., Carruthers, T. J., and Waycott, M. (2002). Testing the sediment-trapping paradigm of seagrass: Do seagrasses influence nutrient status and sediment structure in tropical intertidal environments? *Bulletin of Marine Science*, 71(3):1215–1226.
- Pedersen, M. F., Duarte, C. M., and Cebrian, J. (1997). Rates of changes in organic matter and nutrient stocks during seagrass *Cymodocea nodosa* colonization and stand development. *Marine Ecology Progress Series*, 159:29–36.
- Pendleton, L., Donato, D. C., Murray, B. C., Crooks, S., Jenkins, W. A., Sifleet, S., Craft, C., Fourqurean, J. W., Kauffman, J. B., Marbà, N., Megonigal, P., Pidgeon, E., Herr, D.,

- Gordon, D., and Baldera, A. (2012). Estimating Global “Blue Carbon” Emissions from Conversion and Degradation of Vegetated Coastal Ecosystems. *PLoS ONE*, 7(9):e43542.
- Peterson, B. J. and Fourqurean, J. W. (2001). Large-scale patterns in seagrass (*Thalassia testudinum*) demographics in south Florida. *Limnology and Oceanography*, 46(5):1077–1090.
- Powell, G. V., Fourqurean, J. W., Kenworthy, W. J., and Zieman, J. C. (1991). Bird colonies cause seagrass enrichment in a subtropical estuary: observational and experimental evidence. *Estuarine, Coastal and Shelf Science*, 32(6):567–579.
- Powell, G. V., Kenworthy, J. W., and Fourqurean, J. W. (1989). Experimental evidence for nutrient limitation of seagrass growth in a tropical estuary with restricted circulation. *Bulletin of Marine Science*, 44(1):324–340.
- Powell, G. V., SM, S., and Holmquist, J. G. (1985). Ecology of Shallow-Water Habitats in Florida Bay. *Final Report, NPS contract CX5280-3-2339, South Florida Research Center, Homestead, Florida.*, 68:405.
- Ricart, A. M., York, P. H., Rasheed, M. A., Pérez, M., Romero, J., Bryant, C. V., and Macreadie, P. I. (2015). Variability of sedimentary organic carbon in patchy seagrass landscapes. *Marine Pollution Bulletin*, 100:476–482.
- Serrano, O., Lavery, P. S., and Rozaimi, M. (2014). Influence of water depth on the carbon sequestration capacity of seagrasses. *Global Biogeochemical Cycles*, 28:950–961.
- Smith, S. V. (1981). Marine macrophytes as a global carbon sink. *Science*, 211(4484):838–840.
- Ward, L. G., Michael Kemp, W., and Boynton, W. R. (1984). The influence of waves and seagrass communities on suspended particulates in an estuarine embayment. *Marine Geology*, 59(1):85–103.
- Westlake, D. (1963). Comparisons of plant productivity. *Biological Reviews*, 38(3):385–425.
- Ziegler, S. and Benner, R. (1999). Dissolved organic carbon cycling in a subtropical seagrass-dominated lagoon. *Marine Ecology Progress Series*, 180:149–160.
- Zieman, J. C., Fourqurean, J. W., and Frankovich, T. A. (1999). Seagrass die-off in Florida Bay: Long-term trends in abundance and growth of turtle grass, *Thalassia testudinum*. *Estuaries*, 22(2):460–470.
- Zieman, J. C., Thayer, G. W., Robblee, M. B., and Zieman, R. T. (1979). Production and export of sea grasses from a tropical bay. In *Ecological processes in coastal and marine systems*, pages 21–33. Springer.
- Zieman, J. C. and Wetzel, R. G. (1980). Productivity in seagrasses: methods and rates. *Garland STPM Press*, pages 87–116.

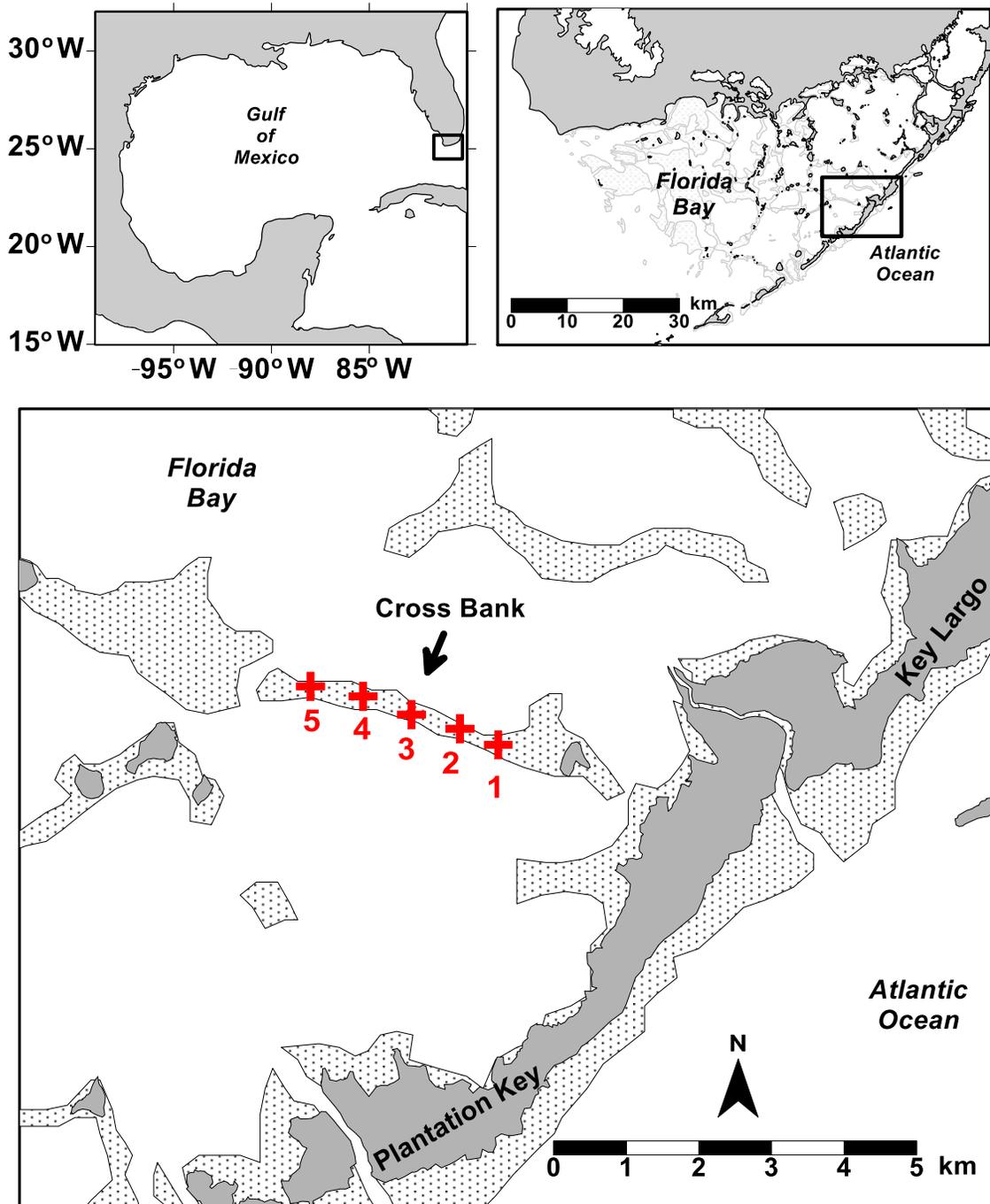


Figure 2.1: Study area showing locations of experiment sites along Cross Bank, Florida Bay. Each site, denoted by a cross, has both an experimental bird perch and a control spaced 10 meters apart.

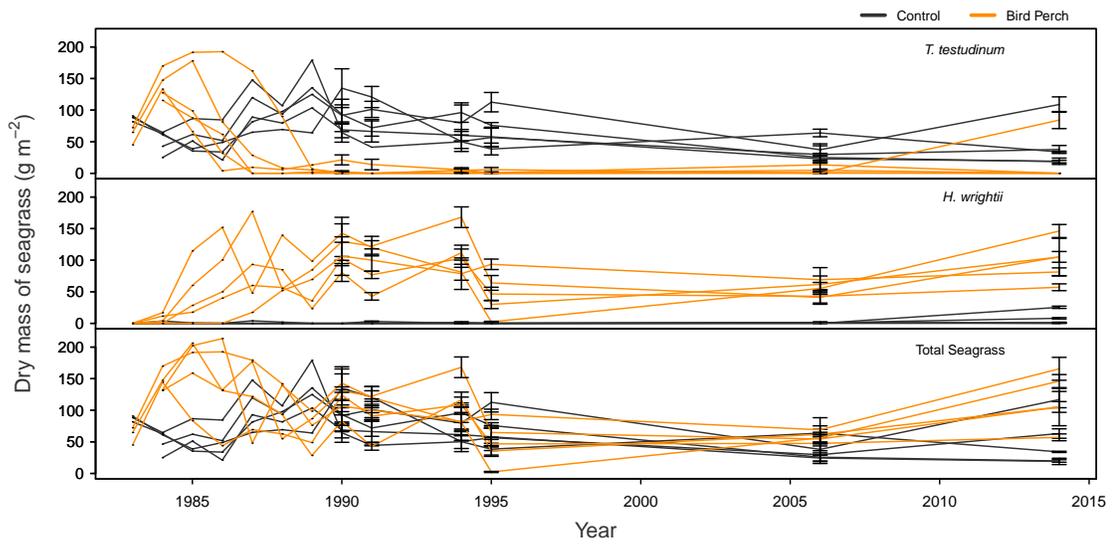


Figure 2.2: Changes in seagrass species composition showing shifts in dominance between *T. testudinum* (first panel) and *H. wrightii* (second panel) under conditions of long-term continuous fertilization compared to control. Total mass of seagrass however showed no clear shift under fertilization treatment (third panel). Data represents mean \pm SE (N = 3, within-site replicates) of aboveground biomass with the exception of data collected prior to 1990 that lacked replicates.

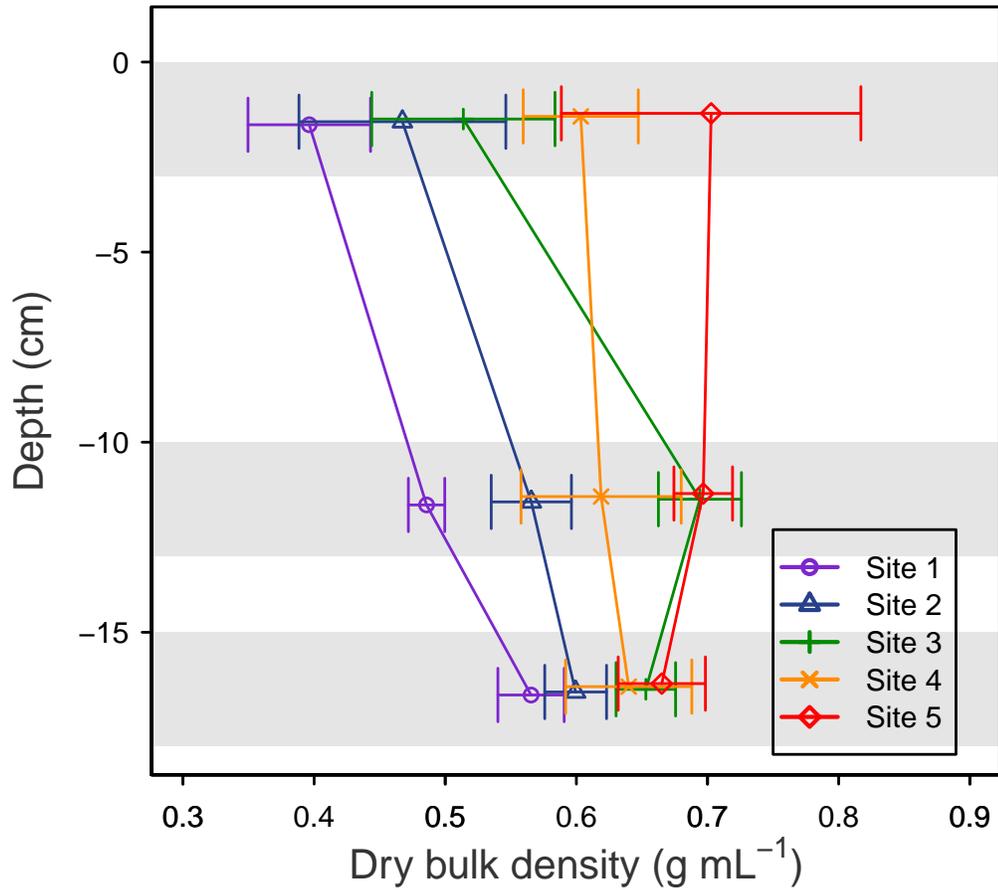


Figure 2.3: Down core profiles of dry bulk density for the five sites (treated as experimental blocks), spaced 600 m apart on Cross Bank, Florida Bay. Points represent mean of samples taken from both experimental and control treatments within each site. Horizontal error bars represent \pm SE (N = 6). Grey horizontal bars represent the depth range sampled and homogenized for soil analyses.

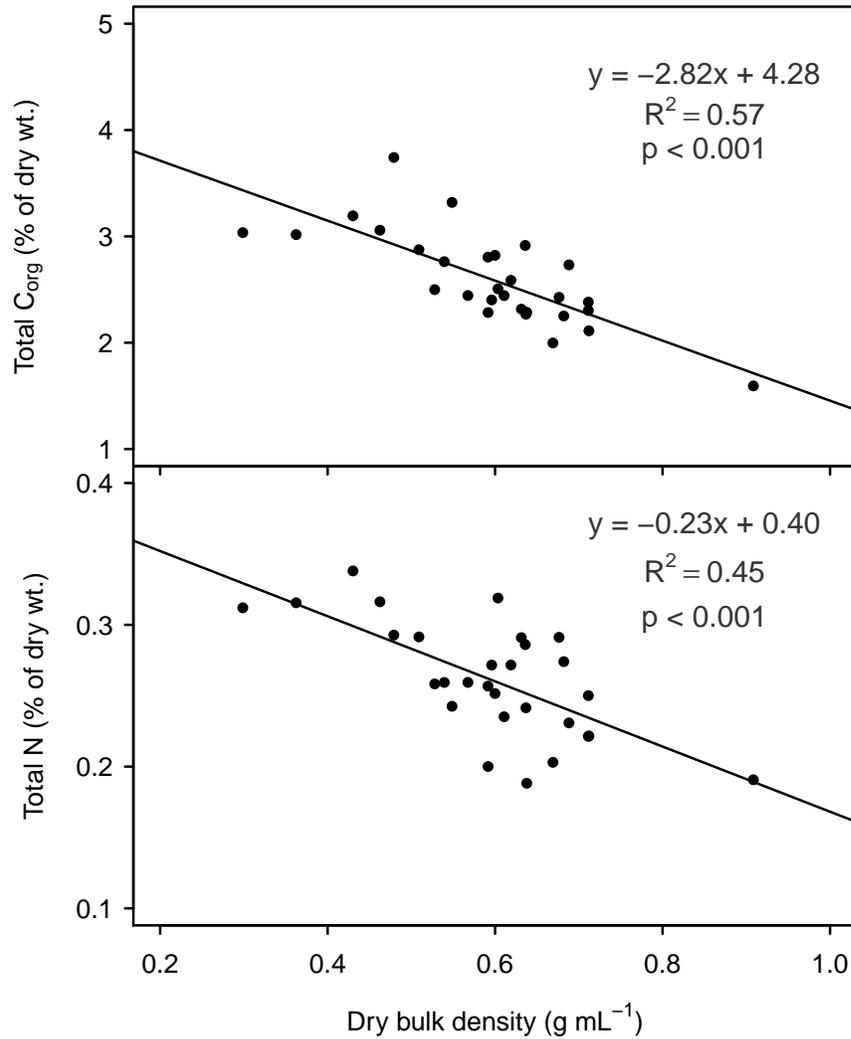


Figure 2.4: Relationships between dry bulk density and C_{org} content (top) as well as dry bulk density and total N content (bottom) of soil samples. These models include averaged values across our five sites, two treatments and three sampled depths.

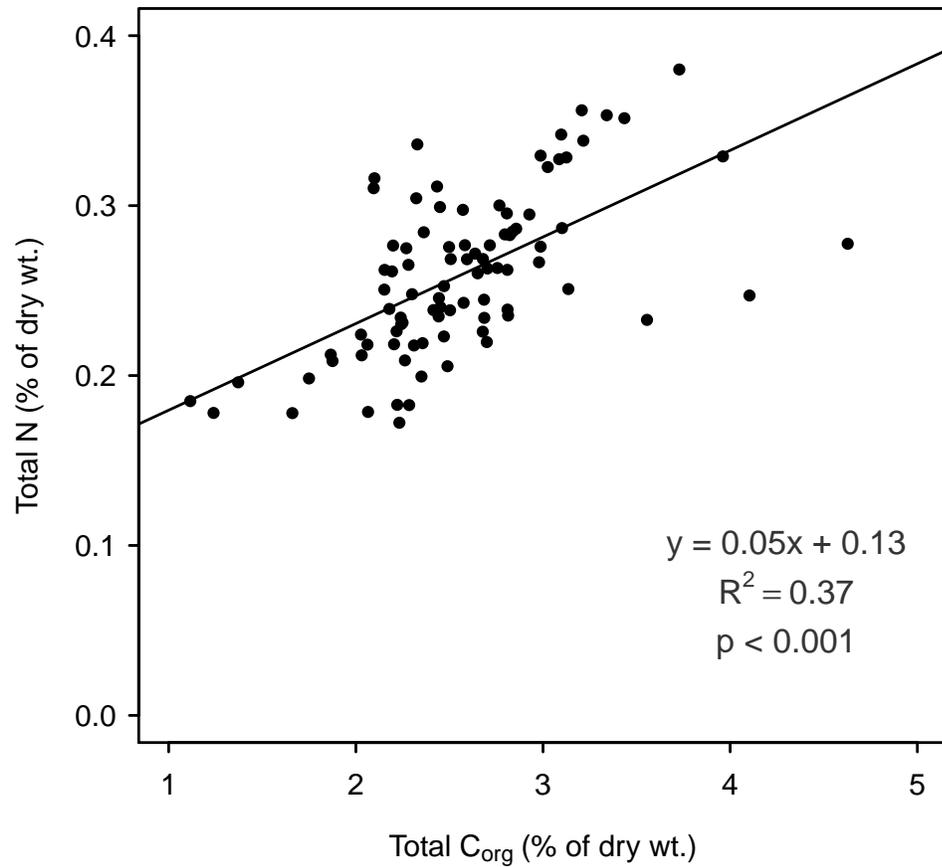


Figure 2.5: Relationship between the C_{org} and total N content of soil samples. Values include all soil samples collected across our five sites, two treatments and three sampled depths.

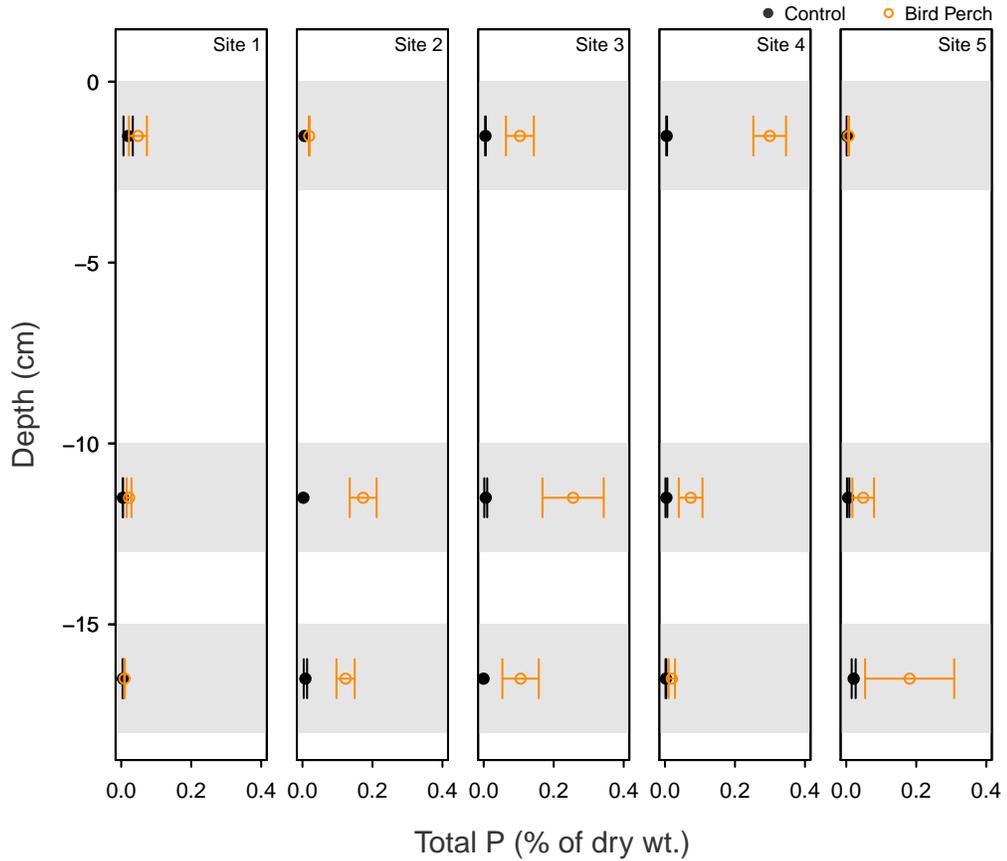


Figure 2.6: Soil phosphorus content changes with depth for bird perch treatments and controls within each experimental block. Points represent mean with horizontal error bars representing \pm SE (N = 3, within-site replicates). Grey horizontal bars represent the depth range sampled and homogenized for soil analyses. The five sites (experimental blocks) are spaced 600 m apart on Cross Bank, Florida Bay.

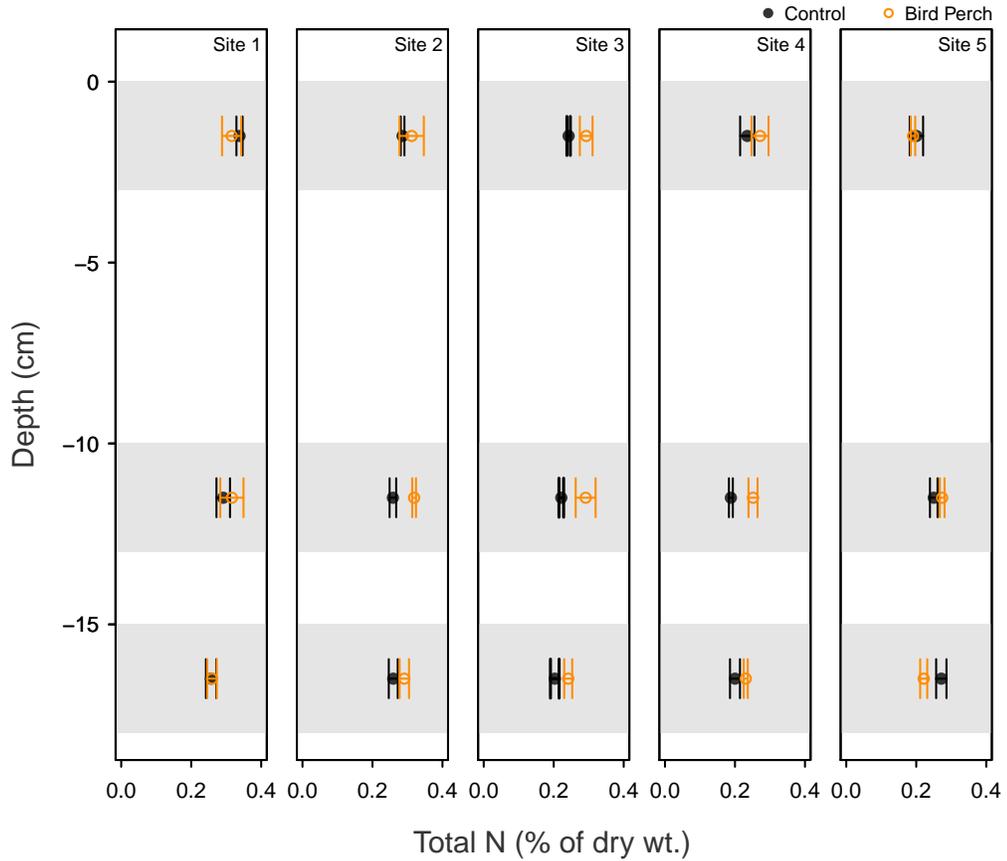


Figure 2.7: Soil nitrogen content changes with depth for bird perch treatments and controls within each experimental block. Points represent mean with horizontal error bars representing \pm SE ($N = 3$, within-site replicates) Grey horizontal bars represent the depth range sampled and homogenized for soil analyses. The five sites (experimental blocks) are spaced 600 m apart on Cross Bank, Florida Bay.

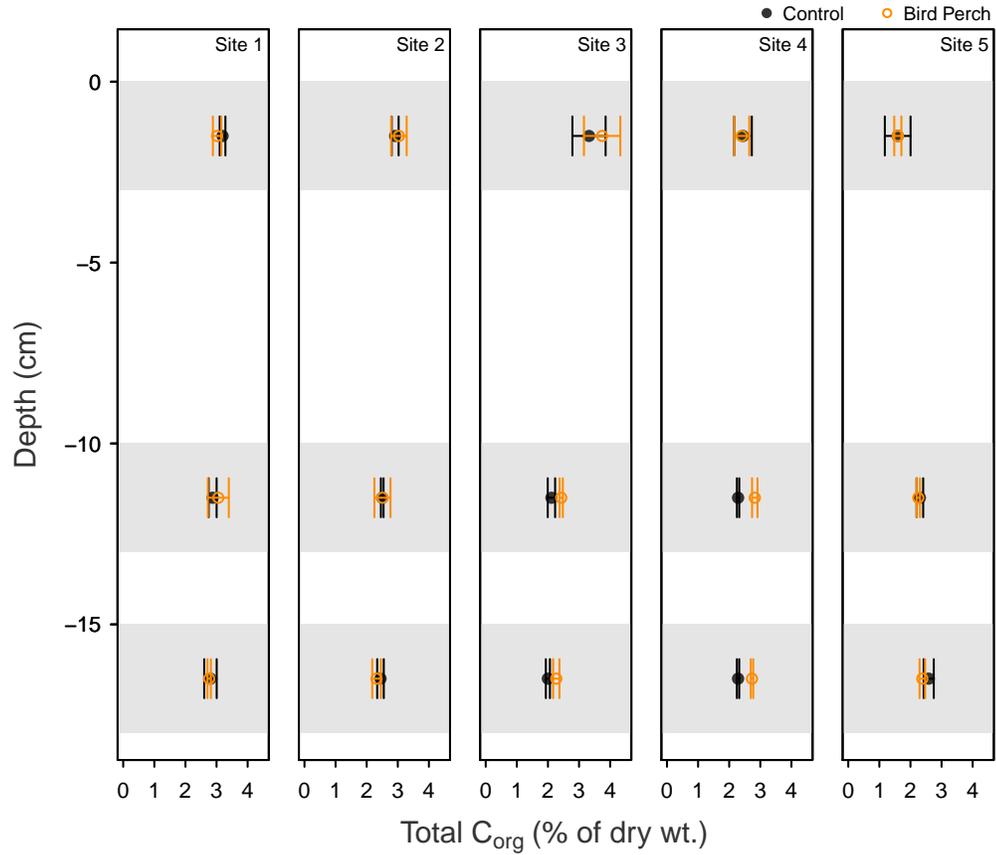


Figure 2.8: Down core profiles of soil C_{org} content from bird perch treatments and controls within each experimental block. Points represent mean with horizontal error bars representing \pm SE (N = 3, within-site replicates). Grey horizontal bars represent the depth range sampled and homogenized for soil analyses. The five sites (experimental blocks) are spaced 600 m apart on Cross Bank, Florida Bay.

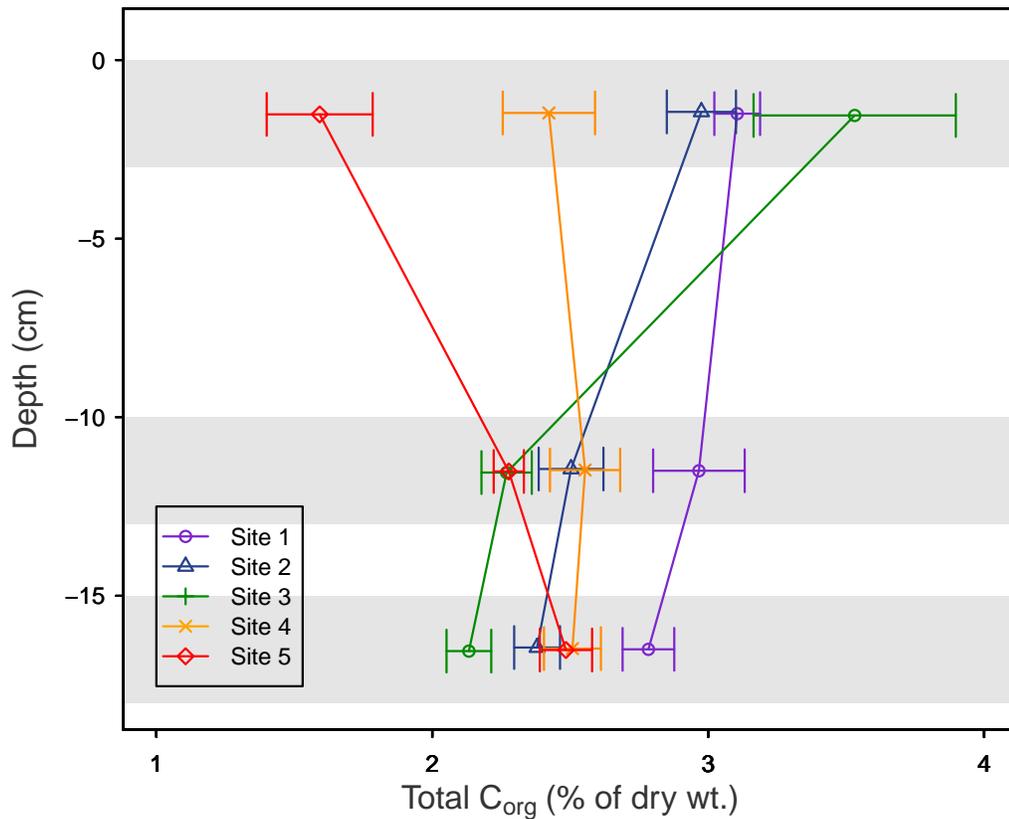


Figure 2.9: Down core profiles of soil C_{org} content for the five sites (treated as experimental blocks), spaced 600 m apart on Cross Bank, Florida Bay. Points represent mean of samples taken from both experimental and control treatments within each site. Horizontal error bars represent ± SE (N = 6). Grey horizontal bars represent the depth range sampled and homogenized for soil analyses.

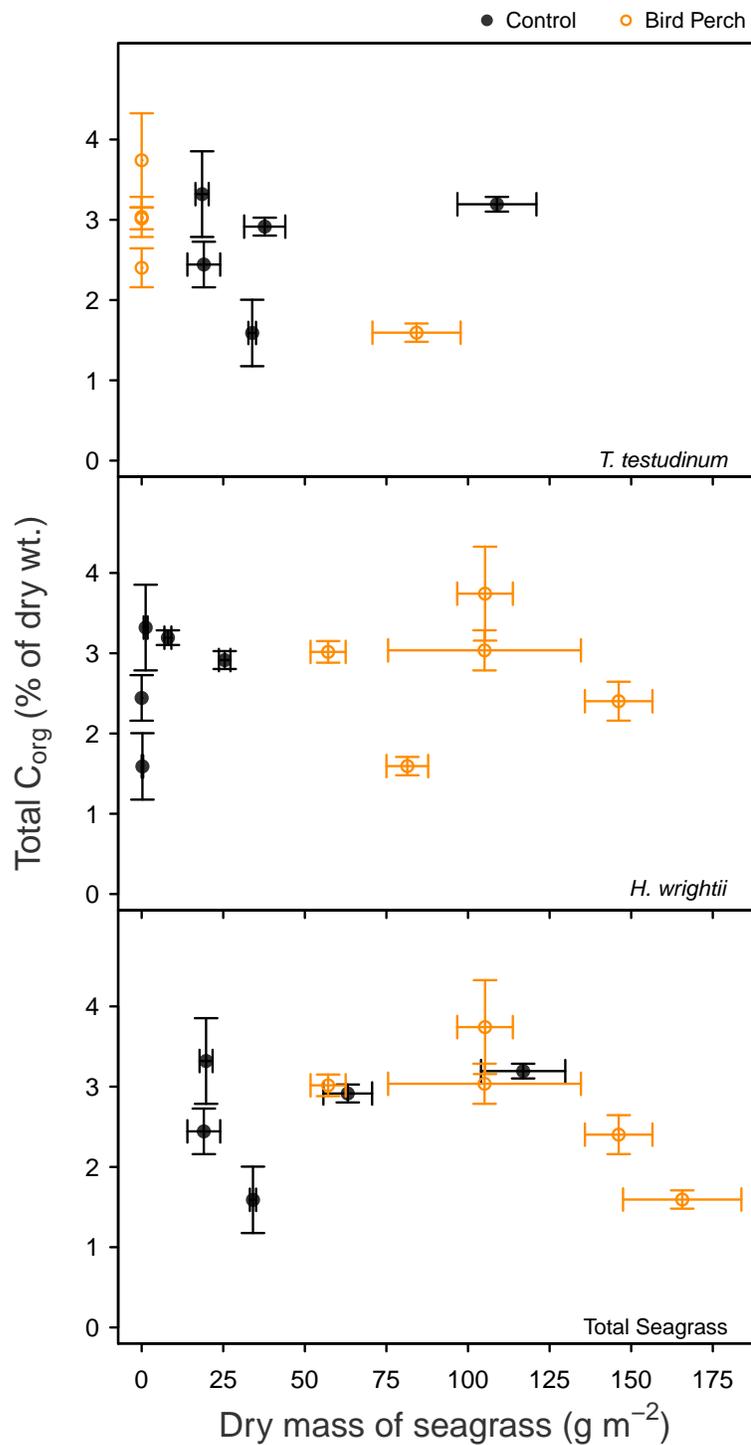


Figure 2.10: Relationship between seagrass biomass (shown as *T. testudinum* only, *H. wrightii* only and total seagrass) and surface soil C_{org} content across bird perch treatments and controls. Points represent mean ± SE (N = 3, within-site replicates) of above ground biomass and total C_{org}.

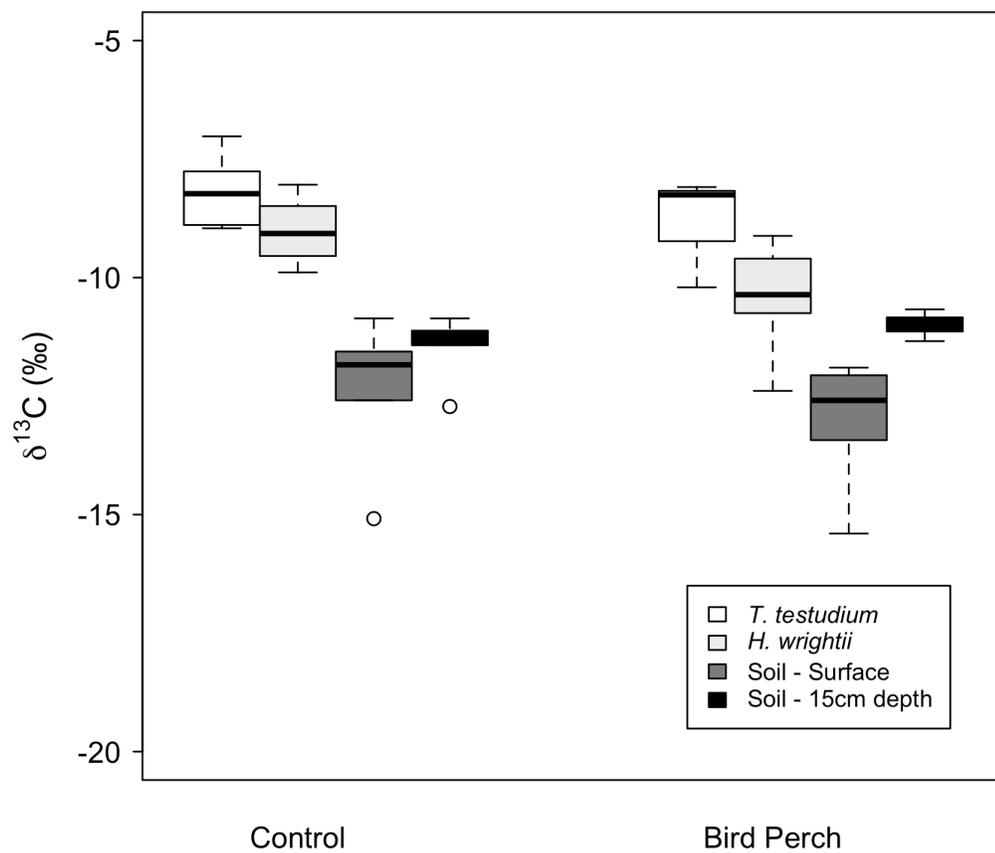


Figure 2.11: Box plots showing the distribution of the $\delta^{13}\text{C}$ for seagrasses and underlying soils at bird perches and controls. Boxes encompass 50% of the values, the line represents the median value, bars extend to the 95% confidence limits, and points represent observations beyond the 95% confidence limits (N = 5).

CHAPTER 3

IMPORTANCE OF SEDIMENT GRAIN SIZE TO STOCKS AND STABILITY OF ORGANIC CARBON BURIED IN SEAGRASS SOILS

Abstract

Seagrass ecosystems are being considered for conservation and management projects aimed at climate change mitigation based on the organic carbon (C_{org}) that they have historically sequestered. Coastal ecosystems inhabited by seagrasses often have more soil C_{org} stored than nearby bare sites, but the environmental and ecological factors that control the quantity and stability of seagrass soil carbon are complex and site specific. Here we measured soil carbon density and organic matter (OM) breakdown rates using a standard substrate deployed both buried and on the soil surface, as well as potential environmental and biological drivers of their variation at 45 seagrass-inhabited sites across the South Florida seascape. Total seagrass abundance was positively correlated with soil C_{org} density, though variance in data was better explained by sediment characteristics (sediment type, dry bulk density, and sediment grain size). The standard substrate was deployed for six months, with an average exponential breakdown rate, k , of $0.33 \pm 0.02 \text{ yr}^{-1}$ across all samples. Burial only increased OM preservation at sites with muddy, fine sediments where breakdown rates of buried OM were reduced by an average of 22 - 39% compared to surficial breakdown. At sites with coarser sediments, breakdown rates of OM were at least 55% greater for buried material. Seagrass abundance had limited (if any) explanatory power for C_{org} stock or OM breakdown rates across our study sites, suggesting other factors like geomorphological and hydrological setting have primary control of sediment characteristics, and thus C_{org} stocks and breakdown rates. We suggest fine sediments limit porewater exchange through sediments, limiting subsurface microbial decomposition and enhancing C_{org} preservation. These findings prompt the reconsideration of Blue Carbon

site selection and management, highlighting the importance of environmental controls of C stocks that can be independent of seagrass abundance in these ecosystems.

Introduction

The capability of some coastal ecosystems to sequester CO₂ and store large carbon stocks is drawing increasing attention as a potential means of inexpensive, conservation-based climate change mitigation (Hiraishi et al., 2014). The term "Blue Carbon" is used to describe the vulnerable organic carbon stocks associated with these coastal vegetated ecosystems (seagrass meadows, mangrove forests, and tidal marshes) that could be lost and emitted as CO₂ during habitat destruction or degradation (McLeod et al., 2011). The term is also tied to those carbon finance policies and frameworks under development to maximize carbon sequestration through the protection and promotion of carbon-rich ecosystems (collectively called "Blue Carbon strategies"; Pendleton et al. 2012). The need to quantify Blue Carbon stocks and assess the relative risk of CO₂ emissions from degraded sites is spurring a flood of investigations into the causal connections between manageable ecosystem attributes and stable, long-term carbon sequestration (Howard et al., 2017; Macreadie et al., 2017). Discussions have progressed to the prioritization of optimal Blue Carbon sites, focusing on those that have high C stocks that can be kept sequestered through effective ecosystem management (Lovelock et al., 2017a).

Seagrass meadows are declining globally and their associated carbon stocks are large enough to be considered in global carbon budgets, making them prime candidates for inclusion in Blue Carbon strategies (Waycott et al., 2009; Fourqurean et al., 2012a). Though, unlike most other ecosystems incorporated into climate change mitigation strategies, seagrasses are included for their existing soil carbon stocks rather than living biomass or current production rates (Fourqurean et al., 2012b). An estimated 299 Tg carbon per year

could be lost globally from remineralized soil carbon stocks resulting from the current loss of seagrass ecosystems (Fourqurean et al., 2012a); the focus of Blue Carbon strategies is to mitigate such CO₂ losses through ecosystem management and conservation. For those preliminary C_{org} loss projections to be accurate and meaningful, the presence of soil C_{org} stocks must be causally linked to the presence of intact seagrass meadows. Further, if seagrass Blue Carbon is to have value in greenhouse gas mitigation strategies, the C_{org} lost from the ecosystems upon seagrass destruction needs to be remineralized and released into the atmosphere where it exacerbates greenhouse gas emissions.

Drivers of C_{org} stocks in Seagrass Ecosystems

Soil C_{org} stocks associated with seagrass ecosystems vary greatly among sites, influenced by local seagrass-related features, but also local geomorphological and hydrological setting as well as soil characteristics (Serrano et al., 2016a). When considered broadly, seagrass ecosystems promote C_{org} storage, with studies showing that seagrass presence (Macreadie et al., 2015; Mazarrasa et al., 2015), density and productivity (Serrano et al., 2014), and recolonization (Greiner et al., 2013; Marbà et al., 2015) are all positively correlated with soil carbon storage. Seagrasses directly contribute to soil C_{org} stocks through the production of belowground roots, rhizomes, and leaves (Kennedy et al., 2010), though the soil retention of carbon derived from both seagrass and non-seagrass sources relies on a depositional environment that is only in part determined by seagrasses (Miyajima et al., 2017). The canopy's complex matrix of seagrass leaves serves to decrease current velocity and alter the turbulence in a way that encourages deposition (Ward et al., 1984; Hendriks et al., 2008; Fonseca and Fisher, 1986). It is important to note that this hydrological effect of seagrass canopy can only occur when the attenuation effects of seagrasses decrease local water velocity below thresholds needed for C_{org} deposition and accumulation (see Hansen and Reidenbach 2013). The depositional threshold for particles is dependent on their

particle size and density, with less dense and/or finer sediments requiring lower energy environments for settlement and accumulation (Bergamaschi et al., 1997; Belshe et al., 2017). When water velocity is too great for seagrasses to induce deposition, seagrass-derived C and other organic particulates may be exported, accounting for a portion of the carbon budget that is often overlooked (Duarte and Krause-Jensen, 2017).

On the other hand, in some locations water velocity can be low enough to encourage deposition and accumulation without the influence of seagrasses. For example, Serrano et al. (2016a) found that C_{org} stocks at sites where seagrasses were small or absent were controlled by the contribution of finer particles to sediments, rather than the presence or density of seagrasses. This may not be surprising as finer particles (mud, silts, clays) often have higher C_{org} content, and fines can accumulate in some depositional environments without the presence of seagrasses (Keil and Hedges, 1993; Bergamaschi et al., 1997). Miyajima et al. (2017) found that in *Zostera marina* meadows and surrounding habitats, sediment C_{org} is positively correlated with the amount of fine sediment grains that have larger surface area per volume. The areal extent of seagrass meadows positively correlated with the surface area of sediments and C_{org} storage; larger, more complex meadows were able to trap smaller particles with higher C_{org} content. At nearby offshore sites, void of vegetation, there was higher sediment C_{org} storage than seagrass meadows. At these sites, high-surface area sediments, and their associated high C_{org} content, were dependent on local geophysical constraints rather than seagrass-mediated hydrology.

The relative importance of seagrass presence versus local geomorphological drivers can be both regional- and scale-dependent; seagrass density positively affects C_{org} accumulation at the plot level in the Virginia Coast Reserve seagrass restoration project, though these biological drivers can be outweighed by those related to location at the meadow-scale (Oreska et al., 2017). In Florida Bay, there is no effect of local seagrass density or community type on underlying C_{org} stocks at the plot level after 30 years of experimental

fertilization that increased seagrass density and species composition, indicating that trends in C_{org} storage may be driven by local hydrology and depositional environments (Howard et al., 2016). However there are clear effects of seagrass density and productivity on regional C_{org} storage in the same embayment at a larger scale (Armitage and Fourqurean, 2016), underscoring the importance of seagrasses to South Florida C_{org} stocks. As we seek to understand how to manage C_{org} storage in seagrass ecosystems, we may have to expand on relationships between seagrass abundance and C_{org} storage to form a more holistic understanding of soil C_{org} drivers.

Decomposition and CO_2 Production in Seagrass Ecosystems

Mapping dense seagrass organic carbon stocks has taken primacy to date in Blue Carbon efforts, though for stocks to be relevant in discussions of greenhouse gas emissions, there must be evidence that seagrass-mediated attributes are linked to changes in organic matter remineralization, and hence, CO_2 production rates. In other words, for seagrasses to be important in controlling seagrass soil C_{org} stocks, seagrass presence must prevent decomposition and remineralization that would otherwise occur in their absence. In seagrasses, like other Blue Carbon ecosystems, the production of CO_2 is driven mainly by respiratory processes linked to the decomposition and remineralization of organic matter (OM). The stability and permanence of C_{org} stocks in Blue Carbon ecosystems is typically attributed to suppressed microbial activity and resultant low breakdown rates when buried in the relatively stable, low redox, anoxic soils (Duarte et al., 2011; Fourqurean et al., 2012a). Loss of seagrasses is suggested to be accompanied by an erosional environmental that would expose once buried C_{org} from anoxic to oxic conditions (Lovell et al., 2017b). Further, exposure of buried material to labile OM associated with DOC and fresh detritus of the sediment-water interface may induce a priming effect, where the decomposition of recalcitrant OM is enhanced in response to additional labile organic inputs (Trevathan-

Tackett et al., 2018). Seagrass presence and abundance may enhance preservation of C_{org} via stable, anoxic sediment conditions, though there are other drivers can provide similar conditions in unvegetated sediments.

In seagrass meadows, anoxia has been shown to develop millimeters beneath the sediment surface (Borum et al., 2005) and plant density reduces the oxygen input via pore-water advective transport (Burdige and Zimmerman, 2002). Anoxia and stability in sediments can also be reached independently of benthic vegetation by mechanisms like restricted hydrological movement, supply of low $[O_2]$ overlying water, and decomposition of both autochthonous and allochthonous organic matter (see Middelburg and Levin 2009). More importantly, there is no consensus regarding the suppression of OM remineralization or enhancement of soil C_{org} storage due to anoxia. Some experimental evidence (e.g., Moodley et al. 2005; Dauwe et al. 2001) suggests that remineralization rates of OM in marine sediments are suppressed under anoxic conditions, while other work suggests that anoxic conditions may even accelerate breakdown of some OM (Harrison, 1989). Others have suggested that the sensitivity of OM remineralization rates to oxygen availability is dependent upon the chemical composition and therefore the recalcitrance of the OM, where decomposition rates of fresh, labile OM are independent of O_2 availability and breakdown of “aged”, recalcitrant OM is accelerated with oxygen (Kristensen et al., 1995; Hulthe et al., 1998; Kristensen and Holmer, 2001; Burdige, 2007).

The aim of this study was to identify correlates of seagrass soil C_{org} density and breakdown rates across a spectrum of seagrass characteristics and environmental conditions. Specifically, this study addresses the importance of seagrass species, seagrass abundance, and soil type to C_{org} storage and breakdown rates. As erosion and oxygen exposure have been discussed as primary drivers of decomposition and a likely fate of seagrass soil C_{org} following ecosystem loss, we also investigate the effect of OM burial on breakdown rates. The South Florida seascape hosts massive stretches continuous seagrass meadows, with

high variability in seagrass abundance, productivity, and community type as well as soil C_{org} stocks. We document 45 sites across the diverse seascape, hypothesizing that C_{org} stocks would be tightly correlated with sediment grain size, and we expected sediment grain size would be determined by a combination of seagrass canopy-induced effects and local environmental characteristics. As the benefits of burial to OM preservation is a foundational assumption of seagrass Blue Carbon strategies, we also address the hypothesis that breakdown rates of OM are suppressed in buried conditions compared those on the sediment surface across the range in sedimentary environments of our study area.

Materials and Methods

The Florida Keys National Marine Sanctuary and Florida Bay cover over 11,000 km² and host the largest documented continuous seagrass ecosystem in the world (Fourqurean et al., 2002). Seagrass communities across the south Florida seascape are composed primarily of *Thalassia testudinum*, *Halodule wrightii*, and/or *Syringodium filiforme* depending on local nutrient availability, sediment type, salinity, and light availability, among other factors (Fourqurean et al., 1995, 2003). During the summer and winter seasons of 2015 and 2016, 45 sites were surveyed for water depth, sediment type, average canopy height, and species-specific seagrass abundance, as part of ongoing seagrass monitoring programs that have been underway for over 20 years (Fourqurean et al., 2002). A map of the region with study sites can be found in Figure 3.1.

For all surveys at each of our long-term monitoring sites, ten quadrats (0.25 m²) were placed along a permanent 50 m transect at pre-determined random distances from the primary marker. In each quadrat, all seagrass species were listed and scored for abundance using a modified Braun–Blanquet scale: 0 = absent; 0.1 = one individual and < 5%; 0.5 = few individuals and < 5%; 1 = many individuals and < 5%; 2 = 5 - 25%; 3 = 25

- 50%; 4 = 50 - 75%; and 5 = 75 - 100% (Table 3.1; Fourqurean et al. 2001). Each of these same quadrats were also assessed for average seagrass canopy height (measured in situ with a ruler) as well as visual/tactile classification of sediments into one of 9 categories of increasing grain size (Table 3.2).

In addition to these routinely collected variables, sediment cores were taken during the January 2016 campaign at each site for C_{org} content, dry bulk density, and grain size analysis. Four surface sediment cores were taken at each site during the January 2016 campaign using 60 mL plastic syringes that had been modified into small piston cores (~2.6 cm diameter) able to sample the top ~15 cm of surface sediment with minimal compaction. Two cores of each set were dried at 65 °C and homogenized before being analyzed for dry bulk density (DBD) and C_{org} content. Samples were processed in duplicate for each site then used to calculate mean. Dry bulk density was calculated as the dry weight of the soil divided by the volume of the original soil sample and expressed as gram dry weight per cubic centimeter. C_{org} content was calculated using the instrumental analyzer-dry oxidation procedures described by Fourqurean et al. (2012b). Briefly, powdered samples were analyzed for total carbon (C_{total}) using a CHN analyzer. Subsamples of dried material were weighed, ashed at 550 °C for 4 h, and reweighed, enabling organic content to be calculated as loss on ignition (LOI). The ashed soil samples remaining after the LOI technique were reanalyzed using a CHN analyzer to quantify the C content of the inorganic fraction. C_{org} was calculated by difference between C_{total} and inorganic carbon (C_{inorg}), using LOI values to correct the C_{inorg} measurements to the pre-ashed soil mass. Carbon density, presented as $C_{\text{org}} \text{ mg cm}^{-3}$ is the product of C_{org} content and DBD.

The remaining two sediment cores from each site were used for grain size analysis using methods described by Erftemeijer and Koch (2001) for wet sieving. Approximately 60 mL of wet sediment was treated with 20 - 30 mL of 30% H_2O_2 to remove organics. After bubbling subsided, the slurry was sieved using a vibrating shaker plate and rotating

shower head that supplied a continuous flow of water. Sieve sizes 4 (> 4.76 mm), 10 (> 2.00 mm), 40 (> 0.42 mm), and 200 (> 0.07 mm) were chosen for easy comparison to other South Florida research projects and used to separate gravel, coarse, medium, and fine sand fractions. Water and all sediments passing through the 200 sieve were collected in 2000 mL graduated cylinders for pipette analysis to separate silt from clay contributions (Folk, 1980). The combination of procedures yielded percent contributions (by weight) of five sediment categories (clay, silt, fine sand, medium sand, coarse sand, and gravel). Clay and silt were combined for a “mud” category. Grain size analysis was done in duplicate for each site, presented data are the site means.

We assessed local OM breakdown rates beginning during the January 2016 campaign. Organic matter breakdown rates were measured using the canvas strip assay, where the loss of tensile strength of a standardized cellulose material is used as a proxy for OM decay (Harrison et al., 1988; Tiegs et al., 2007a). As described by Slocum et al. (2009), Fredrix brand 12-ounce duck, style number 548 artist canvas was cut into uniform strips 10 x 2 cm, each with the same number of warp threads in the long direction. These strips were deployed at each site where sediments allowed, with 10 deployed on the surface of the sediment and another 10 below the rhizosphere at 20 cm depth (Figure 3.2). Some sites had shallow to no sediment, preventing the assay deployment at all study sites. For deployment below the rhizosphere, sediment cores (4 cm wide x 20 cm deep) were extracted, followed immediately by the insertion of buried strips and the return of extracted sediment. Buried strips were tethered to surface strips and a small foam buoy using 5 mm nylon cord, allowing breakdown rates of buried, anoxic strips to be compared to strips exposed to the above sediment/water interface at each site while being easily relocated and recovered. Strips were deployed in January 2016 and recovered in June - July 2016 for incubation times spanning from 154 to 179 days. After the deployment period, strips were retrieved and kept on ice until processing. In the lab, strips were brushed gently

to remove sediments and epiphytes, soaked in freshwater for 20 minutes to remove salts and air-dried. Strip tensile strength was determined using a Dillon Quantrol Snapshot tensometer set to an expansion rate of 250 mm min⁻¹ and reported in Newtons (N).

To relate loss of tensile strength to weight loss, a separate, controlled experiment was conducted to correlate these variables. Identical strips of artist canvas (n = 190) were cut, weighed to the 0.1 mg, and individually labeled. To induce controlled oxidation equally across replicates, strips were incubated at ambient temperature under low light in 30% H₂O₂. Fifteen (15) strips were removed from the H₂O₂ bath daily for 12 days. Removed strips were lightly rinsed with water to stop the oxidation reaction, air dried, and reweighed. Tensile strengths for the 180 H₂O₂ - treated strips and a control group of 10 strips were measured in newtons (N) using a tensometer set up as described for the field experiment.

Data Processing

The Braun-Blanquet scale is an effective method for the rapid assessment of seagrass abundance, though the 0 - 5 scale is both non-linear and categorical, greatly limiting statistical usefulness. Species-specific Braun-Blanquet scores were converted to percent abundance by assigning the median percent abundance of each score's abundance range for each quadrat along the transect. Thus, a score of "5", representing 75% - 100% abundance, was converted to 87.5% abundance (Table 3.1). The calculated species-specific percent abundances at each quadrat were added together for total seagrass abundance. Species-specific and total seagrass abundance percentages were averaged across all quadrats from each site's 50 m transect (n = 10), then site-specific abundance averages (in %) were averaged again across sampling campaigns over two years (n = 4) to account for both minor spatial and temporal variations in a site's seagrass abundance. Similar procedures were applied to categorical sediment type data; sediment categories were assigned numbers

one through nine of increasing coarseness, where "1" is mud and "9" is rock (Table 3.2). These scores were averaged across a site's transect, then across sampling campaigns for a representational sediment score. Numerical scores were back-calculated to original categorical nomenclature for easy interpretation. Average canopy height for each site was calculated by averaging measurements across each site's transect, then averaging across sampling campaigns.

Data Analysis

When making pairwise comparisons of continuous variables (seagrass abundance, C_{org} content, sediment mud content, et cetera), linear regressions among sites were used, abiding by assumptions of the analysis. Organic carbon density and breakdown rates were analyzed across gradients of the categorical variable sediment type, thus ANOVA was used. The average tensile strength of recovered strips from each site and placement (exposed vs buried) was calculated and translated to percent weight loss. Breakdown rates (k) were then calculated using a first-order exponential decay function (Olson, 1963). The canvas strip assay as utilized here only considers initial and final weights in the breakdown rate calculations, so assumptions regarding model fit need to be made. We used the first-order exponential decay model for easy comparison to existing literature (Table 3.3).

Results

Soil C_{org}

Soil C_{org} content ranged from 0.7% to 8.6% averaging $2.4 \pm 0.3\%$ of dry wt. (Table 3.4). Organic carbon content was lower ($< 2\%$ dry wt) in waters deeper than 10 m and in more exposed areas found off the oceanside of the Florida Keys, whereas shallow waters nearshore and within Florida Bay generally had higher soil C_{org} (Figure 3.3a; Figure 3.4).

Dry bulk density ranged from 0.22 g cm^{-3} to 1.45 g cm^{-3} , averaging $0.73 \pm 0.04 \text{ g cm}^{-3}$. Dry bulk density was positively correlated with water depth (Figure 3.4; linear regression, $p < 0.05$, $R^2 = 0.53$) with deeper sites consistently having denser sediments. Carbon density ranged from 6.2 mg cm^{-3} to 27.7 mg cm^{-3} , averaging $13.8 \pm 0.8 \text{ mg cm}^{-3}$. Sites with a deeper water column ($> 10 \text{ m}$) had lower C_{org} density than shallow sites nearshore and within Florida Bay (Figure 3.4; linear regression, $p < 0.05$, $R^2 = 0.16$). Two shallow sites (water depth $\sim 1 \text{ m}$) within the extremely P-limited region of Florida Bay also supported low C_{org} density, under 11 mg cm^{-3} (Figure 3.4a).

Seagrass Characteristics

Seagrass was present at 96% of sites during sampling period. *Thalassia testudinum* was the most commonly found species, present at 94% of sites, with *Syringodium filiforme* and *Halodule wrightii* found less frequently (at 49% and 34% of sites, respectively). There was no correlation between the abundance of any of the three individual seagrass species and C_{org} density (linear regression, $p > 0.05$). When species identity was disregarded and seagrasses were considered collectively, there was a positive correlation between seagrass abundance and C_{org} density (Figure 3.6a; linear regression, $p < 0.05$) with seagrass abundance explaining 13% of the variation in C_{org} density. Average canopy height also positively correlated with soil C_{org} density (Figure 3.6b; linear regression, $p < 0.05$, $R^2 = 0.24$).

Sediment Grain Size

Sediment type varied greatly across the South Florida seascape with sites within the protected water of Florida Bay and the Gulf of Mexico side of the lower Florida Keys containing sediments categorized exclusively as mud or sandy mud (Figure 3.4b). Other sites showed a greater variation in sediment type, with deeper oceanside sites generally having coarser (muddy sand, sand, or gravel) sediments. Categorical sediment

classifications collected through long-term monitoring correlated with results from our grain size analyses; sites with lower sediment index scores (i.e., mud and sandy mud) had higher fractions of mud (Figure 3.5a; ANOVA, $p < 0.05$) and generally lower dry bulk densities (Figure 3.5b; ANOVA, $p < 0.05$) and higher C_{org} content and density (Figure 3.5c, Figure 3.5d; ANOVA, $p < 0.05$). There was a weak positive correlation between total seagrass abundance and mud content (Figure 3.6c; linear regression, $p < 0.05$, $R^2 = 0.19$) and between height and mud content (Figure 3.6d; linear regression, $p < 0.05$, $R^2 = 0.39$). Sites with muddier sediments had higher C_{org} density (linear regression, $p < 0.05$), and mud content alone explained 34% of the variability in C_{org} density between sites.

Organic Matter Breakdown

During the longest exposure to hydrogen peroxide in the lab calibration experiment (12 days), canvas strips decreased in tensile strength from an average of 238.7 ± 7.2 N to 10.7 ± 1.4 N, and decreased in mass from 741.9 ± 4.6 mg to 613.8 ± 8.4 mg. A logarithmic model was used to explain the relationship between tensile strength and weight loss, yielding a best fit equation of $wtloss = 29.5 - 12.4 \times \log_{10}(tensstrgth)$ with $R^2 = 0.77$, where $wtloss$ represents % weight loss of canvas strip and $tensstrgth$ represents the final tensile strength of deployed strip (Figure 3.7).

Canvas strips were successfully retrieved from 23 of the sites, accounting for sites unsuitable for deployment and sites where deployed strips were lost (Figure 3.1). Breakdown rates, k , averaged 0.33 ± 0.02 yr⁻¹ across all sites and conditions, ranging from 0.07 to 0.59 mg mg⁻¹ yr⁻¹ (Table 3.5). Considering all 23 sites, there was not an effect of burial on breakdown rates (paired t-test, $p > 0.05$; Figure 3.9), nor was there an effect of seagrass density (surface or buried; linear regression, $p > 0.05$). Breakdown rates of surface-deployed strips were generally lower on the southeastern, ocean-exposed side of the Florida Keys archipelago. Breakdown rates were generally lower for buried strips in

the areas of Florida Bay, the Gulf of Mexico side of the lower keys, and other shallow sites. When sites were divided into sediment type categories, breakdown rates of buried strips increased with increasing sediment coarseness (Figure 3.9; ANOVA, $p < 0.05$) while rates decreased for surface deployed strips decreased with increasing coarseness (Figure 3.9; ANOVA, $p < 0.05$). Breakdown rates in sediments categorized as “mud” and “sandy mud” were decreased 39 and 22% for buried canvas strips relative to those deployed on the sediment surface (Figure 3.9; ANOVA, $p < 0.05$). For sites with courser sediments (muddy sand, sand, and gravel), the opposite was true: breakdown rates of buried strips were at least of 55% faster than surface deployed strips (Figure 3.9; ANOVA, $p < 0.05$).

Discussion

Successful Blue Carbon management in seagrass ecosystems relies on the protection of large seagrass C_{org} stocks where OM remineralization rates are low. Here we show that seagrass density and canopy height are related to surface C_{org} density, across the South Florida seascape, though sediment type and grain size (not necessarily driven by seagrasses) better explain variation in C_{org} soil density. Sediment characteristics, rather than seagrass characteristics, controlled OM breakdown rates. The general hypothesis that burial enhances OM preservation was not supported at our study sites, rather only at a subset of sites where fine-grained, high C_{org} soils were found. Conversely, rates of OM breakdown were higher when buried in coarse-grained, low C_{org} seagrass sediments than they were at the sediment surface. These finding have direct bearing on the development of Blue Carbon strategies, as they bring into question the categorical importance of burial to C_{org} preservation, suggesting that only sites with fine sediments, regardless of seagrass presence, enhance preservation of C_{org} through burial.

The sediment C_{org} content across South Florida (averaging $2.4 \pm 0.3\%$) was slightly higher than global values (1.4% median, $2.0 \pm 0.1\%$ mean) and slightly higher than previously reported from Florida Bay exclusively ($2.1 \pm 0.3\%$; Fourqurean et al. 2012a,b). Dry bulk density across South Florida averaged $0.73 \pm 0.04 \text{ g cm}^{-3}$, lower than previously published global (Fourqurean et al., 2012a), and south Florida (Fourqurean et al., 2012b) values (1.03 ± 0.02 and $1.0 \pm 0.1 \text{ g cm}^{-3}$, respectively). Finer particles with higher organic content commonly have lower dry bulk densities (Figure 3.5b, c; Fourqurean et al. 2012a) justifying the high C_{org} content / low DBD values reported here.

The positive correlation between seagrass presence and C_{org} storage observed across South Florida has been noted previously (Macreadie et al., 2015; Armitage and Fourqurean, 2016). This trend was only significant when seagrass species was disregarded and total seagrass abundance was considered. Seagrass species vary in C production, plant C allocation, and tissue recalcitrance (Chapter 5; Howard et al. 2016; Trevathan-Tackett et al. 2017a), thus C_{org} stocks may have been expected to relate to seagrass community composition as has been observed elsewhere (Lavery et al., 2013). However, if soil C content was driven primarily by the decrease in shear stress at the sediment surface provided by seagrass canopy complexity, individual species presence or density would not matter as much as the overall canopy complexity produced. Gullström et al. (2017) found that above-ground characteristics (abundance, canopy, and aboveground biomass) had no significant effect on soil C_{org} storage, whereas below-ground biomass did. The differences in seagrass morphology and local environmental conditions between our study sites and those of Gullström et al. (2017) could explain the contrasting drivers of C_{org} storage in the disparate locations. Alternatively, seagrass characteristics and C_{org} density could be strictly correlative, where proximity to land and depth affect seagrass morphology, abundance and sediment characteristics simultaneously via altered hydrodynamics, nutrient availability and light availability (Hemminga and Duarte, 2000; Schanz and Asmus,

2003). If this is the case, both seagrass characteristics and C_{org} stocks could be dependent on local landscape configuration and geomorphology; this may explain interspecies variation in C_{org} stocks documented in some Australian habitats (Lavery et al., 2013).

Sediment characteristics better explained variations in C_{org} stocks than did seagrass abundance. We found that finer, less dense sediments contained greater C_{org} stocks, supporting previously published work (Dahl et al., 2016; Röhr et al., 2016; Serrano et al., 2016a; Gullström et al., 2017). Like Serrano et al. (2014), we found that deeper sites (> 10 m) contained lower C_{org} stocks, though we explain the low soil C_{org} content soils at these sites by their coarse sediments resulting from a higher energy environment, rather than the lower carbon inputs stemming from lower light availability. Conversely, shallow muddy sites found sheltered between small islands and embayments had the highest C_{org} stocks. These high C_{org} sites are positioned within a matrix of land, protecting sediments from high energy, high velocity water and promoting an environment more conducive to the settling of fine, low DBD sediment particles (Röhr et al., 2016). This landscape also promotes C_{org} inputs from nearby mangroves and other terrestrial sources that can augment seagrass inputs (Bouillon and Connolly, 2009). There are two exceptions; two sampling sites within the shallow matrix of Florida Bay islands had values below the regional average DBD (0.7 g cm^{-3}) but lower C_{org} content than all other protected sites. These sites are within the extremely P-limited portion of Florida Bay where water hydrodynamics allow for the accumulation of fine particulates but nutrient limitation prevents a general source for C_{org} input (Fourqurean and Zieman, 2002). The P availability gradient within Florida Bay is so strong that C_{org} stocks can be driven by seagrass characteristics and primary productivity rather than hydrologically-driven sediment characteristics that dominate the South Florida seascape more broadly (Armitage and Fourqurean, 2016).

The presence of seagrass has been suggested to decrease grain size in sediments and soils, in turn altering the soil C_{org} content (Bos et al., 2007; Miyajima et al., 2017); we

noted positive, albeit weak, relationships between both seagrass abundance and canopy height with mud content in our study region (Figure 3.6). The net accumulation of silts and clays is determined by the balance between particulate input, sedimentation, and losses from erosion. Sites with seagrasses can both provide fine particulate material and the depositional environment to promote its burial, though local hydrology and allochthonous inputs independently promote net sedimentation of fine particles regardless of seagrass presence. Given the diversity of seagrass abundance, hydrologic conditions and sedimentary inputs between our study sites at the landscape scale, the lack of a strong correlation was perhaps not unexpected.

Degradation of seagrass ecosystem ecosystems may lead to significant carbon losses and emissions of CO₂ as carbon is oxidized, thus a primary justification for seagrass conservation in Blue Carbon strategies is to maintain the stable, anoxic sediments they create (Lovelock et al., 2017a,b). Burial in such stable, anoxic environments is thought to suppress decomposition and remineralization of OM, particularly that of more refractory compounds (Burdige, 2007; Lovelock et al., 2017b). Across our study sites, we saw no general trend for the preservation of buried OM compared to exposed material (Figure 3.8) with approximately half of sites displaying faster breakdown rates below the rhizosphere at 20 cm depth compared to the sediment-water column interface. The categorical importance of burial to OM decomposition has been repeatedly questioned, giving way to a more complex hypothesis where enhanced decomposition by O₂ exposure and the priming effect is only important to some more recalcitrant, aged OM (Harrison, 1989; Kristensen et al., 1995; Hulthe et al., 1998; Burdige, 2007; Bianchi, 2011).

The decay rates reported here are low on average compared to those previously reported for seagrass ecosystems, though still within the reported range (Table 3.6; Table 3.3). To investigate the importance of burial to OM breakdown, we utilized the cotton strip assay and converted results to units of weight loss for comparison to the literature. The vast

majority of previous studies use litter bags to measure breakdown rates despite the well known obstacles. Variations of this methodology make use of raw, natural material that are naturally inconstant between species and source. This may not be a problem if the decay of a particular substrate is the research focus, though if establishing and comparing the influence of environmental setting on decay rates is the research goal, this could add unwanted variation. We avoided these obstacles by minimizing any variance in recalcitrance through the use of standardized organic material (Tiegs et al., 2007b). Even more problematic for the litter bag method is the fluctuation of material weight not related to microbial mediated decomposition that could lead to an overestimation of decay rates (Valiela et al., 1985; Moran and Hodson, 1989). This shortcoming could explain our comparably low decay rates, though there could be another explanation. The standard organic substrate used for the cotton strip assay is > 95% cellulose (Tiegs et al., 2007a) representing only a single type of OM amongst a plethora of compounds found in sediments, all varying greatly in their recalcitrance. Canvas strips do not fully capture the full range of recalcitrance of naturally occurring seagrass OM, particularly the more labile OM fractions. These fractions of fresh OM can be leached out or quickly mineralized regardless of redox conditions (Harrison, 1989). The lack of these OM fractions in our canvas strips would likely results in decay rates lower than those that utilize fresh and whole tissue OM, like that typically used in previous literature (Table 3.3). Trevathan-Tackett et al. (2017b) used dead leaf detritus rather than fresh, resulting in a lower leaf decay rate than average (Table 3.3). These labile OM fractions excluded from our experimental design are likely to be unimportant for long term Blue Carbon stocks anyway.

The canvas strip assay is not without its methodological shortcomings. Cellulose can be considered one of the more recalcitrant organic compounds produced by seagrasses (Trevathan-Tackett et al., 2017a), though our standard organic substrate lacks the more complex, more recalcitrant OM fractions that could be important to long term storage (see

Trevathan-Tackett et al. 2017a. The canvas strip assay has been used previously in multiple settings and ecosystems (Harrison et al., 1988; Tiegs et al., 2007b; Kirwan et al., 2014), though never before has it been converted to the commonly used units of weight loss. The lab bench experiment using H_2O_2 as an oxidant yielded a clear correlation between tensile strength and weight loss ($R^2 = 0.77$), though the rates of loss are very different from one another. Regardless of the unit of decay, there was no difference between the breakdown rates for OM on the surface compared to that buried (Table 3.5). (Fourqurean and Schrlau, 2003) found differences in decay rates between species of coastal plants, but no difference between buried and surface-deployed litter bags. The seagrass literature contains decay rates spanning two orders of magnitude, though the variation relies on study methodology, type of substrate, and environmental condition that do not typically address burial. However, Godshalk and Wetzel (1978) did note faster decomposition rates in aerated conditions, though only at the highest experimental temperature. Increased CO_2 emissions (related to decomposition) were measured in mangrove forests where soils were disturbed (Kristensen et al., 2008) and sediments exposed and augmented with labile OM (Trevathan-Tackett et al., 2018). The stable, anoxic conditions of seagrass soil may encourage the long-term preservation of soil C_{org} , though there is little empirical support of universality or effect size, despite published rates (Table 3.6; Lovelock et al. 2017b).

The varying effect of burial on breakdown rates is elucidated when sites were separated by sediment type (Figure 3.9). Burial depresses OM breakdown rates by an average of 39% at sites with muddy sediments and 22% at sites with sandy mud. Sites with coarser sediments (muddy sand, sand, and gravel) show the opposite trend, where buried canvas strips had accelerated rates of breakdown compared to strips deployed on the sediment surface. This may be explained by advective processes occurring in highly permeable, sandy sediments that allows solutes (O_2 , nutrients, labile DOM, etc) to be transported through the sediment depth profile (Janssen et al., 2005; Burdige, 2007). In the sandy,

coarse-grained carbonate sands of the Bahamas (geologically similar to the oceanside of the Florida Keys in our study area), (Burdige and Zimmerman, 2002) found that measurable O₂ concentrations related to pore water advection at depths over 20 cm. Porewater exchange of solutes through coarse sediments leads to faster turnover rates of organics introduced to sediments and lower C_{org} retention (Huettel et al., 2014). Fine-grained, muddy sediments have lower porosity and pore water exchange, leading to decreased solute penetration and a reliance on sulfate reduction rather than aerobic decomposition (Cook et al., 2007; Silburn et al., 2017). Limited solute renewal and delivery in fine sediments decreases OM remineralization and thus increases OM preservation (Burdige, 2007). Breakdown of buried OM (including deployed canvas strips) in fine muds is thus only a fraction of that in coarse sediments. The maintenance of uneroded, buried OM is important to its preservation at some sites as previously suggested (Lovelock et al., 2017b; Fourqurean et al., 2012a), though possibly only at sites with stable, fine-grained sediments.

Breakdown rates of canvas strips deployed on the sediments surface were notably faster in fine compared to coarse sediments, suggesting that decomposition rates of OM are not universally slower in fine-grained depositional environments (Figure 3.9). Oxygen uptake rate by microbial decomposition on the sediment surface is negatively correlated with grain size, thus sediments containing higher C_{org} content and greater surface area for microbial substrate have faster breakdown rates (Hargrave, 1972; DeFlaun and Mayer, 1983; Huettel et al., 2014). Faster decomposition and consumption of solutes at the sediment surface in fine sediments can lead to fewer solutes being transported through the sediments for bacteria to use when remineralizing buried C_{org}; this compounded with limited permeability of muds, creates a large gradient in oxygen consumption and decomposition down the sediment profile (Silburn et al., 2017).

Implications for Management and Blue Carbon Strategies

Our results indicate, despite widely-held assumptions, that seagrass abundance is not always a primary driver of C_{org} density in coastal environments, and that burial of OM in seagrasses does not necessarily decrease decomposition rates and enhance storage. Rather, environmental context is important in determining whether OM in seagrass meadows would be at risk of being returned to the atmosphere, and hence have value in Blue Carbon accounting, upon loss of the seagrass ecosystems. In places where seagrasses lead to deposition of finer-grained soils than would occur in their absence and where grain size is fine enough to slow decomposition of buried compared to surficial soil C_{org} , it is likely that loss of seagrasses would result in the net release of stored soil carbon to the atmosphere. However, in environments with coarser-grained sediments, burial of OM under seagrass actually increases the rate of OM breakdown. It remains to be determined if these increased cellulose degradation rates in seagrasses could lead to less C_{org} storage in some seagrass meadows in coarse-grained sediments than in nearby unvegetated areas.

There was a 4.5-fold difference in surface C_{org} density across South Florida stocks that was driven primarily by sediment type that in turn was more reliant on landscape arrangement and local hydrogeological characteristics than the density or species identity of the seagrasses themselves. These findings, along with others (Röhr et al., 2016; Dahl et al., 2016; Serrano et al., 2016b) bring to question the categorical importance of seagrasses to soil C_{org} stocks and suggest that management considerations should be expanded beyond seagrass conservation as a guiding rule.

In the context of Blue Carbon strategies, we might want to reconsider how sites are selected and managed for carbon conservation. Here we note that sediment type, regardless of the driving factor behind it, is important to both C_{org} stock and C_{org} preservation. We have already identified seagrasses, marshes and mangroves as more important for Blue

Carbon strategies. Perhaps we should further prioritize sites, taking more consideration in likelihood that C_{org} stocks can be preserved.

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Work Cited

- Armitage, A. R. and Fourqurean, J. W. (2016). Carbon storage in seagrass soils: long-term nutrient history exceeds the effects of near-term nutrient enrichment. *Biogeosciences*, 13(1):313–321.
- Belshe, E. F., Hoeijmakers, D., Herran, N., Mtolera, M., and Teichberg, M. (2017). Seagrass community-level controls over organic carbon storage are constrained by geo-physical attributes within meadows of Zanzibar, Tanzania. *Biogeosciences*, pages 1–27.
- Bergamaschi, B. A., Tsamakis, E., Keil, R. G., Eglinton, T. I., Montluçon, D. B., and Hedges, J. I. (1997). The effect of grain size and surface area on organic matter, lignin and carbohydrate concentration, and molecular compositions in Peru Margin sediments. *Geochimica et Cosmochimica Acta*, 61(6):1247–1260.
- Bianchi, T. S. (2011). The role of terrestrially derived organic carbon in the coastal ocean: A changing paradigm and the priming effect. *Proceedings of the National Academy of Sciences*, 108(49):19473–19481.
- Borum, J., Pederson, O., Greve, T. M., Frankovich, T. A., Zieman, J., Fourqurean, J. W., and Madden, C. J. (2005). The potential role of plant oxygen and sulphide dynamics in die-off events of the tropical seagrass, *Thalassia testudinum*. *Journal of Ecology*, 93(1):148–158.

- Bos, A. R., Bouma, T. J., de Kort, G. L. J., and Van Katwijk, M. M. (2007). Ecosystem engineering by annual intertidal seagrass beds: Sediment accretion and modification. *Estuarine, Coastal and Shelf Science*, 74(1-2):344–348.
- Bouillon, S. and Connolly, R. (2009). Carbon Exchange Among Tropical Coastal Ecosystems. In Nagelkerken, I., editor, *Ecological connectivity among tropical coastal ecosystems*, pages 45–70. Springer.
- Burdige, D. J. (2007). Preservation of Organic Matter in Marine Sediments: Controls, Mechanisms, and an Imbalance in Sediment Organic Carbon Budgets? *Chemical Reviews*, 107(2):467–485.
- Burdige, D. J. and Zimmerman, R. C. (2002). Impact of sea grass density on carbonate dissolution in Bahamian sediments. *Limnology and Oceanography*, 47(6):1751–1763.
- Cook, P. L., Wenzhöfer, F., Glud, R. N., Janssen, F., and Huettel, M. (2007). Benthic solute exchange and carbon mineralization in two shallow subtidal sandy sediments: Effect of advective pore-water exchange. *Limnology and Oceanography*, 52(5):1943–1963.
- Dahl, M., Deyanova, D., Gütschow, S., Asplund, M. E., Lyimo, L. D., Karamfilov, V., Santos, R., Björk, M., and Gullström, M. (2016). Sediment Properties as Important Predictors of Carbon Storage in *Zostera marina* Meadows: A Comparison of Four European Areas. *PLoS ONE*, 11(12):e0167493.
- Dauwe, B., Middelburg, J., and Herman, P. (2001). Effect of oxygen on the degradability of organic matter in subtidal and intertidal sediments of the North Sea area. *Marine Ecology Progress Series*, 215:13–22.
- DeFlaun, M. F. and Mayer, L. M. (1983). Relationships between bacteria and grain surfaces in intertidal sediments. *Limnology and Oceanography*, 28(5):873–881.
- Duarte, C. M., Kennedy, H., Marbà, N., and Hendriks, I. (2011). Assessing the capacity of seagrass meadows for carbon burial: Current limitations and future strategies. *Ocean and Coastal Management*, 83:32–38.
- Duarte, C. M. and Krause-Jensen, D. (2017). Export from Seagrass Meadows Contributes to Marine Carbon Sequestration. *Frontiers in Marine Science*, 4:2107.
- Erfemeijer, P. and Koch, E. W. (2001). Sediment geology methods for seagrass habitat. In *Global seagrass research methods*, pages 345–367. Elsevier Science.
- Folk, R. L. (1980). *Petrology of sedimentary rocks*. Hemphill Publishing Company.
- Fonseca, M. S. and Fisher, J. S. (1986). A comparison of canopy friction and sediment movement between four species of seagrass with reference to their ecology and restoration. *Marine Ecology Progress Series*, 29(1):15–22.
- Fourqurean, J. W., Boyer, J. N., Durako, M. J., Hefty, L. N., and Peterson, B. J. (2003). Forecasting responses of seagrass distributions to changing water quality using monitoring data. *Ecological Applications*, 13(2):474–489.
- Fourqurean, J. W., Duarte, C. M., Kennedy, H., Marbà, N., Holmer, M., Mateo, M. A., Apostolaki, E. T., Kendrick, G. A., Krause-Jensen, D., McGlathery, K. J., and Ser-

- rano, O. (2012a). Seagrass ecosystems as a globally significant carbon stock. *Nature Geoscience*, 5(7):505–509.
- Fourqurean, J. W., Durako, M. J., Hall, M. O., and Hefty, L. N. (2002). Seagrass distribution in south florida: a multi-agency coordinated monitoring program. CRC Press.
- Fourqurean, J. W., Kendrick, G. A., Collins, L. S., Chambers, R. M., and Vanderklift, M. A. (2012b). Carbon, nitrogen and phosphorus storage in subtropical seagrass meadows: examples from Florida Bay and Shark Bay. *Marine and Freshwater Research*, 63(11):967.
- Fourqurean, J. W., Powell, G. V., Kenworthy, W. J., and Zieman, J. C. (1995). The effects of long-term manipulation of nutrient supply on competition between the seagrasses *Thalassia testudinum* and *Halodule wrightii* in Florida Bay. *Oikos*, 72(3):349–358.
- Fourqurean, J. W. and Schrlau, J. E. (2003). Changes in nutrient content and stable isotope ratios of C and N during decomposition of seagrasses and mangrove leaves along a nutrient availability gradient in Florida Bay, USA. *Chemistry and Ecology*, 19(5):373–390.
- Fourqurean, J. W., Willsie, A., Rose, C. D., and Rutten, L. M. (2001). Spatial and temporal pattern in seagrass community composition and productivity in south Florida. *Marine Biology*, 138(2):341–354.
- Fourqurean, J. W. and Zieman, J. C. (2002). Nutrient content of the seagrass *Thalassia testudinum* reveals regional patterns of relative availability of nitrogen and phosphorus in the Florida Keys USA. *Biogeochemistry*, 61(3):229–245.
- Godshalk, G. L. and Wetzel, R. G. (1978). Decomposition of aquatic angiosperms. III. *Zostera marina* L. and a conceptual model of decomposition. *Aquatic Botany*, 5:329–354.
- Greiner, J. T., McGlathery, K. J., Gunnell, J., and McKee, B. A. (2013). Seagrass restoration enhances “blue carbon” sequestration in coastal waters. *PLoS ONE*, 8(8):e72469.
- Gullström, M., Lyimo, L. D., Dahl, M., Samuelsson, G. S., Eggertsen, M., Anderberg, E., Rasmusson, L. M., Linderholm, H. W., Knudby, A., Bandeira, S., Nordlund, L. M., and Björk, M. (2017). Blue Carbon Storage in Tropical Seagrass Meadows Relates to Carbonate Stock Dynamics, Plant– Sediment Processes, and Landscape Context: Insights from the Western Indian Ocean. *Ecosystems*, pages 1–16.
- Hansen, J. C. R. and Reidenbach, M. A. (2013). Seasonal Growth and Senescence of a *Zostera marina* Seagrass Meadow Alters Wave-Dominated Flow and Sediment Suspension Within a Coastal Bay. *Estuaries and Coasts*, 36(6):1099–1114.
- Hargrave, B. T. (1972). Aerobic decomposition of sediment and detritus as a function of particle surface area and organic content. *Limnology and Oceanography*, 17(4):583–586.
- Harrison, A. F., Latter, P. M., and Walton, D. W. H. (1988). *Cotton strip assay: an index of decomposition in soils*. ITE.

- Harrison, P. G. (1989). Detrital processing in seagrass systems: a review of factors affecting decay rates, remineralization and detritivory. *Aquatic Botany*, 35(3-4):263–288.
- Hemminga, M. A. and Duarte, C. M. (2000). *Seagrass ecology*. Cambridge University Press.
- Hendriks, I. E., Sintes, T., Bouma, T. J., and Duarte, C. M. (2008). Experimental assessment and modeling evaluation of the effects of the seagrass *Posidonia oceanica* on flow and particle trapping. *Marine Ecology Progress Series*, 356:163–173.
- Hiraishi, T., Krug, T., Watanabe, K., Srivastava, N., Baasansuren, J., Fukuda, M., and Troxler, T. (2014). 2013 Supplement to the 2006 IPCC guidelines for national greenhouse gas inventories: wetlands . IPCC, Switzerland.
- Howard, J., Sutton-Grier, A., Herr, D., Kleypas, J., Landis, E., Mcleod, E., Pidgeon, E., and Simpson, S. (2017). Clarifying the role of coastal and marine systems in climate mitigation. *Frontiers in Ecology and the Environment*, 15(1):42–50.
- Howard, J. L., Perez, A., Lopes, C. C., and Fourqurean, J. W. (2016). Fertilization Changes Seagrass Community Structure but not Blue Carbon Storage: Results from a 30-Year Field Experiment. *Estuaries and Coasts*, 39(5):1422–1434.
- Huettel, M., Berg, P., and Kostka, J. E. (2014). Benthic Exchange and Biogeochemical Cycling in Permeable Sediments. *Annual Review of Marine Science*, 6(1):23–51.
- Hulthe, G., Hulth, S., and Hall, P. O. (1998). Effect of oxygen on degradation rate of refractory and labile organic matter in continental margin sediments. *Geochimica et Cosmochimica Acta*, 62(8):1319–1328.
- Janssen, F., Huettel, M., and Witte, U. (2005). Pore-water advection and solute fluxes in permeable marine sediments (II): Benthic respiration at three sandy sites with different permeabilities (German Bight, North Sea). *Limnology and Oceanography*, 50(3):779–792.
- Keil, R. G. and Hedges, J. I. (1993). Sorption of organic matter to mineral surfaces and the preservation of organic matter in coastal marine sediments. *Chemical Geology*, 107(3):385–388.
- Kennedy, H., Beggins, J., Duarte, C. M., Fourqurean, J. W., Holmer, M., Marbà, N., and Middelburg, J. J. (2010). Seagrass sediments as a global carbon sink: Isotopic constraints. *Global Biogeochemical Cycles*, 24(4):GB4026.
- Kirwan, M. L., Guntenspergen, G. R., and Langley, J. A. (2014). Temperature sensitivity of organic-matter decay in tidal marshes. *Biogeosciences*, 11(17):4801–4808.
- Kristensen, E., Ahmed, S. I., and Devol, A. H. (1995). Aerobic and anaerobic decomposition of organic matter in marine sediment: Which is fastest? *Limnology and Oceanography*, pages 1430–1437.
- Kristensen, E., Flindt, M. R., Ulomi, S., Borges, A. V., Abril, G., and Bouillon, S. (2008). Emission of CO₂ and CH₄ to the atmosphere by sediments and open waters in two Tanzanian mangrove forests. *Marine Ecology Progress Series*, 370:53–67.

- Kristensen, E. and Holmer, M. (2001). Decomposition of plant materials in marine sediment exposed to different electron acceptors O₂, NO₃, and SO₄⁻², with emphasis on substrate origin, degradation kinetics, and the role of bioturbation. *Geochimica et Cosmochimica Acta*, 65(3):419–433.
- Lavery, P. S., Mateo, M. A., Serrano, O., and Rozaimi, M. (2013). Variability in the Carbon Storage of Seagrass Habitats and Its Implications for Global Estimates of Blue Carbon Ecosystem Service. *PLoS ONE*, 8(9):e73748.
- Lovelock, C. E., Atwood, T., Baldock, J., Duarte, C. M., Hickey, S., Lavery, P. S., Masqué, P., Macreadie, P. I., Ricart, A. M., Serrano, O., and Steven, A. (2017a). Assessing the risk of carbon dioxide emissions from blue carbon ecosystems. *Frontiers in Ecology and the Environment*, 15(5):257–265.
- Lovelock, C. E., Fourqurean, J. W., and Morris, J. T. (2017b). Modeled CO₂ Emissions from Coastal Wetland Transitions to Other Land Uses: Tidal Marshes, Mangrove Forests, and Seagrass Beds. *Frontiers in Marine Science*, 4:143.
- Macreadie, P. I., Nielsen, D. A., Kelleway, J. J., Atwood, T. B., Seymour, J. R., Petrou, K., Connolly, R. M., Thomson, A. C., Trevathan-Tackett, S. M., and Ralph, P. J. (2017). Can we manage coastal ecosystems to sequester more blue carbon? *Frontiers in Ecology and the Environment*, 57:1492.
- Macreadie, P. I., Trevathan-Tackett, S. M., Skilbeck, C. G., Sanderman, J., Curlevski, N., Jacobsen, G., and Seymour, J. R. (2015). Losses and recovery of organic carbon from a seagrass ecosystem following disturbance. *Proceedings of the Royal Society B: Biological Sciences*, 282(1817):20151537.
- Marbà, N., Arias-Ortiz, A., Masqué, P., Kendrick, G. A., Mazarrasa, I., Bastyan, G. R., Garcia-Orellana, J., and Duarte, C. M. (2015). Impact of seagrass loss and subsequent revegetation on carbon sequestration and stocks. *Journal of Ecology*, 103:296–302.
- Mazarrasa, I., Marba, N., Lovelock, C. E., Serrano, O., Lavery, P. S., Fourqurean, J. W., Kennedy, H., Mateo, M. A., Krause-Jensen, D., Steven, A. D. L., and Duarte, C. M. (2015). Seagrass meadows as a globally significant carbonate reservoir. *Biogeosciences*, 12(5):4107–4138.
- McLeod, E., Chmura, G. L., Bouillon, S., Salm, R., Björk, M., Duarte, C. M., Lovelock, C. E., Schlesinger, W. H., and Silliman, B. R. (2011). A blueprint for blue carbon: toward an improved understanding of the role of vegetated coastal habitats in sequestering CO₂. *Frontiers in Ecology and the Environment*, 9(10):552–560.
- Middelburg, J. and Levin, L. (2009). Coastal hypoxia and sediment biogeochemistry. *Biogeosciences*, 6(7):1273–1293.
- Miyajima, T., Hori, M., Hamaguchi, M., Shimabukuro, H., and Yoshida, G. (2017). Geophysical constraints for organic carbon sequestration capacity of *Zostera marina* seagrass meadows and surrounding habitats. *Limnology and Oceanography*, 62(3):954–972.
- Moodley, L., Middelburg, J. J., Herman, P. M. J., Soetaert, K., and de Lange, G. J. (2005). Oxygenation and organic-matter preservation in marine sediments: Direct experimental evidence from ancient organic carbon-rich deposits. *Geology*, 33(11):889.

- Moran, M. A. and Hodson, R. E. (1989). Bacterial secondary production on vascular plant detritus: relationships to detritus composition and degradation rate. *Applied and Environmental Microbiology*, 55(9):2178–2189.
- Olson, J. S. (1963). Energy storage and the balance of producers and decomposers in ecological systems. *Ecology*, 44(2):322–331.
- Oreska, M. P. J., McGlathery, K. J., and Porter, J. H. (2017). Seagrass blue carbon spatial patterns at the meadow-scale. *PLoS ONE*, 12(4):e0176630.
- Pendleton, L., Donato, D. C., Murray, B. C., Crooks, S., Jenkins, W. A., Sifleet, S., Craft, C., Fourqurean, J. W., Kauffman, J. B., Marbà, N., Megonigal, P., Pidgeon, E., Herr, D., Gordon, D., and Baldera, A. (2012). Estimating Global “Blue Carbon” Emissions from Conversion and Degradation of Vegetated Coastal Ecosystems. *PLoS ONE*, 7(9):e43542.
- Röhr, M. E., Boström, C., Canal-Vergés, P., and Holmer, M. (2016). Blue carbon stocks in Baltic Sea eelgrass (*Zostera marina*) meadows. *Biogeosciences*, 13(22):6139–6153.
- Schanz, A. and Asmus, H. (2003). Impact of hydrodynamics on development and morphology of intertidal seagrasses in the Wadden Sea. *Marine Ecology Progress Series*, 261:123–134.
- Serrano, O., Lavery, P. S., Duarte, C. M., Kendrick, G. A., Calafat, A., York, P. H., Steven, A., and Macreadie, P. I. (2016a). Can mud (silt and clay) concentration be used to predict soil organic carbon content within seagrass ecosystems? *Biogeosciences*, 13(17):4915.
- Serrano, O., Lavery, P. S., and Rozaimi, M. (2014). Influence of water depth on the carbon sequestration capacity of seagrasses. *Global Biogeochemical Cycles*, 28:950–961.
- Serrano, O., Ricart, A. M., Lavery, P. S., Mateo, M. A., Arias-Ortiz, A., Masqué, P., Steven, A., and Duarte, C. M. (2016b). Key biogeochemical factors affecting soil carbon storage in *Posidonia* meadows. *Biogeosciences*, 13:4581–4594.
- Silburn, B., Kröger, S., Parker, E. R., Sivyer, D. B., Hicks, N., Powell, C. F., Johnson, M., and Greenwood, N. (2017). Benthic pH gradients across a range of shelf sea sediment types linked to sediment characteristics and seasonal variability. *Biogeochemistry*, 135(1):69–88.
- Slocum, M. G., Roberts, J., and Mendelssohn, I. A. (2009). Artist canvas as a new standard for the cotton-strip assay. *Journal of Plant Nutrition and Soil Science*, 172(1):71–74.
- Tiegs, S., Langhans, S., Tockner, K., and Gessner, M. O. (2007a). Cotton strips as a leaf surrogate to measure decomposition in river floodplain habitats. *Journal of the North American Benthological Society*, 26(1):70–77.
- Tiegs, S., Langhans, S., Tockner, K., and Gessner, M. O. (2007b). Cotton strips as a leaf surrogate to measure decomposition in river floodplain habitats. *Journal of the North American Benthological Society*, 26(1):70–77.
- Trevathan-Tackett, S. M., Macreadie, P. I., Sanderman, J., Baldock, J., Howes, J. M., and Ralph, P. J. (2017a). A Global Assessment of the Chemical Recalcitrance of Seagrass Tissues: Implications for Long-Term Carbon Sequestration. *Frontiers in plant science*, 8:561.

- Trevathan-Tackett, S. M., Seymour, J. R., Nielsen, D. A., Macreadie, P. I., Jeffries, T. C., Sanderman, J., Baldock, J., Howes, J. M., Steven, A. D. L., and Ralph, P. J. (2017b). Sediment anoxia limits microbial-driven seagrass carbon remineralization under warming conditions. *FEMS Microbiology Ecology*, 93(6).
- Trevathan-Tackett, S. M., Thomson, A. C., Ralph, P. J., and Macreadie, P. I. (2018). Fresh carbon inputs to seagrass sediments induce variable microbial priming responses. *Science of The Total Environment*, 621:663–669.
- Valiela, I., Teal, J. M., Allen, S. D., Van Etten, R., Goehring, D., and Volkmann, S. (1985). Decomposition in salt marsh ecosystems: the phases and major factors affecting disappearance of above-ground organic matter. *Journal of Experimental Marine Biology and Ecology*, 89(1):29–54.
- Ward, L. G., Michael Kemp, W., and Boynton, W. R. (1984). The influence of waves and seagrass communities on suspended particulates in an estuarine embayment. *Marine Geology*, 59(1):85–103.
- Waycott, M., Duarte, C. M., Carruthers, T. J. B., Orth, R. J., Dennison, W. C., Olyarnik, S., Calladine, A., Fourqurean, J. W., Heck, K. L., Hughes, A. R., Kendrick, G. A., Kenworthy, W. J., Short, F. T., and Williams, S. L. (2009). Accelerating loss of seagrasses across the globe threatens coastal ecosystems. *Proceedings of the National Academy of Sciences*, 106(30):12377–12381.

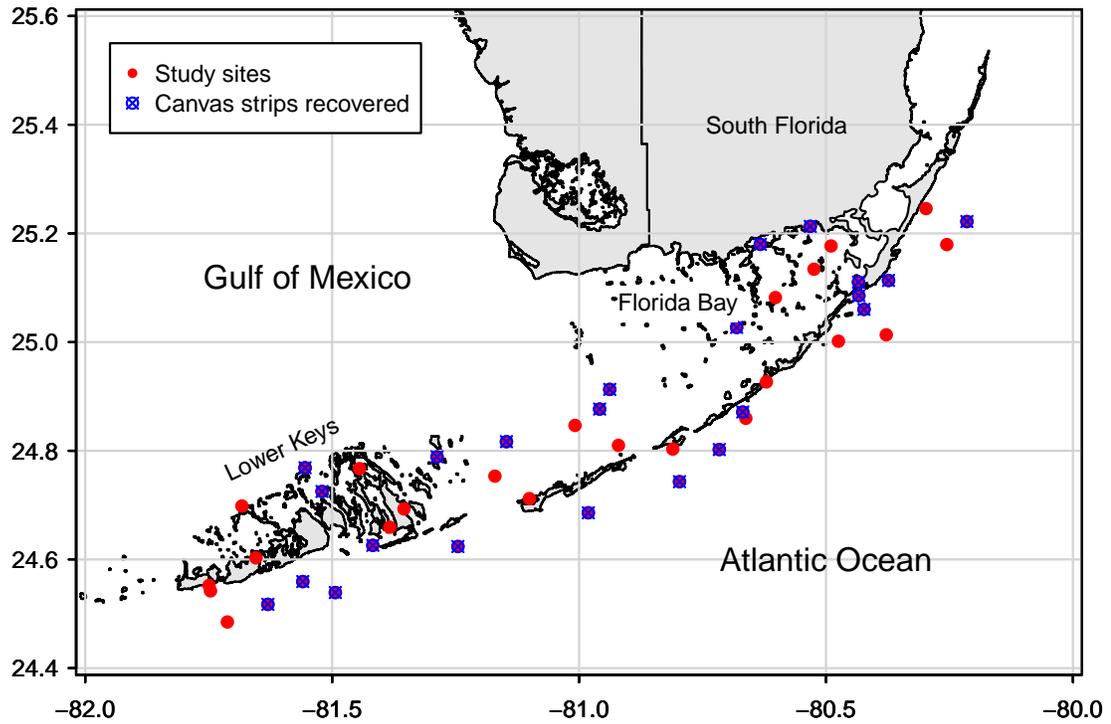


Figure 3.1: Map of South Map including study sites and sites where canvas strips were successfully recovered

| BB Score | Description | Assigned percent coverage |
|----------|--|---------------------------|
| 0 | Species absent from quadrat | 0 |
| 0.1 | Species represented by a solitary short shoot, <5% cover | 0.1 |
| 0.5 | Species represented by a few (<5) shoots, <5% cover | 0.5 |
| 1 | Species represented by many (>5) shoots, <5% cover | 2.5 |
| 2 | 5% - 25% cover | 15 |
| 3 | 25% - 50% cover | 37.5 |
| 4 | 50% - 75% cover | 62.5 |
| 5 | 75% - 100% cover | 87.5 |

Table 3.1: Modified Braun-Blanquet abundance scores, their description, and their assigned percent coverage

| Sediment Category | Numerical Value | Description |
|-------------------|-----------------|---|
| Mud | 1 | individual grains indistinguishable, easily compress in hand, sediment remains clumped after compression |
| Sandy Mud | 2 | majority of grains indistinguishable but textured upon touch, easily compress in hand, sediment remains clumped after compression |
| Muddy Sand | 3 | sandy texture upon touch but compresses in hand, sediment dissociates upon release with most grain falling in water column |
| Sand | 4 | clearly distinguishable grains, difficult to compress in hand, grains fall quickly in water |
| Coarse Shell | 5 | shell and shell remains dominate sediments (approx. 5-10 mm in size) |
| Halimeda-Hash | 6 | Remains of carbonate segments from Halimeda detritus (approx. 5-10 mm in size) |
| Rubble | 7 | medium size rock (approx. 10-25 mm in size) |
| Live Coral | 8 | continuous living coral |
| Rock | 9 | bedrock or solid biogenic carbonate formations |

Table 3.2: Sediment categories and their assigned ranking of increasing coarseness

| Substrate | Details | Additional Notes | Breakdown rate (day ⁻¹) | Citation |
|---------------------|----------------------|------------------------|-------------------------------------|---------------------------------|
| Mixed litter | <i>Z. marina</i> | Laboratory experiment | 0.004 | (Godshalk and Wetzel, 1978) |
| Seagrass leaves | <i>Z. marina</i> | Laboratory experiment | 0.0035 | (Harrison, 1982) |
| Seagrass leaves | <i>Z. marina</i> | Laboratory experiment | 0.018 | (Harrison, 1982) |
| Seagrass leaves | <i>T. testudinum</i> | Litterbag measurements | 0.0149 | (Ruble and Roman, 1982) |
| Seagrass leaves | <i>Z. marina</i> | Litterbag measurements | 0.0136 | (Pellikaan, 1982) |
| Seagrass leaves | <i>Z. marina</i> | Laboratory experiments | 0.0357 | (Pellikaan, 1984) |
| Mixed litter | <i>Z. marina</i> | Laboratory experiments | 0.0357 | (Pellikaan, 1984) |
| Seagrass leaves | <i>Z. marina</i> | Litterbag measurements | 0.0124 | (Kenworthy and Thayer, 1984) |
| Seagrass leaves | <i>C. nodosa</i> | Litterbag measurements | 0.023 | (Kenworthy and Thayer, 1984) |
| Seagrass rhizomes | <i>T. testudinum</i> | Litterbag measurements | 0.0007 | (Kenworthy and Thayer, 1984) |
| Seagrass roots | <i>T. testudinum</i> | Litterbag measurements | 0.0183 | (Kenworthy and Thayer, 1984) |
| Seagrass roots | <i>Z. marina</i> | Litterbag measurements | 0.0048 | (Kenworthy and Thayer, 1984) |
| Seagrass rhizomes | <i>Z. marina</i> | Litterbag measurements | 0.0035 | (Kenworthy and Thayer, 1984) |
| Seagrass leaves | <i>H. stipulacea</i> | Litterbag measurements | 0.0032 | (Wahbeh and Mahasneh, 1985) |
| Seagrass leaves | <i>T. testudinum</i> | Litterbag measurements | 0.0048 | (Newell et al, 1984) |
| Seagrass leaves | <i>T. testudinum</i> | Litterbag measurements | 0.0279 | (Newell et al, 1984) |
| Seagrass leaves | <i>T. testudinum</i> | Literature review | 0.0007 | (Harrison, 1989) |
| Seagrass leaves | <i>Z. marina</i> | Literature review | 0.007 | (Harrison, 1989) |
| Seagrass leaves | <i>T. testudinum</i> | Literature review | 0.017 | (Harrison, 1989) |
| Seagrass leaves | <i>T. testudinum</i> | Literature review | 0.0085 | (Harrison, 1989) |
| Seagrass leaves | <i>T. testudinum</i> | Literature review | 0.008 | (Harrison, 1989) |
| Seagrass leaves | <i>P. australis</i> | Literature review | 0.0013 | (Harrison, 1989) |
| Seagrass leaves | <i>H. tasmanica</i> | Literature review | 0.004 | (Harrison, 1989) |
| Seagrass leaves | <i>C. nodosa</i> | Laboratory experiments | 0.0039 | (Peduzzi and Herndl, 1991) |
| Seagrass leaves | <i>P. oceanica</i> | Litterbag measurements | 0.0088 | (Romero et al, 1992) |
| belowground biomass | <i>P. oceanica</i> | lepidochronology | 0.0002 | (Romero et al, 1992) |
| belowground biomass | <i>P. oceanica</i> | lepidochronology | 0.0006 | (Romero et al, 1992) |
| belowground biomass | <i>P. oceanica</i> | lepidochronology | 0.0003 | (Romero et al, 1992) |
| Seagrass leaves | <i>Z. noltii</i> | Litterbag measurements | 0.0164 | (Bourgues et al, 1996) |
| Seagrass leaves | <i>P. oceanica</i> | Oxygen uptake | 0.003 | (Mateo and Romero, 1996) |
| Seagrass leaves | <i>P. oceanica</i> | Litterbag measurements | 0.0068 | (Mateo and Romero, 1996) |
| Seagrass leaves | <i>P. oceanica</i> | Litterbag measurements | 0.0091 | (Cebrian et al, 1997) |
| Seagrass leaves | <i>Z. marina</i> | Litterbag measurements | 0.019 | (Cebrian et al, 1997) |
| Seagrass leaves | <i>C. nodosa</i> | Litterbag measurements | 0.024 | (Cebrian et al, 1997) |
| Seagrass leaves | <i>P. oceanica</i> | Litterbag measurements | 0.0205 | (Mateo and Romero, 1997) |
| Seagrass leaves | <i>C. nodosa</i> | Litterbag measurements | 0.0086 | (Pérez et al, 2001) |
| Seagrass leaves | <i>C. nodosa</i> | Litterbag measurements | 0.0157 | (Pérez et al, 2001) |
| Seagrass leaves | <i>T. testudinum</i> | Litterbag measurements | 0.017 | (Fourqurean and Schrlau, 2003) |
| Seagrass rhizomes | <i>T. testudinum</i> | Litterbag measurements | 0.0032 | (Fourqurean and Schrlau, 2003) |
| Mangrove leaves | <i>R. mangle</i> | Litterbag measurements | 0.0064 | (Fourqurean and Schrlau, 2003) |
| Seagrass leaves | <i>Z. noltii</i> | Litterbag measurements | 0.016 | (Machás et al, 2006) |
| Seagrass leaves | <i>P. sinuosa</i> | Litterbag measurements | 0.0068 | (Moore and Fairweather, 2006) |
| Seagrass leaves | <i>A. griffithii</i> | Litterbag measurements | 0.0078 | (Moore and Fairweather, 2006) |
| Seagrass leaves | <i>A. antarctica</i> | Litterbag measurements | 0.0116 | (Moore and Fairweather, 2006) |
| Seagrass leaves | Mixed species | Litterbag measurements | 0.0094 | (Moore and Fairweather, 2006) |
| Seagrass leaves | <i>Z. muelleri</i> | Litterbag measurements | 0.0152 | (Nicastro et al, 2012) |
| Seagrass leaves | <i>T. hemprichii</i> | Litterbag measurements | 0.011 | (Chiu et al, 2013) |
| Seagrass rhizomes | <i>T. hemprichii</i> | Litterbag measurements | 0.0268 | (Yano et al, 2013) |
| Seagrass leaves | <i>T. hemprichii</i> | Litterbag measurements | 0.0394 | (Yano et al, 2013) |
| Seagrass leaves | <i>Z. muelleri</i> | Litterbag measurements | 0.0055 | (Trevathan-Tackett et al, 2017) |

Table 3.3: Literature review of decay rates in seagrass ecosystems

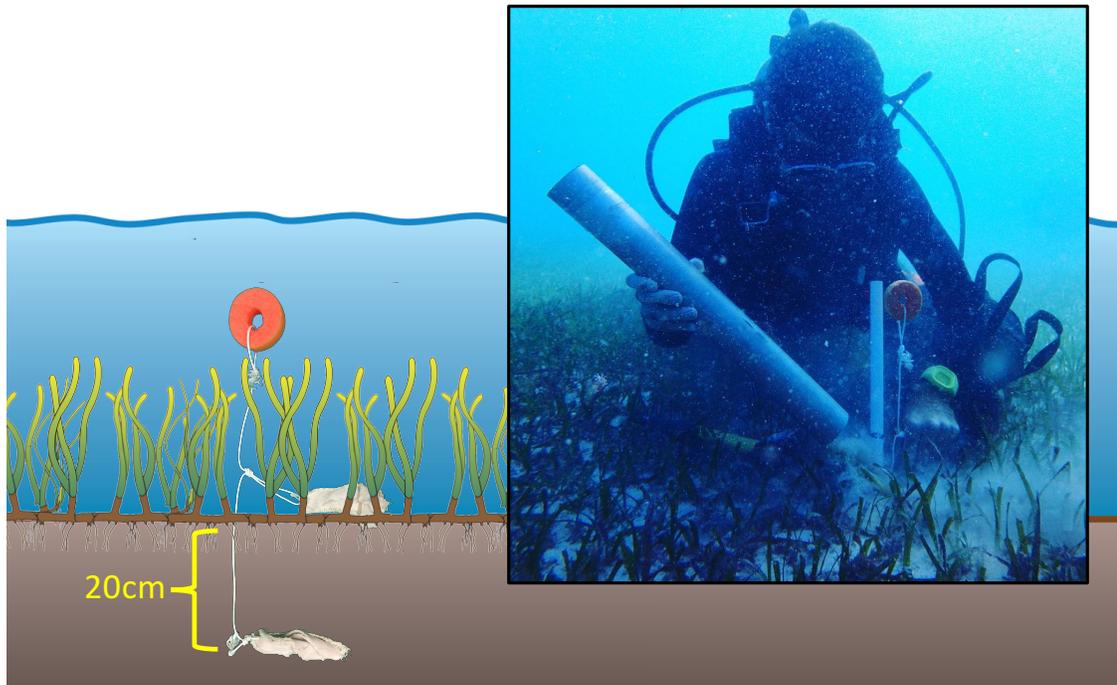


Figure 3.2: Depiction of single canvas assay deployment apparatus. Strips were deployed at each site (n=10) at the sediment-water interface and 20 cm depth with foam buoy for easy detection and recovery.

| | n | Fraction of sites where present (%) | mean | SE | median | min | max |
|--|----|-------------------------------------|------|-----|--------|-----|------|
| LOI (%) | 46 | - | 6.9 | 0.6 | 5 | 3.3 | 19.5 |
| C _{org} content (%) | 46 | - | 2.4 | 0.3 | 1.7 | 0.7 | 8.6 |
| dry bulk density (g cm ⁻³) | 46 | - | 0.7 | 0 | 0.7 | 0.2 | 1.5 |
| C stock (mg cm ⁻³) | 46 | - | 13.8 | 0.8 | 12.9 | 6.2 | 27.7 |
| Mud content (%) | 45 | - | 33.1 | 3.7 | 28 | 1.4 | 90.1 |
| Thalassia coverage (%) | 46 | 93.5 | 17.8 | 2.3 | 15.6 | 0 | 60.9 |
| Syringodium coverage (%) | 46 | 50 | 7.9 | 2.2 | 0.4 | 0 | 73.3 |
| Halodule coverage (%) | 46 | 34.8 | 1.5 | 0.7 | 0 | 0 | 22.3 |
| Total seagrass coverage (%) | 46 | 95.7 | 1.5 | 0.7 | 0 | 0 | 22.3 |
| seagrass canopy ht. (cm) | 44 | - | 18.8 | 1.2 | 17.3 | 7.9 | 41.2 |

Table 3.4: Summary of sediment and seagrass characteristics measured at sampled south Florida sites.

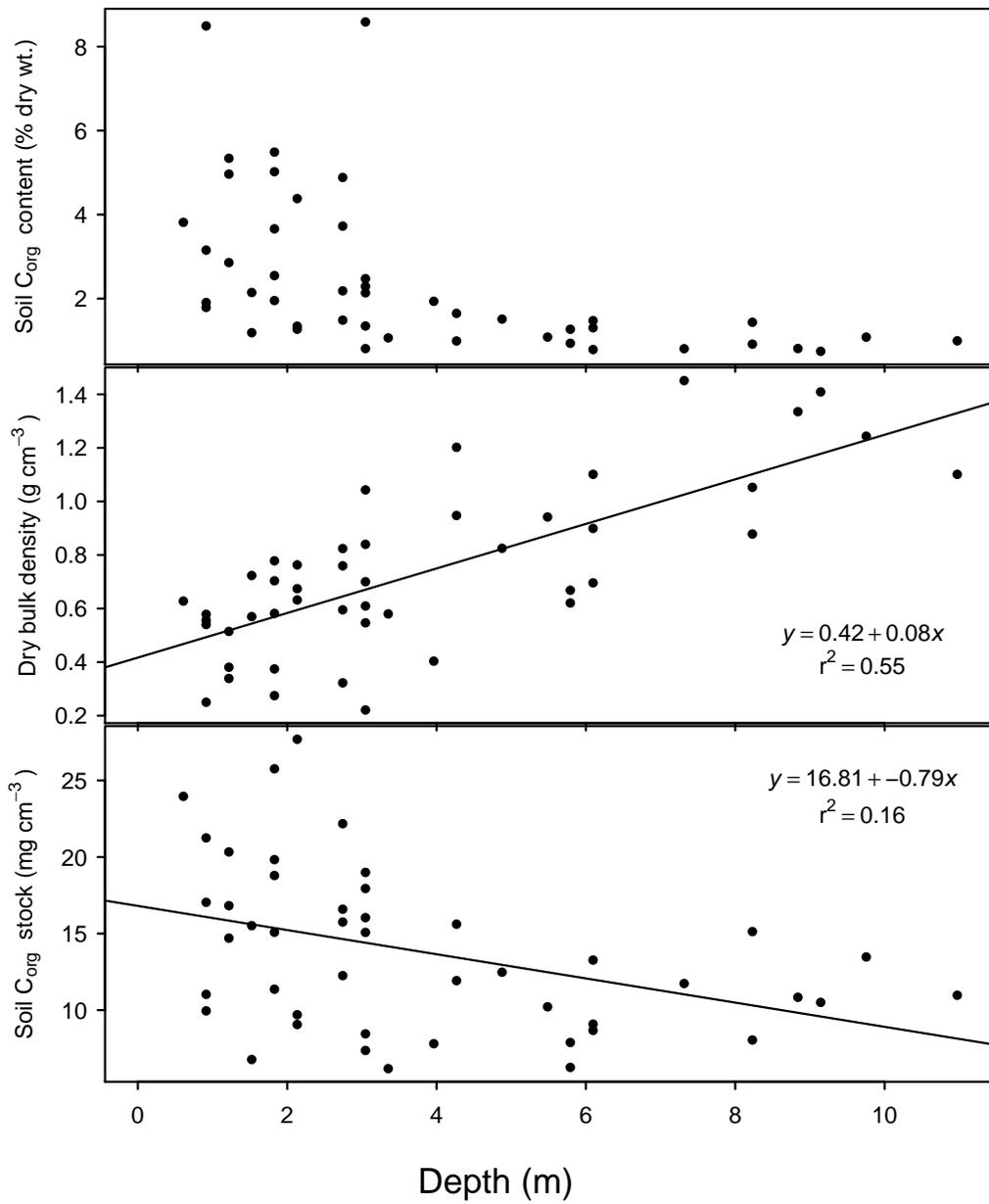


Figure 3.3: Sediment characteristics for study sites as a function of water column depth

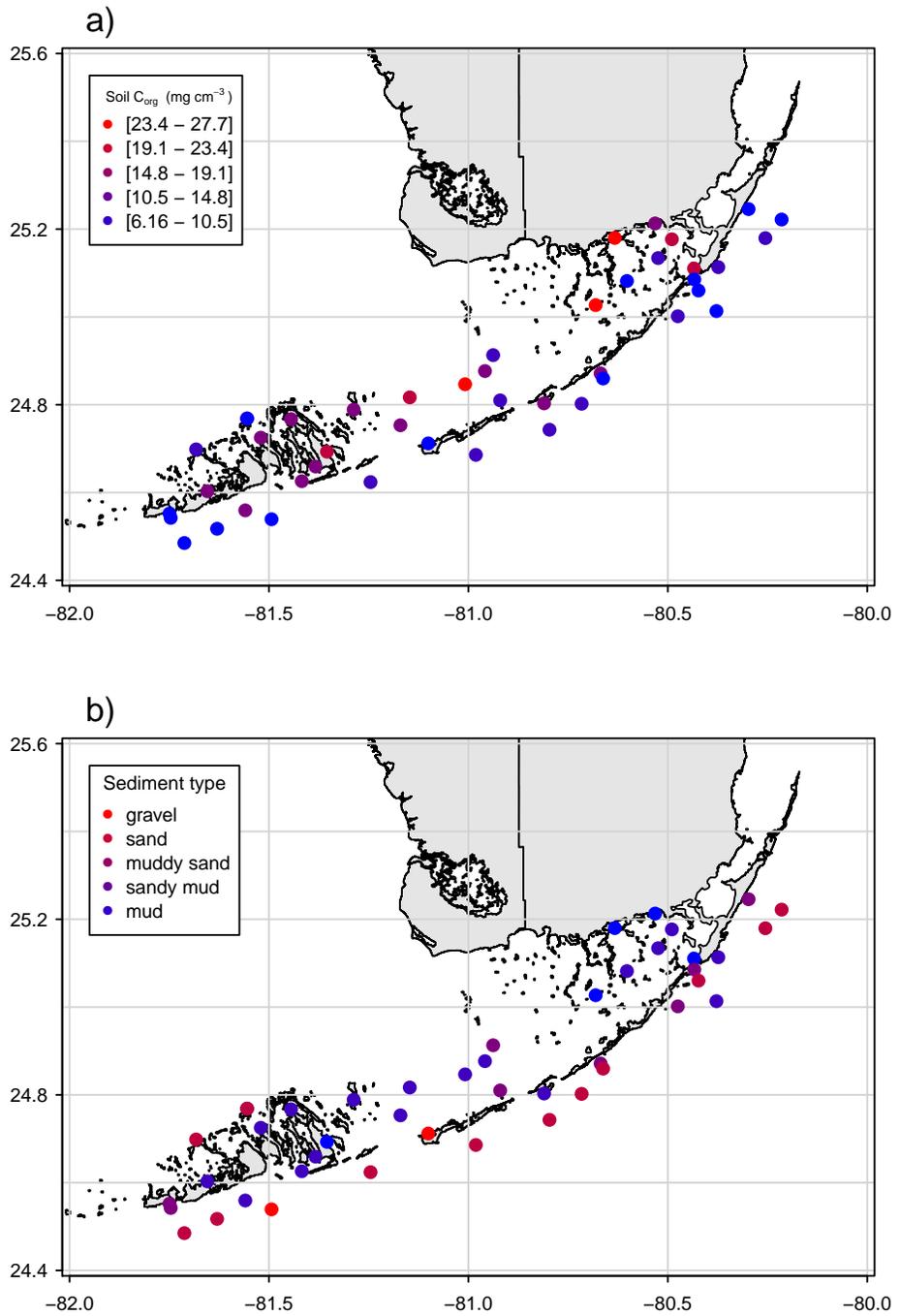


Figure 3.4: Map showing a) surface soil C_{org} stocks, and b) sediment type across 45 study sites of Florida Bay and the Florida Keys.

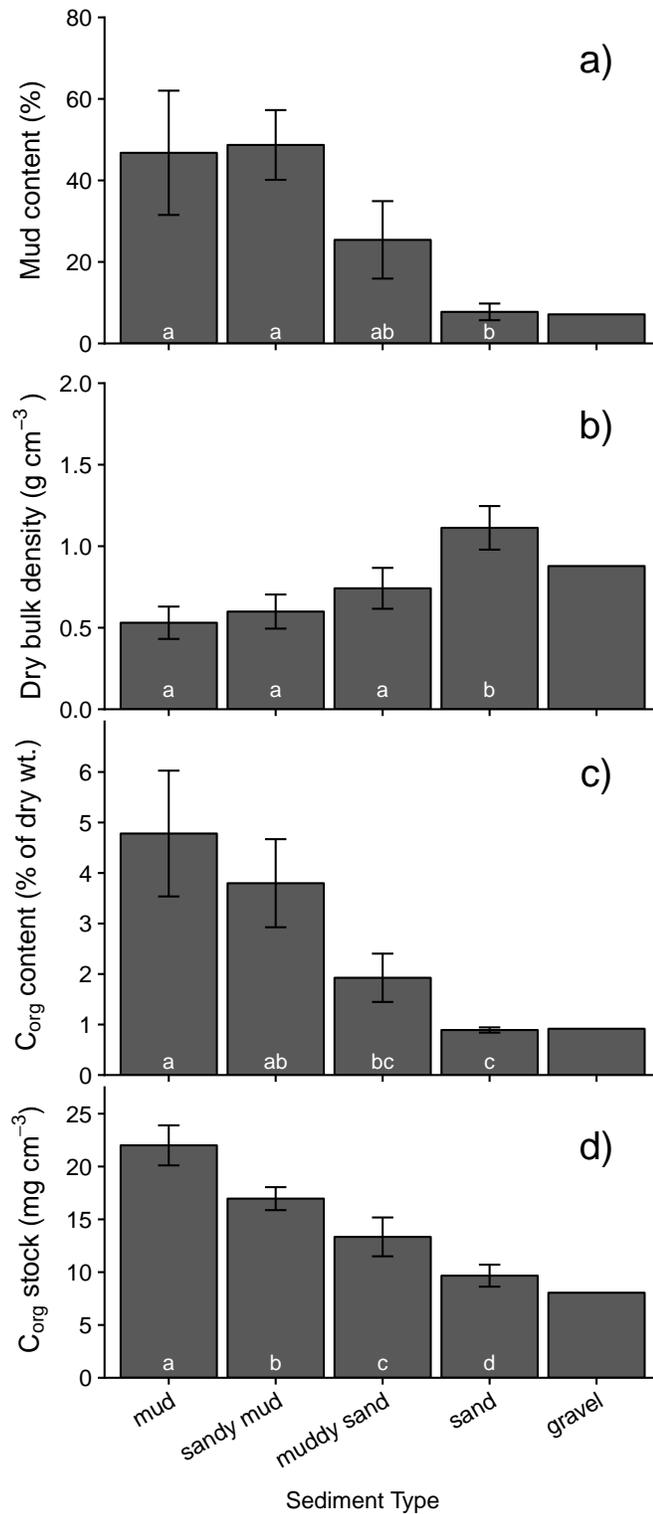


Figure 3.5: Relationship between sediment type and sediment characteristics. Sediment type represents averages across ten quadrats per site and four sampling periods from January 2015 and July 2016. Letters represent groupings from Tukey post-hoc tests. Gravel had only one replicate thus was excluded from significance tests.

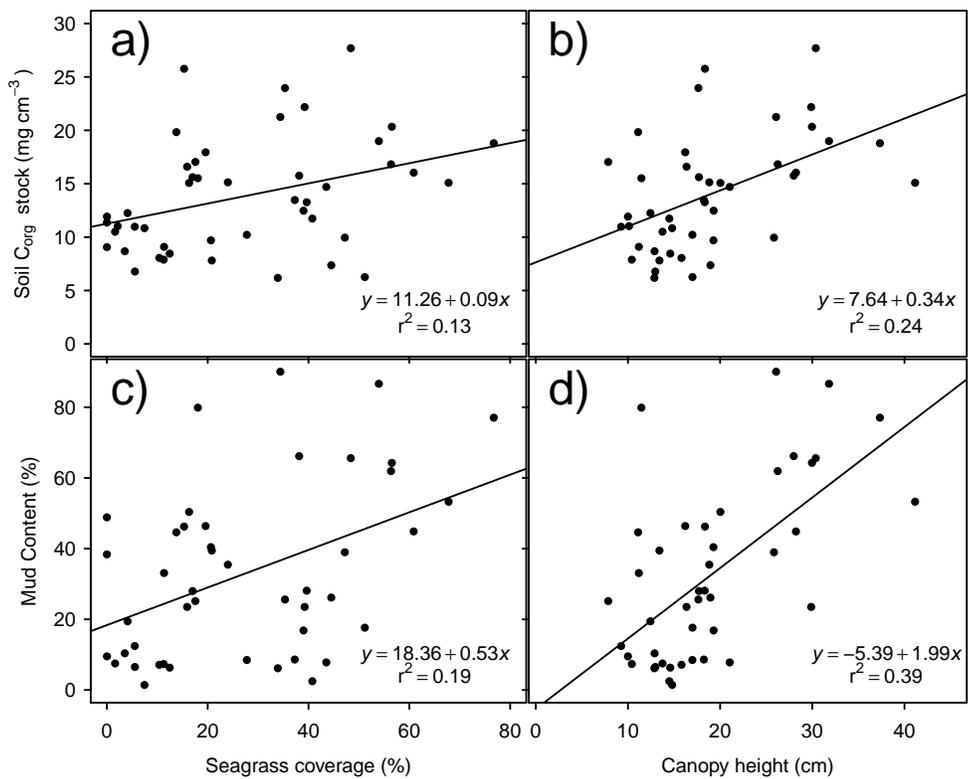


Figure 3.6: Relationships between seagrasses and sediment characteristics. Each data point represents averages across ten quadrats per site and four sampling periods from January 2015 and July 2016.

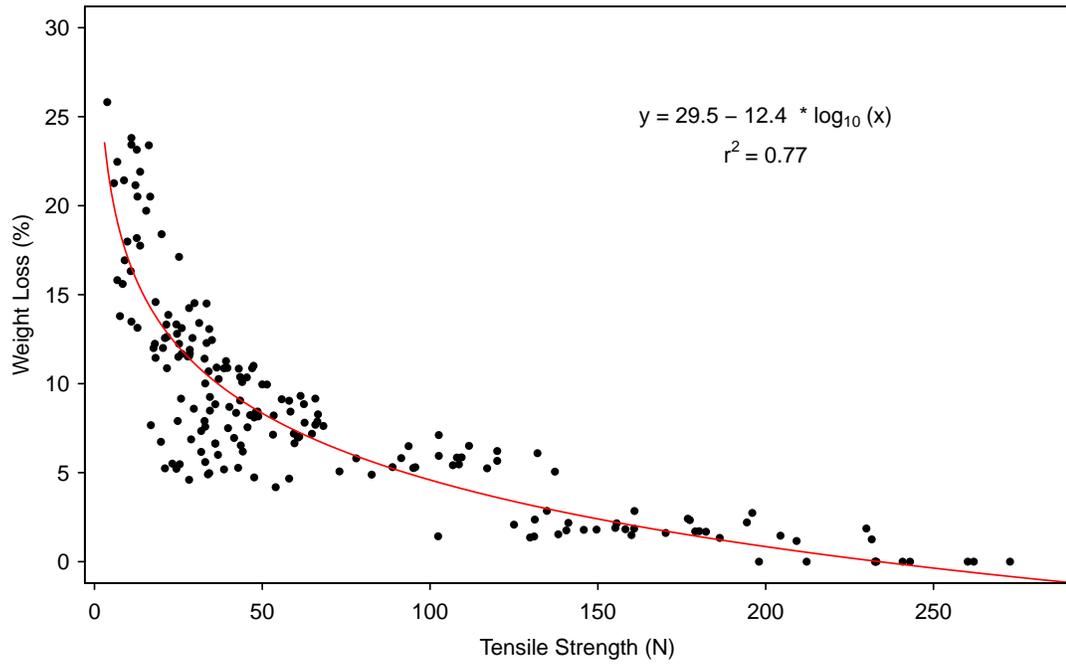


Figure 3.7: Correlation between tensile strength and weight loss of canvas strips incubated in H_2O_2 for bench top calibration experiment.

| | Tensile strength at T_{final} (N) | | Tensile strength loss ($\% \text{ day}^{-1}$) | | Weight loss ($\% \text{ day}^{-1}$) | | Decay rate, k (year^{-1}) | | Decay rate, k (day^{-1}) | |
|---------------|-------------------------------------|---------|---|---------|---------------------------------------|---------|--|---------|---------------------------------------|----------|
| | Buried | Surface | Buried | Surface | Buried | Surface | Buried | Surface | Buried | Surface |
| Mean | 18.377 | 31.508 | 0.00529 | 0.00499 | 0.0877 | 0.077 | 0.3504 | 0.3054 | 0.00096 | 0.000837 |
| SE | 2.683 | 6.556 | 0.00006 | 0.00018 | 0.005 | 0.0066 | 0.022 | 0.0277 | 0.00006 | 0.000076 |
| Median | 15.948 | 16.41 | 0.00528 | 0.0052 | 0.0815 | 0.0806 | 0.3215 | 0.3178 | 0.000881 | 0.000871 |
| Max | 49.229 | 127.051 | 0.00603 | 0.00628 | 0.1394 | 0.1221 | 0.5854 | 0.5028 | 0.001604 | 0.001377 |
| Min | 2.326 | 4.138 | 0.00456 | 0.00261 | 0.051 | 0.0191 | 0.1952 | 0.0708 | 0.000535 | 0.000194 |
| All sites | | | | | | | | | | |
| Mean \pm SE | 24.942 \pm 3.636 | | 0.00514 \pm 0.00009 | | 0.0824 \pm 0.0042 | | 0.3279 \pm 0.0178 | | 0.000898 \pm 0.000046 | |

Table 3.5: Summarized breakdown rates of canvas strips buried at 20 cm depth and deployed on the sediment surface.

| Ecosystem | Details | Breakdown rate, k (day^{-1}) | | |
|---|---|---|----------------------|--------|
| | | Oxic | Anoxic | |
| <i>Generalized Rates (Lovelock et al 2017b)</i> | | | | |
| Tidal marsh | Aboveground biomass | 0.01 | 0.005 | |
| | Blowground biomass | 0.007 | 0.0032 | |
| | Sediment C_{org} | 0.0005 | 0.00005 | |
| Mangrove | Leaves | 0.06 | 0.03 | |
| | Wood | 0.0007 | 0.0004 | |
| | Sediment C_{org} | 0.0005 | 0.00005 | |
| Seagrass | Aboveground biomass | 0.02 | 0.01 | |
| | Blowground biomass | 0.002 | 0.001 | |
| | Sediment C_{org} | 0.0005 | 0.00005 | |
| <i>This study</i> | | Breakdown rate, k (day^{-1}) | | |
| Seagrass | Canvas strip assay | Surface Deployed | Buried | |
| | | 0.00083 ± 0.00008 | 0.0010 ± 0.00007 | |
| <i>Summarized literature</i> | | Breakdown rate, k (day^{-1}) | | |
| Seagrass | Various conditions (see Online Resource 10) | Average \pm SE | Min | Max |
| | | 0.0117 ± 0.0014 | 0.0002 | 0.0394 |

Table 3.6: Generalized breakdown rates in oxic and anoxic conditions for coastal ecosystems (from Lovelock et al 2017b) as well as rates reported here and summarized data from the literature.

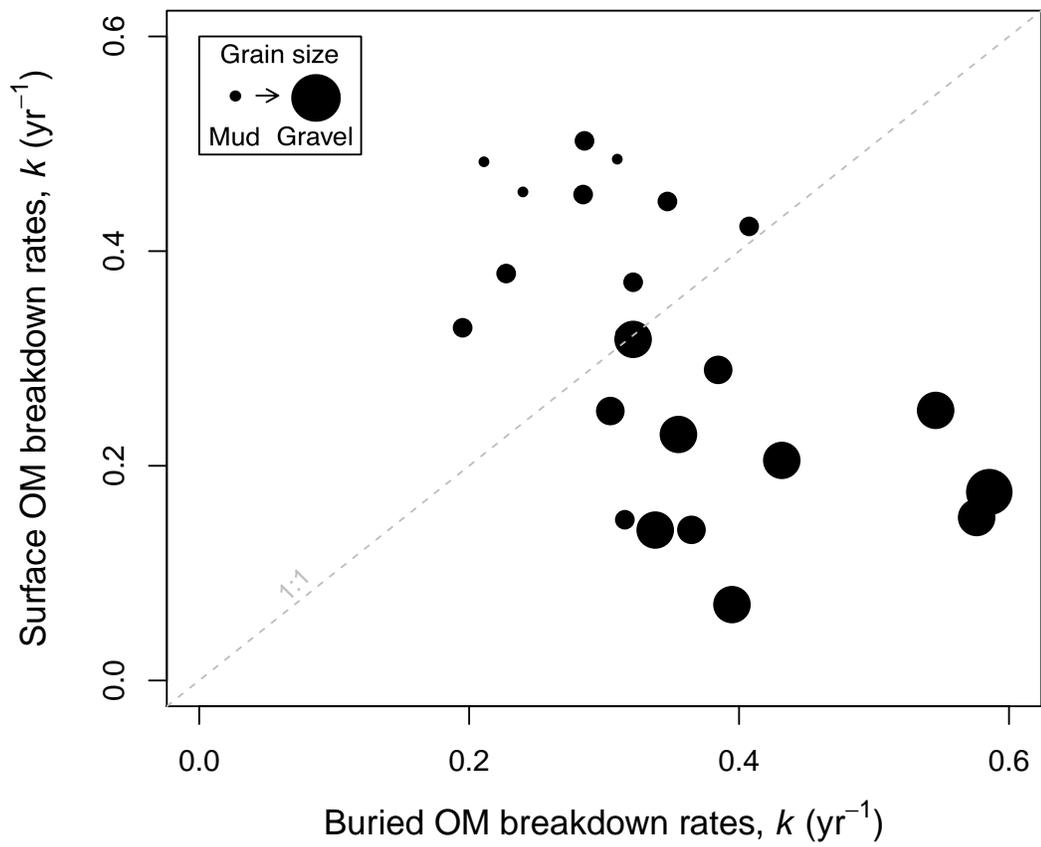


Figure 3.8: Comparison of breakdown rates for canvas strip assays deployed at 20 cm depth (*buried*) and at the sediment-water interface (*surface*). Increasing symbol size indicates categories of increasing grain size.

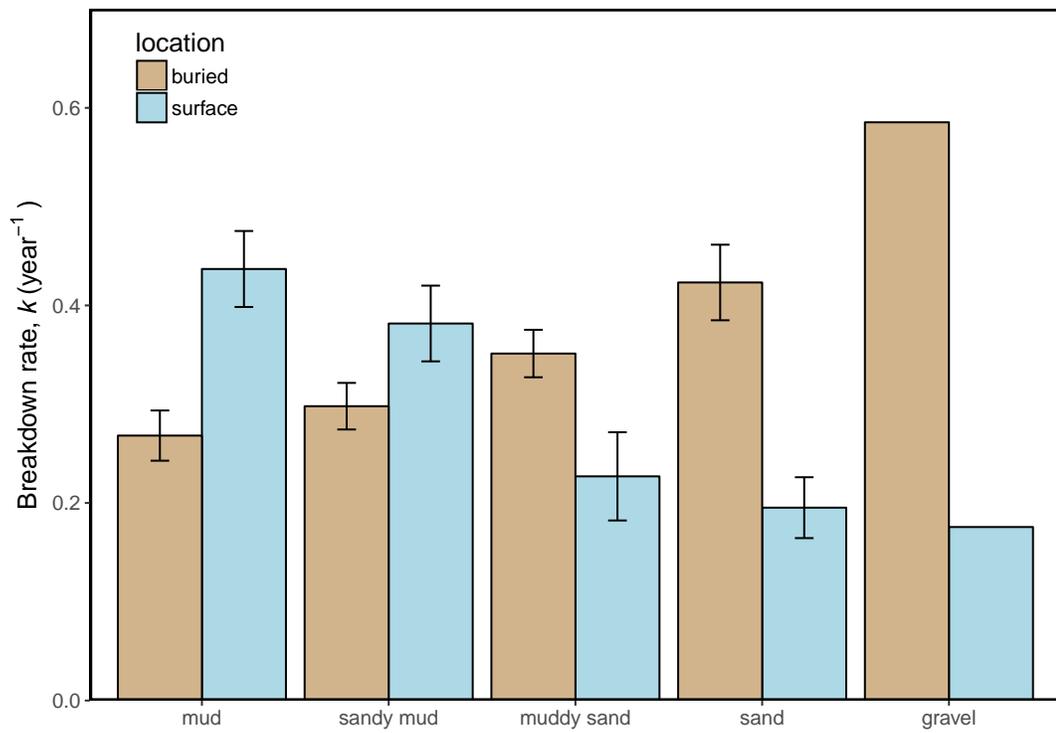


Figure 3.9: Comparison of breakdown rates for canvas strip assays deployed at 20 cm depth (*buried*) and at the sediment-water interface (*surface*) for sites with increasingly large sediment grain size categories.

CHAPTER 4

CO₂ RELEASED BY CARBONATE SEDIMENT PRODUCTION IN SOME COASTAL AREAS MAY OFFSET THE BENEFITS OF SEAGRASS "BLUE CARBON" STORAGE

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 CO₂ mitigation disregard the co-occurring inorganic carbon cycle, whose antagonist effect on CO₂ 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 Brazil and compares values to Florida Bay (USA), a well-studied system known for both high autotrophy and calcification, representing extremes of CaCO₃ soil content. Seagrass soils in SE Brazil contain an average of 67.6 ± 14.7 Mg C_{org} ha⁻¹ in the top 1m, compared to an average of 175.0 ± 20.4 Mg C_{org} ha⁻¹ for their counterparts in Florida Bay. C_{inorg} as CaCO₃ 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 CO₂ evasion related to CaCO₃ production is considered, seagrass ecosystems with high CaCO₃ content may have CO₂ sequestered via C_{org} accumulation negated by CO₂ produced by calcification. These findings prompt the reconsideration of carbon inventory methods and encourage regionally- and community-specific assessments of CO₂ sequestration abilities of seagrass ecosystems.

Introduction

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 CO₂ capture (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 CO₂ with the atmosphere need to be understood. Gaps in knowledge regarding the link between organic carbon (C_{org}) soil stocks in seagrasses and CO₂ sequestration are actively being addressed, however the influence of calcification and carbonate dissolution, both of which directly affect CO₂ partial pressure (pCO₂) in the water column and thus CO₂ 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 (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 $p\text{CO}_2$ 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 (Ward et al., 1984; 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 and Perillo, 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 $p\text{CO}_2$ 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 (Campbell et al., 2014), 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 towards 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 $p\text{CO}_2$, 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 Jr 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 (Smith 2013; Millero 2007), though some fraction will alter the $\Delta p\text{CO}_2$ 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 effect

the carbonate saturation state (Millero, 2007). For example, sulfide oxidation and aerobic remineralization during sediment organic matter decomposition decrease porewater 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 (Romero, 1988; 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., 2010; Camp et al., 2016). 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; Green and Short, 2003; 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 CO₂ sink tendencies of autotrophic seagrass ecosystems. Further, if net CaCO₃ production is positively correlated with net primary production, then CO₂ sequestration capacity of seagrasses as well as any respiration related CO₂ 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 CO₂ with the atmosphere and the pCO₂ in seawater (Suzuki, 1998; Lerman and Mackenzie, 2005). Net autotrophy and the net storage of C_{org} suggest seagrass ecosystems are long-term CO₂ 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 CO₂ 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 CO₂ 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 Jr 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 morphometrics (shoot density, above/belowground biomass, and leaf length) as they have been correlated with C_{org} storage previously (Serrano et al., 2015). We measure leaf CNP ratios 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).

Materials and Methods

Seagrass characteristics and underlying soil carbon stocks were measured between June and August 2015 at 14 sites along the southeastern Brazilian coastline (Figure 4.1, Table 4.1) 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). 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 to 25 °C (Creed 2003).

Data from SE Brazil were compared to existing data from Florida Bay, USA (Figure 4.2, Table 4.2; Fourqurean et al. 2012a; Armitage and Fourqurean 2016; Howard et al. 2016), 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 $\delta^{13}\text{C}$ using 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 (‰): $\delta \text{ (‰)} = [(R_{\text{sample}}/R_{\text{standard}}) - 1] \times 1000$. 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 $\pm 0.08 \text{ ‰}$.

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 pre-drilled sampling ports as described by Campbell et al. (2014). 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 ($\text{g dry soil mL wet soil}^{-1}$). Soil samples were homogenized using a motorized mortar and pestle then analyzed for C_{org} and C_{inorg} using previously described methods

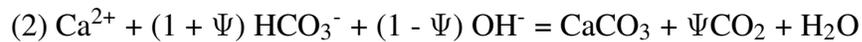
(Fourqurean et al., 2012b). Surface soil samples from each site were acid-fumed to remove carbonates and analyzed for $\delta^{13}\text{C}$ of C_{org} .

Data Analysis

Stocks of inorganic and organic carbon were measured using methods reported by Campbell et al. (2014). C_{org} and C_{inorg} content data were converted from % of dry wt to stock ($\text{mol C mL soil}^{-1}$) by multiplying carbon content (% dry wt) by dry bulk density ($\text{g dry soil mL wet soil}^{-1}$) 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. 2014), which were then used to compute site specific $\text{C}_{\text{org}}:\text{C}_{\text{inorg}}$ areal stock ratios. Carbon stock values (in $\text{mol C mL soil}^{-1}$) 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:

$$(1) \text{C}_{\text{org stored}} - \Psi \times \text{C}_{\text{inorg stored}} = \text{CO}_2 \text{ net sequestered}$$

Where $\text{C}_{\text{org stored}}$ 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), $\text{C}_{\text{inorg stored}}$ 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.



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., 2012a; 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 CO₂ uptake driven by NEP and C_{org} storage as used previously (Fourqurean et al. 2012a; Pendleton et al. 2012; Mazarrasa et al. 2015). Positive values of CO₂ net sequestered were interpreted to indicate net CO₂ sequestration while negative values indicate net CO₂ evasion, assuming sea-air CO₂ 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. $\delta^{13}\text{C}$ 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 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 with the exception of Table 3, which presents standard deviation 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 < 2m depth in

Urca, and *Halodule emarginata* found at sites near Vitória (see Figure 4.1 and Table 4.1) for locations of sampling sites). Total seagrass biomass was low across the region, averaging $37.5 \pm 7.2 \text{ g m}^{-2}$ across sites with a maximum of 91.1 g m^{-2} for the sampling period (Table 4.3). 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 $4.1 \pm 0.1 \text{ cm}$ for *H. wrightii* and $3.8 \pm 0.1 \text{ cm}$ for *H. 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 $4063 \pm 853 \text{ shoots m}^{-2}$ 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 4.4). Seagrasses leaf tissue N:P molar ratios fell below the “Seagrass Redfield Ratio” of 30:1 with the exception of the most northern site, Santa Cruz. Both C:N and C:P were low across sites, averaging 11.3 ± 0.3 and 271.2 ± 19.9 , respectively. These values can be compared to average ratios of *H. wrightii* from Florida Bay (22.7 ± 0.4 for C:N, 1014.1 ± 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 $\delta^{13}\text{C}$ values of leaf tissue from Brazilian sites ranged from -13.4 ‰ to -7.7 ‰ with an average of $-10.1 \pm 0.4 \text{ ‰}$ (Table 2). The C_{org} component of surface soils collected beneath sampled seagrasses showed $\delta^{13}\text{C}$ values ranging between -11.3 ‰ and -27.7 ‰ averaging $-18.3 \pm 1.3 \text{ ‰}$. These values, with the exception of one sample from Bracuí, fell within the global range of $\delta^{13}\text{C}$ seagrass surface sediment values (-26.6 ‰ to -7.2 ‰ ; Kennedy et al 2010), though the majority of sites sampled in Brazil were depleted in $\delta^{13}\text{C}$ in comparison when adjusted for seagrass $\delta^{13}\text{C}$ values using the Kennedy et al. (2010) global model (see Figure 4.3). Seagrass surface sediment C_{org} from SE Brazil was on average more depleted in $\delta^{13}\text{C}$ than Florida Bay ($-18.3 \pm 1.3 \text{ ‰}$ compared to $-12.7 \pm 0.5 \text{ ‰}$, ANOVA, $F_{1,24}$, $p < 0.05$).

Sediment density at Brazilian sites ranged between 0.61 and 1.60 g mL⁻¹ with an average of 1.09 ± 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 ± 0.15 % of dry wt. across all study sites in SE Brazil, ranging between 0.10 % and 1.95 % of dry weight (Figure 4.4, Figure 4.6). 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 ± 0.1 % across sites and down the sampled depth profile, while sediments collected on the southern side of Cabo Frio averaged 0.6 ± 0.1 %. The Brazilian samples were lower in soil C_{org} content than those from Florida Bay (which averaged 2.3 ± 0.1 % of dry wt across sites and downcore; Figure 4.4; Figure 4.7; 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 δ¹³C 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 ± 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. (Figure 4.5; Figure 4.6). 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 ± 0.3 % across sites and down the sampled depth profile. Those sediments collected on the southern side of Cabo Frio averaged 0.12 ± 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 (Figure 4.5; Figure 4.7; ANOVA, $F_{1,16}$, $p < 0.05$), which averaged 9.45 ± 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 top 1m of soil (Figure 4.8, 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} (Figure 4.9). 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 equation 1 (see Table 3).

Discussion

Seagrasses meadows are typically autotrophic ecosystems whose positive net ecosystem production acts as a sink for CO_2 while producing and storing C_{org} (Duarte et al., 2010; Fourqurean et al., 2012a). 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. (1999b) 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 4.5) 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-inhabiting 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., 2012a) and were significantly lower than

those measured in Florida Bay (Fourqurean et al., 2012b; Howard et al., 2016). Using $\delta^{13}\text{C}$ values of surface soils as indicators 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} (Figure 4.3). 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 seagrass biomass and underlying soil C_{org} stocks, or between soil C_{org} source (as implied by $\delta^{13}\text{C}$ 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 (Figure 4.8; Armitage and Fourqurean 2016). While *Halodule wrightii* is common in Florida Bay, the morphology of the more common *Thalassia 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 % and 6.34 % of dry weight. Translated to areal stock, SE Brazil averaged $141.5 \pm 59.9 \text{ Mg } C_{inorg} \text{ ha}^{-1}$, putting it well below the global mean of $654 \pm 24 \text{ Mg } C_{inorg} \text{ ha}^{-1}$ 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 four-fold 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 sea water (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 (Melo et al., 1975; da Rocha 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 (Shinn et al., 1989; Robbins and Blackwelder, 1992). Autochthonous precipitation in Florida Bay has been reported to be high enough

to be 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., 1999a) and there is some empirical evidence for such a mutualistic relationship (Semese 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 porewater 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 significant portions of gross shallow water 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. The “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 (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 $\text{C}_{\text{org}}:\text{C}_{\text{inorg}}$ content of seagrass sediments, indicating a slight trend towards 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 $p\text{CO}_2$ 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 Equation 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 Equation 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 re-released 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, 2012). 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 CO₂ 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 CO₂ 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 ecosystem production of CO₂, as is suggested for other carbonate-producing systems (Ware et al., 1992; Gattuso et al., 1999b). Considered a synergistic couplet, C_{org} and C_{inorg} processes could buffer one another's effect on CO₂ production, cushioning long-term changes in CO₂. 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 CO₂ production.

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Work Cited

- Anthony, K. R. N., A Kleypas, J., and Gattuso, J.-P. (2011). Coral reefs modify their seawater carbon chemistry - implications for impacts of ocean acidification. *Global Change Biology*, 17(12):3655–3666.
- Armitage, A. R. and Fourqurean, J. W. (2016). Carbon storage in seagrass soils: long-term nutrient history exceeds the effects of near-term nutrient enrichment. *Biogeosciences*, 13(1):313–321.
- Arndt, S., Jørgensen, B. B., LaRowe, D. E., Middelburg, J., Pancost, R. D., and Regnier, P. (2013). Quantifying the degradation of organic matter in marine sediments: A review and synthesis. *Earth-Science Reviews*, 123:53–86.
- Atkinson, M. J. and Smith, S. V. (1983). C:N:P ratios of benthic marine plants. *Limnology and Oceanography*, 28(3):568–574.
- Bosence, D. (1989). Biogenic carbonate production in Florida Bay. *Bulletin of Marine Science*, 44(1):419–433.
- Bosence, D. W., Rowlands, R. J., and Quine, M. L. (1985). Sedimentology and budget of a Recent carbonate mound, Florida Keys. *Sedimentology*, 32(3):317–343.
- Burdige, D. J., Hu, X., and Zimmerman, R. C. (2010). The widespread occurrence of coupled carbonate dissolution/precipitation in surface sediments on the Bahamas Bank. *American Journal of Science*, 310(6):492–521.
- Burdige, D. J. and Zimmerman, R. C. (2002). Impact of sea grass density on carbonate dissolution in Bahamian sediments. *Limnology and Oceanography*, 47(6):1751–1763.
- Camp, E., Suggett, D. J., Gendron, G., Jompa, A., Manfrino, C., and Smith, D. J. (2016). Mangrove and seagrass beds provide different biogeochemical services for corals threatened by climate change. *Frontiers in Marine Science*, 3:52.
- Campbell, J. E. and Fourqurean, J. W. (2009). Interspecific variation in the elemental and stable isotope content of seagrasses in South Florida. *Marine Ecology Progress Series*, 387:109–123.

- Campbell, J. E., Lacey, E. A., Decker, R. A., Crooks, S., and Fourqurean, J. W. (2014). Carbon Storage in Seagrass Beds of Abu Dhabi, United Arab Emirates. *Estuaries and Coasts*, 38(1):242–251.
- Collado-Vides, L., Caccia, V. G., Boyer, J. N., and Fourqurean, J. W. (2007). Tropical seagrass-associated macroalgae distributions and trends relative to water quality. *Estuarine, Coastal and Shelf Science*, 73:680–694.
- Copertino, M. S., Creed, J. C., Lanari, M. O., Magalhães, K., Barros, K., Lana, P. C., Sordo, L., and Horta, P. A. (2016). Seagrass and submerged aquatic vegetation habitats off the coast of Brazil: state of knowledge, conservation and main threats. *Brazilian Journal of Oceanography*, 64(SPE2):53–80.
- Creed, J. C. (1997). Morphological variation in the seagrass *Halodule wrightii* near its southern distributional limit. *Aquatic Botany*, 59(1):163–172.
- Creed, J. C. (1999). Distribution, seasonal abundance and shoot size of the seagrass *Halodule wrightii* near its southern limit at Rio de Janeiro state, Brazil. *Aquatic Botany*, 65(1):47–58.
- da Rocha, J., Milliman, J. D., Santanan, C. I., and Vicalvi, M. A. (1975). Continental margin sedimentation off Brazil, part 5: southern Brazil. *Contr Sedimentology*, 4:117–150.
- De Falco, G., Magni, P., Teräsvuori, L. M. H., and Matteucci, G. (2004). Sediment grain size and organic carbon distribution in the Cabras lagoon (Sardinia, Western Mediterranean). *Chemistry and Ecology*, 20:367–377.
- Duarte, C. M. (1990). Seagrass nutrient content. *Marine Ecology Progress Series*, 6(2):201–207.
- Duarte, C. M. and Krause-Jensen, D. (2017). Export from Seagrass Meadows Contributes to Marine Carbon Sequestration. *Frontiers in Marine Science*, 4:2107.
- Duarte, C. M., Marbà, N., Gacia, E., Fourqurean, J. W., Beggins, J., Barrón, C., and Apostolaki, E. T. (2010). Seagrass community metabolism: Assessing the carbon sink capacity of seagrass meadows. *Global Biogeochemical Cycles*, 24(4):GB4032.
- Duarte, C. M., Merino, M., and Gallegos, M. (1995). Evidence of iron deficiency in seagrasses growing above carbonate sediments. *Limnology and Oceanography*, 40(6):1153–1158.
- Enríquez, S. and Schubert, N. (2014). Direct contribution of the seagrass *Thalassia testudinum* to lime mud production. *Nature communications*, 5:3835.
- Fonseca, M. S. and Fisher, J. S. (1986). A comparison of canopy friction and sediment movement between four species of seagrass with reference to their ecology and restoration. *Marine Ecology Progress Series*, 29(1):15–22.
- Fourqurean, J. W., Duarte, C. M., Kennedy, H., Marbà, N., Holmer, M., Mateo, M. A., Apostolaki, E. T., Kendrick, G. A., Krause-Jensen, D., McGlathery, K. J., and Serrano, O. (2012a). Seagrass ecosystems as a globally significant carbon stock. *Nature Geoscience*, 5(7):505–509.

- Fourqurean, J. W., Kendrick, G. A., Collins, L. S., Chambers, R. M., and Vanderklift, M. A. (2012b). Carbon, nitrogen and phosphorus storage in subtropical seagrass meadows: examples from Florida Bay and Shark Bay. *Marine and Freshwater Research*, 63(11):967.
- Fourqurean, J. W. and Robblee, M. B. (1999). Florida Bay: a history of recent ecological changes. *Estuaries*, 22(2):345–357.
- Fourqurean, J. W., Zieman, J., and Powell, G. V. (1992). Phosphorus limitation of primary production in Florida Bay: Evidence from C: N: P ratios of the dominant seagrass *Thalassia testudinum*. *Limnology and Oceanography*, 37(1):162–171.
- Frankignoulle, M., Pichon, M., and Gattuso, J.-P. (1995). Aquatic calcification as a source of carbon dioxide. In *Carbon sequestration in the biosphere*, pages 265–271. Springer.
- Frankovich, T. A. and Zieman, J. C. (1994). Total epiphyte and epiphytic carbonate production on *Thalassia testudinum* across Florida Bay. *Bulletin of Marine Science*, 54(3):679–695.
- Gacia, E., Duarte, C. M., and Middelburg, J. (2002). Carbon and nutrient deposition in a Mediterranean seagrass (*Posidonia oceanica*) meadow. *Limnology and Oceanography*, 47(1):23–32.
- Gattuso, J. P., Allemand, D., and Frankignoulle, M. (1999a). Photosynthesis and calcification at cellular, organismal and community levels in coral reefs: a review on interactions and control by carbonate chemistry. *American Zoologist*, 39(1):160–183.
- Gattuso, J. P., Frankignoulle, M., and Smith, S. V. (1999b). Measurement of community metabolism and significance in the coral reef CO₂ source-sink debate. *Proceedings of the National Academy of Sciences of the United States of America*, 96(23):13017–13022.
- Green, E. P. and Short, F. (2003). *World atlas of seagrasses*. Univ of California Press.
- Hejnowicz, A. P., Kennedy, H., Huxham, M. R., and Rudd, M. A. (2015). Harnessing the climate mitigation, conservation and poverty alleviation potential of seagrasses: prospects for developing blue carbon initiatives and payment for ecosystem service programmes. *Frontiers in Marine Science*, page 32.
- Hendriks, I. E., Bouma, T. J., Morris, E. P., and Duarte, C. M. (2010). Effects of seagrasses and algae of the *Caulerpa* family on hydrodynamics and particle-trapping rates. *Marine Biology*, 157(3):473–481.
- Holmer, M. and Perillo, G. (2009). Productivity and biogeochemical cycling in seagrass ecosystems. *Coastal Wetlands: An Integrated Ecosystem Approach*. Elsevier Science, Amsterdam, pages 377–402.
- Howard, J., Hoyt, S., Isensee, K., Telszewski, M., Pidgeon, E., et al. (2014). *Coastal blue carbon: methods for assessing carbon stocks and emissions factors in mangroves, tidal salt marshes, and seagrasses*. Conservation International, Intergovernmental Oceanographic Commission of UNESCO, International Union for Conservation of Nature, Arlington, Va, USA.

- Howard, J. L., Perez, A., Lopes, C. C., and Fourqurean, J. W. (2016). Fertilization Changes Seagrass Community Structure but not Blue Carbon Storage: Results from a 30-Year Field Experiment. *Estuaries and Coasts*, 39(5):1422–1434.
- Johannessen, S. C. and Macdonald, R. W. (2016). Geoengineering with seagrasses: is credit due where credit is given? *Environmental Research Letters*, 11(11):1–10.
- Keil, R. G. and Hedges, J. I. (1993). Sorption of organic matter to mineral surfaces and the preservation of organic matter in coastal marine sediments. *Chemical Geology*, 107(3):385–388.
- Kennedy, H., Beggins, J., Duarte, C. M., Fourqurean, J. W., Holmer, M., Marbà, N., and Middelburg, J. J. (2010). Seagrass sediments as a global carbon sink: Isotopic constraints. *Global Biogeochemical Cycles*, 24(4):GB4026.
- Kennedy, H., Gacia, E., Kennedy, D. P., Papadimitriou, S., and Duarte, C. M. (2004). Organic carbon sources to SE Asian coastal sediments. *Estuarine, Coastal and Shelf Science*, 60(1):59–68.
- Ku, T., Walter, L. M., Coleman, M. L., Blake, R. E., and Martini, A. M. (1999). Coupling between sulfur recycling and syndepositional carbonate dissolution: evidence from oxygen and sulfur isotope composition of pore water sulfate, South Florida Platform, USA. *Geochimica et Cosmochimica Acta*, 63(17):2529–2546.
- Langdon, C., Takahashi, T., Sweeney, C., Chipman, D., Goddard, J., Marubini, F., Aceves, H., Barnett, H., and Atkinson, M. J. (2000). Effect of calcium carbonate saturation state on the calcification rate of an experimental coral reef. *Global Biogeochemical Cycles*, 14(2):639–654.
- Lavery, P. S., Mateo, M. A., Serrano, O., and Rozaimi, M. (2013). Variability in the Carbon Storage of Seagrass Habitats and Its Implications for Global Estimates of Blue Carbon Ecosystem Service. *PLoS ONE*, 8(9):e73748.
- Lerman, A. and Mackenzie, F. T. (2005). CO₂ Air–Sea Exchange due to Calcium Carbonate and Organic Matter Storage, and its Implications for the Global Carbon Cycle. *Aquatic Geochemistry*, 11(4):345–390.
- Long, M. H., Berg, P., McGlathery, K. J., and Zieman, J. (2015). Sub-tropical seagrass ecosystem metabolism measured by eddy covariance. *Marine Ecology Progress Series*, 529:75–90.
- Macreadie, P. I., Trevathan-Tackett, S. M., Skilbeck, C. G., Sanderman, J., Curlevski, N., Jacobsen, G., and Seymour, J. R. (2015). Losses and recovery of organic carbon from a seagrass ecosystem following disturbance. *Proceedings of the Royal Society B: Biological Sciences*, 282(1817):20151537.
- Magni, P., Montani, S., and Tada, K. (2002). Semidiurnal dynamics of salinity, nutrients and suspended particulate matter in an estuary in the Seto Inland Sea, Japan, during a spring tide cycle. *Journal of Oceanography*, 58(2):389–402.
- Manzello, D. P., Enochs, I. C., Melo, N., Gledhill, D. K., and Johns, E. M. (2012). Ocean acidification refugia of the Florida Reef Tract. *PLoS ONE*, 7(7):e41715.

- Marbà, N., Arias-Ortiz, A., Masqué, P., Kendrick, G. A., Mazarrasa, I., Bastyan, G. R., Garcia-Orellana, J., and Duarte, C. M. (2015). Impact of seagrass loss and subsequent revegetation on carbon sequestration and stocks. *Journal of Ecology*, 103:296–302.
- Marques, L. V. (2010). *Dinâmica populacional de Halodule wrightii Ascherson e sua fauna e flora associada em Cabo Frio – RJ*. PhD thesis, Instituto de Biologia Roberto Alcântara Gomes, Universidade do Estado do Rio de Janeiro.
- Mateo, M., Cebrián, J., Dunton, K., and Mutchler, T. (2006). Carbon flux in seagrass ecosystems. pages 159–192. Springer.
- Mazarrasa, I., Marba, N., Lovelock, C. E., Serrano, O., Lavery, P. S., Fourqurean, J. W., Kennedy, H., Mateo, M. A., Krause-Jensen, D., and Steven, A. (2015). Seagrass meadows as a globally significant carbonate reservoir. *Biogeosciences*, 12:4993–5003.
- McLeod, E., Chmura, G. L., Bouillon, S., Salm, R., Björk, M., Duarte, C. M., Lovelock, C. E., Schlesinger, W. H., and Silliman, B. R. (2011). A blueprint for blue carbon: toward an improved understanding of the role of vegetated coastal habitats in sequestering CO₂. *Frontiers in Ecology and the Environment*, 9(10):552–560.
- Melo, U., Summerhayes, C. P., and P, E. J. (1975). Upper continental margin sedimentation off Brazil, part IV: Salvador to Vitoria, southeastern Brazil. *Contr Sedimentology*, 3:80–118.
- Millero, F. J. (2007). The Marine Inorganic Carbon Cycle. *Chemical Reviews*, 107(2):308–341.
- Muehlllehner, N., Langdon, C., Venti, A., and Kadko, D. (2016). Dynamics of carbonate chemistry, production, and calcification of the florida reef tract (2009–2010): Evidence for seasonal dissolution. *Global Biogeochemical Cycles*, 30(5):661–688.
- Nelsen Jr, J. E. and Ginsburg, R. N. (1986). Calcium carbonate production by epibionts on *Thalassia* in Florida Bay. *Journal of Sedimentary Research*, 56(5).
- Orr, J. C., Fabry, V. J., Aumont, O., Bopp, L., Doney, S. C., Feely, R. A., Gnanadesikan, A., Gruber, N., Ishida, A., Joos, F., Key, R. M., Lindsay, K., Maier-Reimer, E., Matear, R., Monfray, P., Mouchet, A., Najjar, R. G., Plattner, G.-K., Rodgers, K. B., Sabine, C. L., Sarmiento, J. L., Schlitzer, R., Slater, R. D., Totterdell, I. J., Weirig, M.-F., Yamanaka, Y., and Yool, A. (2005). Anthropogenic ocean acidification over the twenty-first century and its impact on calcifying organisms. *Nature*, 437(7059):681–686.
- Pendleton, L., Donato, D. C., Murray, B. C., Crooks, S., Jenkins, W. A., Sifleet, S., Craft, C., Fourqurean, J. W., Kauffman, J. B., Marbà, N., Megonigal, P., Pidgeon, E., Herr, D., Gordon, D., and Baldera, A. (2012). Estimating Global “Blue Carbon” Emissions from Conversion and Degradation of Vegetated Coastal Ecosystems. *PLoS ONE*, 7(9):e43542.
- Robbins, L. L. and Blackwelder, P. L. (1992). Biochemical and ultrastructural evidence for the origin of whittings: a biologically induced calcium carbonate precipitation mechanism. *Geology*, 20(5):464–468.
- Romero, J. (1988). Epífitos de las hojas de *Posidonia oceanica*: variaciones estacionales y batimétricas de biomasa en la pradera de las islas Medes (Girona). *Oecologia aquatica*, 9:19–25.

- Semesi, I. S., Beer, S., and Björk, M. (2009). Seagrass photosynthesis controls rates of calcification and photosynthesis of calcareous macroalgae in a tropical seagrass meadow. *Marine Ecology Progress Series*, 382:41–48.
- Serrano, O., Lavery, P. S., Duarte, C. M., Kendrick, G. A., Calafat, A., York, P. H., Steven, A., and Macreadie, P. I. (2016). Can mud (silt and clay) concentration be used to predict soil organic carbon content within seagrass ecosystems? *Biogeosciences*, 13(17):4915.
- Serrano, O., Ricart, A. M., Lavery, P. S., Mateo, M. A., Arias-Ortiz, A., Masqué, P., Steven, A., and Duarte, C. M. (2015). Key biogeochemical factors affecting soil carbon storage in *Posidonia* meadows. *Biogeosciences*, 12(22):18913–18944.
- Shinn, E. A., Steinen, R. P., Lidz, B. H., and Swart, P. K. (1989). Whittings, a sedimentologic dilemma: Perspectives. *Journal of Sedimentary Research*, 59(1):147–161.
- Smith, S. V. (1981). Marine macrophytes as a global carbon sink. *Science*, 211(4484):838–840.
- Smith, S. V. (2013). *Parsing the Oceanic Calcium Carbonate Cycle: A Net Atmospheric Carbon Dioxide Source Or a Sink?* Association for the Sciences of Limnology and Oceanography.
- Stockman, K. W., Ginsburg, R. N., and Shinn, E. A. (1967). The Production of Lime Mud by Algae in South Florida. *Journal of Sedimentary Petrology*, 37(2):633–648.
- Stumm, W. and Morgan, J. J. (2012). *Aquatic chemistry: chemical equilibria and rates in natural waters*. John Wiley & Sons.
- Summerhayes, C. P., Melo, U., and Barretto, H. T. (1976). The Influence of Upwelling on Suspended Matter and Shelf Sediments off Southeastern Brazil. *Journal of Sedimentary Petrology*, 46(4):819–828.
- Suzuki, A. (1998). Combined effects of photosynthesis and calcification on the partial pressure of carbon dioxide in seawater. *Journal of Oceanography*, 54(1):1–7.
- Ullman, R., Bilbao-Bastida, V., and Grimsditch, G. (2012). Including Blue Carbon in climate market mechanisms. *Ocean and Coastal Management*, 83:15–18.
- van der Heide, T., Govers, L. L., de Fouw, J., Olf, H., van der Geest, M., van Katwijk, M. M., Piersma, T., van de Koppel, J., Silliman, B. R., Smolders, A. J. P., and van Gils, J. A. (2012). A Three-Stage Symbiosis Forms the Foundation of Seagrass Ecosystems. *Science*, 336(6087):1432–1434.
- Vicalvi, M. A. and Milliman, J. D. (1977). Calcium Carbonate Sedimentation on Continental Shelf off Southern Brazil, with Special Reference to Benthic Foraminifera: Sediments and Diagenesis. *Am. Assoc. Petrol. Geol. Stud. Geol.*, 4:313–328.
- Walter, L. M. and Burton, E. A. (1990). Dissolution of recent platform carbonate sediments in marine pore fluids. *American Journal of Science*, 290(6):601–643.
- Ward, L. G., Michael Kemp, W., and Boynton, W. R. (1984). The influence of waves and seagrass communities on suspended particulates in an estuarine embayment. *Marine Geology*, 59(1):85–103.

- Ware, J. R., Smith, S. V., and Reaka-Kudla, M. L. (1992). Coral reefs: sources or sinks of atmospheric CO₂? *Coral Reefs*, 11(3):127–130.
- Waycott, M., Duarte, C. M., Carruthers, T. J. B., Orth, R. J., Dennison, W. C., Olyarnik, S., Calladine, A., Fourqurean, J. W., Heck, K. L., Hughes, A. R., Kendrick, G. A., Kenworthy, W. J., Short, F. T., and Williams, S. L. (2009). Accelerating loss of seagrasses across the globe threatens coastal ecosystems. *Proceedings of the National Academy of Sciences*, 106(30):12377–12381.
- Yates, K. K., Dufore, C., Smiley, N., Jackson, C., and Halley, R. B. (2007). Diurnal variation of oxygen and carbonate system parameters in Tampa Bay and Florida Bay. *Marine Chemistry*, 104(1-2):110–124.
- Yates, K. K. and Halley, R. B. (2006). Diurnal variation in rates of calcification and carbonate sediment dissolution in Florida Bay. *Estuaries and Coasts*, 29(1):24–39.
- Zieman, J., Fourqurean, J. W., and Iverson, R. L. (1989). Distribution, abundance and productivity of seagrasses and macroalgae in Florida Bay. *Bulletin of Marine Science*, 44(1):292–311.

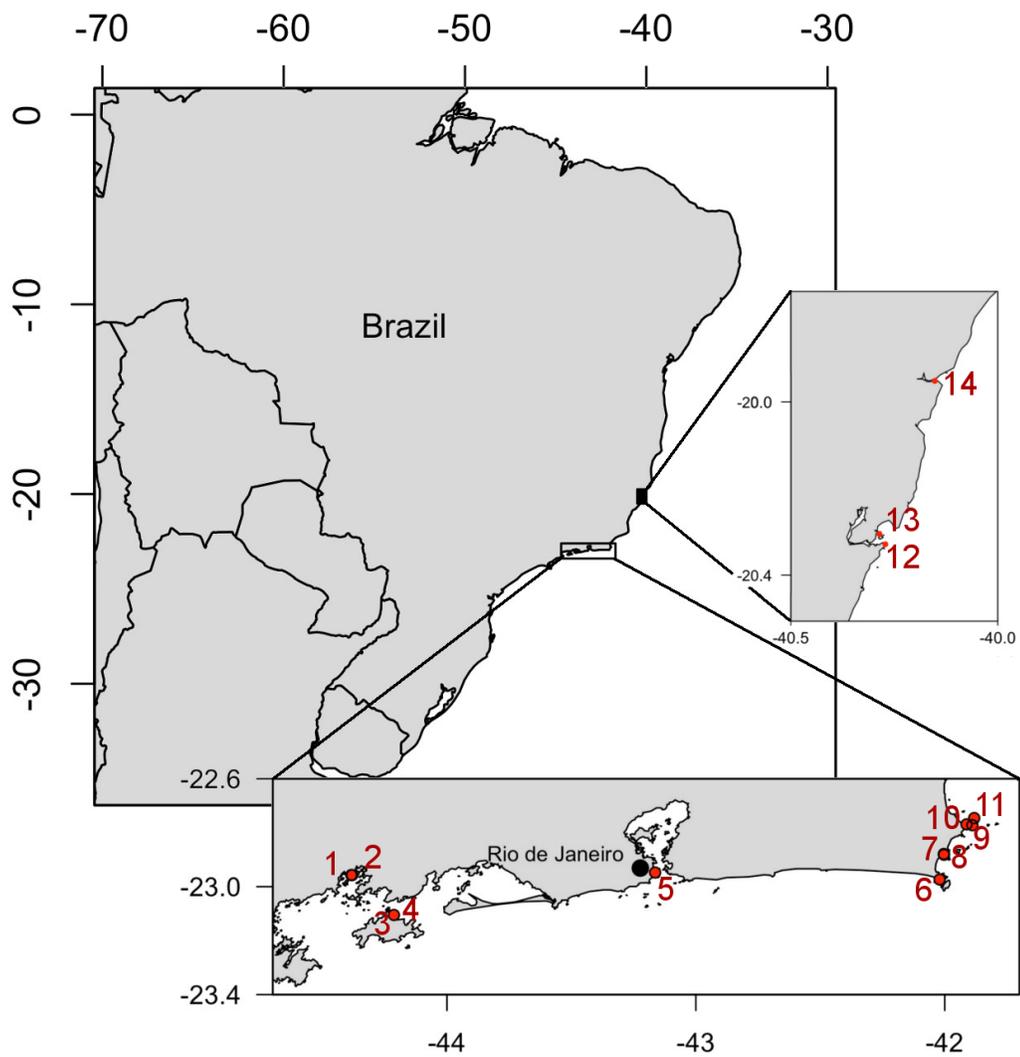


Figure 4.1: Study area showing sampling sites for seagrass and soil cores in southeastern Brazil. Two sediment cores and three seagrass cores were taken at each of the 14 sites. See Table 4.1 for site descriptions.

| Map Key | Site name | Latitude (°N) | Longitude (°E) | Salinity (psu) | Temp (°C) | depth (cm) | Seagrass present | Cohabitants | epiphytes | notes |
|---------|--------------------------|---------------|----------------|----------------|-----------|------------|--|--|-----------|--|
| 1 | Bracuí - site 1 | -22.957100° | -44.384567° | 35 | 24.4 | 30 | <i>Halodule wrightii</i> | epiphytic Rhodophyta | yes | on subtidal sandbank |
| 2 | Bracuí - site 2 | -22.957267° | -44.381133° | 35 | 24.4 | 50 | <i>Halodule wrightii</i> | epiphytic Rhodophyta, benthic cyanobacteria | yes | near mangrove-lined embayment |
| 3 | Ilha Grande - site 1 | -23.104933° | -44.213233° | 35 | 22.7 | 20 | <i>Halodule wrightii</i> | none | no | shallow water beach used for harvesting infauna |
| 4 | Ilha Grande - site 2 | -23.133783° | -44.151083° | 37 | 22.8 | 170 | <i>Halodule wrightii</i> | none | no | near mangrove-lined coast |
| 5 | Urca | -22.947603° | -43.163558° | 36 | 23.4 | 200 | <i>Halophila decipiens</i> | none | no | urban beach near mouth of Guanabara Bay |
| 6 | Arraial do Cabo | -22.973434° | -42.020278° | 36 | 23 | 370 | <i>Halodule wrightii</i> | none | no | long sandy beach with minimal surrounding vegetation |
| 7 | Ilha do Japones - site 1 | -22.881841° | -42.002751° | 31 | 22.8 | 55 | <i>Halodule wrightii</i> | <i>Hypnea musciformis</i> , <i>Ulva</i> sp. | yes | beach located near inlet |
| 8 | Ilha do Japones - site 2 | -22.878932° | -42.003653° | 31 | 22.8 | 40 | <i>Halodule wrightii</i> | <i>Hypnea musciformis</i> , <i>Ulva</i> sp. | yes | beach located near inlet, adjacent to tropical forest. |
| 9 | Manguinhos | -22.769126° | -41.912172° | 40 | 21.1 | 40 | <i>Halodule wrightii</i> | none | no | long sandy beach adjacent to urban area |
| 10 | Praia da Ferradura | -22.772383° | -41.888983° | 37 | 21.9 | 210 | <i>Halodule wrightii</i> | epiphytic Rhodophyta | yes | long sandy beach with minimal surrounding vegetation |
| 11 | Praia dos Ossos | -22.745867° | -41.881450° | 37 | 21.5 | 180 | <i>Halodule wrightii</i> | none | no | long sandy beach adjacent to urban area |
| 12 | Vila Velha | -20.325117° | -40.271533° | 36 | 25.7 | 30 | <i>Halodule emarginata</i> | none | no | small embayment used for ship storage |
| 13 | Vitoria | -20.301767° | -40.285967° | 36 | 23.7 | 40 | <i>Halodule emarginata</i> | bryopsis sp | no | long sandy beach adjacent to urban area |
| 14 | Santa Cruz | -19.953650° | -40.152067° | 34 | 24 | 40 | <i>H. decipiens</i> & <i>H. wrightii</i> | <i>Ulva</i> sp., Rhodophyta | no | beach located at river mouth |

Table 4.1: Location and site characteristics of seagrass survey sites in SE Brazil.

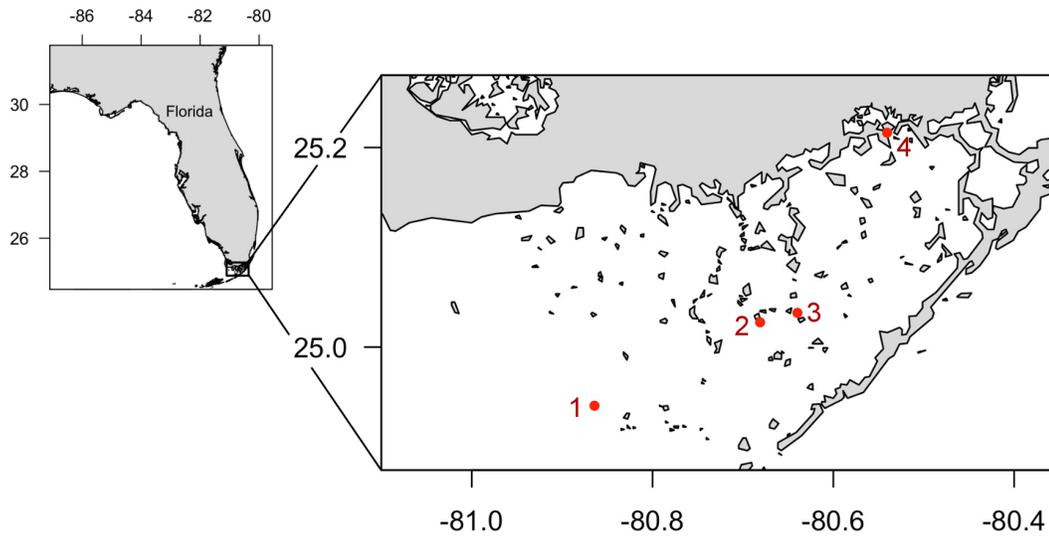


Figure 4.2: Referenced study areas showing sampling sites for seagrasses and soil cores in Florida Bay, USA. See Table 4.2 for site descriptions.

| Map Key | Site name | Latitude (°N) | Longitude (°E) | Seagrass present | Cohabitants | epiphytes | notes |
|---------|----------------|---------------|----------------|--|--|-----------|--|
| 1 | Nine Mile Bank | 24.9412° | -80.8642° | <i>T. testudinum</i> | sparse <i>Penicillus</i> spp., <i>Halimeda</i> spp. | yes | Dense seagrass on shallow bank. Data from Armitage and Fourqrean 2016; Fourqrean unpublished |
| 2 | Bob Allen Keys | 25.0248° | -80.6810° | <i>T. testudinum</i> | <i>Batophora</i> spp., <i>Penicillus</i> spp. | yes | Sparse seagrass in fine sediment. Data from Armitage and Fourqrean 2016; Fourqrean unpublished |
| 3 | Russell Bank | 25.0343° | -80.6397° | <i>T. testudinum</i> | rare | yes | Sparse seagrass in fine sediment. Data from Armitage and Fourqrean 2016; Fourqrean unpublished |
| 4 | Trout Cove | 25.2148° | -80.5404° | <i>T. testudinum</i> & <i>H. wrightii</i> | rare | yes | Sparse seagrass in fine sediment. Data from Armitage and Fourqrean 2016; Fourqrean unpublished |

Table 4.2: Location and site characteristics of referenced seagrass survey sites in Florida Bay.

| 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 | <i>Halodule wrightii</i> | 1886.3 ± 349.3 | 5.4 ± 0.4 | 1.1 ± 0.2 | 6.5 ± 1.3 | 7.7 ± 1.5 | 0.2 ± 0.1 |
| 2 | Bracui—site 2 | <i>Halodule wrightii</i> | 1848.6 ± 105.0 | 3.7 ± 0.3 | 0.9 ± 0.1 | 4.4 ± 0.6 | 5.3 ± 0.7 | 0.2 ± 0.1 |
| 3 | Ilha Grande—site 1 | <i>Halodule wrightii</i> | 2735.1 ± 690.2 | 3.9 ± 0.2 | 15.3 ± 2.3 | 10.0 ± 0.4 | 25.3 ± 2.5 | 1.5 ± 0.9 |
| 4 | Ilha Grande—site 2 | <i>Halodule wrightii</i> | 1659.9 ± 132.0 | 5.2 ± 0.3 | 1.6 ± 0.0 | 16.8 ± 1.1 | 18.4 ± 1.1 | 0.1 ± 0.1 |
| 5 | Urca | <i>Halophila decipiens</i> | - | - | 14.1 ± 1.9 | 21.6 ± 1.0 | 35.7 ± 1.7 | 0.7 ± 0.4 |
| 6 | Arraial do Cabo | <i>Halodule wrightii</i> | 9450.3 ± 1428.2 | 4.4 ± 0.3 | 29.1 ± 0.4 | 62.1 ± 20.7 | 91.1 ± 21.1 | 0.6 ± 0.4 |
| 7 | Ilha do Japones—site 1 | <i>Halodule wrightii</i> | 2489.9 ± 214.2 | 4.9 ± 0.3 | 28.9 ± 0.2 | 33.7 ± 3.0 | 62.6 ± 2.9 | 0.9 ± 0.5 |
| 8 | Ilha do Japones—site 2 | <i>Halodule wrightii</i> | 1905.2 ± 207.5 | 4.0 ± 0.2 | 25.5 ± 0.6 | 30.8 ± 7.5 | 56.3 ± 8.1 | 1.0 ± 0.6 |
| 9 | Manguinhos | <i>Halodule wrightii</i> | 6677.4 ± 385.2 | 3.3 ± 0.1 | 4.6 ± 0.1 | 51.7 ± 5.7 | 56.3 ± 5.8 | 0.1 ± 0.1 |
| 10 | Praia da Ferradura | <i>Halodule wrightii</i> | 2093.8 ± 471.2 | 3.5 ± 0.1 | 24.7 ± 0.1 | 43.7 ± 4.4 | 68.4 ± 4.5 | 1.5 ± 0.9 |
| 11 | Praia dos Ossos | <i>Halodule wrightii</i> | 7054.7 ± 1700.3 | 4.8 ± 0.2 | 26.8 ± 0.1 | 42.8 ± 6.8 | 69.6 ± 6.8 | 0.7 ± 0.4 |
| 12 | Vila Velha | <i>Halodule emarginata</i> | 603.6 ± 68.0 | 3.9 ± 0.2 | 0.6 ± 0.1 | 7.6 ± 1.5 | 8.2 ± 1.5 | 0.1 ± 0.1 |
| 13 | Vitoria | <i>Halodule emarginata</i> | 2207.0 ± 598.9 | 3.8 ± 0.1 | 8.8 ± 5.8 | 13.4 ± 2.8 | 22.2 ± 8.6 | 0.6 ± 0.3 |
| 14 | Santa Cruz | <i>Halodule wrightii</i> | 10,468.9 ± 1044.0 | 2.0 ± 0.1 | 1.4 ± 0.2 | 29.1 ± 0.4 | 30.6 ± 0.6 | 0.1 ± 0.0 |
| 14 | Santa Cruz | <i>Halophila decipiens</i> | 5809.8 ± 796.5 | - | 1.6 ± 0.2 | 3.3 ± 0.4 | 4.8 ± 0.6 | 0.5 ± 0.3 |

Table 4.3: Shoot densities and biomass of seagrasses inhabiting study sites in SE Brazil. Data are mean ± SE (n = 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 | δ ¹³ C (‰) |
|---------|------------------------|----------------------------|-----------------------|-----------------------|-----------------------|------------|--------------|------------|-----------------------|
| 1 | Bracui—site 1 | <i>Halodule wrightii</i> | 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 | <i>Halodule wrightii</i> | 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 | <i>Halodule wrightii</i> | 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 | <i>Halodule wrightii</i> | 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 | <i>Halophila decipiens</i> | 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 | <i>Halodule wrightii</i> | 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 | <i>Halodule wrightii</i> | 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 | <i>Halodule wrightii</i> | 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 | <i>Halodule wrightii</i> | 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 | <i>Halodule wrightii</i> | 41.0 | 4.8 | 0.48 | 9.9 | 222.2 | 22.5 | -9.9 |
| 11 | Praia dos Ossos | <i>Halodule wrightii</i> | 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 | <i>Halodule emarginata</i> | 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 | <i>Halodule emarginata</i> | 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 | <i>Halodule wrightii</i> | 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 | <i>Halophila decipiens</i> | - | - | - | - | - | - | -8.7 ± 0.4 |

Table 4.4: Elemental and stable isotope composition of seagrass leaves collected across sites in SE Brazil. Data are mean ± SE (n = 1-3).

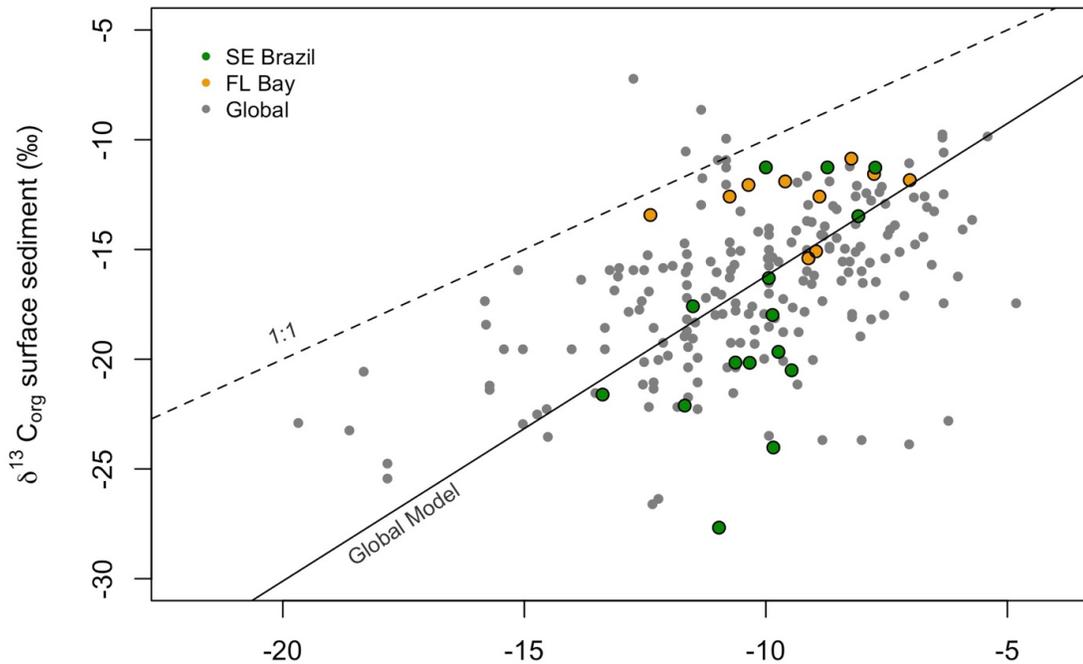


Figure 4.3: The relationship between $\delta^{13}\text{C}$ of seagrass and $\delta^{13}\text{C}$ of organic fraction of underlying surface sediments. Dark blue points are from this study, orange points are comparable data from Florida Bay (Howard et al. 2016) and black points are the global data set for reference (Kennedy et al. 2010).

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

Table 4.5: Regional comparisons of C_{org} (Fourqurean et al., 2012a) and C_{inorg} areal stocks (Mazarrasa et al., 2015) in seagrass ecosystems with calculated CO_2 net sequestration.

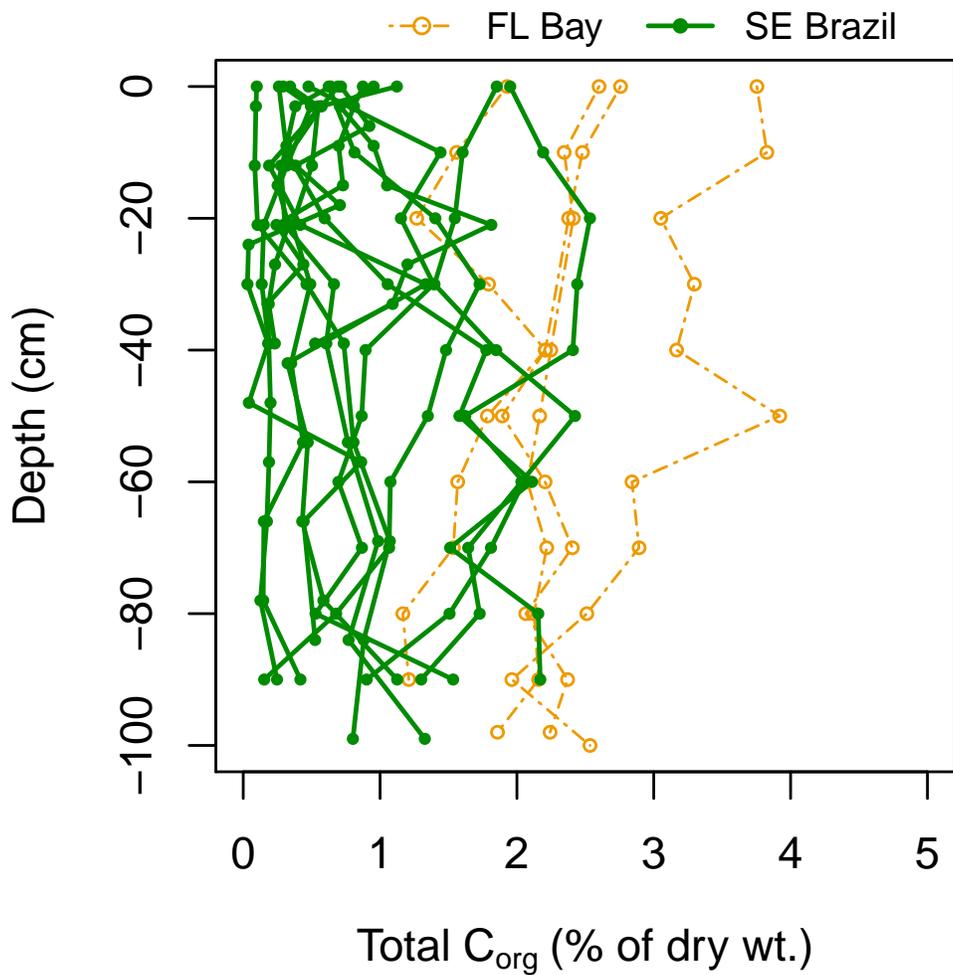


Figure 4.4: Down core profiles of mean soil C_{org} content across all sites in SE Brazil and FL bay (mean, n=2-3). Error associated with mean are displayed in Figure 4.6 and Figure 4.7.

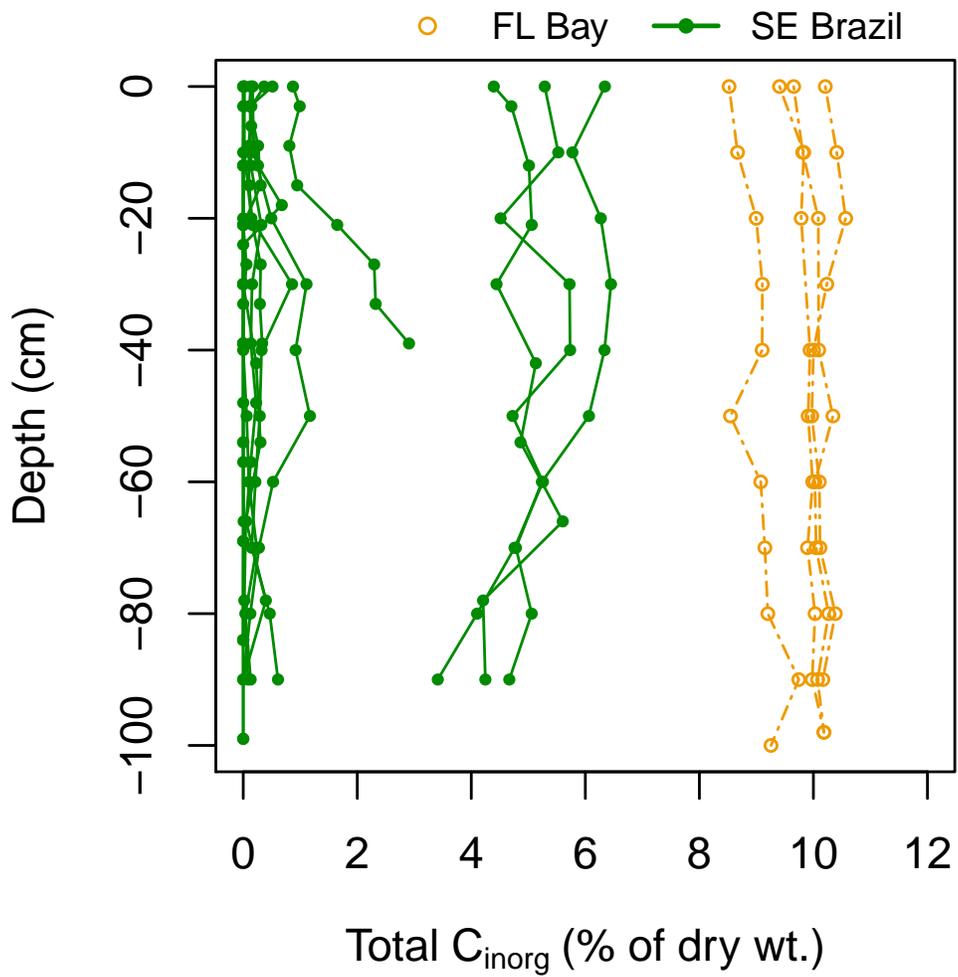


Figure 4.5: Down core profiles of mean soil C_{inorg} content across all sites in SE Brazil and FL bay (mean, n=2-3). Error associated with mean are displayed in Figure 4.6 and Figure 4.7.

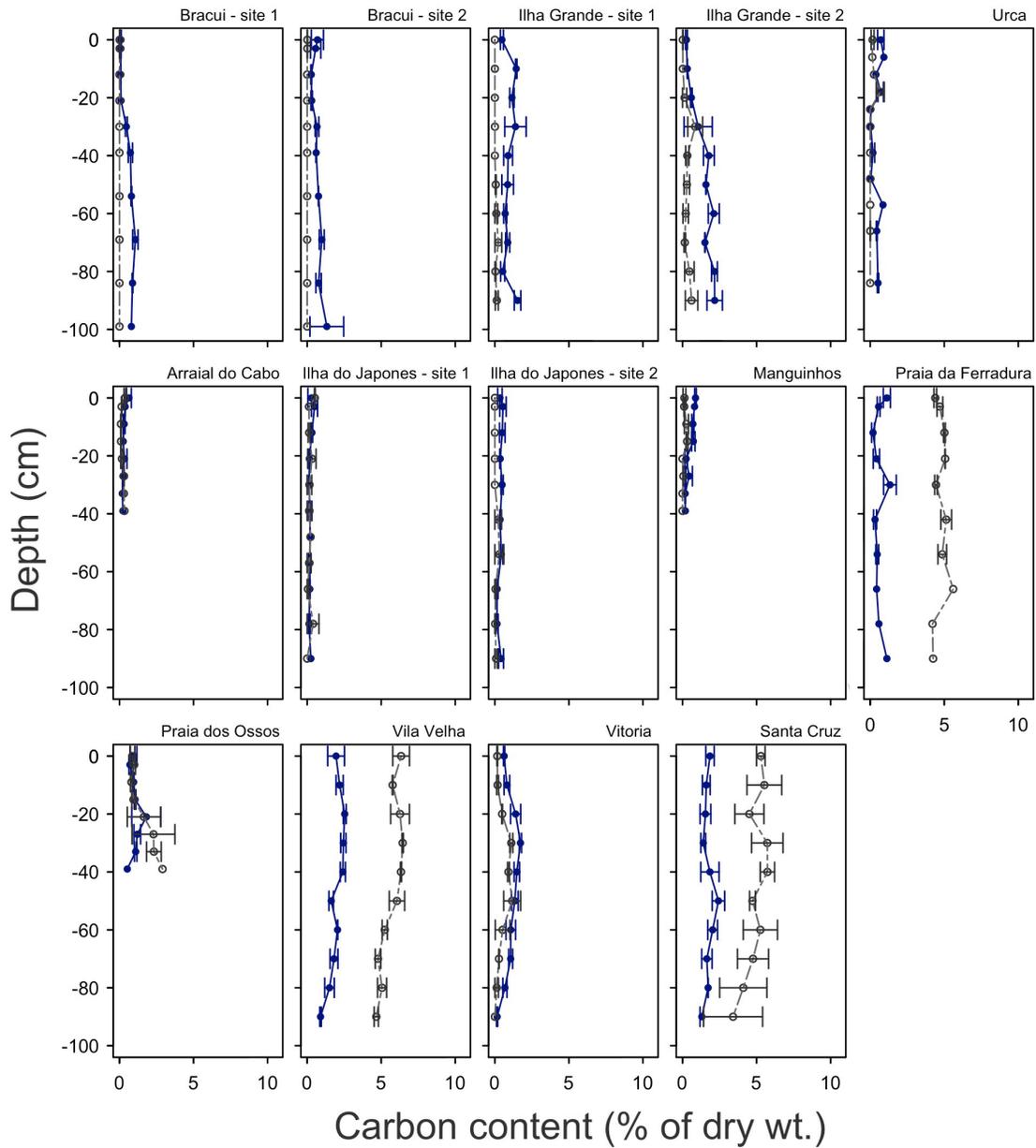


Figure 4.6: Down core profiles of soil C_{org} (—) and C_{inorg} (---) (means \pm 1 SE, $n = 1 - 3$) across 14 sampling sites. Sites are arranged from most southern to northern.

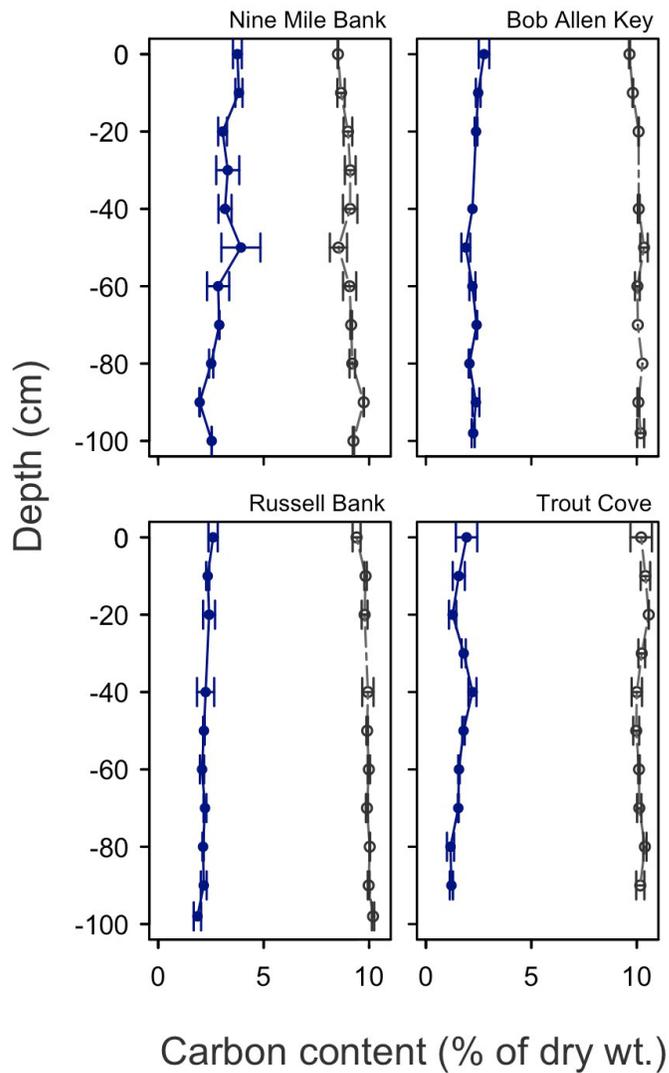


Figure 4.7: Down core profiles of soil C_{org} (—) and C_{inorg} (---) (means ± 1 SE, $n = 2$) across 4 sites in Florida Bay, USA (Fourqurean, unpublished). Sites are arranged from most southern to northern, also following a nutrient availability gradient from replete to limited.

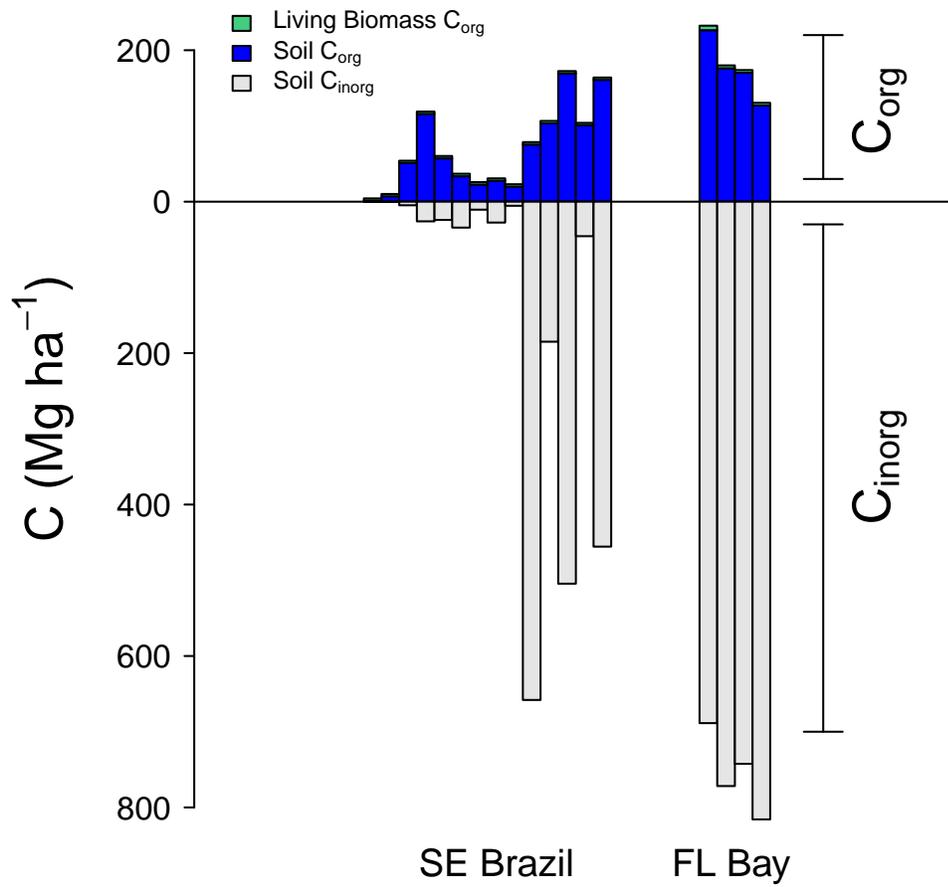


Figure 4.8: Site specific carbon areal stocks including C_{org} and C_{inorg} associated with living biomass and soils. Sites are arranged from southernmost survey site on the left to northernmost site on the right.

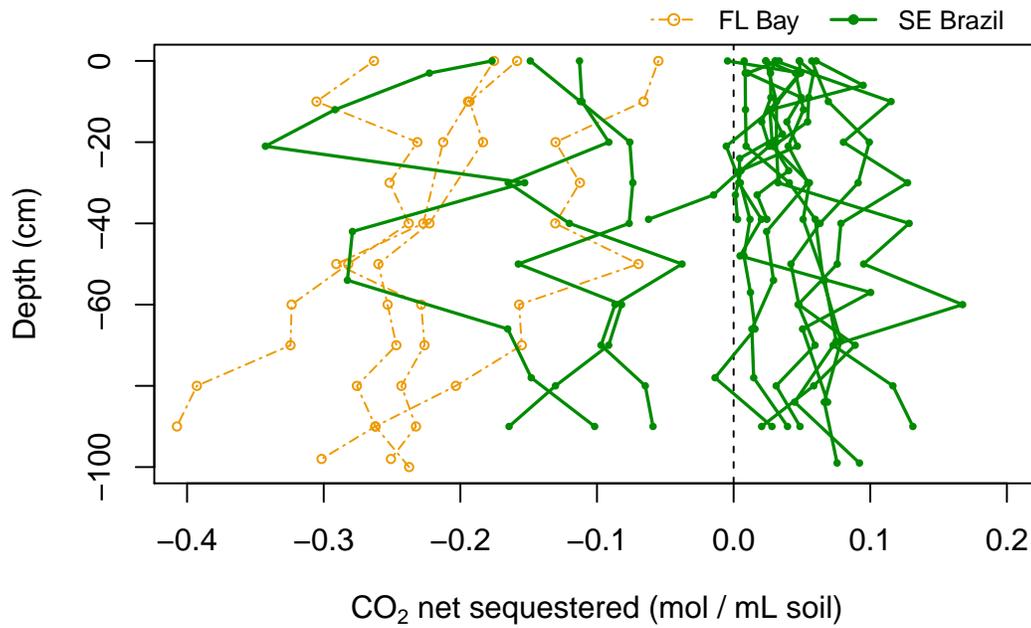


Figure 4.9: Down core profiles of mean CO₂ sequestration equivalents across survey sites. Positive values indicate that CO₂ is consumed during soil production while negative values indicate that the production of soil carbon resulted in net CO₂ production. Data derived from both C_{org} and C_{inorg}, assuming standard gas exchange:reaction ratios.

CHAPTER 5

SPATIAL VARIATION IN ORGANIC MATTER RECALCITRANCE AND $\delta^{13}\text{C}$ OF ORGANIC AND INORGANIC CARBON IN SEAGRASS SEDIMENTS AS INDICATORS OF CARBON CYCLING AND EXCHANGE PROCESSES

Abstract

The soils underlying seagrass ecosystems have been identified as globally important stocks of organic carbon (C_{org}) that, if compromised, could significantly exacerbate global greenhouse gas emissions. However, total soil C_{org} stock beneath seagrasses is likely to be different than the C_{org} vulnerable to remineralization and CO_2 efflux, with the amount at risk likely varying between environmental and ecological conditions. Here we measured 93 seagrass-inhabited sites across the South Florida seascape to characterize the recalcitrance and $\delta^{13}\text{C}$ values of surface sediments to understand the variability in vulnerable C_{org} and its likely fate after remineralization. We used a stepwise thermo-oxidation process to calculate the relative recalcitrance of soil C_{org} stocks, finding that soils with finer sediments and higher overall C_{org} content contain relatively higher proportions of labile material. We also observed $\delta^{13}\text{C}$ values of carbonates were related to $\delta^{13}\text{C}$ values of seagrasses and soil C_{org} content, suggesting that C_{inorg} processes are tied to organic metabolism. Such findings indicate there are differences in the vulnerability of soil C_{org} to oxidation and the buffering by carbonate processes may influence the links between C_{org} stores and the ocean and atmosphere CO_2 reservoirs.

Introduction

Seagrass ecosystems are pragmatically being evaluated as a low-cost, manageable method of climate change mitigation based on the CO_2 that they have historically se-

questered and continue to keep stored (termed “Blue Carbon”; Mcleod et al. 2011; Pendleton et al. 2012). These systems are typically net autotrophic, consuming more CO₂ from ocean water through photosynthesis than producing through ecosystem respiration, in turn encouraging CO₂ invasion from the atmosphere (Duarte et al., 2010). Global rates of seagrass net productivity is high (0.06 – 1.94 Pg C yr⁻¹, with approximately 15 % of net production being buried (Duarte, 2017). Seagrass-derived carbon, combined with other sources, can accumulate in the underlying soils throughout the lifespan of a meadow to form large, globally significant organic carbon (C_{org}) stocks (Fourqurean et al., 2012a). If the mechanisms controlling C storage and preservation are inherent to seagrass ecosystems, then ecosystem damage or destruction could result in the remineralization of stored C_{org} and the subsequent efflux to the atmosphere, exacerbating climate change. To ensure the stability of seagrass soil C stocks, seagrass conservation and management is being explored as a means to mitigate greenhouse gas emissions (Hiraishi et al., 2014). However, there is great uncertainty regarding the likelihood that soil carbon stocks in damaged seagrass ecosystems could be remineralized and other processes that could alter the fate of remineralized C_{org} (Lovelock et al., 2017a; Macreadie et al., 2017; Howard et al., 2017).

The organic component of soils underlying seagrass meadows is a diverse mixture of macromolecules that vary in their resistance to remineralization (Burdige, 2007). The molecular constituents of soil C_{org} vary spatially and temporally, determined by the source and type of OM inputs, as well as the degree and milieu of processing (Burdige, 2007; Arndt et al., 2013). These contributing OM fractions exist on a scale of recalcitrance that is complicated by environmental factors that can augment a macromolecule’s inherent recalcitrance. Chemical stabilization (Mayer, 1995), physical protection (Keil et al., 1994), anaerobic metabolism (Nierop et al., 2017), nutrient limitation (Enriquez et al., 1993; Lopez et al., 1998), and unachieved energetic thresholds (Guenet et al., 2010)

can limit microbially-driven degradation and remineralization, thus changing the realized recalcitrance of OM. Blue Carbon discussions often consider the recalcitrance of seagrass soil C_{org} as dependent on the stable, low nutrient, anoxic environment in which it is buried rather than inherent properties of the OM (Duarte et al., 2010; Fourqurean et al., 2012a), though this may be an oversimplification given the complicated mixtures of organic compounds that make up soil C_{org} and the complex environmental factors that influence the refractory nature of each of those compounds.

The organic matter in living seagrasses themselves varies greatly in their inherent recalcitrance depending on species, tissue component and latitudinal origin (Trevathan-Tackett et al., 2017), and other common contributors to seagrass C_{org} stocks, like adjacent terrestrial inputs and algae, vary even more in their ability to be decomposed (Enriquez et al., 1993). This being the case, it is unlikely that litter quality and the inherent recalcitrance of OM is equal across sites inhabited by seagrasses, potentially altering the importance of environmental conditions to the long-term preservation of C_{org} . The degree of inherent recalcitrance of soil OM could influence the risk of remineralization that Blue Carbon stocks face (Lovelock et al., 2017a).

The metabolic processes linked to C_{org} storage and potential loss are the foci of most Blue Carbon discussions, though many seagrass meadows also have high inorganic carbon (C_{inorg}) content (Mazarrasa et al., 2015) that may interfere with the proposed pathways and fate of Blue Carbon (Howard et al., 2017). Like soil C_{org} , C_{inorg} affects $p\text{CO}_2$ through its formation (via calcification) and dissolution, though the reaction is reversed (Millero, 2007). Calcifying organisms associated with seagrass meadows (and some seagrasses themselves), utilize dissolved inorganic carbon (DIC) and produce CO_2 during the production of solid CaCO_3 (Frankovich and Ziemann, 1994; Frankignoulle et al., 1995; Enríquez and Schubert, 2014). Carbonate dissolution consumes CO_2 acting as a sink, while producing alkalinity (Millero, 2007). The solubility of CaCO_3 is linked to the

chemical conditions created by metabolic processes, where high pH conditions driven by photosynthesis encourage calcification, and low pH conditions provided by respiration and decomposition promote CaCO_3 dissolution (Hendriks et al., 2014; Semesi et al., 2009; Smith, 2013). Inorganic carbon processes are independent from organic metabolism, though they are mutually influential. Considering their antagonistic effects on pCO_2 , the interrelated $\text{C}_{\text{org}} - \text{C}_{\text{inorg}}$ reactions may buffer overall CO_2 uptake and production from the ecosystem (Smith, 2013; Macreadie et al., 2017).

Studies of seagrass meadows in particular have demonstrated correlations between sediment C_{org} and C_{inorg} content (Gullström et al., 2017) and how spatial differences in C_{inorg} may affect overall CO_2 exchange (Howard et al., 2017), though there are uncertainties regarding the temporal scales and impact of C_{inorg} processes relative to organic metabolism and carbon sequestration (Macreadie et al., 2017). Many of the most expansive seagrass meadows (Mediterranean Sea, Florida Bay, coastal Australia) are found in soils consisting primarily of carbonates (Duarte et al., 1995; Green and Short, 2003) and seagrass ecosystems have been identified as large reservoirs of C_{inorg} (Mazarrasa et al., 2015). For those C_{inorg} stocks to be pertinent to contemporary CO_2 fluxes and estimates of C loss, they need to be vulnerable to change. Yates and Halley (2006) noted that sediment carbonate dissolution relies on seagrass productivity and sediment respiration in Florida Bay. Further, carbonate dissolution is well documented in porewaters related to respiratory-driven decreases in pH (Walter and Burton, 1990; Ku et al., 1999). Values of carbonate $\delta^{13}\text{C}$ have been used to suggest the presence and degree of carbonate dissolution and mineralization (Walter et al., 2007; Hu and Burdige, 2007), thus being potentially valuable for determining site specific activity of C_{inorg} to buffer C_{org} processes.

We expect areas with rapid OM decomposition and turnover to have lower C_{org} stocks with higher fractions of recalcitrant C_{org} remaining after remineralization. Considering previous work (Chapter 3 and its references) we expect these areas to have coarse sedi-

ments. We also expect C_{inorg} processes to relate to C_{org} processes through the common use of DIC or direct influence of carbonate buffering through dissolution. In this study, we test these hypotheses by investigating the variability of seagrass soil C_{org} recalcitrance and the relationship between soil C_{org} and C_{inorg} across a range of seagrass inhabited sites. Specifically, we use a simple and inexpensive method based on stepwise thermogravimetry to characterize the recalcitrance of soil C_{org} at sites across Florida Bay and the Florida Keys. We then investigate $\delta^{13}\text{C}$ values of seagrasses, soil C_{org} and soil C_{inorg} for potential feedbacks between organic and inorganic cycles that could signify a relationship between CO_2 -related processes.

Materials and Methods

This study was conducted across the seagrass meadows of Florida Bay and the Florida Keys that together form the largest documented continuous seagrass ecosystem in the world (Fourqurean et al., 2002). Sediments across the region consist primarily of biogenic carbonates (Bosence, 1989a) supporting seagrass meadows primarily of *Thalassia testudinum* with *Halodule wrightii*, and/or *Syringodium filiforme*, along with *Ruppia maritima* and *Halophila* sp. in lower abundances (Bosence, 1989b; Zieman et al., 1989). Seagrasses are often interspersed with calcareous macroalgae species of *Penicillus*, *Halimeda*, *Batophora*, *Dictyota* and *Laurencia*, which contribute to primary production as well as sediment-forming carbonates (Stockman et al., 1967; Zieman et al., 1989). Environmental factors vary across the seascape that is dominated by seagrasses, leading us to group our sampling sites into groups of similar environmental condition. Eastern Florida Bay is severely phosphorus limited because of high N:P in freshwater runoff and low mobility of P across the landscape owing to the adsorption of P onto carbonate sediments (Fourqurean et al., 1992), thus has been distinguished from FKNMS sites and Western

Florida Bay (Figure 5.1). The delineation of Eastern and Western Florida was made by dividing Florida Bay study sites longitudinally around the site with the median longitude. More thorough descriptions of South Florida sedimentology, benthic communities and their controlling factors can be found elsewhere (Fourqurean et al., 1995, 2003).

Sediment cores taken in the Florida Keys National Marine Sanctuary were collected January 2016 using 60-mL plastic syringes that were modified into small piston cores (~2.6 cm diameter) that extract ~15 cm deep of surface sediment. These 46 sites were sampled in quadruplicate. Samples collected at the 47 sites within Florida Bay were collected from September to October 2016, using a 2" hand sediment corer, that was repeatedly used to sample the top 20cm of sediment until ~1000 ml was retrieved.

A stepwise, ramped temperature analysis of C loss was used to investigate relative recalcitrance of soil C_{org} , modeled after thermogravimetric analysis and ramped pyrolysis (Kristensen, 1990; Capel et al., 2006; Trevathan-Tackett et al., 2015, 2017). We used sequential mass loss on ignition at set temperatures to remove organics combined with the pre- and post-ignition C content as determined with an elemental analyzer (Fisons NA1500). This allowed for both weight loss and C loss to be calculated across the range of temperatures.

Soil samples were dried, homogenized to a fine powder using a motorized mortar and pestle, and re-dried at 65 °C for a minimum of two weeks. Prepared samples were analyzed using a CHN analyzer to measure total C (C_{total}) in soil sample (which included both C_{org} from OM and C_{inorg} from carbonate minerals). Subsamples of dried material (~1.5g) were added to ashed, dry, preweighed vials and weighed to the nearest 0.1 mg. Samples were then oxidized at 180 °C for 4 hours and reweighed for the calculation of temperature-specific LOI (LOI_{180}). A small (~20 µg) subsample of oxidized material was then analyzed for post-oxidation carbon content. The remaining oxidized material was reweighed and oxidized at the subsequent temperature (300 °C) for 4 hours. The LOI_{300}

was calculated and a subsample was taken for elemental analysis. This sequential process was conducted at 180 °C, 300 °C, 400 °C, 500 °C, 550 °C, and 600 °C, corresponding to primary OM categories of marine macroalgae and seagrass (Trevathan-Tackett et al., 2015, 2017). Each temperature step yielded temperature-specific LOI and C content values, that were scaled to calculate the C lost at each temperature step relative to initial sample weight. C loss across temperatures were used to create a Recalcitrance Index (RI), defined as C lost at 500 - 550 °C, representing the high, most recalcitrant C_{org}, divided by total C_{org} lost between 180 - 550 °C. The 600 °C temperature step was excluded from RI calculation because common methods of C_{org} determination used in the literature are calculated at 550 °C and lower.

Samples were then analyzed for total C_{org} and C_{inorg} content as well as bulk $\delta^{13}\text{C}_{\text{org}}$ and $\delta^{13}\text{C}_{\text{inorg}}$ values of soils. Analysis for total C_{org} and C_{inorg} content followed procedures similar to those for stepwise oxidation, though consisted of a single temperature step at 550 °C for four hours. Ashed material was analyzed for C_{inorg} content, and scaled to C_{inorg} content of the original sample using calculated LOI. The difference between C_{total} and C_{inorg} was used to compute C_{org} content. Analysis of $\delta^{13}\text{C}_{\text{inorg}}$ used the ashed material remaining from C_{org} content determination. An elemental analyzer was used to combust the samples and to subsequently reduce the formed carbon-containing gases to CO₂, which was then measured on a Finnigan MAT Delta C IRMS in a continuous flow mode. For determining $\delta^{13}\text{C}_{\text{org}}$ of soils, subsamples of dry, homogenized soil were fumed with HCl for >14 days to remove C_{inorg} before similar mass spectrometer procedures. Isotopic values were reported in the standard delta notation (‰): $\delta (\text{‰}) = [(R_{\text{sample}}/R_{\text{standard}}) - 1] \times 1000$. 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 $\pm 0.08 \text{ ‰}$.

Intact sediments were wet sieved using methods described by Erftemeijer and Koch (2001) using sieve sizes 4, 10, 40, 200 to separate gravel, course, medium and fine sand fractions. All sediments fine enough to pass through the #200 sieve (thus smaller than 74 μm) were considered mud. For Florida Bay sites, muds were separated into silts and clays using hydrometer analysis, where as muds from the remaining FL Keys sites were separated by gravimetric pipette analysis (Folk, 1980). The combination of procedures yielded percent contributions (by weight) of five sediment categories (clay, silt, fine sand, medium sand, course sand, and gravel). Percent mud was calculated by dividing clay + silt weight contributions by total weight. The mean grain size was calculated and presented using phi (ϕ) units.

Seagrass $\delta^{13}\text{C}$ values were assessed at sites within the Florida Keys National Marine Sanctuary during both winter and summer months of 2015 and 2016 for a total of four samples per site. At each site, short shoots of each seagrass species present were haphazardly collected, placed on ice, and transported back to the laboratory for analysis. In the lab, seagrass leaves were separated by species, cleaned of epiphytes by scraping with a razor blade and dried to a constant weight at 65 $^{\circ}\text{C}$. Prior to analyses, seagrasses tissue was ground to a fine powder with an automated mortar and pestle. Seagrass tissue was analyzed for $\delta^{13}\text{C}$ using the same procedures and precision as soils. An average $\delta^{13}\text{C}$ value for each site was calculated using values of the dominant species.

Data Analysis

Correlations between RI values and mud content were tested using linear regressions. Values of $\delta^{13}\text{C}_{\text{org}}$ and $\delta^{13}\text{C}_{\text{inorg}}$ were compared to one another as well as soil C_{org} content using linear regression. The comparisons of $\delta^{13}\text{C}_{\text{org}}$ and $\delta^{13}\text{C}_{\text{inorg}}$ to seagrass $\delta^{13}\text{C}$ were tested similarly on a subset of sites where data for values were determined. The assumptions of linear regression were not met for testing the Correlation between C_{org}

and RI. Considering the very different upper and lower boundaries of the relationship, a quantile regression was used, testing the correlation of quantiles ranging from 5 % to 95 %. Quantile regression estimates multiple slopes from the minimum to maximum response, providing a description of the relationships between variables that are missed by regression methods focused on prediction of the mean values (Ellison and Gotelli, 2004).

Results

Soil C_{org} content in the top 15 cm of sampled sites averaged 2.8 ± 0.2 ranging from 0.7 to 8.6 %. Soils from Western FL Bay had higher C_{org} compared to Eastern FL Bay and the Florida Keys (4.0 ± 0.3 compared to 2.3 ± 0.2 and 2.4 ± 0.3 , respectively; Figure 5.2a; ANOVA, $p < 0.05$). These values are comparable to previous reports of Florida Bay (2.1 ± 0.3 %, (Fourqurean et al., 2012b) showing similar spatial patterns, with northwestern Florida Bay and some nearshore sites displaying the highest values (Figure 5.3). Soil C_{inorg} content averaged 9.2 ± 0.2 and correlated inversely to C_{org} content (linear regression, $p < 0.05$, $R^2 = 0.95$). Both Eastern and Western FL Bay had higher mud content than sites along the FL Keys (Figure 5.2b). Mud content correlated positively with soil C_{org} content, but only for FL Keys and Western Florida Bay regions (Figure 5.4).

When the stepwise carbon loss analysis was performed, there was weight loss at all temperature steps from 65 °C to 600 °C (Figure 5.5), with the largest decreases in weight between 180 - 300 °C and 400 - 500 °C where 22.4 ± 0.5 and 25.1 ± 0.7 % of the total weight loss occurred, respectively. LOI values correlated positively with C loss at each temperature step except for 180 °C temperature step, where there was no C loss associated with the weight loss (Figure 5.6). Where significance tests were positive, linear models consistently had $R^2 > 0.88$ with slopes ranging from 0.13 to 0.48. Slopes were highest at

300 °C and 400 °C steps, indicating the organic matter oxidized at this temperature had higher C content per mass than the OM lost at other temperatures.

Carbon content decreased from 12.0 ± 0.1 at 65 °C to 9.8 ± 0.1 through the stepwise oxidation process, decreasing in C content at each temperature step except for 180 °C (Figure 5.7; ANOVA, $p < 0.05$). Carbon loss occurred at all temperature steps with two clear peaks at 300 °C and 500 °C where 35.1 ± 1.0 and 28.0 ± 0.8 % of C_{org} loss occurred, respectively (Figure 5.7). The temperature step from 65 °C to 180 °C included the lowest average carbon loss where 2.4 ± 1.0 % of total carbon was lost.

Recalcitrance Index values averaged 0.44 ± 0.1 , ranging from 0.28 to 0.80. There was a negative correlation between mud content and RI, where soils with muddy sediments contained relatively more labile carbon (Figure 5.8; linear regression, $p < 0.05$). RI values tended to decrease with increasing soil C_{org} content (Figure 5.9), though this was not linear (the assumption of heteroskedasticity was not met). As C_{org} content increases, the range of RI values decrease, with most RI values being low when C_{org} content is high. In other words, there was a negative relationship between soil C_{org} and RI, but this relationship was not consistent across all study sites.

Seagrass and soil $\delta^{13}C$

Average $\delta^{13}C$ values of seagrass leaf tissue for the sampling period was -9.4 ± 0.2 ‰ across all sites with data, ranging from -6.9 to -12.8 ‰. The average $\delta^{13}C$ of the organic component of soil of sites was -15.0 ± 0.2 ‰, ranging from -11.2 to -17.7 ‰. For the inorganic, carbonate component of sediments, $\delta^{13}C$ averaged -0.7 ± 0.3 ‰ ranging from 3.9 to -7.2 ‰. There was no measurable relationship between the $\delta^{13}C$ of seagrasses and that of the C_{org} component of the underlying soils (linear regression, $p > 0.05$), though there was a positive correlation between the $\delta^{13}C$ of seagrasses and that of the C_{inorg} component (Figure 5.10; linear regression, $p < 0.05$). Values of $\delta^{13}C$ for both

organic and inorganic components were compared to overall soil C_{org} content. There was a positive relationship between soil C_{org} content and soil $\delta^{13}\text{C}_{\text{org}}$ values (Figure 5.11; linear regression, $p < 0.05$). There was also a relationship between soil C_{inorg} content and $\delta^{13}\text{C}_{\text{org}}$ values, though the direction was reversed (Figure 5.11; linear regression, $p < 0.05$).

Discussion

We found that C_{org} input and sediment grain size both influence soil C_{org} in south Florida seagrasses communities, though the importance of each driver varies geographically. We also show that not all soil C_{org} is equally at risk of remineralization, suggesting that vulnerable C_{org} is related to sediment grain size and is relatedly non-linearly to the total soil C_{org} content. Supporting the interaction between organic metabolism and C_{inorg} processes (calcification and dissolution), we find found that $\delta^{13}\text{C}$ values of surface soil carbonates were related to both $\delta^{13}\text{C}$ values of seagrasses and soil C_{org} content.

The average soil C_{org} content for sampled sites (averaging $2.8 \pm 0.2\%$) was slightly higher than previously published local ($2.1 \pm 0.3\%$; Fourqurean et al. 2012b) and global values (1.4% median, $2.0 \pm 0.1\%$ mean; Fourqurean et al. 2012a) though varied significantly between regions of south Florida (Figure 5.2, Figure 5.3). Sediment grain size is a primary driver of soil C_{org} stock in seagrasses (Chap 3, Röhr et al. 2016; Dahl et al. 2016; Miyajima et al. 2017) and while we saw a similar relationship here, it is limited to Western Florida Bay and the FL Keys regions. Not only was there a lack of relationship between sediment grain size and C_{org} content in Eastern FL Bay, the high C_{org} content predicted by the high average mud content was absent. Eastern FL Bay is phosphorus limited, restricting autochthonous production and overall C_{org} input for the region (Fourqurean et al., 1992; Armitage and Fourqurean, 2016). The fine sediments of the region have high

surface areas suitable for C_{org} sorption, though general lack of OM in the region causes C_{org} concentration to be low regardless of particle surface area and local hydrology. Western Florida Bay has autochthonous seagrass production and allochthonous inputs from the nearby ecosystems. Waters in the region in this region are shallow and embedded in a matrix of small islands, preventing strong hydrological energy and promoting the accumulation of fine sediments. The combination of factors results in high soil C_{org} content. The Florida Keys region varies greatly in benthic ecology and sedimentology, though the lower average mud content and larger grain size in the region may explain the lower C_{org} content lower compared to Western Florida Bay. The influence of these two C_{org} drivers (C_{org} delivery and sediment surface area) have been discussed previously for continental shelf sediments (Mayer, 1994a). Regardless of the study region, all of our study sites have at least 0.7 % C_{org} by weight, even in nutrient limited regions. C_{org} delivery may be low in some regions but a low background C_{org} concentration is expected, particularly in carbonate sands, where C_{org} can be incorporated into the mineral matrix (Mayer, 1994a).

Popular methods of of OM determination and C_{org} content rely on LOI and thermo-oxidation processes, typically at 500 °C or 550 °C for organic determination (Dean, 1974; Kristensen and Andersen, 1987; Wang et al., 2010; Fourqurean et al., 2012b; Howard et al., 2014). Additional information regarding the lability of soil C_{org} can be produced using the similar procedures over a range of oxidation temperatures. Thermal stability of biogenic material has been used as a proxy for its propensity for decomposition, where higher oxidation temperature correspond to a higher recalcitrance (Persson et al., 1986; Kristensen, 1990; Capel et al., 2006; Trevathan-Tackett et al., 2017). In our study, soil samples subjected to the stepwise thermo-oxidation process lost weight at every temperature step from 65 to 600 °C. While the loss-on-ignition determination method is used to partition organic from inorganic material, loss of volatile salts, structural water of clay minerals and/or metal oxides can also confound LOI data as they is also lost

during thermo-oxidative processes (Heiri et al., 2001) resulting in continued weight loss at temperatures lower and higher than the assumed oxidation temperature for organics (Kristensen, 1990; Wang et al., 2010).

Known discrepancies between LOI and C_{org} content (Wang et al., 2012), along with a primary interest in the C_{org} portion of OM (Fourqurean et al., 2012a) have led the LOI methodology to be coupled with elemental analysis to analysis C loss rather than weight loss alone (i.e., Fourqurean et al. 2012b; Campbell et al. 2014). Here, our stepwise thermo-oxidation process additionally yielded C loss. There was a tight correlation between temperature specific weight loss and computed C loss at all temperature besides 160 °C (Figure 5.6; $R^2 > 0.88$), suggesting that weight loss at 160 °C can be attributed to water rather than OM oxidation. Temperature steps at 300 °C and 400 °C had linear models with the highest slopes (0.48 and 0.41, respectively) suggesting that weight loss at these temperatures also included highest fractions of C. These are the temperatures at which C-rich organic matter (i.e., cellulose) oxidizes (Kristensen, 1990). Higher temperatures (500 and 550 °C) have lower but significant slopes, suggesting that C is still loss but less of the total weight can be attributed to C-rich organics.

Soil C content decreases from 180 to 600 °C and significant losses of C were measured at every temperature step (Figure 5.7). This may be interpreted in two ways: C_{org} oxidation started below 200 °C and continued to at least 600 °C. If this is the case, oxidation methods used to determine C_{org} using 500 °C or 550 °C may be underestimating C_{org} content. Assuming that all C lost during each oxidation steps is 1) complete and 2) from the oxidation of C_{org} , we missed an average of 9.8 % of C_{org} using the 550 °C temperature delineation. When soil carbon inventories use C_{org} content to extrapolate to regional C_{org} stocks, these discrepancies in C_{org} content related to temperature may heavily influence C inventories and comparisons. Alternatively, continued C loss across all temperature steps may be due a transition of C_{org} oxidation to C_{inorg} oxidation at temperatures above

500 °C. Though this is a possibility, our methods cannot differentiate C origin, and previous literature suggests that C_{inorg} begins to oxidize at temperatures between 600 and 950 °C (Heiri et al., 2001; Wang et al., 2010). There were two peaks of carbon loss (300 and 500 °C), consistent with previous reports of a bimodal combustion patterns for seagrass tissue (Trevathan-Tackett et al., 2017) and biogenic material in marine sediments (Kristensen, 1990). We interpreted this pattern as two primary OM oxidation points with the lower peak corresponding to low molecular weight volatile compounds and relatively more labile macromolecules. The second peak was interpreted as the oxidation point of char and polyphenolic compounds like lignin, humic substances and kerogens that are thermally more stable. These compounds are also considered more resistant to microbial driven decomposition (Burdige, 2005; Arndt et al., 2013).

The Recalcitrance Index compares relatively more labile and recalcitrant fractions by comparing C_{org} loss starting at the second combustion peak (including 500 and 550 °C) to the total C loss. The scale ranges from 0 – 1, where higher values denote higher proportions of recalcitrant C_{org} material and lower values suggest a relatively higher amounts of labile C_{org} . There was a negative correlation between mud content and RI values (Figure 5.8); linear regression, $p < 0.05$), suggesting that soils with a higher mud content and lower average grain size have a relatively higher fraction of labile C_{org} . Chapter 3 suggests that burial depresses OM breakdown in muddy sites because of decreased microbial decomposition. That could explain why such high proportions of labile, microbially accessible C_{org} remain at muddy sites. There is also a negative relationship between RI values and total soil C_{org} content, though the correlation is not linear (Figure 5.9). There is a non-obligatory relationship between the two variables, where high C_{org} is likely to have proportionally more labile C_{org} , but low C_{org} sites contain a large range in recalcitrance. Sites with high C_{org} content are likely to contain C_{org} that is vulnerable to remineralization during environmental change or over time. Low C_{org} may be similar, though higher RI

values at some sites suggest that soil C_{org} may be resistant to microbial decomposition regardless of environmental setting. There is also a minimum RI value of ~ 0.3 , suggesting that approximately 30 % of C_{org} is always in the “higher recalcitrance” category. This may be related to a background level of recalcitrant C_{org} associated with mineral surface area and the carbonate matrix (Mayer, 1994b). Seagrass soil C_{org} content varies 18-fold between sample sites, though the differences in C_{org} recalcitrance between sites suggests an even greater variance in potential CO_2 produced during remineralization.

Seagrass and soil $\delta^{13}C$

Seagrass tissue $\delta^{13}C$ values reported here average -9.4 ± 0.2 , comparable to previously reported values for the region (Campbell and Fourqurean, 2009). The combination of an enzymatic discrimination against ^{13}C during photosynthesis and a limited CO_2 availability for seagrass photosynthesis causes tissue $\delta^{13}C$ to be less negative than terrestrial plants and more negative than the CO_2/DIC pool (Raven et al., 2002). Seagrass $\delta^{13}C$ values are typically distinct from other sources of OM, thus their relative contribution to higher trophic levels and OM pools can be determined (Fry et al., 1977; Gacia et al., 2002). Kennedy et al. (Kennedy et al., 2010) concluded that approximately 50 % of the surface soil C_{org} was derived from seagrass, with higher seagrass $\delta^{13}C$ corresponding to higher soil $\delta^{13}C_{org}$. Correlations between seagrass $\delta^{13}C$ and soil $\delta^{13}C$ have been shown globally (Kennedy et al., 2010) and regionally (Howard et al., 2017) but we found no such correlation at the spatial scale of this study (Figure 5.3; linear regression, $p > 0.05$). The lack of correlation could be due to a high homogenization and mixing of sediments in the region; this was the suggested mechanism for similar soil $\delta^{13}C$ values within plots of differing macrophytes (Howard et al., 2016), though is questionable given the wide geographic range of our study sites. Seagrasses in south Florida show a strong seasonal variation in $\delta^{13}C$ values (Campbell and Fourqurean, 2009); perhaps our seagrass values (averaged across seasons)

do not represent the integrated C_{org} of soils. The lack of correlation between seagrass and $\delta^{13}\text{C}$ – soil C_{org} could also be related to variance in non-seagrass inputs (Oreska et al., 2017) or $\delta^{13}\text{C}$ values of particular OM compounds that could preferentially be preserved in soils (Benner et al., 1984).

There was a positive correlation between average seagrass tissue $\delta^{13}\text{C}$ and soil $\delta^{13}\text{C}_{\text{inorg}}$ (Figure 5.10). This relationship has been noted previously with seagrasses and carbonate shell material (Lin et al., 1991), and may be explained by the common DIC source for both calcification and photosynthesis. For example, nearshore waters have $\delta^{13}\text{C}$ values for DIC that is more negative than elsewhere due the respiratory CO_2 derived from mangrove and other terrestrial OM. The relatively ^{13}C -replete DIC nearshore will translate to tissues that are ^{13}C -replete (Hemminga et al., 1994). Similar mechanisms would explain variance in C_{inorg} and solid phase carbonates (Lin et al., 1991). This correlation may also be interpreted as temporally overlapping C_{org} and C_{inorg} processes, where the DIC pool was shared.

There was a correlation between soil C_{org} content and soil $\delta^{13}\text{C}$ for both C_{org} and C_{inorg} fractions (Figure 5.11; linear regression, $p < 0.05$). High soil C_{org} corresponds to a higher proportion of labile C_{org} (Figure 5.9, Figure 5.10). In Chapter 3, high C_{org} content of some of these sites is due, in part, to the fine, muddy sediments that reduce OM breakdown. Fourqurean and Schrlau (Fourqurean and Schrlau, 2003) found that seagrass significantly and steadily declines in $\delta^{13}\text{C}$ during decomposition. Benner et al (Benner et al., 1987) found differences in the $\delta^{13}\text{C}$ values of polysaccharides and lignin across various plants, suggesting that shifts in the isotopic composition of bulk OM may occur as particular OM fractions are preferentially decomposed. The variance in soil $\delta^{13}\text{C}$ could correspond to the intensity of decomposition and the relative recalcitrance of the remaining OM fractions. Alternatively, if a simpler carbon mixing model is considered, higher $\delta^{13}\text{C}$ values could represent a higher influence of seagrass C to soil stocks. The comparison with soil C_{org}

content could suggest that sites with high seagrass input may be responsible for increased soil C_{org} .

Soil C_{org} content also correlated to $\delta^{13}\text{C}$ of the soil C_{inorg} fraction (Figure 5.11). The correlation is negative and it is importance to note that values converge with $\delta^{13}\text{C}$ of soil C_{org} as C_{org} increases. We interpret this as an intensified CO_2 buffering by carbonates at sites where C_{org} content high. As soil C_{org} is remineralized, the porewater pH decreases in concert with increases in pCO_2 . The acidic conditions can then dissolve buried carbonates, buffering CO_2 production and pH changes, while increasing alkalinity (Walter et al., 2007; Burdige et al., 2008). Addition to the accumulation and export of alkalinity and an overall reduction of pCO_2 , some carbonate recrystallization may occur, forming more stable, sometimes larger carbonate structures (Burdige et al., 2010). In terms of $\delta^{13}\text{C}$ values, the CO_2 produced from remineralized C_{org} will have low $\delta^{13}\text{C}$ values that reflect the C source. As carbonate dissolve, they introduced ^{13}C enriched DIC into the porewater, altering the porewater $\delta^{13}\text{C}$ initially influenced C_{org} remineralization (Hu and Burdige, 2007). The re-precipitation of carbonate will fix DIC from remineralized OM, causing newly formed carbonates to have more negative $\delta^{13}\text{C}$ values than before. We understand decreased $\delta^{13}\text{C}$ values of soil C_{inorg} to be evidence of carbonate dissolution and re-precipitation due to increased metabolic processes. Sites with high C_{org} content have typically finer sediments and more seagrasses (Chapter 3). Carbonate dissolution and re-precipitation related to porewater processes have been suggested to be enhanced when grain size is small and seagrasses can introduce O_2 and labile exudates into the porewater (Hu and Burdige, 2007; Burdige et al., 2010).

Conclusions

Inventories of Blue Carbon soil stocks are often equated with amount of CO_2 historically sequestered. More important to Blue Carbon strategies is the CO_2 emissions avoided

when soil C_{org} stocks are preserved through habitat management. The environmental context of soil C_{org} has been linked to its likelihood of remineralization and efflux as CO_2 (Lovelock et al., 2017b) and has been shown to alter OM breakdown rates in particular environments (Trevathan-Tackett et al. 2018; Chapter 3). Here we show that differences in C_{org} vulnerability are linked to molecular characteristics inherent to OM. The environmental context provided by seagrasses may help preserve C_{org} stocks in some areas, though large fractions of C_{org} stocks in may be too recalcitrant to be oxidized, regardless of changes in the surrounding environment. The relative contribution of labile C_{org} varies with mud and total C_{org} content, suggesting that sediments with fine grain sizes have more C_{org} as well as relatively more labile C_{org} to their sandy counterparts.

Calcification and carbonate dissolution have been acknowledged for their antagonistic effect on CO_2 sequestration and storage via primary production (Howard et al., 2017; Macreadie et al., 2017), but there is concern whether the fate of CO_2 flux and the temporal scales related to C_{inorg} processes are relevant to Blue Carbon processes. Here we suggest that seagrass and carbonate production are both influenced by contemporary, spatially explicit DIC. We also suggest that C_{org} remineralization is buffered by carbonate processes, and these processes have a more marked effect in areas with high C_{org} content. These conclusions, along with the variability in soil C_{org} recalcitrance complicates our understanding of Blue Carbon stored in seagrass meadows and its likelihood to be returned to the atmosphere as CO_2 upon environmental change. Given these conclusions, managers and Blue Carbon strategists may want to reconsider how sites are selected and managed for carbon conservation, taking into account the likelihood of remineralization and local C_{inorg} processes.

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Work Cited

- Armitage, A. R. and Fourqurean, J. W. (2016). Carbon storage in seagrass soils: long-term nutrient history exceeds the effects of near-term nutrient enrichment. *Biogeosciences*, 13(1):313–321.
- Arndt, S., Jørgensen, B. B., LaRowe, D. E., Middelburg, J., Pancost, R. D., and Regnier, P. (2013). Quantifying the degradation of organic matter in marine sediments: A review and synthesis. *Earth-Science Reviews*, 123:53–86.
- Benner, R., Fogel, M. L., Sprague, E. K., and Hodson, R. E. (1987). Depletion of ^{13}C in lignin and its implications for stable carbon isotope studies. *Nature*, 329(6141):708–710.
- Benner, R., Maccubbin, A. E., and Hodson, R. E. (1984). Anaerobic biodegradation of the lignin and polysaccharide components of lignocellulose and synthetic lignin by sediment microflora. *Applied and Environmental Microbiology*, 47(5):998–1004.
- Bosence, D. (1989a). Biogenic carbonate production in Florida Bay. *Bulletin of Marine Science*, 44(1):419–433.
- Bosence, D. (1989b). Surface sublittoral sediments of Florida Bay. *Bulletin of Marine Science*, 44(1):434–453.
- Burdige, D. J. (2005). Burial of terrestrial organic matter in marine sediments: A re-assessment. *Global Biogeochemical Cycles*, 19(4):GB4011.

- Burdige, D. J. (2007). Preservation of Organic Matter in Marine Sediments: Controls, Mechanisms, and an Imbalance in Sediment Organic Carbon Budgets? *Chemical Reviews*, 107(2):467–485.
- Burdige, D. J., Hu, X., and Zimmerman, R. C. (2010). The widespread occurrence of coupled carbonate dissolution/precipitation in surface sediments on the Bahamas Bank. *American Journal of Science*, 310(6):492–521.
- Burdige, D. J., Zimmerman, R. C., and Hu, X. (2008). Rates of carbonate dissolution in permeable sediments estimated from pore-water profiles: The role of seagrasses. *Limnology and Oceanography*, 53(2):549.
- Campbell, J. E. and Fourqurean, J. W. (2009). Interspecific variation in the elemental and stable isotope content of seagrasses in South Florida. *Marine Ecology Progress Series*, 387:109–123.
- Campbell, J. E., Lacey, E. A., Decker, R. A., Crooks, S., and Fourqurean, J. W. (2014). Carbon Storage in Seagrass Beds of Abu Dhabi, United Arab Emirates. *Estuaries and Coasts*, 38(1):242–251.
- Capel, E. L., de la Rosa Arranz, J. M., González-Vila, F. J., González-Perez, J. A., and Manning, D. A. (2006). Elucidation of different forms of organic carbon in marine sediments from the Atlantic coast of Spain using thermal analysis coupled to isotope ratio and quadrupole mass spectrometry. *Organic Geochemistry*, 37(12):1983–1994.
- Dahl, M., Deyanova, D., Gütschow, S., Asplund, M. E., Lyimo, L. D., Karamfilov, V., Santos, R., Björk, M., and Gullström, M. (2016). Sediment Properties as Important Predictors of Carbon Storage in *Zostera marina* Meadows: A Comparison of Four European Areas. *PLoS ONE*, 11(12):e0167493.
- Dean, Jr, W. E. (1974). Determination of carbonate and organic matter in calcareous sediments and sedimentary rocks by loss on ignition: comparison with other methods. *Journal of Sedimentary Research*, 44(1):242–248.
- Duarte, C. M. (2017). Reviews and syntheses: Hidden forests, the role of vegetated coastal habitats in the ocean carbon budget. *Biogeosciences*, 14(2):301.
- Duarte, C. M., Marbà, N., Gacia, E., Fourqurean, J. W., Beggins, J., Barrón, C., and Apostolaki, E. T. (2010). Seagrass community metabolism: Assessing the carbon sink capacity of seagrass meadows. *Global Biogeochemical Cycles*, 24(4):GB4032.
- Duarte, C. M., Merino, M., and Gallegos, M. (1995). Evidence of iron deficiency in seagrasses growing above carbonate sediments. *Limnology and Oceanography*, 40(6):1153–1158.
- Ellison, G. N. and Gotelli, N. J. (2004). A primer of ecological statistics. *Sinauer, Sunderland, Massachusetts, USA*.
- Enriquez, S., Duarte, C. M., and Sand-Jensen, K. (1993). Patterns in decomposition rates among photosynthetic organisms: the importance of detritus C:N:P content. *Oecologia*, 94(4):457–471.

- Enríquez, S. and Schubert, N. (2014). Direct contribution of the seagrass *Thalassia testudinum* to lime mud production. *Nature communications*, 5:3835.
- Erfteimeijer, P. and Koch, E. W. (2001). Sediment geology methods for seagrass habitat. In *Global seagrass research methods*, pages 345–367. Elsevier Science.
- Folk, R. L. (1980). *Petrology of sedimentary rocks*. Hemphill Publishing Company.
- Fourqurean, J. W., Boyer, J. N., Durako, M. J., Hefty, L. N., and Peterson, B. J. (2003). Forecasting responses of seagrass distributions to changing water quality using monitoring data. *Ecological Applications*, 13(2):474–489.
- Fourqurean, J. W., Duarte, C. M., Kennedy, H., Marbà, N., Holmer, M., Mateo, M. A., Apostolaki, E. T., Kendrick, G. A., Krause-Jensen, D., McGlathery, K. J., and Serrano, O. (2012a). Seagrass ecosystems as a globally significant carbon stock. *Nature Geoscience*, 5(7):505–509.
- Fourqurean, J. W., Durako, M. J., Hall, M. O., and Hefty, L. N. (2002). Seagrass distribution in south florida: a multi-agency coordinated monitoring program. CRC Press.
- Fourqurean, J. W., Kendrick, G. A., Collins, L. S., Chambers, R. M., and Vanderklift, M. A. (2012b). Carbon, nitrogen and phosphorus storage in subtropical seagrass meadows: examples from Florida Bay and Shark Bay. *Marine and Freshwater Research*, 63(11):967.
- Fourqurean, J. W., Powell, G. V., Kenworthy, W. J., and Zieman, J. C. (1995). The effects of long-term manipulation of nutrient supply on competition between the seagrasses *Thalassia testudinum* and *Halodule wrightii* in Florida Bay. *Oikos*, 72(3):349–358.
- Fourqurean, J. W. and Schrlau, J. E. (2003). Changes in nutrient content and stable isotope ratios of C and N during decomposition of seagrasses and mangrove leaves along a nutrient availability gradient in Florida Bay, USA. *Chemistry and Ecology*, 19(5):373–390.
- Fourqurean, J. W., Zieman, J., and Powell, G. V. (1992). Phosphorus limitation of primary production in Florida Bay: Evidence from C:N:P ratios of the dominant seagrass *Thalassia testudinum*. *Limnology and Oceanography*, 37(1):162–171.
- Frankignoulle, M., Pichon, M., and Gattuso, J.-P. (1995). Aquatic calcification as a source of carbon dioxide. In *Carbon sequestration in the biosphere*, pages 265–271. Springer.
- Frankovich, T. A. and Zieman, J. C. (1994). Total epiphyte and epiphytic carbonate production on *Thalassia testudinum* across Florida Bay. *Bulletin of Marine Science*, 54(3):679–695.
- Fry, B., Scalan, R. S., and Parker, P. L. (1977). Stable carbon isotope evidence for two sources of organic matter in coastal sediments: seagrasses and plankton. *Geochimica et Cosmochimica Acta*, 41:1875–1877.
- Gacia, E., Duarte, C. M., and Middelburg, J. (2002). Carbon and nutrient deposition in a Mediterranean seagrass (*Posidonia oceanica*) meadow. *Limnology and Oceanography*, 47(1):23–32.

- Green, E. P. and Short, F. (2003). *World atlas of seagrasses*. Univ of California Press.
- Guenet, B., Danger, M., Abbadie, L., and Lacroix, G. (2010). Priming effect: bridging the gap between terrestrial and aquatic ecology. *Ecology*, 91(10):2850–2861.
- Gullström, M., Lyimo, L. D., Dahl, M., Samuelsson, G. S., Eggertsen, M., Anderberg, E., Rasmusson, L. M., Linderholm, H. W., Knudby, A., Bandeira, S., Nordlund, L. M., and Björk, M. (2017). Blue Carbon Storage in Tropical Seagrass Meadows Relates to Carbonate Stock Dynamics, Plant– Sediment Processes, and Landscape Context: Insights from the Western Indian Ocean. *Ecosystems*, pages 1–16.
- Heiri, O., Lotter, A. F., and Lemcke, G. (2001). Loss on ignition as a method for estimating organic and carbonate content in sediments: reproducibility and comparability of results. *Journal of paleolimnology*, 25(1):101–110.
- Hemminga, M., Slim, F., Kazungu, J., Ganssen, G., Nieuwenhuize, J., and Kruyt, N. (1994). Carbon outwelling from a mangrove forest with adjacent seagrass beds and coral reefs (Gazi Bay, Kenya). *Marine Ecology Progress Series*, pages 291–301.
- Hendriks, I. E., Olsen, Y. S., Ramajo, L., Basso, L., Steckbauer, A., Moore, T. S., Howard, J., and Duarte, C. M. (2014). Photosynthetic activity buffers ocean acidification in seagrass meadows. *Biogeosciences*, 11(2):333–346.
- Hiraishi, T., Krug, T., Watanabe, K., Srivastava, N., Baasansuren, J., Fukuda, M., and Troxler, T. (2014). 2013 Supplement to the 2006 IPCC guidelines for national greenhouse gas inventories: wetlands . IPCC, Switzerland.
- Howard, J., Hoyt, S., Isensee, K., Telszewski, M., Pidgeon, E., et al. (2014). *Coastal blue carbon: methods for assessing carbon stocks and emissions factors in mangroves, tidal salt marshes, and seagrasses*. Conservation International, Intergovernmental Oceanographic Commission of UNESCO, International Union for Conservation of Nature, Arlington, Va, USA.
- Howard, J. L., Creed, J. C., Aguiar, M. V. P., and Fouquerean, J. W. (2017). CO₂ released by carbonate sediment production in some coastal areas may offset the benefits of seagrass “Blue Carbon” storage. *Limnology and Oceanography*, 17:3655.
- Howard, J. L., Perez, A., Lopes, C. C., and Fourqurean, J. W. (2016). Fertilization Changes Seagrass Community Structure but not Blue Carbon Storage: Results from a 30-Year Field Experiment. *Estuaries and Coasts*, 39(5):1422–1434.
- Hu, X. and Burdige, D. J. (2007). Enriched stable carbon isotopes in the pore waters of carbonate sediments dominated by seagrasses: Evidence for coupled carbonate dissolution and reprecipitation. *Geochimica et Cosmochimica Acta*, 71(1):129–144.
- Keil, R. G., Tsamakidis, E., Fuh, C. B., Giddings, J. C., and Hedges, J. I. (1994). Mineralogical and textural controls on the organic composition of coastal marine sediments: hydrodynamic separation using SPLIT-fractionation. *Geochimica et Cosmochimica Acta*, 58(2):879–893.
- Kennedy, H., Beggins, J., Duarte, C. M., Fourqurean, J. W., Holmer, M., Marbà, N., and Middelburg, J. J. (2010). Seagrass sediments as a global carbon sink: Isotopic constraints. *Global Biogeochemical Cycles*, 24(4):GB4026.

- Kristensen, E. (1990). Characterization of biogenic organic matter by stepwise thermogravimetry (STG). *Biogeochemistry*, 9(2):135–159.
- Kristensen, E. and Andersen, F. Ø. (1987). Determination of organic carbon in marine sediments: a comparison of two CHN-analyzer methods. *Journal of Experimental Marine Biology and Ecology*, 109(1):15–23.
- Ku, T., Walter, L. M., Coleman, M. L., Blake, R. E., and Martini, A. M. (1999). Coupling between sulfur recycling and syndepositional carbonate dissolution: evidence from oxygen and sulfur isotope composition of pore water sulfate, South Florida Platform, USA. *Geochimica et Cosmochimica Acta*, 63(17):2529–2546.
- Lin, G., Banks, T., and Sternberg, L. d. S. L. O. (1991). Variation in $\delta^{13}\text{C}$ values for the seagrass *Thalassia testudinum* and its relations to mangrove carbon. *Aquatic Botany*, 40(4):333–341.
- Lopez, N., Duarte, C. M., Vallespinos, F., Romero, J., and Alcoverro, T. (1998). The effect of nutrient additions on bacterial activity in seagrass (*Posidonia oceanica*) sediments. *Journal of Experimental Marine Biology and Ecology*, 224:155–166.
- Lovelock, C. E., Atwood, T., Baldock, J., Duarte, C. M., Hickey, S., Lavery, P. S., Masqué, P., Macreadie, P. I., Ricart, A. M., Serrano, O., and Steven, A. (2017a). Assessing the risk of carbon dioxide emissions from blue carbon ecosystems. *Frontiers in Ecology and the Environment*, 15(5):257–265.
- Lovelock, C. E., Fourqurean, J. W., and Morris, J. T. (2017b). Modeled CO₂ Emissions from Coastal Wetland Transitions to Other Land Uses: Tidal Marshes, Mangrove Forests, and Seagrass Beds. *Frontiers in Marine Science*, 4:143.
- Macreadie, P. I., Serrano, O., Maher, D. T., Duarte, C. M., and Beardall, J. (2017). Addressing calcium carbonate cycling in blue carbon accounting. *Limnology and Oceanography Letters*, 31:513.
- Mayer, L. M. (1994a). Relationships between mineral surfaces and organic carbon concentrations in soils and sediments. *Chemical Geology*, 114(3-4):347–363.
- Mayer, L. M. (1994b). Surface area control of organic carbon accumulation in continental shelf sediments. *Geochimica et Cosmochimica Acta*, 58(4):1271–1284.
- Mayer, L. M. (1995). Sedimentary organic matter preservation: an assessment and speculative synthesis. *Marine Chemistry*, 49(2-3):123–126.
- Mazarrasa, I., Marba, N., Lovelock, C. E., Serrano, O., Lavery, P. S., Fourqurean, J. W., Kennedy, H., Mateo, M. A., Krause-Jensen, D., and Steven, A. (2015). Seagrass meadows as a globally significant carbonate reservoir. *Biogeosciences*, 12:4993–5003.
- McLeod, E., Chmura, G. L., Bouillon, S., Salm, R., Björk, M., Duarte, C. M., Lovelock, C. E., Schlesinger, W. H., and Silliman, B. R. (2011). A blueprint for blue carbon: toward an improved understanding of the role of vegetated coastal habitats in sequestering CO₂. *Frontiers in Ecology and the Environment*, 9(10):552–560.
- Millero, F. J. (2007). The Marine Inorganic Carbon Cycle. *Chemical Reviews*, 107(2):308–341.

- Miyajima, T., Hori, M., Hamaguchi, M., Shimabukuro, H., and Yoshida, G. (2017). Geophysical constraints for organic carbon sequestration capacity of *Zostera marina* seagrass meadows and surrounding habitats. *Limnology and Oceanography*, 62(3):954–972.
- Nierop, K. G. J., Reichart, G.-J., Veld, H., and Damsté, J. S. S. (2017). The influence of oxygen exposure time on the composition of macromolecular organic matter as revealed by surface sediments on the Murray Ridge (Arabian Sea). *Geochimica et Cosmochimica Acta*, 206:40–56.
- Oreska, M. P. J., Wilkinson, G. M., McGlathery, K. J., Bost, M., and McKee, B. A. (2017). Non-seagrass carbon contributions to seagrass sediment blue carbon. *Limnology and Oceanography*, 103:29.
- Pendleton, L., Donato, D. C., Murray, B. C., Crooks, S., Jenkins, W. A., Sifleet, S., Craft, C., Fourqurean, J. W., Kauffman, J. B., Marbà, N., Megonigal, P., Pidgeon, E., Herr, D., Gordon, D., and Baldera, A. (2012). Estimating Global “Blue Carbon” Emissions from Conversion and Degradation of Vegetated Coastal Ecosystems. *PLoS ONE*, 7(9):e43542.
- Persson, J. A., Johansson, E., and Albano, C. (1986). Quantitative thermogravimetry of peat. A multivariate approach. *Analytical Chemistry*, 58(6):1173–1178.
- Raven, J. A., Johnston, A. M., Kübler, J. E., Korb, R., McInroy, S. G., Handley, L. L., Scrimgeour, C. M., Walker, D. I., Beardall, J., and Vanderklift, M. (2002). Mechanistic interpretation of carbon isotope discrimination by marine macroalgae and seagrasses. *Functional Plant Biology*, 29(3):355–378.
- Röhr, M. E., Boström, C., Canal-Vergés, P., and Holmer, M. (2016). Blue carbon stocks in Baltic Sea eelgrass (*Zostera marina*) meadows. *Biogeosciences*, 13(22):6139–6153.
- Semesi, I. S., Beer, S., and Björk, M. (2009). Seagrass photosynthesis controls rates of calcification and photosynthesis of calcareous macroalgae in a tropical seagrass meadow. *Marine Ecology Progress Series*, 382:41–48.
- Smith, S. V. (2013). *Parsing the Oceanic Calcium Carbonate Cycle: A Net Atmospheric Carbon Dioxide Source Or a Sink?* Association for the Sciences of Limnology and Oceanography.
- Stockman, K. W., Ginsburg, R. N., and Shinn, E. A. (1967). The Production of Lime Mud by Algae in South Florida. *Journal of Sedimentary Petrology*, 37(2):633–648.
- Trevathan-Tackett, S. M., Kelleway, J. J., and Macreadie, P. I. (2015). Comparison of marine macrophytes for their contributions to blue carbon sequestration. *Ecology*.
- Trevathan-Tackett, S. M., Macreadie, P. I., Sanderman, J., Baldock, J., Howes, J. M., and Ralph, P. J. (2017). A Global Assessment of the Chemical Recalcitrance of Seagrass Tissues: Implications for Long-Term Carbon Sequestration. *Frontiers in Plant Science*, 8:561.
- Trevathan-Tackett, S. M., Thomson, A. C., Ralph, P. J., and Macreadie, P. I. (2018). Fresh carbon inputs to seagrass sediments induce variable microbial priming responses. *Science of The Total Environment*, 621:663–669.

- Walter, L. M. and Burton, E. A. (1990). Dissolution of recent platform carbonate sediments in marine pore fluids. *American Journal of Science*, 290(6):601–643.
- Walter, L. M., Ku, T. C. W., Muehlenbachs, K., Patterson, W. P., and Bonnell, L. (2007). Controls on the $\delta^{13}\text{C}$ of dissolved inorganic carbon in marine pore waters: An integrated case study of isotope exchange during syndepositional recrystallization of biogenic carbonate sediments (South Florida Platform, USA). *Deep Sea Research Part II: Topical Studies in Oceanography*, 54(11-13):1163–1200.
- Wang, Q., Li, Y., and Wang, Y. (2010). Optimizing the weight loss-on-ignition methodology to quantify organic and carbonate carbon of sediments from diverse sources. *Environmental Monitoring and Assessment*, 174(1-4):241–257.
- Wang, X., Wang, J., and Zhang, J. (2012). Comparisons of three methods for organic and inorganic carbon in calcareous soils of northwestern china. *PLoS one*, 7(8):e44334.
- Yates, K. K. and Halley, R. B. (2006). Diurnal variation in rates of calcification and carbonate sediment dissolution in Florida Bay. *Estuaries and Coasts*, 29(1):24–39.
- Zieman, J., Fourqurean, J. W., and Iverson, R. L. (1989). Distribution, abundance and productivity of seagrasses and macroalgae in Florida Bay. *Bulletin of Marine Science*, 44(1):292–311.

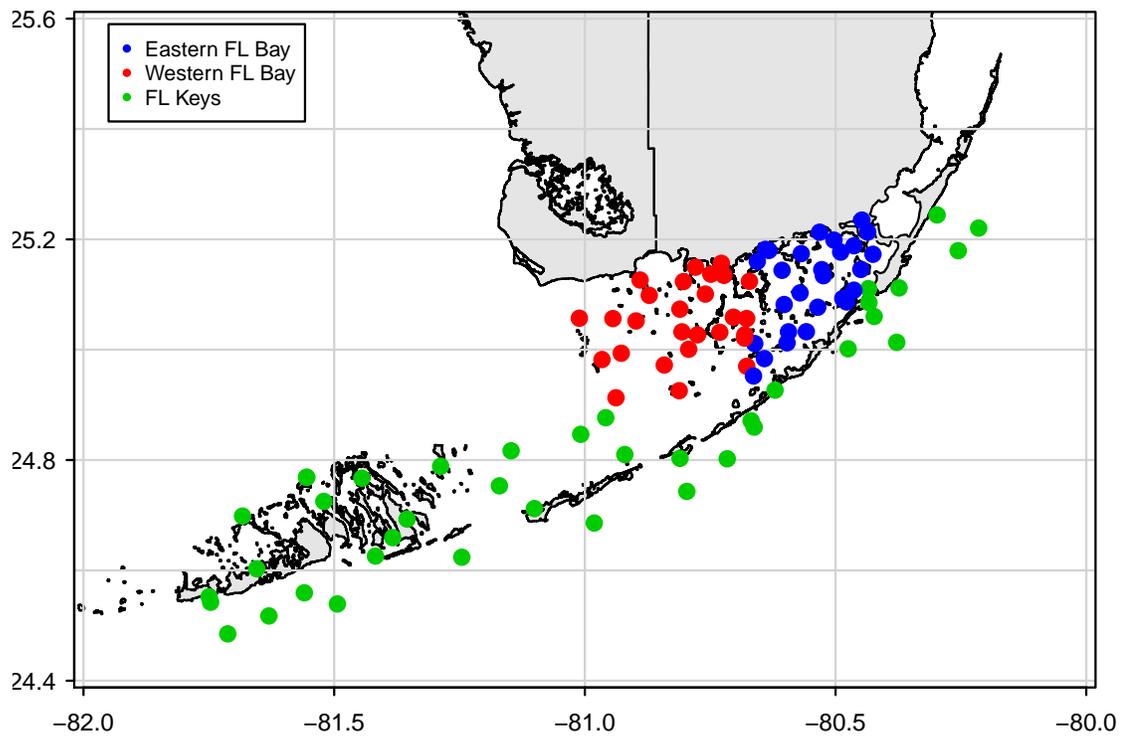


Figure 5.1: South Florida sampling sites, with sites categorized as FL Keys (within the Florida Keys National Marine Sanctuary), and Florida Bay (within the Everglades National Park) divided into eastern and western regions.

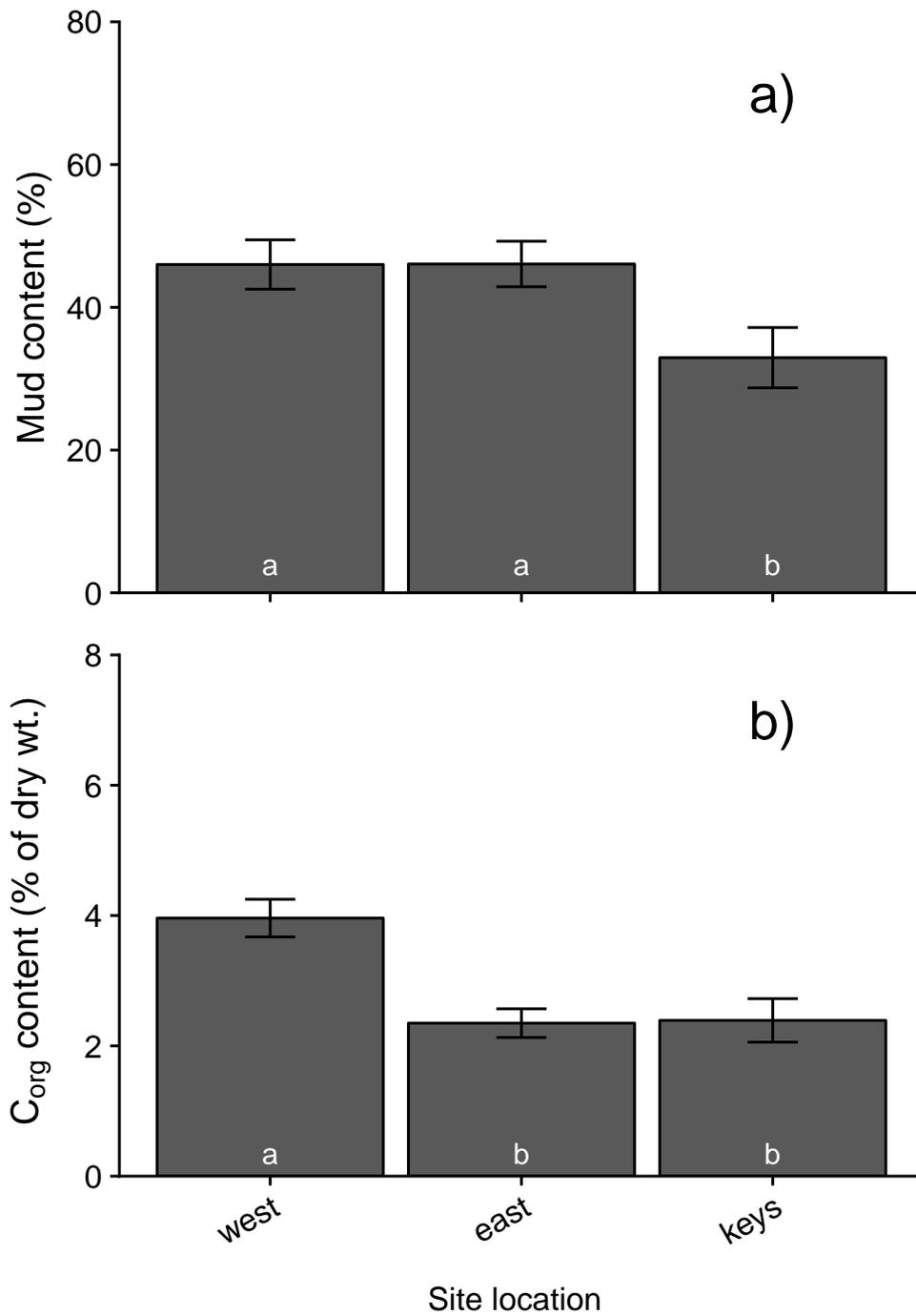


Figure 5.2: Comparison of surface soil a) mud content and b) C_{org} content between three regions sampled. Figures represent mean \pm SE with letters representing groups determined by Tukey post-hoc test.

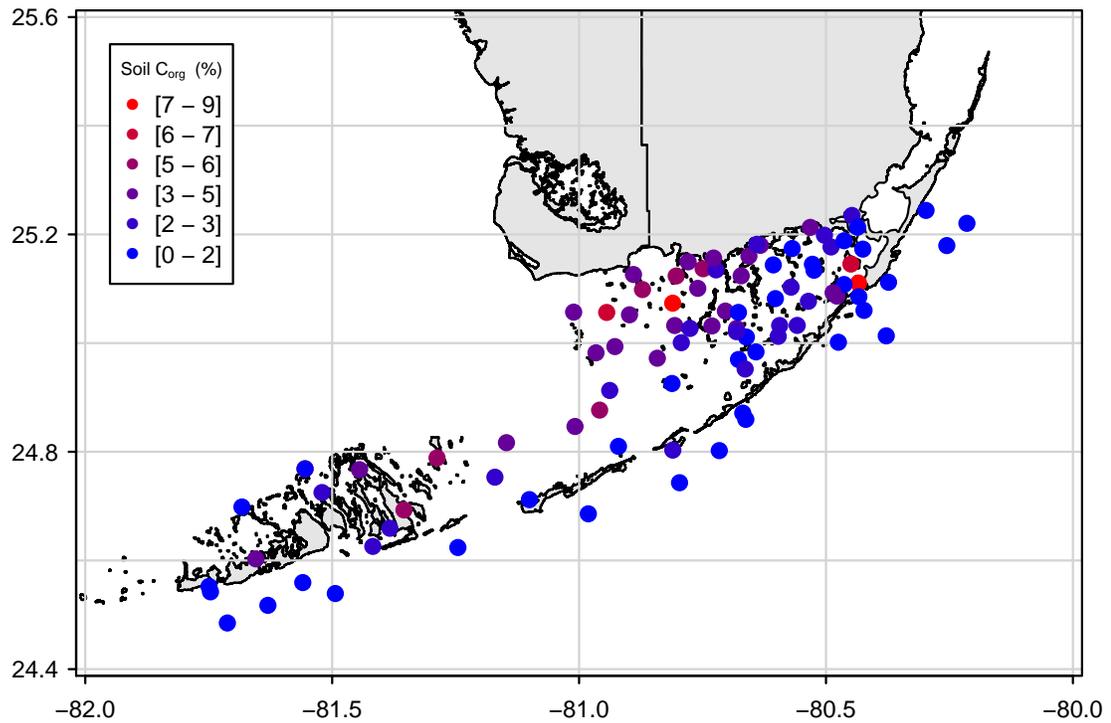


Figure 5.3: C_{org} content in surface soils across South Florida sampling sites.

| Quartile | Intercept \pm SE | Slope \pm SE | p value |
|--------------|--------------------|-----------------|---------|
| 0.05 | 2.0 ± 0.6 | -2.0 ± 1.0 | 0.06 |
| 0.5 (median) | 6.0 ± 0.5 | -7.9 ± 0.7 | 0.00 |
| 0.95 | 11.1 ± 1.8 | -13.6 ± 3.4 | 0.00 |

Table 5.1: Parameters and their standard errors and statistics for the fitted quantile regression equations between Recalcitrance Index values and soil C_{org} content represented in Figure 5.9.

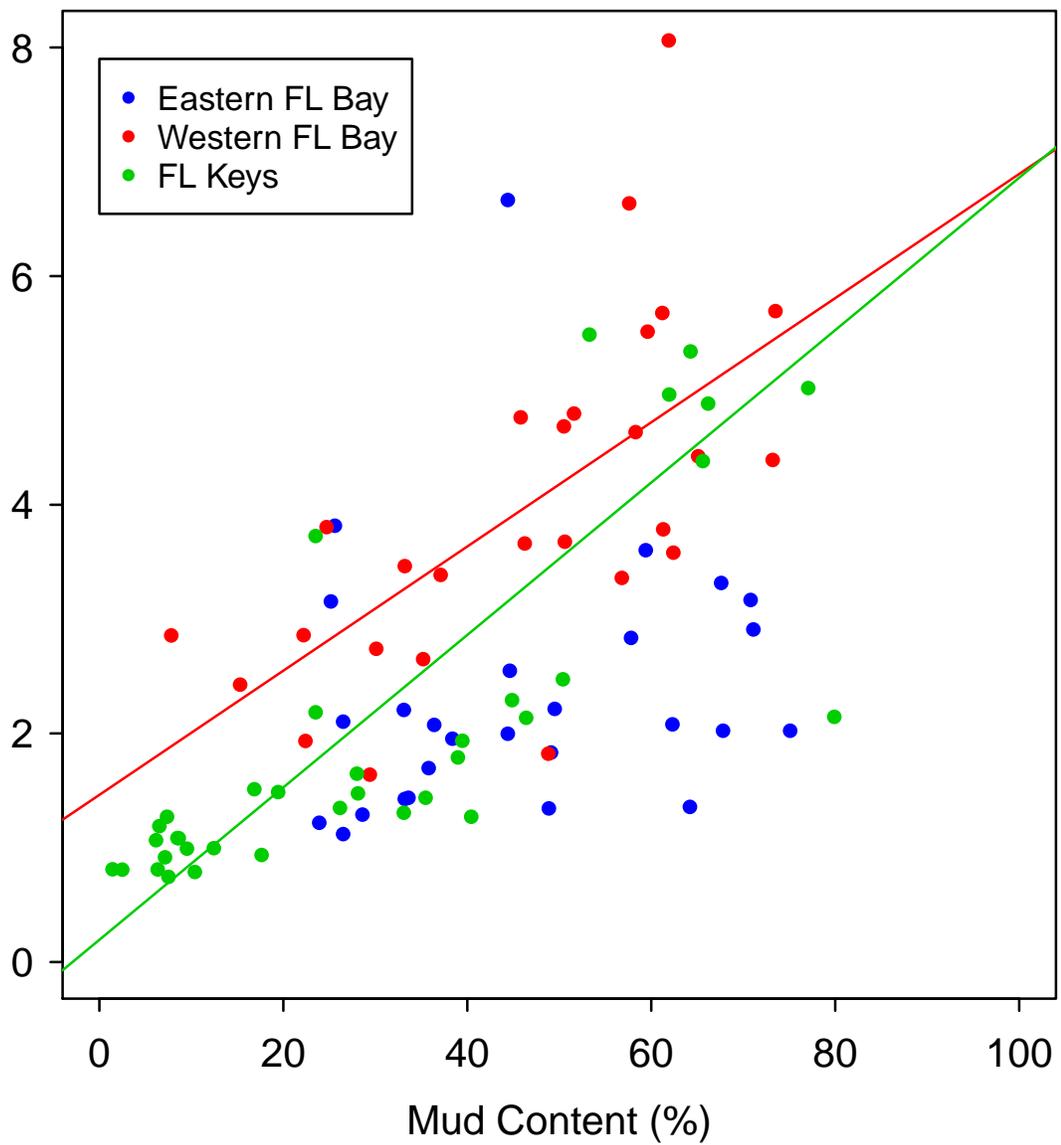


Figure 5.4: Relationship between surface soil mud content and C_{org} content for three study regions. Lines represent significant correlations (linear regression, $p < 0.05$).

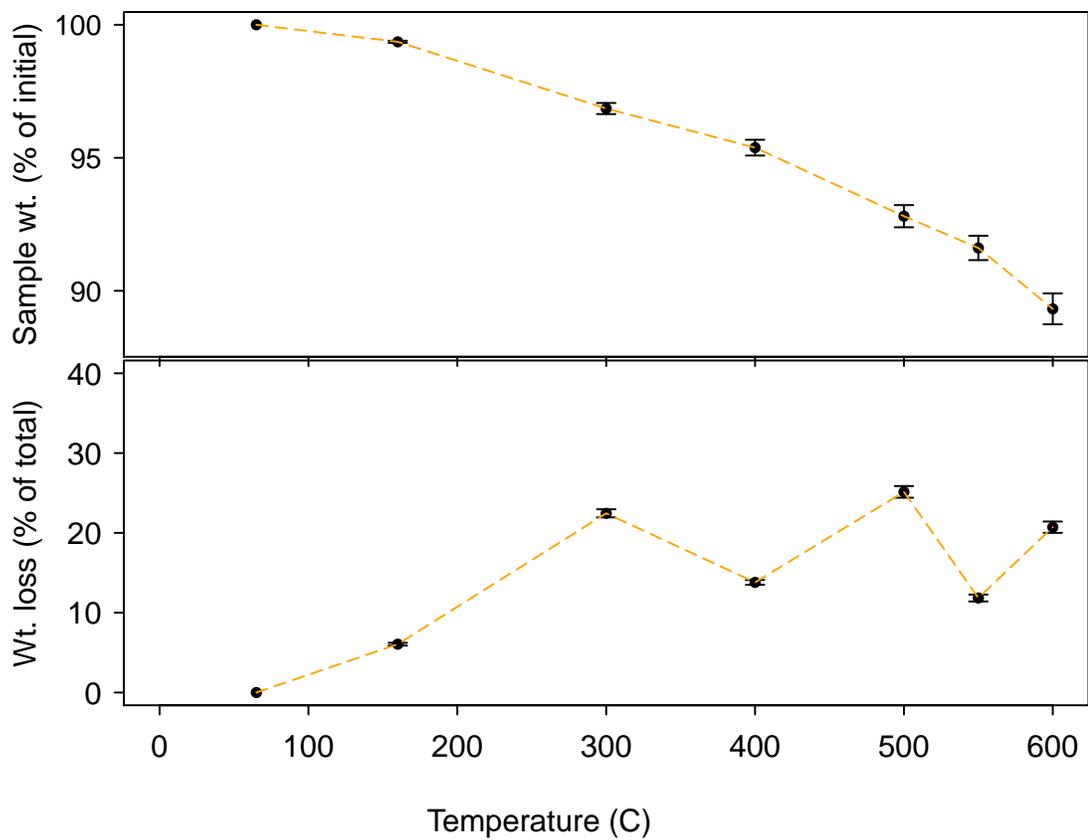


Figure 5.5: Weight loss during controlled oxidation from from 65 °C to 600 °C. Top pannel shows decrease in sample weight as temperature increases, while bottom pannel shows percent of total weight loss at each oxidation step. Data represent mean \pm SE (n = 90).

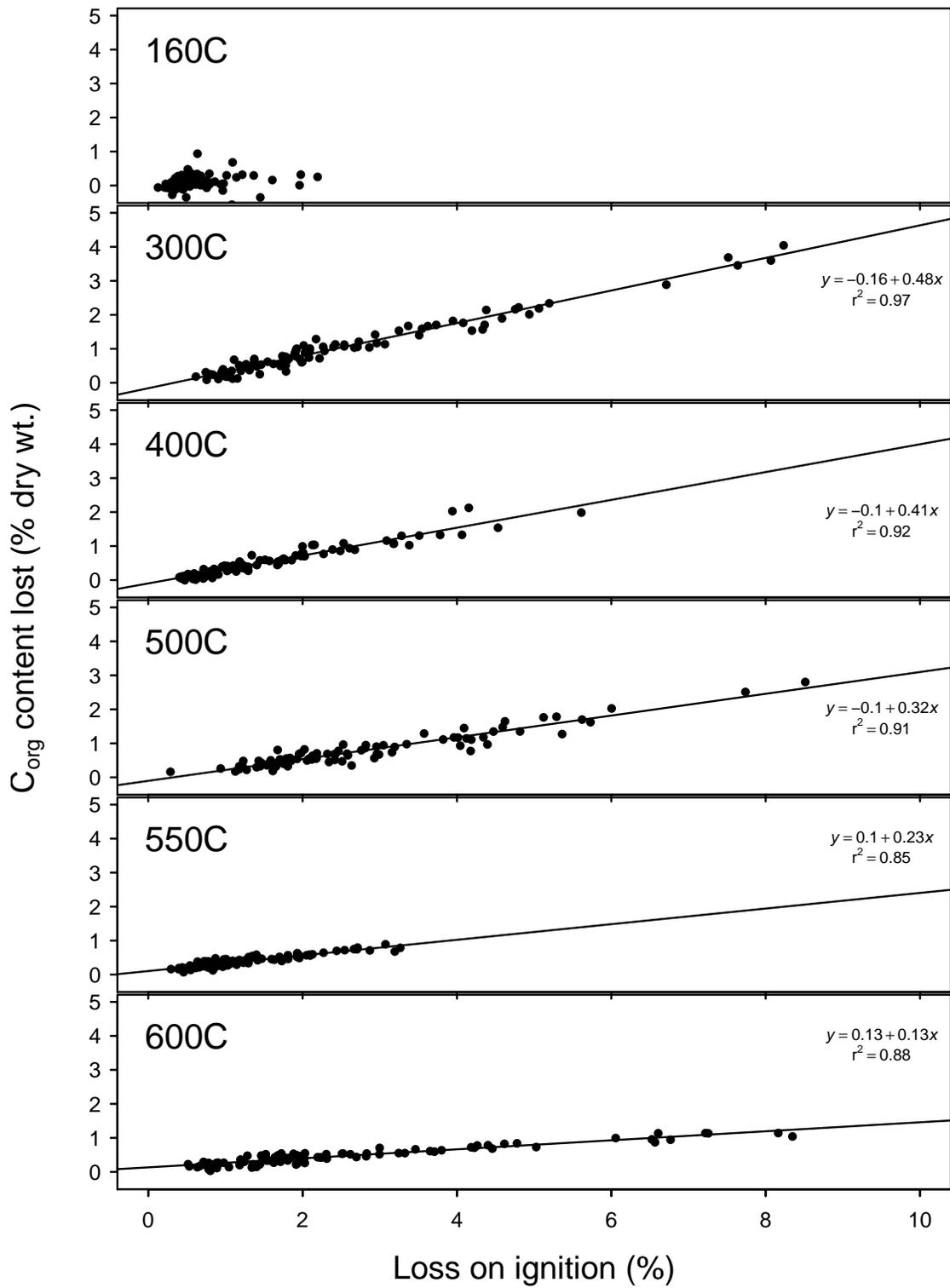


Figure 5.6: Relationship between LOI and decrease in C content for each temperature step. Lines represent significant correlations (linear regression, $p < 0.05$).

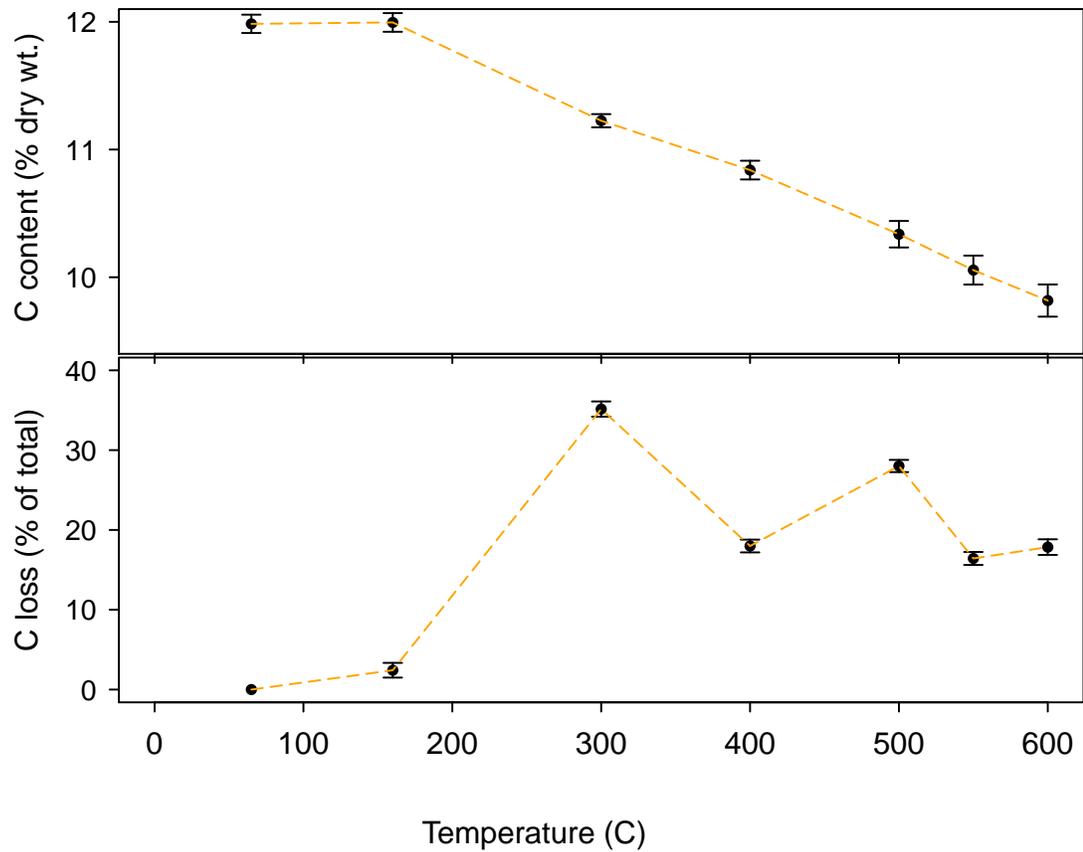


Figure 5.7: Carbon loss during controlled oxidation from from 65 °C to 600 °C. Top pannel shows decrease in sample carbon content as temperature increases, while bottom pannel shows fraction of total carbon lost as each oxidation step. Data represent mean \pm SE (n = 90).

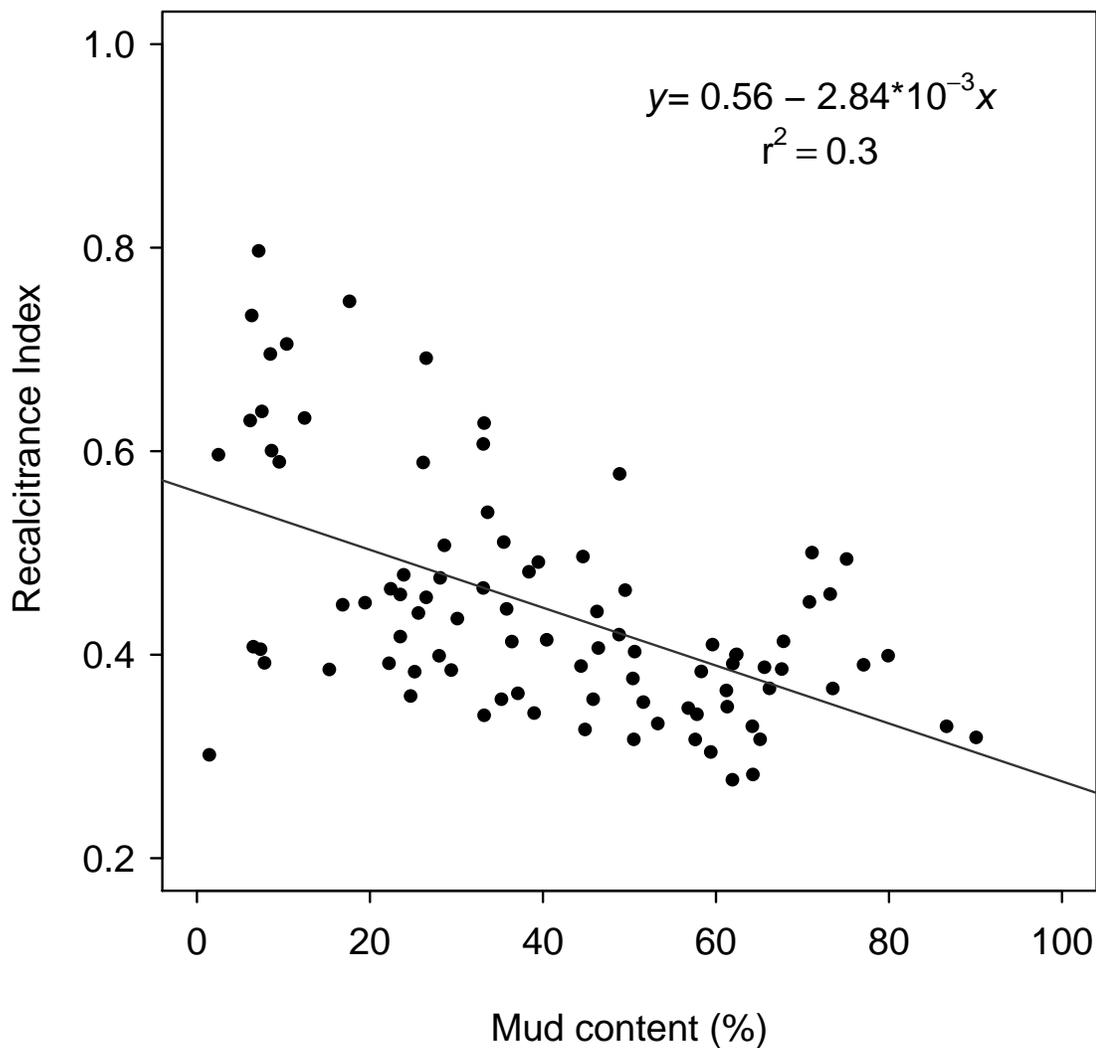


Figure 5.8: Ratio of carbon lost above 400 °C to total carbon lost from 180-550 °C (Recalcitrance Index) as function of mud content of soils. Relationship between LOI and decrease in C content for each temperature step. Lines represent significant correlations (linear regression, $p < 0.05$).

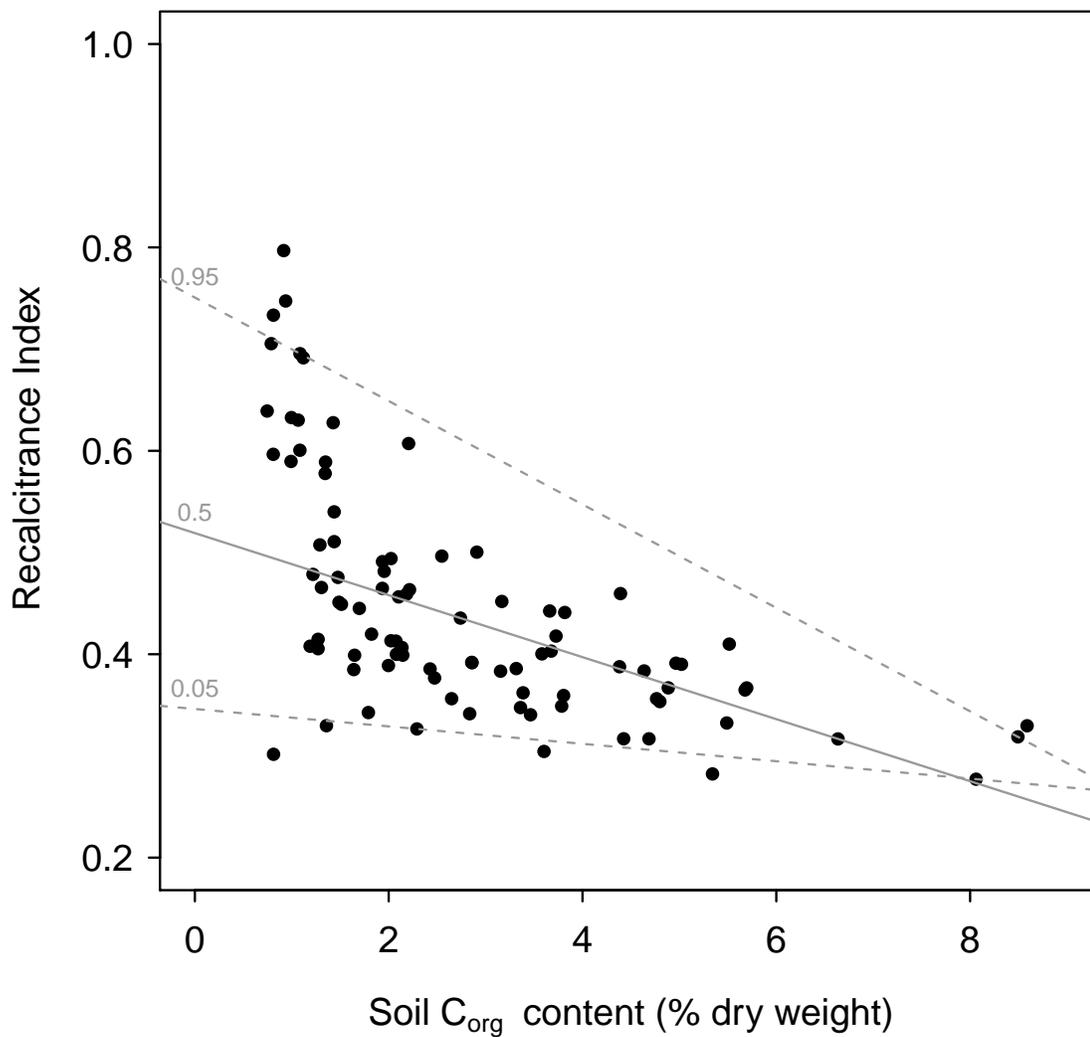


Figure 5.9: Ratio of carbon lost above 400 °C to total carbon lost from 180-550 °C (Recalcitrance Index) as function of total C_{org} content of soils. The solid line represents the fitted regression for the median or the 50 % quartile. Dashed lines represent the fitted regression for the 95 and 10 % quantiles. Statistics for the regression lines are summarized in Table 5.1.

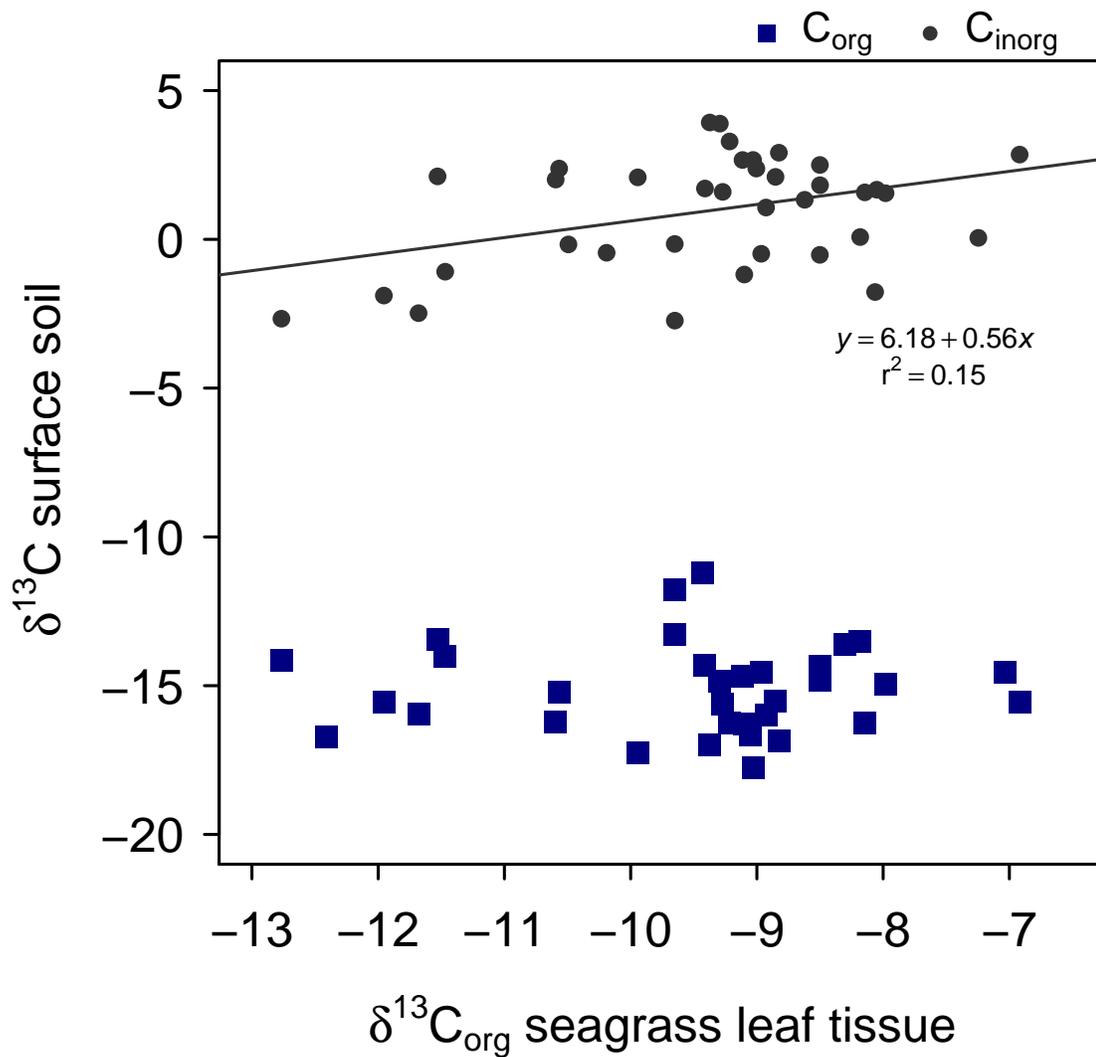


Figure 5.10: Comparison of average $\delta^{13}\text{C}$ values of seagrass tissue to $\delta^{13}\text{C}$ values of organic and inorganic fractions of underlying surface soil.

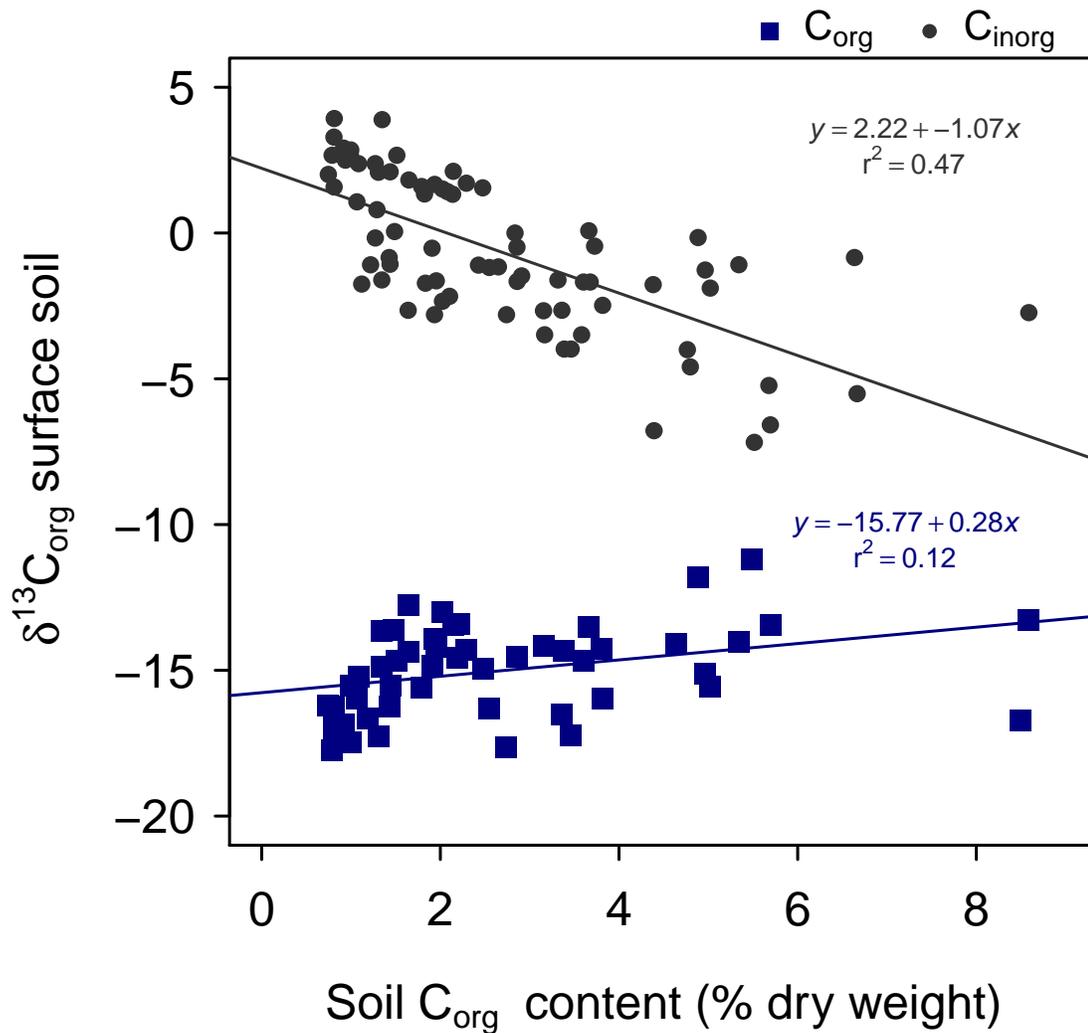


Figure 5.11: Values $\delta^{13}\text{C}$ of organic and inorganic fractions of surface soils as function of total C_{org} content.

CHAPTER 6

CONCLUSIONS

The ability of seagrasses to sequester and store carbon has been of academic interest for over two decades (Orth, 1977; Smith, 1981), though it is being reconsidered pragmatically in light of climate change mitigation efforts. High atmospheric levels of CO₂ are spurring wide and diverse changes in our environment, encouraging a reassessment of carbon stocks and sources of CO₂ to the atmosphere, particularly in natural ecosystems. Seagrasses have been acknowledged as containing globally important stocks of C_{org} (Fourqurean et al., 2012) as well as hotspots for marine productivity and burial (Duarte et al., 2005), despite covering only a narrow belt around the shoreline of the world's oceans. With high light demands and sensitivity to many impacts related to coastal development, global seagrass coverage has been declining rapidly at approximately 7 % yr⁻¹ in recent times (Waycott et al., 2009). The consequences are twofold; first, seagrass meadows are importance ecosystems that provide services like erosional control, nutrient processing, and habitat for commercially important species that are valued at over \$28,000 hect⁻¹ yr⁻¹ (Costanza et al., 2014). Loss of seagrass habitat directly brings about the loss of these ecosystem services. Secondly there is a fear that carbon stocks associated with seagrasses would be lost upon habitat destruction, increasing carbon emissions and exacerbating climate change (Pendleton et al., 2012; Fourqurean et al., 2012).

Resource managers and policy makers are often forced to make trade-offs between human alteration and development of coastal areas and the ecosystem services provided by intact, healthy habitats. Seagrass Blue Carbon offers an additional ecosystem service that is capable of drawing international funding for local conservation projects, supporting climate change mitigation and well as a financial incentive for conservation and appropriate management. Existing programs aimed at the value of carbon mitigation focus on the likelihood of emissions after ecosystem loss or degradation; seagrasses are no different

(Lovelock et al., 2017a). A clear expression of the risks to seagrass soil carbon may help further development Blue Carbon projects along with the prioritization of particularly vulnerable sites. This has been particularly difficult in discussions of seagrass carbon stocks, that have focused chiefly on total C_{org} inventories rather than realistic threats to stocks and the likelihood that carbon loss could equate to CO_2 emissions. This dissertation has attempted to fill in gaps in our understanding of C_{org} storage variability as well as those factors that may protect against the remineralization of C_{org} soils and overall CO_2 production.

It is clear that seagrasses are not categorically important for soil C_{org} stocks or their preservation. Chapter II is an extremely rare case where the effect of seagrasses on long-term soil C_{org} stocks was isolated from the milieu of other potential drivers of sediment characteristics. There was no effect of seagrasses, despite known differences in seagrass type, abundance, and productivity. Chapter III found that there was a positive, albeit weak, correlation between seagrass abundance and C_{org} stocks. Characteristics related to sediment grain size better explained C_{org} stocks, with finer, muddier sites having higher C_{org} content. It is likely that seagrasses influence C_{org} stocks via the alteration of local hydrology that in turn encourages a deposition environment for smaller grain sediments and less-dense organic matter. However, the depositional threshold may not be reached in all seagrasses and local geomorphology and hydrology may cause the accumulation of C_{org} -rich muds independently of benthic vegetation. In south Florida, soil C_{org} stocks become notable not because of seagrasses, but rather a balance environmental and ecological characteristics, that may or may not include seagrasses.

Seagrasses are included in Blue Carbon strategies because of potential conversion of C stocks to CO_2 emissions after habitat destruction. This assumes that both stored C_{org} can be remineralized and that habitat destruction would bring about changes that induce remineralization. The greatest threat to seagrass Blue Carbon is the increase

in decomposition rates associated with the erosion and exposure of buried soil to an environment rich in oxygen, labile OM (for microbial priming), and nutrients (Duarte et al., 2010; Fourqurean et al., 2012; Lovelock et al., 2017b). Chapter V found that only a fraction of total C_{org} bound in sediments may be vulnerable to oxidation, and that fraction varies with sediment grain size and overall C_{org} stock. Chapter III suggests that burial as a means of C stock preservation may only be important when sediments are fine. The amount of C_{org} that may be important in Blue Carbon strategies is less than the total C_{org} stock, varies greatly between sites, and is only marginally influenced by the measurements of seagrass presented here.

Chapters IV and V introduce C_{inorg} processes (calcification – carbonate dissolution) as buffers to both C sequestration and CO_2 production that occur during decomposition. Stocks of C_{org} represent historic sinks of CO_2 that could be lost; in the same vein, C_{inorg} stocks represent historic production of C_{org} and can decrease pCO_2 through dissolution. Chapter V finds that C_{inorg} may be buffering CO_2 production via decomposition but only at sites where C_{org} content is high. C_{inorg} processes have the potential to buffer traditional Blue Carbon processes, though it is limited to environments where thermodynamics and ecology promote calcification.

Conservation of seagrasses is important for established reasons (Costanza et al., 2014) and while carbon sequestration could be a valuable service to add to the list, the relationship between Blue Carbon stores and seagrasses is a complicated issue that includes species-specific characteristics and environmental contexts. We have already identified seagrasses, marshes and mangroves as more important for Blue Carbon strategies. Perhaps we should

further prioritize sites, taking more consideration of the drivers of C storage and the likelihood that C_{org} stocks can be preserved.

Work Cited

- Costanza, R., de Groot, R., Sutton, P., van der Ploeg, S., Anderson, S. J., Kubiszewski, I., Farber, S., and Turner, R. K. (2014). Changes in the global value of ecosystem services. *Global Environmental Change*, 26:152–158.
- Duarte, C. M., Marbà, N., Gacia, E., Fourqurean, J. W., Beggins, J., Barrón, C., and Apostolaki, E. T. (2010). Seagrass community metabolism: Assessing the carbon sink capacity of seagrass meadows. *Global Biogeochemical Cycles*, 24(4):GB4032.
- Duarte, C. M., Middelburg, J., and Caraco, N. (2005). Major role of marine vegetation on the oceanic carbon cycle. *Biogeosciences*, 2(2):1–8.
- Fourqurean, J. W., Duarte, C. M., Kennedy, H., Marbà, N., Holmer, M., Mateo, M. A., Apostolaki, E. T., Kendrick, G. A., Krause-Jensen, D., McGlathery, K. J., and Serrano, O. (2012). Seagrass ecosystems as a globally significant carbon stock. *Nature Geoscience*, 5(7):505–509.
- Lovelock, C. E., Atwood, T., Baldock, J., Duarte, C. M., Hickey, S., Lavery, P. S., Masqué, P., Macreadie, P. I., Ricart, A. M., Serrano, O., and Steven, A. (2017a). Assessing the risk of carbon dioxide emissions from blue carbon ecosystems. *Frontiers in Ecology and the Environment*, 15(5):257–265.
- Lovelock, C. E., Fourqurean, J. W., and Morris, J. T. (2017b). Modeled CO₂ Emissions from Coastal Wetland Transitions to Other Land Uses: Tidal Marshes, Mangrove Forests, and Seagrass Beds. *Frontiers in Marine Science*, 4:143.
- Orth, R. J. (1977). The importance of sediment stability in seagrass communities. In *Ecology of Marine Benthos*, pages 281–300. Published for the Belle W. Baruch Institute, by the University of South Carolina Press.
- Pendleton, L., Donato, D. C., Murray, B. C., Crooks, S., Jenkins, W. A., Sifleet, S., Craft, C., Fourqurean, J. W., Kauffman, J. B., Marbà, N., Megonigal, P., Pidgeon, E., Herr, D., Gordon, D., and Baldera, A. (2012). Estimating Global “Blue Carbon” Emissions from Conversion and Degradation of Vegetated Coastal Ecosystems. *PLoS ONE*, 7(9):e43542.
- Smith, S. V. (1981). Marine macrophytes as a global carbon sink. *Science*, 211(4484):838–840.
- Waycott, M., Duarte, C. M., Carruthers, T. J. B., Orth, R. J., Dennison, W. C., Olyarnik, S., Calladine, A., Fourqurean, J. W., Heck, K. L., Hughes, A. R., Kendrick, G. A., Kenworthy, W. J., Short, F. T., and Williams, S. L. (2009). Accelerating loss of seagrasses across the globe threatens coastal ecosystems. *Proceedings of the National Academy of Sciences*, 106(30):12377–12381.

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PUBLICATIONS

Hendriks, IE, YS Olsen, L Ramajo, L Basso, A Steckbauer, TS Moore, JL Howard, and CM Duarte. 2014. Photosynthetic activity buffers ocean acidification in seagrass meadows. *Biogeosciences* 11:333–346.

Howard JL, JC Creed, MVP Aguiar, and JW Fourqurean. 2017. CO₂ released by carbonate sediment production in some coastal areas may offset the benefits of seagrass “Blue Carbon” storage. *Limnology and Oceanography*, 63(1), 160–172.

Howard JL, A Perez, CC Lopes, and JW Fourqurean. 2016. Fertilization changes seagrass community structure but not Blue Carbon stores: results from a 30-year field experiment. *Estuaries and Coasts*, 39(5), 1422-1434.

Zandonà E, SK Auer, SS Kilham, JL Howard, A López-Sepulcre, MP O'Connor, RD Bassar, A Osorio, CM Pringle, and DN Reznick. 2011. Diet quality and prey selectivity correlate with life histories and predation regime in Trinidadian guppies. *Functional Ecology*, 25:964–973.

Zandonà E, C Dalton, RW El-Sabaawi, JL Howard, MC Marshall, SS Kilham, DN Reznick, J Travis, TJ Kohler, AS Flecker, SA Thomas, and CM Pringle. 2017. Population variation in the trophic niche of the Trinidadian guppy from different predation regimes. *Scientific Reports*. 7:5770