Seagrass contribution to blue carbon in a shallow karstic coastal area of the Gulf of Mexico

Tania C. Cota-Lucero[1] and Jorge A. Herrera-Silveira [1]

[1] Marine Resources, Centro de Investigación y de Estudios Avanzados del Instituto Politécnico, Mérida, YUC, México
Corresponding Author:
Tania C. Cota Lucero[1]
Km. 6 Carretera Antigua a Progreso. Mérida, Yuc. 97310, Mexico
Email address: tania.cota@cinvestav.mx

Abstract

Seagrass meadows provide multiple ecosystem services, including carbon sequestration,~~.~~ ~~However, seagrass meadows~~ and are among the most threatened ecosystems worldwide. Determining the magnitude of the carbon stocks in seagrass meadows at the regional scale allows for the estimation of their global magnitude and identification of their importance in regional environmental mitigation strategies; however, few studies have quantified carbon sequestration in ____. The objective of the present study was to determine the structure of seagrass meadows and evaluate their contributions to sinks of carbon in this system in the Los Petenes Biosfera Reserve (LPBR)~~ and evaluate their contributions to sinks of carbon in this system~~. LPBR is ~~,~~located in Yucatan~~, which~~ and is ~~considered the region with~~includes the largest seagrass extension in Mexico. Analyses of the seagrass meadows ~~were executed following~~ followed standardized protocols (spectral analysis, and isotope and carbon stock analyses)~~. The~~ suggested that LPBR ~~stores~~ stored ~~an average of~~ 2.2 ± 1.7 Mg C ha^{-1} in living biomass and 318 ± 215 Mg C ha^{-1} in the top 1 m of sediment~~s (top 1 m)~~.~~,~~ ~~and t~~This carbon stock ~~decreases~~ decreased with water depth~~. The seagrass community extends 149,613 ha, which~~ and represents the largest organic carbon stock (47 Tg C) documented in seagrass meadows in Mexico. Macroalgae and seagrass represent 76% of the organic carbon stored in sediment. If LPBR seagrass meadows ~~are~~ were lost ~~due to natural or anthropogenic impacts,~~ 173 Tg CO_{2eq} emissions ~~could~~ would be released, which corresponds to the emissions generated by fossil fuel combustion of 27% of the current Mexican population. ~~This information emphasizes the importance of~~

Style Definition: Unresolved Mention

Commented [LMG1]: Provide the ecosystem typ
(subtropical?)

Commented [LMG2]: Present your results in pas

~~seagrass meadows as a carbon sink in the region and their contribution to climate change mitigation, thus allowing for the implementation of necessary conservation strategies.~~

Commented [LMG3]: Adds little

Key words Autochthonous, Blue carbon, Mangroves, Seagrasses

Introduction

Seagrasses provide numerous ecosystem services, such as serving as a habitat and refuge for a high diversity of species, ~~providing~~ retaining sediment ~~retention~~ and ~~protection~~ protecting ~~of~~ the coastal zone; healthy seagrass meadows~~,~~ ~~improving~~ improve water quality, and ~~helping to~~ regulate the impacts of greenhouse gases, particularly CO_2 (Hemminga & Nieuwenhuize, 1990, Constanza et al., 2014;). ~~and 50%~~ Indeed, seagrass are more efficient than tropical forests in carbon sequestration (McLeod et al., 2011).

Half of the carbon buried in marine sediments is found in ~~all~~ coastal blue carbon habitats combined (i.e., mangrove, salt marshes and seagrass) (Duarte et al., 2013). Seagrasses have a ~~greater~~ larger distribution (0.33 x 10^6 km^2) than salt marshes and mangroves, whose habitats are restricted to intertidal areas along the coast (Charpy-Roubaud & Sournia, 1990; Duarte & Cebrian, 1996; Short et al., 2007). Because of their wide distrubtion and high productivity it is important to quantify the contribution of seagrass meadows to ~~are currently being considered for use in climate change mitigation strategies and have high productivity and contributions to the coastal carbon balance for reconciling~~ continent-scale carbon budgets (Duarte & Chiscano, 1999; Laffoley & Grimsditch, 2009; Nellemann et al., 2009). ~~Seagrass is recognized as being more efficient than tropical forests in carbon sequestration (McLeod et al., 2011), and 50% of the carbon buried in marine sediments is found in all coastal blue carbon habitats combined (i.e., mangrove, salt marshes and seagrass) (Duarte et al., 2013).~~

Shoot density, leaf area, and the specific characteristics of seagrass species regulate carbon storage (Mazarrasa et al., 2018). The structural complexity of seagrasses is related to both the above- and belowground biomass and contributes to sediment retention processes by trapping particles ~~that come from within the same or adjacent ecosystems,~~ accumulating in sediments for millennia in the form of organic carbon (Hendrix et al. 2008; McLeod et al. 2011; Duarte & Krause-Jensen 2017). Carbon ~~that is captured and~~

Commented [LMG4]: I assume some particles ar
generated within the system too

stored in seagrass sediments comes from both the detritus produced by the degradation of its biomass (leaves, rhizomes, and roots), considered autochthonous carbon (Agawin & Duarte, 2002; Hendriks et al., 2008; Tanaya et al., 2018), and from allochthonous sources such as the contributions of river sediments ~~that are dragged along the basin and finally deposited in coastal areas~~ (Signa et al., 2017; Maklin et al., 2019). The origin of the carbon in seagrass ecosystems differs at the regional level. ~~since there are records of~~In some areas ~~where~~ the proportion of allochthonous carbon in seagrass meadows exceeds autochthonous carbon (Gacia et al., 2002; Bouillon et al., 2008); these differences ~~can be an indicator of~~indicate the degree of connectivity between seagrass meadows and other ecosystems.

Anthropogenic impacts threaten seagrasses worldwide and have caused the disappearance of these habitats (Orth et al., 2006; Waycott et al., 2009). These impacts must be monitored ~~since the habitat decrease is not the same~~ at the regional scale ~~where seagrasses are distributed~~ (Carmen et al., 2019~~). Monitoring at a regional or local level allows the following information gaps~~ to ~~be~~ improve~~d~~: 1) estimates of carbon stocks and the contribution of seagrass meadows ~~across the world are derived from scarce data, resulting in the tendency~~ to ~~generalize~~ global carbon stocks ~~in these ecosystems~~ (Serrano et al., 2014); 2) ~~in subtropical regions, insufficient reports exist regarding how the structural complexity of seagrasses is~~ relate~~d~~ ~~to~~ carbon sources and their ability to store organic carbon with the influence of groundwater; and 3) ~~there is scarcity of~~provide data on the contribution of autochthonous vs allochthonous materials in carbon stocks.

Few studies have ~~related to the~~ quantified~~cation of~~ organic carbon in seagrass ecosystems in Mexico ~~are insufficient,~~ ~~and~~ or ~~few studies~~ related habitat health and the structure of these ~~seagrass community~~meadows (Samper-Villarreal et al., 2016, Herrera Silveira et al., 2020). In this context, it is important to determine the carbon stocks both in seagrass biomass and sediments associated with these habitats, as well as their sources, the structural complexity of the seagrass, and the water quality ~~in which they are found~~. Here, we hypothesized that the seagrass carbon stocks and their contribution to sediments differ ~~among~~ with water depth~~s~~ and that habitat-forming seagrass is the main source of the accumulated organic matter in associated sediments.

This may help improve carbon estimations on a global scale and the variables associated with those stocks. The study area corresponds to the marine protected area of Los Petenes Biosphere Reserve (LPBR), in the Gulf of Mexico. This region, of 151,200 ha (Perez-

Espinoza et al., 2019), is one of ~~may be~~ the largest continuous extension of seagrass on the Mexican coast~~, covering 151,200 ha (Perez-Espinoza et al., 2019)~~. Therefore, the primary objective of the present study was to characterize the structural complexity of seagrass meadows and determine their relationship with the spatial distribution of organic carbon stocks ~~according~~ along ~~to~~ environmental gradients related to water depth. A secondary objective was to identify the main sources of this carbon and the influences of environmental variables.

Materials & Methods

Study Area

~~We performed the present study at~~The LPBR ~~located southeast of the Gulf of Mexico~~, one of the largest marine reserves (282,857 ha) in the southeast region of the Gulf of Mexico ~~region~~ (Fig. 1). Mangroves and petenes (vegetation islands similar to hammock ecosystems in Florida, USA) cover 23% of the terrestrial surface. The coastal zone is estuarine (181,991 ha), showing a substrate enriched in carbonates due to the karst characteristics of the continental shelf in this region. The largest extension of seagrasses in Mexico is distributed in this protected area, and the community is composed of three species (*Thalassia testudinum*, *Syringodium filiforme* and *Halodule wrightii*) that have been recorded at depths of up to 5 m. This community shares substrates with a large diversity of macroalgae (Mateo Cid et al., 2013). This region maintains strong coastal hydrological connectivity since its karst nature favors groundwater discharges to the coast, thus contributing to the supply of nutrients there (Grivel-Piña, 1992; CONAGUA, 2006). Along its 100 km coastline, there are only two communities of less than 1000 inhabitants each, so it is ~~considered~~ an area of low anthropic environmental impact~~, unlike the coasts of the other two states of the Yucatan Peninsula (Yucatan and Quintana Roo)~~. This region is ~~considered~~ an area of biological, ecological, and scientific importance as a result of its conservation and diversity (Corbalá et al., 2007). "

Water Quality

We visited the LPBR in May, 2017 and 2018 under CONANP permission (F.OO.9.DRPYyCM/060/2021). Transects were established perpendicular to the coast traveling ~25 km considering a depth gradient of 1 to 5 m (Fig. 1). At ~~the~~ sampling stations, physicochemical water quality data and seagrass samples were collected. Water depth was measured using a portable depth gauge (Hondex Ps-7); temperature, salinity, and dissolved oxygen (OD) were measured in situ using a YSI-2030 multiparameter probe at 50 cm depth intervals from the surface to the bottom. Incident light data (%) were obtained using a LI-250A spherical sensor (LICOR) that collected measurements every 50 cm deep across the entire water column. Water samples were collected in the immediate vicinity of the seagrass meadows for dissolved inorganic nutrient analysis (n=79). The nutrients analyzed were nitrates + nitrites ($NO_3^- + NO_2^-$), soluble reactive phosphate (SRP), ammonium (NH_4^+), and soluble reactive silicate (SRSi). These analyses were performed according to the standard methods described in Strickland and Parsons (1972). The concentration of chlorophyll-a (Chl-a) was also determined using the method of Parsons et al. (1984). ~~With~~ From these environmental variables, the trophic index "TRIX" was calculated (Vollenweider et al., 1998; Jorgensen et al., 2005; Melaku et al., 2003).

Seagrass Community Characterization

The extension of the seagrass meadows in this protected marine area was determined using a Sentinel 2A multispectral image, which has a pixel size of 10 m and a radiometric resolution of 12 bits. This image corresponds to May 8, 2017 (Path/Row: 21/46) (ESA, 2019), in which the image composition was generated by means of the blue (490 nm), green (560 nm), and red (665 nm) bands. Once this image composition was obtained, ground masking and radiometric correction (DOS-Dark Object Subtraction) were performed (Chavez, 1988). For the classification of the image, four classes were considered based on an analysis of conglomerates with 80% similarity. From these classes and field verifications of 117 sites, spectral signatures of four types of seagrass beds were generated (coverage%, Table 1, Supporting Information): monospecific meadows of *Thalassia testudinum* (TtMa), mixing seagrass meadows (*T. testudinum, S. filiforme, H. wrightii*) with macroalgae (MxMa), mixing meadows dominated by *Syringodium fliforme* (MxSf), and *Syringodium filiforme* and *Thalassia testudinum* beds (SfTt). In the latter class, just one sample with *H. wrigthii* was found (Supplementary material, Table 1). The supervised classification was carried out by means of the maximum likelihood estimation. To determine the accuracy of the classification, we determined the Kappa statistic, which measures the level of agreement between the classes (Song et al., 2001). Sampling campaigns were designed to collect data and samples at several stations according to the area of each type of seagrass meadow. The characterization of the seagrass beds consisted of determining coverage (%) and density, following the Seagrass-Watch percent cover standard (Mckenzie et al. 2001), and they were established at each station using a random scheme. Duplicate samples of seagrass biomass (leaves, rhizomes, and roots) were collected at each station using the standing crop method with a 15 cm diameter core (CARICOMP, 2001). In the laboratory, ~~the~~ biomass samples were cleaned and ~~the~~ epiphytes were removed. Once cleaned, ~~the~~ samples were subdivided into two components (aboveground and belowground) and dried at 70°C until a constant weight was obtained. ~~The s~~Specific morphometric shoot variables evaluated were the maximum length of the leaves of each species, the width of the leaf and number of leaves per shoot (only for *T. testudinum*), and the leaf area index (LAI), which was calculated for *T. testudinum* (Bulthuis, 1990). To estimate the average carbon content in the biomass (C_{bio}) of above- and belowground seagrass components, the values of the dry weights (g Dw m^{-2}) were converted to carbon equivalents using conversion factors for each species: *Thallasia testudinum* (0.36), *Syringodium filiforme* (0.32), and *Hallodule wrightii* (0.34) (Fourqurean & Zieman 2002; Short et al., 1985, Papiol et al., *unpublished data*). Afterwards, these values were finally extrapolated to Mg C ha^{-1}.

Soil Characteristics

To determine the carbon storage in the sediments, we used PVC cores 1 m in length (n=62). These cores were inserted by manual hammering. Due to the karst characteristics of the continental shelf, ~~the~~ core penetration varied from 0.20 to 1 m~~,~~. ~~and a~~All cores were extrapolated to 1 m long (Howard et al., 2014). Core compaction was less than 5% in all cases, and compaction was not considered for correction in this study due to the coarse sediment composition. In the lab, the cores revealed high heterogeneity over several layers of sediment and were sliced into 5 cm sections at different intervals (Supplementary material Data base). Slices were selected for LOI, OM% and C_{ing} %, C_{org}%, TN%, and TP % determination.

Organic and Carbonate Content

Each slice (n=298) was weighed before and after drying at 70°C for 48 h to determine bulk density (BD). Bulk density was calculated as the dry weight of the soil subsamples divided by the volume of the subsample (5 cm^{-3}) and expressed as g cm^{-3}. All samples were homogenized and combusted at 500°C for 4 h to determine LOI (OM%) and then for 2 h at 900 °C to determine the carbonate content C_{ing} (%) (Kendrick and Lavery, 2001;

Heiri et al. 2001). C_{org}% (after acidification with 1 N HCl to remove carbonates) and nitrogen content (TN%) were analyzed using a CHN ThermoQuest autoanalyzer (model Flash EA 112, Italy). The C_{org} content (Ccorg; g C_{org} cm^3) of each 5 cm slice was calculated from the measured C_{org} and the BD of the slice following Eq. (1):

$$\mathrm{Ccorg} = z\mathrm{slice} * \mathrm{BD}_{\mathrm{slice}} * \mathrm{Corg}_{\mathrm{slice}}/100 \qquad (1)$$

where zslice is the slice thickness (cm), and the C_{org}% content of the slice is divided by 100 to convert % to grams of C_{org} per gram of dry weight. The amount of carbon stored in each core was calculated by summing the C_{org} content in each depth increment (slice). C_{org} stocks (Mg C ha^{-1}) were converted to $CO_{2equivalents}$ by multiplying by 3.67 (conversion factor, ratio of molecular weight CO_2 to C_{org}). Total phosphorus (TP %) was determined by the colorimetric method described by Strickland & Parsons (1972) and Aspila et al., (1976).

Carbon Source

To determine the organic carbon sources in the sediment, isotopic analysis of $\delta^{13}C$ and $\delta^{15}N$ was performed. Surface layers (0-5 cm) of sedimentary cores (n = 24) distributed in the north, center, and south of the reserve were selected, considering a water depth gradient of 1 to 5 m with a maximum distance of 25 km from the coast. The subsample for organic carbon analysis was dried, weighed, and then dry-sieved through a 1 mm mesh to remove coarse inorganic particles. The remaining samples were then acidified with acid 10% (HCl). The residual samples were redried and then capsulated for analyses using a mass spectrometer (Delta V Plus) with an instrumental precision of 0.2%. The Standard material for carbon is Pee Dee Belemnite (PDB) limestone, and the nitrogen standard is atmospheric nitrogen. The $\delta^{13}C$ carbon signal was expressed in parts per thousand (‰), which was obtained by the isotopic ratio of the heavy isotope in relation to the light isotope (Eq. 2):

$$\delta^{13}C(‰)\left[\left(\frac{R_{sample}}{R_{standar}} - 1\right)\right] \times 1000, R = \frac{\delta^{13}C}{\delta^{12}C}$$

(2)

The relative contribution of different primary producers as potential sources of organic matter in seagrass sediments was estimated using Fits Stable Isotope Mixing Models

(SIMMR V. 0. 3) (Parnell et al., 2010, 2013). We ran the mixing models separately for each water depth (1-5 m) sediment, and we only included as potential sources those primary producers for which both $\delta^{13}C$ and $\delta^{15}N$ values were available: macroalgae blades ($\delta^{13}C$-13±0.2 ‰, $\delta^{15}N$ 1.74±1.59 ‰), seagrass leaves ($\delta^{13}C$ -11±0.3 ‰, $\delta^{15}N$ 2±0.2 ‰), and mangrove leaves ($\delta^{13}C$ -29±2 ‰, $\delta^{15}N$ 1.1±0.09 ‰) (Duarte et al., 2018, Campbell & Fourqurean 2009, Vaslet et al., 2015).

Statistical Analysis

The frequency distributions of the water quality characteristics, vegetation structures, and sediments (storage and isotopic signatures) of this study generally did not show normality (based on the normality test of Shapiro-Wilk), so ~~the ~~differences in the characteristics of these components between depths were evaluated using the nonparametric Kruskal-Wallis test. ~~The v~~Variables that showed normality were analyzed using ANDEVA. These analyses were performed using SigmaPlot 12® software with a significance level of 0.05. Tables 1 and 3 in the Results section show the variables with significant differences according to the depth gradient.

Results

Water Quality

The trophic state of the water column estimated through the TRIX index showed an average of 3.85±0.12, which is in the oligotrophic range. However, this value varied between oligotrophic and mesotrophic. The LPBR coastal water temperature averaged 29±0.12°C, while the average water salinity was 35±2.43 ups (Table 1). ~~The ~~DO concentrations averaged 6.92±0.16 mg l^{-1}, and no hypoxia concentrations were recorded at any depth (Table 1). ~~The percentage of l~~Light incidence was greatest at 1 m depth, (52±11~~.38~~%)~~,~~ and ~~decreasing ~~decreased with ~~respect to ~~depth ~~until it reached~~to <20% at 5 m (Table 1). NO_{3-} + NO_{2-} in the water column of LPBR averaged 5.26±0.79 µmol l^{-1}, with the maximum concentration at 3 m depth (Table 1). ~~The average concentration of~~ SRP ~~in the area was~~averaged 0.35±0.02 µmol l^{-1}, with the highest values at greater depths (Table 1). ~~The average ~~NH_4^+ ~~value was~~averaged 1.20±0.08 µmol l^{-1}, with the highest values at the lowest depths~~;~~. SRSi concentrations in the study area averaged 21.6~~2~~±2.7 µmol l^{-1}, varying from higher to lower concentrations following the depth gradient or coastal distance (Table 1). Chlorophyll-a (Ch-*a*) values averaged 2.59±0.42 µg l^{-1}, with the highest concentrations at the lower depths (Table 1).

Sediment Characteristics

~~The s~~Sediments in the LPBR had an average bulk density (BD) of 0.31±0.25 g cm^{-3}, and ~~they~~ exhibited no significant differences due to the water depth gradient (gl= 4, H=5.69, P= 0.223). Concentrations of OM% ranged from 8 to 35%, and these values did show significant differences (gl= 4, H=126.28, P < 0.001). ~~Meanwhile,~~ C$_{org}$% ~~yielded values of~~ ranged from 7 to 15%, and ~~decreasing~~ decreased with depth (Table 2, gl= 4, H=29.31, P < 0.001). ~~The~~ C$_{ing}$% increased with water depth and maximun concentration was found at 5 m (gl= 4, H=8.12, P =0.087). ~~The spatial distribution of~~ TN% and TP% did not show significant spatial variation (gl=49, F=01.81, P = 0.142, and gl=49, F=2.10, P = 0.097, respectively), while the TN:TP ratio varied between 22 and 42 in the depth gradient (Table 2).

Seagrass Community

~~From the marine extension of the LPBR (181,991 ha), s~~Seagrass meadows and macroalgae ~~occupy~~ occupied 82% ~~of this area~~ (149,613 ha) of the LPBR (181,991 ha).~~,~~ ~~while~~ T~~t~~he remainder ~~is~~ was substrate without vegetation (31,069 ha) (Fig. 2a). ~~This area is dominated by mixing~~ Mixing meadows dominated this area with 51,884 ha of MxMa macroalgae (Fig. 2b). The supervised classification allowed for mapping with 73% accuracy.

Three species, *T. testudinum*, *S. filiforme*, and *H. wrightii*, were recorded in different abundances in both monospecific and mixed meadows ~~in this study~~. ~~The dominant species *was*~~ *T. testudinum* dominated, with an average coverage of 54 ± 24% and greater coverage at depths of 1 and 2 m (Table 3). *Syringodium filiforme* showed an average coverage of 45 ± 27%, with the greatest abundance at 3 m depth (50%). ~~For~~ *H. wrightii*, ~~the~~ showed an average coverage ~~was~~ of 27 ± 21%, with the highest value at 3 m (38%). Shoot density of the seagrass species in the LPBR averaged 432 ± 34 shoots m^{-2}, registering wide variations between depths. ~~Regarding morphometry, the l~~Length of ~~the leaves in the study area~~ averaged 32 ± 1.33 cm. ~~For~~ *T. testudinum*~~, the average leaf length~~ leaves averaged ~~was~~ 33 ± 1.61 cm, with the longest leaves (≈ 80 cm) at a depth of 2 m. At 5 m, *T. testudinum* had the widest leaves (1.2 ± 0.11 cm), and the smallest leaves were found at 1 m (Table 3). ~~The l~~Leaf area index (LAI) averaged 4.06 ± 0.44, and the highest average was found at 2 m depth (7.75 ± 1.41). *Syringodium filiforme* showed the longest leaves at 5 m (44 ± 4.67 cm), while *H. wrightii* had the smallest average leaves (15.6 ± 2 cm). In relation to biomass, seagrass meadows in the LPBR averaged 119 ± 13 and 510 ± 46 g Dw m^{-2} in aboveground and belowground biomass, respectively, with the greatest values measured at 2 m depth (aboveground at 196 ± 42 g Dw m^{-2}, and belowground at 768 ± 157 g Dw m^{-2}). *Thalassia testudinum* had the largest contribution (79%) to total biomass, which decreased at greater depths when replaced by *S. filiforme* (Tabla 3). ~~Regarding t~~The above/below biomass ratio (AB:BW)~~, the~~ averaged ~~was~~ 0.32, ~~indicating that the belowground tissue~~which corresponded to 81% of the total biomass (Table 3). Macroalgae coverage decreased with water depth, and there were no significant differences between water depths (Table 4, gl=4, H=10.51, P=0.033).

Seagrass Carbon Stocks and Sources

Biomass organic carbon averaged 2.2 ± 1.7 Mg C ha^{-1}, with statistically significant differences between water depths (gl=4, H=13.49, P=0.009, Table 5). *T. testudinum* averaged 2 ±1.7 Mg C ha^{-1} and decreased with water depth (Fig. 3a). *S. filiforme* and *H. wrightii* averaged 0.88±0.78 and 0.89±1 Mg C ha^{-1}, respectively, and did not present a trend in the gradient (Fig. 3 b,c). Statistical differences between species were found (gl=4, H = 22.44, P = <0.001). In sediment (C_{sed}), Corg storage net averaged 131 ± 118 Mg C ha^{-1} (gl=4, H=13.77, P=0.008). In the top 1 m, this stock was 318 ± 215 Mg C ha^{-1}, with a maximum of 463 ± 267 Mg C ha^{-1} at 1 m water (gl= 4, H=6.02, P=0.197) (Table 5). The C_{ing} stock averaged 133 ± 104 Mg C_{ing} ha^{-1}, varying with respect to depth (gl=4, H= 0.64, P=0.958; Table 5). The ecosystem carbon stock (C_{bio} + C_{sed}) in Los Petenes Biosphere Reserve was 47Tg C (Table 6). Considering the extension of each type of meadow, those in the MxMa stored the largest C_{org} of the study area (34%). The seagrass meadows dominated by SfTt represented the smallest stock in the area, with 8% of the total (Fig. 4).

The surface of seagrass sediments averaged δ^{13}C of -17 ± 3 ‰ and δ^{15}N of 3 ± 1 ‰. ~~Regarding the spatial distribution of the potential sources of C_{org} stored in the surface sediments, it was observed that i~~In ~~the~~ shallow areas (1-2 m), the δ^{13}C varied between -10 and -24 ‰; in the deeper areas (4 -5 m), δ^{13}C varied between -12 and -17 ‰, with statistically significant differences between water depths (gl=23, F=3.37, P=0.030, Table 7).

~~The~~ $\delta^{15}N$ of LPBR sediment ranged from 2 to 3%, and there were no significant differences in the depth gradient (gl=23, F= 0.64 P=0.637; Table 6). Mean $\delta^{13}C$ and $\delta^{15}N$ values of seagrass sediments were within the region defined by $\delta^{13}C$ and $\delta^{15}N$ mean values of primary producers (Fig. 5a). The SMMIR mixing models identified sources of organic matter in seagrass sediments (Fig. 5b and Table 7). Seagrass leaves and macroalgae blades were the major potential contributors in seagrass sediments (mean ± SD proportion = 0.39 ± 0.19 and 0.36 ± 0.21, respectively), while mangrove leaves had a minor contribution (0.24 ± 0.21). The seagrass contribution increased with water depth (Table 7).

Discussion

Water Quality and Sediment Characteristics

The marine area Los Petenes Biosphere Reserve showed general oligotrophic conditions. This area, which is on a karstic geomorphological coast, receives groundwater discharge from springs and runoff from channels that connect mangrove areas with the sea (Agraz-Hernandez et al., 2012). ~~The e~~Exchange of nutrients at the site ~~is also reflected~~ reflects ~~in the characteristics of the sediments, such as the~~ high concentrations of OM%, C_{org}%, and TN% in the areas near the coastline (1-2 m water depth) (Table 2). The concentration of these nutrients in the sediment is associated with ~~various characteristics, such as~~ the type of organic matter that they receive from both ~~the~~ mangroves and ~~the~~ submerged aquatic vegetation (SAV), as well as degradation patterns, residence times of the accumulated matter, and the chemical balance of carbonate (Koch et al., 2001). ~~In this study, c~~Carbonate ~~was measured at~~ concentrations ~~greater than~~exceeded 20% in the deep zone (Table 2). ~~The~~ N/P ratios show that ~~the~~ sediments in the reserve are marine type and are influenced by terrigenous material (Hernández, 2000). ~~The i~~Isotopic mangrove signatures in the superficial sediments at 1 m depth support this finding (Fig. 5;Table 7). In general, ~~the~~ concentrations of registered nutrients indicate that there is no limitation of primary production, at least in the first meters of water depth, since the concentrations are in the tolerance range for seagrasses. In karst systems, it is common to observe P limitations (Álvarez-Góngora and Herrera-Silveira, 2006); the connectivity between mangroves and seagrasses in this area, provides favorable conditions for the development of quality SAV. However, this leads to significant vulnerability if groundwater discharges begin to show signs of pollution, as they have in the northern and eastern regions of the Yucatan Peninsula (Herrera-Silveira & Morales-Ojeda, 2009; Arcega-Cabrera et al., 2014; Kantún et al., 2018). However, due to the connectivity between mangroves and seagrasses, the light and concentration of nutrients in this area favor conditions for the healthy development of SAV.

Seagrass Complexity

The large area covered by SAV ~~in this protected area, in addition to being the largest in the Gulf of Mexico in the marine portion of Mexico (not in lagoons or bays),~~ indicates good conditions, as reflected in the spatial continuity of the seagrass meadows, morphometric characteristics, and their biomass (Table 3). These characteristics of ~~the~~ LPBR seagrasses are useful as baseline data for monitoring the health of the ecosystem. ~~since the r~~Rapid coastal development experienced by these areas may allow for the identification of responses to different environmental stressors (Tomasko & Lapointe, 1991; Lirman & Cropper, 2003; Lee et al., 2007). There was also spatial variability in the specific morphometric and structural characteristics of the seagrass community in the study area with respect to the depth gradient and distance from the coast. This implies changes in variables such as salinity and transparency (Table 1), which ~~have been identified as key variables for development and~~control seagrass productivity (Fourqurean et al., 1992).

The structural variability of seagrass beds with respect to depth gradient (Table 3) indicates an area where *T. testudinum* dominates at lower depths, with the presence of patches of *H. wrightii* (coverage of <5%); at greater depths, the dominant species was *S. filiforme*, which is consistent with ~~the findings observed in~~ tropical locations ~~(the western Caribbean)~~ (Tribble, 1981). ~~The spatial species replacement observed in~~ In the LPBR, ~~suggests that~~ *T. testudinum* and *H. wrightii* dominated areas with greater salinity variability; *S. filiforme* ~~is~~ was common in areas of less salinity variation and lower light requirements, which encouraged its dominance in deeper areas (Zieman et al., 1989; Hall et al., 1999; Lirman & Cropper, 2003). ~~In this reserve, the specific morphometric and structural variables of *T. testudinum* yielded the lowest values (b~~Biomass, coverage, density, and LAI~~)~~ of *T. testudinum* was lowest in the deepest zone (5 m) (Table 3)~~. These variables decreased with depth, mainly~~ due to the lowest incidence of light ~~there~~ (Olesen et al., 2002; Enríquez & Pantoja-Reyes, 2005). Additionally, the primary roots of *T. testudinum* were observed to be approximately 30 cm long. Greater belowground biomass and rhizomal elongation determine the depth of anchorage of the species and allow it to ~~be tolerant to~~tolerate erosion processes, therefore contributing to the C_{org} stock. In contrast, the dominant seagrass at 5 m was *S. filiforme*, suggesting that the light requirements vary between species due to the physiological characteristics and morphological adaptations of each (Lee et al., 2007)~~, which again supports the zoning observed in this study~~.

~~The e~~Environmental conditions in the ~~study area~~LPBR favor the ~~development of leaves and belowground tissue, as reflected in the leaf length values~~ growth of seagrasses (Table 3).~~,~~ ~~the~~ Leaf lengths ~~average of which was~~were greater than ~~that~~ lengths reported for other regions of the Gulf of Mexico and the Caribbean (Hackney & Durako, 2004; Arellano-Méndez et al., 2016; Gallegos et al., 1993; van Tussenbroek, 1998). Additionally, the total biomass (above + belowground = 863 ± 478 g Dw m^{-2}) was higher than the reported global scale value of ~461 g Dw m^{-2} (Duarte & Chiscano, 1999) and lower than estuarine zone estimates (879 g Dw m^{-2}). The ~~high~~ structural complexity and favorable environmental conditions in ~~which the seagrass of~~ the LPBR is ~~developed should be~~ reflected in the quantity and quality of the ecosystem services seagrasses provide, such as storing carbon in high concentrations (Fig. 2; Table 6).

Carbon Stocks and Sources Along a Depth Gradient

In the study area, carbon stored as biomass in seagrasses showed a lower average (2.2 ± 1.17 Mg C ha^{-1}) than those reported on a global scale (3 ± 0.4 Mg C ha^{-1}), but they were greater than values from the South Atlantic meadows (1± 0.5 Mg C ha^{-1}; Fourqurean et al., 2012a). ~~For the underground components, the m~~Mean sediment stock at the top 1 m (318 ± 215 Mg C ha^{-1}) was in the range reported for seagrasses in the tropical region of Australia (268 Mg C ha^{-1}) and was greater than the global estimates (194 ± 20 Mg C ha^{-1}) (Fourqurean et al., 2012a). These results suggest that the study area has a high capacity to capture and store coastal carbon, making it highly relevant for the mitigation of greenhouse gas emissions; it must therefore ~~be~~ remain protected~~ from impacts that threaten this ecosystem’s integrity via the coastal connectivity approach~~.

Both aerial and underground carbon storage showed spatial variability related to depth/distance to the shoreline (Table 5). Some studies for other species have indicated that C_{org} storage and sequestration rates in seagrass sediments are higher in shallow meadows and at moderate salinities (Mateo & Romero, 1997; Serrano et al., 2014). The increase in depth implies a reduction in irradiance and a decrease in salinity, which in part affect the productivity of the seagrasses, their structural complexity, and the species composition, with ultimate consequences on carbon stocks. Hydrodynamics ~~is an environmental characteristic that~~ influences the structural complexity of seagrasses and probably influences the storage and carbon fluxes in seagrasses (Mateo & Romero 1997; Koch et al., 2006; Serrano et al., 2014; Dahl et al., 2016). Although this variable was not evaluated in this study, ~~it has been reported that the speed of the~~ currents in this area ~~is~~ are the lowest (1 m sec $^{-1}$) of the three coasts of the Yucatan Peninsula (López and Sierra, 1998), Furthermore, in combination with the low tidal range (<1 m), hydrodynamic energy must be low, favoring processes such as sedimentation, retention, and decomposition of materials produced both locally and regionally. Such is the case for the area near the coast that receives contributions of organic matter from the adjacent mangrove forest (Fig. 5).

Isotopic values of δ^{13}C from surface sediments varied between -10 and -24 ‰ in relation to ~~the~~ distance to the coast.~~,~~ This ~~indicating~~ indicates different sources of organic carbon in the seagrass soils of this area. Near the coast, and up to 7 km from the coast, the isotopic signatures averaged δ^{13}C of -21 ± 4~~.2~~ ‰ (Table 7), which ~~was~~ is similar to mangrove sediments enriched with carbonates ~~the values reported by (~~Garcias-Bonet et al., (2019)~~ of -21 ± 0.57 ‰ in mangrove sediments enriched with carbonates~~. The inverse pattern of the isotopic signal of seagrass is observed (Table 7). Macroalgae blades and seagrass leaves in seagrass sediments were strongly negatively correlated (-0.94) (Fig 5a). This ~~result is indicative of~~indicates the model ~~being unable to~~could not determine the principal carbon source in sediment, indicating that if macroalgae blades contributed to seagrass sediments at the top of their outcome probability range, seagrass leaves most likely contributed at the bottom of their probability range (Fig. 5a). ~~The s~~Stocks of organic carbon in ~~the~~ sediments of ~~the~~ seagrasses of this protected area ~~are~~ were 24% allochthone sources (mangroves), while 76% ~~are~~ were of autochthon origin (macroalgae and seagrass) (Fig 5b). Therefore, the identification of potential sources and contributions to sediments based on stable isotopes needs to be interpreted with care. These results ~~indicate~~confirm, first, the connectivity between two coastal ecosystems (mangroves and seagrasses) (de Boer 2000; Serrano et al., 2014) and, simultaneously, the role of seagrasses as sediment traps and sequestrants of allochthonous carbon (Mellors et al., 2002; Hendrix et al., 2008; Samper-Villareal et al., 2016).

Commented [LMG5]: revise

Conservation Implications

~~The c~~Carbon stocks in ~~the~~ seagrass meadows of this protected natural area vary according to the extent of each type of seagrass meadow, with a total of 47 Tg C_{org} (Table 6). This value contrasts with the estimate of Thorhaug et al., (2017) of 37~~.2~~ -38~~7.5~~ Tg C_{org} for the first 20 cm of sediments in the entire Gulf of Mexico ~~in the first 20 cm of sediment cores, as well as~~and estimates ~~made in~~ for Mexico (48 Tg C_{org}), where the higher stock is located in the Yucatan Peninsula (Herrera-Silveira et al., 2020). ~~It is important to consider that disturbances of s~~Seagrasses, mangroves, and salt marshes~~,~~ are collectively called blue carbon ecosystems (Howard et al., 2014; Howard et al., 2017).~~,~~ Disturbance of these systems can ~~lead to modified~~increase CO_2 emissions as the carbon in the necromass and surface sediment oxidizes. ~~The oxidation processes that generate~~ ~~CO_{2eq}~~ ~~emissions are regulated by natural and anthropic factors that generate disturbances in ecosystems.~~ ~~This new information related to the carbon storage in the seagrass beds of this protected marine area reveals that its disappearance due to natural and anthropic impacts~~ Mineralization of the carbon stored in LPBR could ~~result in maximum emissions of~~release 173 Tg of CO_{2eq}. This ~~value is based on all of the carbon being remineralized and released to the atmosphere; it also implies mitigation of the~~corresponds to emissions generated by 27% of the current Mexican population, based on per capita emissions from fossil fuel consumption estimated for 2009 (3.72 t CO_2) (Cavazos et al., 2013). The loss of vegetation cover in the Gulf of Mexico has been progressively decreasing, with an estimated 50% decrease from 1,927,500 ha in 1992 to 947,327 ha in 2017 (Duke et al., 1992; Thorhaug et al., 2017); this loss is equivalent to an estimated annual loss rate of vegetation in the region of approximately ~~2.78~~3% over a span of 25 years. The seagrass meadows in the LPBR have the largest extension of seagrasses in Mexico, with 149,613 ha currently reported. Therefore, if the coastal vegetation in this reserve disappeared at the same estimated annual rate, in 25 years, only 30% of the current extension would remain. This would likely significantly reduce the ability of the LPBR to offer its current environmental benefits.

The coastal platform of the Yucatan Peninsula is shallow with a steep slope of ~1:1000 (Zavala-Hidalgo et al., 2003); the bottom in areas near the coast, therefore, are covered with submerged aquatic vegetation, mainly seagrasses dominated by *T. testudinum* (Espinoza-Avalos, 1996; van Tussenbroek et al., 2014). ~~However, it is likely that h~~Hydrodynamic conditions, such as the speed of the currents and their exposure to hydrometeorological events, such as hurricanes, storms, and cold fronts, ~~are~~ ~~factors that determine~~ could explain the differences in the seagrass cover of the three coasts of the Yucatan Peninsula (Day et al., 2019). On the coast of Quintana Roo, ~~the speed of the~~ currents ~~is on~~ average 25 cm sec^{-1}, and patches of scattered seagrasses covering between 10 and 50% of the available area~~s are observed in the landscape~~ (Badan et al., 2005; Arellano-Méndez et al., 2005). On the northern Yucatan coast, ~~the~~ currents range between 10 and 20 cm sec^{-1}, with seagrass patches covering between 40 and 80% of the available area~~ in the landscape of the seabed~~ (Appendini et al., 2012; Kantun -Manzano et al., 2018). Finally, on the coast of Campeche, where the Los Petenes protected area is located, ~~the marine~~ currents are very low at ~10 cm sec^{-1} (López and Sierra, 1998), favoring the extension and coverage of seagrasses~~, which is probably the largest occurrence in the marine environment of Mexico~~.

Conclusions

~~The results of this study contribute to improving the estimations of organic carbon storage (47 Tg) in a marine protected area the~~ The LPBR ~~which~~ has the largest extension of the seagrass community in the Gulf of Mexico~~ and represents the ecological importance of this area~~. ~~The c~~Carbon stored (76%) is from seagrass and macroalgae sources. ~~The a~~Allochthon contribution decreased ~~with water depth, but the~~ and seagrass contribution increased with depth. The results of this study improve estimations of organic carbon storage (47 Tg) in a marine protected area~~Our results reveal the importance of generating local data to support regional estimates~~ and demonstrate ~~the depth variability of~~the importance of blue carbon stocks in ~~seagrass beds~~ in the subtropics.

Acknowledgements

We thanks to Primary Production Lab group from the Centro de Investigación y de Estudios Avanzados del Instituto Politécnico-Unidad Mérida (CINVESTAV-IPN, Unidad Mérida). Special thanks to the Consejo Nacional de Ciencia y Tecnologia (CONACYT) for the PhD., scholarship awarded to Tania Cota Lucero. Thanks to M. Sc. Juan Enrique Mendoza Martínez for his technical support. Thanks to National Commission of Natural Protected Areas (CONANP) especially to the Yucatan Peninsula and Mexican Caribbean Regional Direction, as well to Direction of the natural protected area of the Biosfera Reserve Los Petenes for the support and facilities to seagrasses sampling field trips.

References

Agraz-Hernández, CM, Osti-Sáenz J, Chan-Keb G, Expósito-Díaz E, Márquez-García J, Acosta S, Reyes-Castellanos JE, Conde-Medina KP, Cach-Ruiz MY. 2012.Los ecosistemas de manglar en el estado de Campeche: Diagnóstico de la conservación e identificación de áreas potenciales para la restauración. Informe final. Fondos Mixtos del Gobierno del estado de Campeche y Ciencia y Tecnología (CONACyT-Fomix). Universidad Autónoma de Campeche. Clave 1264430, 179.

Álvarez-Góngora, C, Herrera-Silveira JA. 2006. Variations Of Phytoplankton Community Structure Related To Water Quality Trends In A Tropical Karstic Coastal Zone. *Marine Pollution Bulletin* 52:48-60 DOI: 10.1016/j.marpolbul.2005.08.006

Arcega-Cabrera F, Noreña Barroso E, Oceguera-Vargas I. 2014. Lead from hunting activities and its potential environmental threat to wildlife in a protected wetland in Yucatan, Mexico. *Ecotoxicology and Environmental Safety* 100:251–257 DOI: 10.1016/j.ecoenv.2013.11.002

Arellano-Méndez L, Morales-Ojeda SM, Herrera-Silveira JA. 2015. Carbono orgánico de las praderas de *Thalassia testudinum* en Bahía de la Ascensión (Quintana Roo, México). Una primera estimación del contenido de carbono azul en una laguna costera del Caribe Mexicano. In: Estado Actual del Conocimiento del Ciclo del Carbono y sus Interacciones en México: Síntesis, eds. Paz F, Wong J. Texcoco, Estado de México, México. 421-427.

Arellano-Méndez LU, Bello-Pineda J, Aké-Castillo JA, Pérez-España H, Martínez-Cárdenas L. 2016. Distribución espacial y estructura morfométrica de las praderas de *Thalassia testudinum* (Hydrocharitaceae) en dos arrecifes del Parque Nacional Sistema Arrecifal Veracruzano, México. *Revista de Biología Tropical*. 64(2): 427-448.

Aspila KI, Agemian H, Chau SY. 1976. A Semi-automated method for determination of inorganic, organic and total phosphate in sediments. *Analyst* 101:187-197. DOI:10.1039/AN9760100187

Appendini CM, Salles P, Mendoza ET, López J, Torres-Freyermuth A. 2012. Longshore sediment transport on the northern coast of the Yucatan Peninsula. *Journal of Coastal Research*. 28(6):1404-1417 DOI: 10.2112/JCOASTRES-D-11-00162.1

Badan Jr A, Candela J, Sheinbaum J, Ochoa J. 2005. Upper-layer circulation in the approaches to Yucatan Channel. Washington DC *American Geophysical Union Geophysical Monograph Series* 161:57-69.

Bouillon S, Borges AV, Castaneda-Moya E, Diele K, Dittmar T, Duke NC, Kristensen E, Lee SY, Marchand C, Middelburg JJ, Rivera-Monroy VH, Smith III TJ, Twilley RR. 2008. Mangrove production and carbon sinks: A revision of global Budget estimates. *Global Biogeochemical Cycles* 22(2) DOI:10.1029/2007GB003052.

Carmen B, Krause-Jensen D, Alcoverro T, Marbà N, Duarte CM, Van Katwijk MM, Pérez M, Romero J, Sanchez-Lizaso JL, Roca G, Jankowska E. 2019. Recent trend reversal for declining European seagrass meadows. *Nature communications* 10~~(1)~~:1-8 DOI: 10.1038/s41467-019-11340-4

CARICOMP. 2001. CARICOMP Methods Manual - Level I: Manual of methods for mapping and monitoring of physical and biological parameters in the coastal zone of the Caribbean Mona, Kingston, Jamaica. U.S.A. 93

Campbell JE, Fourqurean JW. 2009. Interspecific variation in the elemental and stable isotope content of seagrasses in South Florida. *Marine Ecology Progress Series* 387:109-123 DOI:10.3354/meps08093

Cavazos T, Salinas JA, Martínez B, Colorado G, de Grau P, Prieto-González R, Bravo ME. 2013. Actualización de escenarios de cambio climático para México como parte de los productos de la Quinta Comunicación Nacional. informe, México, *Instituto Nacional de Ecología y Cambio Climático* 150 pages?

Charpy-Roubaud C, Sournia A. 1990. The comparative estimation of phytoplanktonic, Microphytobenthic and macrophytobenthic primary production in the oceans. *Marine Microbial Food Webs* 4~~(1)~~:31-57

Chavez Jr PS. 1988. An improved dark-object subtraction technique for atmospheric scattering correction of multispectral data. *Remote ~~sensing~~ Sensing of ~~environment~~ Environment* 24~~(3)~~:459-479.

Formatted: Font: Italic

Commented [LMG6]: pages?

CONAGUA. 2006. Programa Hidráulico Regional 2002-2006, Península de Yucatán, Región xii. SEMARNAT.

Corbalá JA, Del Río J, García MJ. 2007. Diversidad, distribución y abundancia de moluscos en la región de Los Petenes. Escuela Superior de Ciencias Agropecuarias. Universidad Autónoma de Campeche. Bol. Inf. *JAINA* 17: 1-15.

Costanza R, de Groot R, Sutton P, Van der Ploeg S, Anderson SJ, Kubiszewski I, Farber S, Turner K. 2014. Changes in the global value of ecosystem services. *Global ~~environmental~~ Environmental ~~change~~ Change* 26:152-158 DOI:10.1016/j.gloenvcha.2014.04.002

Dahl M, Deyanova D, Lyimo LD, Näslund J, Samuelsson GS, Mtolera MS, Bjork M, Gullstrom M. 2016. Effects of shading and simulated grazing on carbon sequestration in a tropical seagrass meadow. *Journal of Ecology* 104~~(3)~~:654-664 DOI: 10.1111/1365-2745.12564

Day JW, Domínguez ALL, Herrera-Silveira JA, Kemp GP. 2019. Climate change in areas of the Gulf of Mexico with high freshwater input a review of impacts and potential mitigation. *JAINA. Costas y Mares ante el Cambio Climático* 1~~(1)~~: 87-108.

de Boer WF. 2000. Biomass dynamics of seagrasses and the role of mangrove and seagrass vegetation as different nutrient sources for an intertidal ecosystem. *Aquatic Botany* 66~~(3)~~:225-239 DOI:10.1016/S0304-3770(99)00072-8

Duarte CM, Cebrián J. 1996. The fate of marine autotrophic production. *Limnology and Oceanography* 41:1758-766 DOI: 10.4319/lo.1996.41.8.1758

Duarte CM, Chiscano CL. 1999. Seagrass biomass and production: a reassessment. *Aquatic ~~botany~~ Botany* 65~~(1-4)~~:159-174 DOI: 10.1016/S0304-3770(99)00038-8

Duarte CM, Sintes T, Marbà N. 2013. Assessing the CO_2 capture potential of seagrass restoration projects. *Journal of Applied Ecology* 50~~(6)~~:~~-~~1341-1349 DOI: 10.1111/1365-2664.12155

Duarte CM, Krause-Jensen D. 2017. Export from seagrass meadows contributes to marine carbon sequestration. *Frontiers in Marine Science* volume 4-13 DOI:10.3389/fmars.2017.00013

Duarte CM, Delgado-Huertas A, Anton Gamazo A, Carrillo-de-Albornoz P, López-Sandoval D. C, Duarte A, Manuel C, Delgado-Huertas, Antonio; Anton, Andrea; Carrillo-de-Albornoz, Paloma; López-Sandoval, Daffne C, Agusti S, Hanan A, Marbà N, Hendriks I, Krause-Jensen D, Garcias-Bonet N.2018. Stable isotope ($\delta^{13}C$, $\delta^{15}N$, $\delta^{18}O$, δD) composition and nutrient concentration of Red Sea primary producers. *Frontiers in Marine Science* 5:298 DOI:10.3389/fmars.2018.00298

Duke T, Kruczynski W. 1992. A summary of the report: Status and trends of emergent and submerged vegetated habitats of the Gulf of Mexico, USA. The Environmental and Economic Status of the Gulf of Mexico Gulf of Mexico Program, Stennis, Mississippi. 11-28.

Enríquez S, Pantoja-Reyes NI. 2005. Form-function analysis of the effect of canopy morphology on leaf self-shading in the seagrass *Thalassia testudinum*. *Oecologia* 145~~(2)~~: 234-242. DOI:10.1007/s00442-005-0111-7

Espinoza-Avalos J. 1996. Distribution of seagrasses in the Yucatan Peninsula, Mexico. *Bulletin of ~~marine~~ Marine ~~science~~ Science* 59~~(2)~~: 449-454.

European Space Agency. 2018. Copernicus Sentinel.https://sentinel.esa.int/web/sentinel/missions/sentinel-2. [Accessed 29 april 2018].

Fourqurean JW, Zieman, JC, Powell GV. 1992. Relationships between pore water nutrients and seagrasses in a subtropical carbonate environment. *Marine Biology*. 114(1):57-65 DOI: 10.1007/BF00350856

Fourqurean JW, Zieman, JC. 2002. Nutrient content of the seagrass *Thalassia testudinum* reveals regional patterns of relative availability of nitrogen and phosphorus in the Florida Keys USA. *Biogeochemistry* 61:229-245 DOI:10.1023/A:1020293503405

Commented [LMG7]: Volume?

Campbell JE, Fourqurean JW. 2009. Interspecific variation in the elemental and stable isotope content of seagrasses in South Florida. *Marine Ecology Progress Series* 387:109-123.

Fourqurean JW, Duarte CM, Kennedy H, Marbà N, Holmer M, Mateo MA, Apostolaki ET, Kendrick GA, Krause-Jensen D, McGlathery KJ, Serrano O. 2012a. Seagrass ecosystems as a globally significant carbon stock. *Nature Geoscience* 5(6): 505-509 DOI: 10.1038/ngeo1477

Gacia E, Duarte CM, Middelburg JJ. 2002. Carbon and nutrient deposition in a Mediterranean seagrass (*Posidonia oceanica*) meadow. *Limnology and Oceanography*. 47:1,23-32. doi:10.4319/lo.2002.47.1.0023

Gallegos-Martínez E, Merino M, Marbá N, Duarte CM. 1993. Biomass and dynamics of *Thalassia testudinum* in the Mexican Caribbean: elucidating rhizome growth. *Marine Ecology Progress Series* 185-192 DOI:10.3354/meps095185

Garcias-Bonet N, Delgado-Huertas A, Carrillo-de-Albornoz P, Anton A, Almahasheer H, Marbà N, Hendriks IE, Krause-Jensen D, Duarte CM. 2019. Carbon and nitrogen concentrations, stocks, and isotopic compositions in Red Sea seagrass and mangrove sediments. *Frontiers in Marine Science* 6:267 DOI: 10.3389/fmars.2019.00267

Grivel-Piña F. 1992. Tablas de Predicción de Mareas. Puertos del Golfo de México y Mar Caribe. Datos Geofísicos Serie A. *Oceanografía. Instituto de Geofísica Universidad Nacional. Autónoma de México*.

Hackney JW, Durako MJ. 2004. Size frequency patterns in morphometric characteristics of the seagrass Thalassia testudinum reflect environmental variability. *Ecological Indicators* 4(1) 55-71 DOI:10.1016/j.ecolind.2003.12.001

Hall MO, Durako MJ, Fourqurean JW, Zieman, JC. 1999. Decadal changes in seagrass distribution and abundance in Florida Bay. *Estuaries* 22(2): 445-459 DOI:10.2307/1353210

Hemminga MA, Nieuwenhuize J. 1990. Seagrass wrack-induced dune formation on a tropical coast (Banc d'Arguin, Mauritania). *Estuarine, Coastal and Shelf Science* 31: 499-502 DOI: 10.1016/0272-7714(90)90040-X

Hendriks IE, Sintes T, Bouma TJ, Duarte CM. 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 DOI:10.3354/meps07316.

Herrera-Silveira JA, Comín FA. 2000. An introductory account of the types of aquatic ecosystems of Yucatan Peninsula (SE Mexico). In: EcoVision World Monographs Series. *Aquatic Ecosystems of Mexico: Status and Scope, eds. Munawar, M, Lawrence SG, Munawar IF, Malley DF. Backhuys Pub., Leiden* 213-227

Herrera-Silveira JA, Morales-Ojeda SM. 2009. Evaluation of the health status of a coastal ecosystem in southeast Mexico: Assessment of water quality, phytoplankton and submerged aquatic vegetation. *Marine Pollution Bulletin* 59:72-86 DOI: 10.1016/j.marpolbul.2008.11.017

Herrera-Silveira JA, Pech-Cardenas MA, Morales-Ojeda SM, Cinco-Castro S, Camacho-Rico A, Sosa JP, Teutli-Hernandez C. 2020. Blue carbon of Mexico, carbon stocks and fluxes: a systematic review. *PeerJ* 8:e8790. DOI:10.7717/peerj.8790

Hernández MVF. 2000. Nitrógeno, fósforo y cociente C/N en los sedimentos superficiales de la laguna de Chacopata, Sucre, Venezuela. *Revista de Biología Tropical* 261-268.

Howard J, Hoyt S, Isensee K, Pidgeon E, Telszewski M. 2014. Coastal Blue Carbon: Methods for assessing carbon stocks and emissions factors in mangroves, tidal salt marshes, and seagrass meadows. Conservation International, Intergovernmental Oceanographic Commission of UNESCO, International Union for Conservation of Nature. Arlington, Virginia, USA. 180.

Howard J, Sutton-Grier A, Herr D, Kleypas J, Landi E, Mcleod E, Pidgeon E, Simpson S. 2017. Clarifying the role of coastal and marine systems in climate mitigation. *Frontiers in Ecology and the Environment* 5(1): 42-50 DOI:10.1002/fee.1451

Jorgensen SE, Xu FL, Salas F, Marques JC. 2005. Application of indicators for the assessment of ecosystem health. Eds. Jurgensen SE, Constanza R. Handbook of Ecological Indicators for Assessment of Ecosystem Health, USA: *Taylor & Francis*.6.

Kantun-Manzano CA, Arcega-Cabrera F, Derrien M, Noreña-Barroso E, Herrera-Silveira JA. 2018. Submerged groundwater discharges as source of fecal material in protected karstic coastal areas. In protected karstic coastal areas. *Geofluids* 11 DOI:10.1155/2018/9736260

Koch EW. 2001. Beyond light: Physical, geological and geochemical parameters as possible submersed aquatic vegetation habitat requirements. *Estuaries* 24: 1-17 DOI:10.2307/1352808

Koch EW, Ackerman JD, Verduin J, van Keulen M. 2006. Fluid dynamics in seagrass ecology from molecules to ecosystems. In Seagrasses: biology, ecology and conservation. Springer, Dordrecht 193-225

Laffoley D, Grimsditch G. 2009. The Management of Natural Coastal Carbon Sinks. IUCN. Gland, Switzerland.

Lee KS, Park SR, Kim YK. 2007. Effects of irradiance, temperature, and nutrients on growth dynamics of seagrasses: a review. *Journal of Experimental Marine Biology and Ecology* 350(1-2):144-175 DOI:10.1016/j.jembe.2007.06.016

Lirman D, Cropper WP. 2003. The influence of salinity on seagrass growth, survivorship, and distribution within Biscayne Bay, Florida: field, experimental, and modeling studies. *Estuaries* 26(1): 131-141 DOI:10.1007/BF02691700

López BM, Sierra AP. 1998. Circulación del Golfo de México inducida por mareas, viento y la corriente de Yucatán. *Ciencias Marinas* 24(1):65-93.

Mateo MA, Romero J. 1997. Detritus dynamics in the seagrass *Posidonia oceanica*: elements for an ecosystem carbon and nutrient budget. *Marine Ecology Progress Series* 151:43-53. DOI:10.3354/meps151043

McKenzie LJ. 2003. Guidelines for the rapid assessment and mapping of tropical seagrass habitats. Department of Primary Industries. *The State of Queensland* 17-18.

Macklin PA, Suryaputra IGNA, Maher DT, Murdiyarso D, Santos IR. 2019. Drivers of CO_2 along a mangrove-seagrass transect in a tropical bay: Delayed groundwater seepage and seagrass uptake. *Continental Shelf Research* 172:57-67 DOI: 10.1016/j.csr.2018.10.008

Mateo-Cid LE, Mendoza-González AC, Ávila-Ortiz AG, Díaz-Martínez S. 2013. Algas marinas bentónicas del litoral de Campeche, México. *Acta botánica mexicana* 104:3-92

McLeod E, Chmura GL, Bouillon S, Salm R, Björk M, Duarte CM, Lovelock CE, Schlesinger WH, Silliman BR. 2011. A blueprint for blue carbon: toward an improved understanding of the role of vegetated coastal habitats in sequestering CO_2. *Frontiers in Ecology and the Environment* 9 (10): 552-560 DOI: 10.1890/110004

Melaku D, Solidoro C, Umgiesser G. 2003. Modelling the responses of the lagoon of Venice ecosystem to variations in physical forcing. *Ecological Modeling* 170:265-289
Mellors J, Marsh H, Carruthers TJ, 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

Nellemann C, Corcoran E, Duarte CM, Valdés L, De Young C, Fonseca L, Grimsditch G. 2009. Blue carbon. A Rapid Response Assessment. United Nations Environment Programme, *GRID-Arendal* 78.

Olesen B, Enríquez S, Duarte CM, Sand-Jensen K. 2002. Depth acclimation of photosynthesis, morphology and demography of *Posidonia oceanica* and *Cymodocea nodosa* in the Spanish Mediterranean Sea. *Marine Ecology Progress Series* 236:89-97 DOI: 10.3354/meps236089

Orth RJ, Carruthers TJB, Dennison WC, Duarte CM, Fourqurean JW, Heck KL, Hughes, Gary AR, Kendrick A, Kenworthy WJ, Olyarnik S, Short FT, Waycott M, Williams SL.2006. A Global Crisis for Seagrass Ecosystems, *BioScience* 56(12): 987-96 DOI:10.1641/0006-3568(2006)56[987:AGCFSE]2.0.CO;2

Parnell AC, Inger R, Bearhop S, Jackson AL. 2010. Source partitioning using stable isotopes: coping with too much variation. *PLoS ONE* 5(3): e9672.

Parnell AC, Phillips DL, Bearhop S, Semmens BX, Ward EJ, Moore JW, Jackson AL, Grey J, Kelly DJ, Inger R. 2013. Bayesian stable isotope mixing models. *Environmetrics* 24(6):387-399 DOI:10.1002/env.2221

Pérez-Espinosa I, Gallegos-Martínez ME, Ressl RA, Valderrama-Landeros LH, Hernández- Cárdenas G. 2019. Spatial distribution of seagrasses and submerged aquatic vegetation of los Petenes, Campeche. *Terra Digitalis* 3(2):1-37 DOI: 10.22201/igg.25940694.2019.2.56

Peterson BJ, Howarth RW. 1987. Sulfur, carbon, and nitrogen isotopes used to trace organic matter flow in the salt-marsh estuaries of Sapelo Island. *Georgia Limnology Oceanography* 32:1195-1213 DOI:10.4319/lo.1987.32.6.1195

Samper-Villarreal J, Lovelock CE, Saunders MI, Roelfsema C, Mumby PJ. 2016. Organic carbon in seagrass sediments is influenced by seagrass canopy complexity, turbidity, wave height, and water depth. *Limnology and Oceanography* 61(3): 938-952 DOI: 10.1002/lno.10262

Serrano O, Lavery PS, Rozaimi M, Mateo MÁ. 2014. Influence of water depth on the carbon sequestration capacity of seagrasses. *Global Biogeochemical Cycles* 28(9): 950-961. DOI:0.1002/2014GB004872

Short FT, Davis MW, Gibson RA, Zimmermann CF. 1985. Evidence for phosphorus limitation in carbonate sediments of the seagrass *Syringodium filiforme*. *Estuarine, Coastal and Shelf Science* 20(4):419-430 DOI: 10.1016/0272-7714(85)90086-1

Short F, Carruthers T, Dennison W, Waycott M. 2007. Global seagrass distribution and diversity: a bioregional model. *Journal of Experimental Marine Biology and Ecology* 350(1): 3-20 DOI: 10.1016/j.jembe.2007.06.012

Signa G, Mazzola A, Kairo J, Vizzini S. 2017. Small-scale variability in geomorphological settings influences mangrove-derived organic matter export in a tropical bay. *Biogeosciences* 14(3): 617-629 DOI: 10.5194/bg-14-617-2017.

Song C, Woodcock CE, Seto KC, Lenney MP, Macomber SA. 2001. Classification and change detection using Landsat TM data: when and how to correct atmospheric effects?. *Remote Sensing of Environment* 75:230-244 DOI: 10.1016/S0034-4257(00)00169-3

Strickland JD, Parsons TR. 1972. A practical handbook of seawater analysis. *Fisheries Research Board of Canada*. Ottawa. 310.

Tanaya T, Watanabe K, Yamamoto S, Hongo C, Kayanne H, Kuwae T. 2018. Contributions of the direct supply of belowground seagrass detritus and trapping of suspended organic matter to the sedimentary organic carbon stock in seagrass meadows. *Biogeosciences* 15(13): 4033-4045. DOI: 10.5194/bg-15-4033-2018

Thorhaug A, Poulos HM, López-Portillo J, Ku TC, Berlyn GP. 2017. Seagrass blue carbon dynamics in the Gulf of Mexico: Stocks, losses from anthropogenic disturbance, and gains through seagrass restoration. *Science of the Total Environment* 605:626-636. DOI: 10.1016/j.scitotenv.2017.06.189

Tribble GW. 1981. Reef-basel herbivores and the distribution of two seagrasses (*Syringodium filiforme* and *Thalassia testudinum*) in the San Blas Islands (Western Caribbean). *Marine Biology* 65(3): 277-281 DOI:10.1007/BF00397122

Tomasko, D. A., & Lapointe, B. E. 1991. Productivity and biomass of *Thalassia testudinum* as related to water column nutrient availability and epiphyte levels: field observations and experimental studies. Marine ecology progress series, 9-17.

Vaslet A, Bouchon-Navarro Y, Harmelin-Vivien M, Lepoint G, Louis M, Bouchon C. (2015). Foraging habits of reef fishes associated with mangroves and seagrass beds in a Caribbean lagoon: A stable isotope approach. *Ciencias marinas* 41(3): 217-232. DOI:10.7773/cm.v41i3.2494

van Tussenbroek BI. 1998. Above-and below-ground biomass and production by *Thalassia testudinum* in a tropical reef lagoon. *Aquatic Botany* 61(1): 69-82 DOI: 10.1016/S0304-3770(98)00058-8 van Tussenbroek BI, Cortés J, Collin R, Fonseca AC, Gayle PM, Guzman HM, Rodríguez-Ramírez, A. 2014. Caribbean-wide, long-term study of seagrass beds reveals local variations, shifts in community structure and occasional collapse. *PloS ONE* 9:3 DOI: 10.1371/journal.pone.0090600

Vollenweider RA, Giovanardi F, Montanari G, Rinaldi A. 1998. Characterization of the trophic conditions of marine coastal waters with special reference to the NW Adriatic Sea: proposal for a trophic scale, turbidity and generalized water quality index. *Environmetrics: The official journal of the International Environmetrics Society* 9(3):329-357.

Waycott M, Duarte CM, Carruthers TJ, Orth RJ, Dennison WC, Olyarnik, S. 2009. Accelerating loss of seagrasses across the globe threatens coastal ecosystems. *Proceedings of the national academy of sciences* 106(30):12377-12381 DOI: 10.1073/pnas.0905620106.

Zieman J, Fourqurean JW, Iverson RL. 1989. Distribution, abundance and productivity of seagrasses and macroalgae in Florida Bay. *Bulletin of marine science* 44(1):292-311.