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The Contribution of Subtidal Seagrass Meadows to the Total Carbon Stocks of Gazi Bay, Kenya

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Abstract: Seagrass beds occur globally in both intertidal and subtidal zones within shallow marine environments, such as bays and estuaries. These important ecosystems support fisheries production, attenuate strong wave energies, support human livelihoods and sequester large amounts of CO_2 that may help mitigate the effects of climate change. At present, there is increased global interest in understanding how these ecosystems could help alleviate the challenges likely to face humanity and the environment into the future. Unlike other blue carbon ecosystems, i.e., mangroves and saltmarshes, seagrasses are less understood, especially regarding their contribution to the carbon dynamics. This is particularly true in regions with less attention and limited resources. Paucity of information is even more relevant for the subtidal meadows that are less accessible. In Kenya, much of the available information on seagrasses comes from Gazi Bay, where the focus has been on the extensive intertidal meadows. As is the case with other regions, there remains a paucity of information on subtidal meadows. This limits our understanding of the overall contribution of seagrasses in carbon capture and storage. This study provides the first assessment of the species composition and variation in carbon storage capacity of subtidal seagrass meadows within Gazi Bay. Nine seagrass species, comprising of *Cymodocea rotundata*, *Cymodocea serrulata*, *Enhalus acoroides*, *Halodule uninervis*, *Halophila ovalis*, *Halophila stipulacea*, *Syringodium isoetifolium*, *Thalassia hemprichii*, and *Thalassodendron ciliatum*, were found. Organic carbon stocks varied between species and pools, with the mean below ground vegetation carbon (bgc) stocks (5.1 ± 0.7 Mg C ha^{-1}) being more than three times greater than above ground carbon (agc) stocks (0.5 ± 0.1 Mg C ha^{-1}). Mean sediment organic carbon stock (sed C_{org}) of the subtidal seagrass beds was 113 ± 8 Mg C ha^{-1}. Combining this new knowledge with existing data from the intertidal and mangrove fringed areas, we estimate the total seagrass ecosystem organic carbon stocks in the bay to be 196,721 Mg C, with the intertidal seagrasses storing about 119,790 Mg C (61%), followed by the subtidal seagrasses 55,742 Mg C (28%) and seagrasses in the mangrove fringed creeks storing 21,189 Mg C (11%). These findings are important in highlighting the need to protect subtidal seagrass meadows and for building a national and global data base on seagrass contribution to global carbon dynamics.

Keywords: subtidal; blue carbon; climate change; Africa

1. Introduction

The value of seagrass ecosystems as natural carbon sinks is currently of interest [1–4], with recent studies highlighting the paucity and restrictive information across the globe [5,6]. Seagrass meadows have a large carbon storage capacity due to their extensive distribution [4,5] and there have been significant efforts to quantify and understand the factors that affect carbon storage from various habitats and across different bioregions [5–10]. Much of this effort, however, has focused on intertidal seagrass meadows (e.g., an ISI Web of Science search reveals 27 peer reviewed articles on intertidal seagrass carbon stocks vs. 12 for subtidal seagrasses), with comparatively fewer studies examining the contribution of subtidal seagrass meadows to carbon storage [6,10–12]. Partly, this is due to the difficulties (and financial costs) of conducting subtidal research and because of poor water quality (e.g., turbidity) in many regions, including the Western Indian Ocean, which hamper accurate estimates of total seagrass extent and structure [13–15]. As a result, it is common for substantial underestimates of the total carbon stocks of seagrass ecosystems in many parts of the globe. Subtidal environments have lower irradiance, due to diffusion through the water column, than intertidal meadows [6,16–18]. This can result in lower primary production and biomass accumulation, when compared to intertidal environments [16,18]. However, because subtidal meadows are subjected to more subtle and less variable environmental conditions, they can, conversely, have higher carbon stocks than intertidal meadows [18,19]. Intermittent exposure to air, higher irradiance, and extreme tidal currents and wave action reduces carbon gains in seagrass tissue, as well as reducing deposition, increasing aeration, and promoting sediment erosion in intertidal meadows [19]. As a result, subtidal meadows are expected to have higher carbon stocks and sequestration rates than intertidal meadows [18]. There is a need to consider subtidal environments and understand habitat conditions that drive carbon storage within these environments, which will assist in obtaining accurate estimates.

The ability of seagrass species to store carbon varies significantly due to differences in primary production, habitat conditions, belowground biomass, and the type of the recalcitrant material that is resistant to decomposition [6,18,20–22]. Additionally, the ability of canopies to filter and accumulate allochthonous carbon also explains some of the variation in carbon storage among species [2,4,6]. Specific factors in their sediments, including granulometry and redox that drive organic carbon preservation, also vary among species and locations [18,21,22]. The diverse range of depositional environments and hydrodynamic factors that act on the sediments affect organic carbon preservation by determining the proportion of fine particles in the soils [18,23]. Anaerobic conditions in the sediments facilitate consolidation of carbon through slow decomposition rates [21,22]. In addition to accumulation of autochthonous carbon, seagrass meadows facilitate the settlement of suspended particles from the water column by reducing water velocity, and thus promote sediment accumulation and stabilization [4], which translates to the deposition of imported carbon from adjacent ecosystems [2,24]. Regardless of the species, seagrass meadows face degradation globally, which can result in the loss of critical ecological goods and services [25,26]. Meadow degradation contributes to global emissions, releasing up to 299 Tg C yr^{-1}, which significantly contributes to global warming [5,26]. Estimating the carbon stock of different species in different environmental settings and measuring their collective contribution to climate change mitigation is critical to raise global awareness of seagrass conservation and protection [1,4,26,27].

The objective of this study was to improve our understanding of the entirety of the seagrass ecosystems of Gazi Bay by pooling information on subtidal, intertidal and fringing meadows. The aims of the study were as follows: (1) to investigate the species composition, distribution and abundance of subtidal seagrass beds of Gazi Bay, (2) assess the physico-chemical properties in the sub tidal area, (3) estimate below and above ground seagrass carbon stocks in the subtidal zone, and (4) to estimate total ecosystem carbon stocks by adding this new data to existing data from intertidal meadows and mangrove lined creeks. Because of its high seagrass diversity and cover, Gazi Bay is one of Kenya's most important ecological sites and a test-case for seagrass systems regionally. The bay contains all the 12 species recognized along the East African coast, and their distribution extends from intertidal to subtidal areas, as well as sandy and rocky substrates. However, the bay's seagrass ecosystem is deteriorating, primarily due to increased herbivory, sedimentation and beach seining practiced by small-scale artisanal fishermen, and it is not under any official protection by the law [14]. This bay was chosen as an excellent case study to quantify the contribution of subtidal seagrass to total carbon stock because recent work on carbon stocks in Gazi Bay [14,15,28] has, up until now, focused on the intertidal seagrasses. To our knowledge, this study is among the few studies globally on carbon storage in subtidal meadows that provides the first estimates of carbon stock data from subtidal meadows in Gazi Bay and contributes to this much-needed information. The findings of this study will inform prospects for incorporating seagrasses into payment for ecosystem services schemes, alongside mangrove ecosystems.

2. Materials and Methods

2.1. Description of the Study Area

This study was conducted in Gazi Bay (4°25′ S, 39°31′ E) located along the Kenyan south coast in Kwale County, 50 km south of Mombasa (Figure 1). The bay is a tropical semi-enclosed shallow coastal water system [29], with a total surface area of approximately 17 km^2 [30].

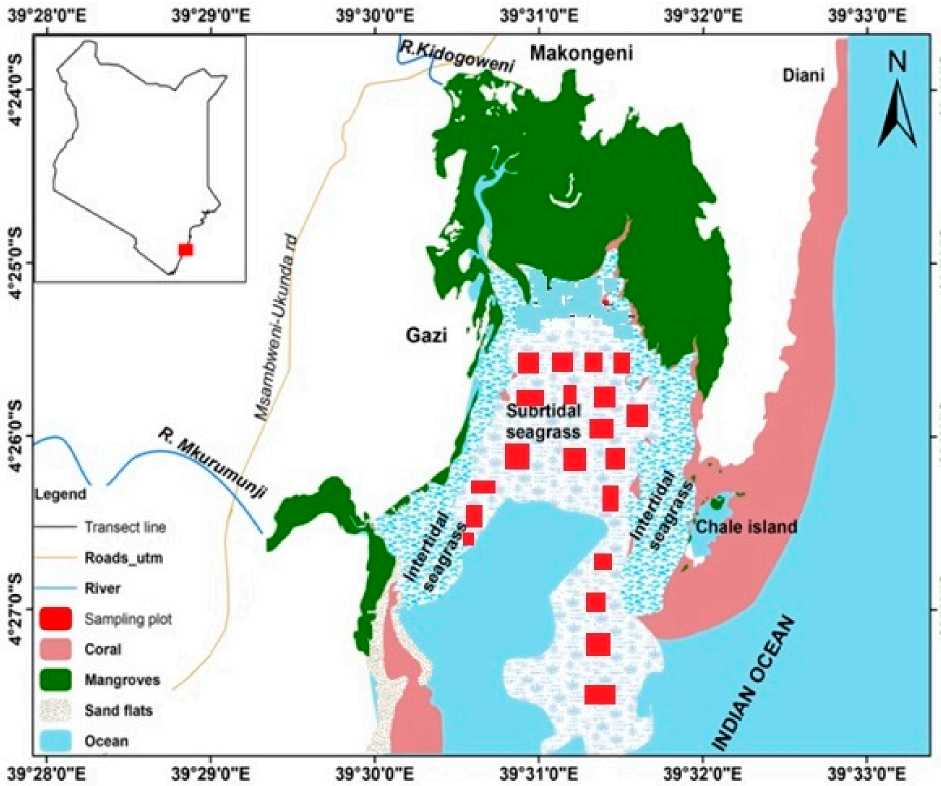

Figure 1. Map of Gazi Bay, indicating the sampling points in subtidal seagrass area. Source: [31].

The embayment is protected from strong waves by the Chale peninsular located to the east and a fringing reef to the south, and has a shallow, wide opening to the open ocean [29]. Freshwater flows into the area via the River Kidogoweni in the northwest and River Mkurumudzi in the southwest of the bay [29]. Kinondo creek, located in the northeastern side of the bay, is the only channel that lacks fresh water supply and is regulated by tidal movements.

The climate of Gazi Bay can be classified as tropical wet/dry according to the Köppen climate classification [32]. The southeast monsoon period (Kuzi) is a wet season associated with heavy rains and rough seas usually from March to August. This is followed by the northeast monsoons (Kazkazi), which is a dry period characterized by calm seas from November to March [33]. Gazi's annual total rainfall ranges from 1000 mm to 1600 mm. Temperatures range from 22 to 34 °C during the northeast monsoon season, and 19 to 29 °C during the southeast monsoon season. Humidity is high, and averages 80% all year round [29]. The tidal cycle in Gazi Bay is semi diurnal, with an amplitude varying between 0.7 m at neap tide and 2.90 m at spring tide [33].

Gazi Bay is characterized by mangroves, seagrasses, macroalgae and coral reefs, with seagrasses covering about 70% of the total bay area [30]. The geomorphological characteristic of Gazi Bay facilitates the exchange and circulation of organic matter across the continuum [34,35]. There is a noticeable gradient in the distribution of organic matter across the ecosystems, which is mainly driven by riverine export and tidal influence [35]. Organic material from the mangrove forest is retained in the adjacent seagrass beds along Kinondo creek, whereas in Kidogoweni creek, mangrove material is widely dispersed into the bay, particularly in the wet season [35,36]. In the southern part of the bay, terrestrial organic matter flows into the bay through River Mkurumudzi [35]. Other less dominant sources of organic matter in Gazi Bay include brown macroalgae and bacteria, which are also the main mineralizers of organic detritus in the Bay [36].

Seagrass meadows in Gazi Bay face pressure from fishing activities, especially the use of seine and drag nets [14,37], as well as sedimentation [38]. In addition, selective fishing, especially for lobsters, leads to increased herbivory. In the last two decades, these are thought to have accelerated the loss of seagrass cover at a pace of 1.68 percent per year [38].

2.2. Sampling Design

The revised Intergovernmental Panel on Climate Change (IPCC) carbon accounting standards for coastal wetlands and the sampling methodologies recommended by the Coastal Blue Carbon manual were applied [14,39,40]. The area of subtidal seagrass in Gazi Bay was estimated after classifying the seagrass area in the bay using shapefiles from [38], as well as field in-situ validation. Seagrass areas less than 3 m deep during high tides in the bay area were classified as inter-tidal, while seagrass areas deeper than 3 m deep were classified as sub-tidal. Based on this classification, the subtidal seagrass area was estimated to be 470 ha. A systematic random sampling approach was used to identify sampling sites within the subtidal zone of the bay.

Four zones in the subtidal area were identified, starting from the mean low water at spring tide (mlws), heading into the lagoon (Figure 2a). In each of these zones, two parallel transects measuring 300 m long and 50 m apart were established, and five sampling points were marked along each transect (Figure 2b). Samples were collected from quadrats measuring 0.25 m^2 placed 60 m apart along each transect. Three divers were sent to collect seagrass and sediment samples, while two field assistants remained on the boat to help with sorting, labelling and packing of the collected samples.

2.2.1. Measurement of Physicochemical Parameters

Measurement of the physicochemical parameters of seawater was carried out in situ, in every quadrat, during low tides. Total dissolved solids (mg/L), water temperature (°C), salinity and pH were measured using the YSI Professional Plus handheld multiparameter meter W14-05. Depth was measured using a dive computer. These measurements were obtained only once. Because environmental variables change with the seasons, these measurements present a snapshot.

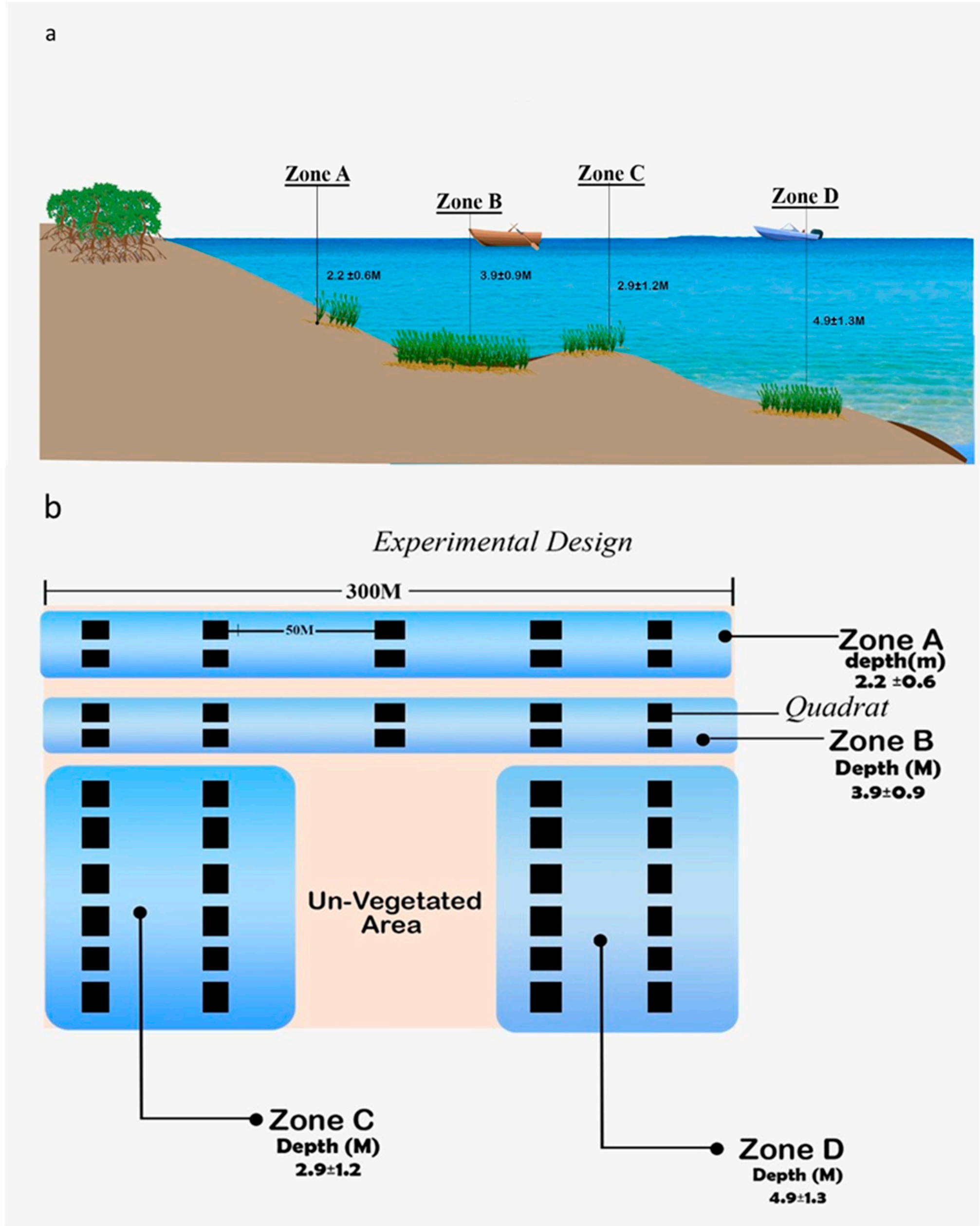

Figure 2. Diagrammatic representations of sampling design within the subtidal zone of Gazi Bay: (**a**) generalized north-to-south transect showing mean depth, and (**b**) aerial view showing the spatial arrangement of replicate sampling sites within each zone.

2.2.2. Determination of Seagrass Meadow Structure

At each sampling point, a quadrat measuring 0.25 m^2 was placed on the vegetation and a photograph was taken from a standard height of 1 m above the surface. Percentage cover was determined, with the aid of percentage cover guide by seagrass net [41]. All the shoots in the quadrat were harvested, packed in pre-labeled zip lock bags and taken to the laboratory. Species identification was carried out in the laboratory using a field identification guide [42], shoots counted, and heights of 10% of the shoots measured. Following this, the shoots and leaves were scrapped gently with a scalpel to remove epiphytes.

2.2.3. Determination of above and belowground Carbon

The harvested aboveground material (shoots and leaves) from each quadrat were weighed and then oven dried at 60 °C for 72 h to achieve a constant weight [14,39], after which a record was taken.

Within the same quadrats where the above ground samples were taken, two cores were taken (totaling 20 cores per sampling zone and 80 cores across the entire subtidal area) using a PVC corer (6 "internal diameter, 50 cm long). The corers were physically pushed into the sediment up to a depth of 50 cm or until bedrock was struck. The corer was then retrieved, and the intact core taken to the boat. The roots, rhizomes and necromass were washed and later sieved to separate from the sediment matrix and put into labeled ziplock bags for transport to the laboratory. The roots, rhizomes and necromass were further rinsed with distilled water, separated into species and oven dried for 72 h at 60 °C to a constant weight. They were then weighed and the dry weights recorded.

Standing stock (both above and belowground) was converted to its carbon equivalent as described by [39,40,43], demonstrated by the following equation:

$$\text{AGB/BGB (kg C/m}^2\text{)} = (\text{plant biomass} \times (0.34))/0.25(\text{m}^2)$$

where 0.34 is the carbon conversion factor, 0.25 m^2 is the area of the quadrat.

The general carbon conversion factor of 0.34 was used due to a lack of site-specific organic carbon values for seagrass in Gazi Bay measured directly using an elemental analyzer. This is recommended in both the coastal blue carbon manual and the IPCC 2014 [39,40].

2.2.4. Determination of Sediment Organic Carbon (Corg)

Two additional PVC cores (3" internal diameters, 50 cm long) were used to obtain sediment samples. These corers were pushed 50 cm into the sediments, retrieved, covered with a stopper and taken to the boat for extraction, in which the corer was placed on a clean cutting board and a wooden plunger inserted at the bottom end of the corer, after which the corer was carefully pulled over the plunger. However, a shallow geological limestone feature across the subtidal area of Gazi Bay meant that some cores obtained were less than 50 cm. The samples were sliced into 5 cm subsamples and stored in pre-labeled ziplock bags and taken to the laboratory. Samples were then oven dried for 72 h at 60 °C to a constant weight. The dry sediment samples were then weighed using a weighing balance and their dry weights recorded.

After that, the dry bulk density (DBD) of each sediment sample was computed, and all the sections in the core were pooled together.

$$\text{Dry bulk density (DBD) (g/cm}^3\text{)} = \text{dry weight of sample (g)/volume of dry soil sample (cm}^3\text{)}$$

where

$$\text{Volume of dry soil sample} = [\pi \times (\text{radius of corer})^2] \times (\text{height of the sample})$$

The dry samples were homogenized using a mortar and pestle and sieved to remove the shell and roots. These were then divided into duplicate sub-samples of 5 g each for determination of organic carbon content using the loss on ignition (LOI) technique [42]. Soil samples were ashed in a furnace at 450 °C for 6 h and organic matter loss used as a proxy for organic carbon. Percentage LOI was calculated as follows:

$$\%\ \text{LOI} = (\text{weight before ashing-weight after ashing})/\text{weight before ashing} \times 100\%$$

Carbon content in the ashed samples was obtained using the carbon conversion factors for seagrass soils [39].

$$(\%\ C_{org} = 0.43 \times \%\text{LOI} - 0.33)\ r^2 = 0.96 \text{ for seagrass soils with } \%\text{LOI} > 0.2$$

$$(\%\ C_{org} = -0.21 + 0.40 \times \%LOI)\ r^2 = 0.87 \text{ in seagrass soils with } \%LOI < 0.2$$

Soil carbon density was calculated for all the soil samples in each core and summed. We present carbon estimates for a maximum depth of 50 cm, or when this was not achieved (due to meeting substrate resistance), for the maximum depth achieved (e.g., the minimum was 30 cm). While some studies and sampling guides recommend extrapolating data to 1 m (to permit global comparison), we did not feel that this was warranted in Gazi Bay due to its unique and relatively shallow geological features. Thus, we feel that the values presented here are a robust and true assessment of the carbon stocks in study area. Because of the core used, compression was found to be <15%. This was assessed by measuring and recording the difference in length from the upper part of the core to the sediment surface, inside and outside the corer, when the corer was in the sediment. This was applied to corrections in core lengths. Total amount of carbon in the subtidal area was determined by summing up the average carbon stocks from each pool (to a maximum depth of 50 cm) and multiplying this with the area of seagrass meadows in the subtidal area. The variabilities and errors associated with the measurements were determined by calculating the standard deviation for each pool and multiplying it by the subtidal area.

2.3. Data Analysis

Statistical analysis was carried out in SPSS (Version 25.0. Armonk, NY, USA: IBM Corp). Assumptions of normality and homogeneity of the response variables (AGB, BGB and sediment carbon) were tested using the Kolmogorov–Smirnov test for normality. Where assumptions were not met, the data were log transformed, and if it failed to conform, a non-parametric equivalent was used. A Student's *t*-test was used to determine the variation in the above and below ground carbon stocks within the subtidal seagrass meadows of the bay. Two-way ANOVA was used to test for significant differences in above, belowground biomass, as well as sediment carbon among the dominant species, as well as among the zones in subtidal zone. *t*-Test was used to test for variation in the sediment carbon stocks between mono-specific and mixed seagrass meadows. The relationships between the above ground parameters and biomass were tested using Spearman's correlation. In all these tests, the level of significance was set at α 0.05.

3. Results

3.1. Physico-Chemical Properties in the Sub Tidal Area

Mean depth in the sub tidal area was 3.4 ± 0.2 m, with a range of 1.2–7.4 m during low spring tide. Mean temperature was 28.6 ± 0.1 °C, with a range of 27.9–29.3 °C. Salinity ranged between 35 and 36.6‰ in the sub tidal area, with a mean value of 35.3 ± 0.2‰, while mean pH was 7.8 ± 0.1, with a range of 7.5–8.1 Turbidity ranged between 34,580 and 35,815 mg/L, with a mean value of 35,003 ± 47.3 mg/L.

All the physico-chemical parameters significantly varied among the four zones in the subtidal area (Table 1). Depth varied significantly among the four zones in the subtidal area ($F(3, 40) = 12.601$, $p < 0.05$). Zone A was significantly shallower than Zone B ($p = 0.001$) and Zone D ($p = 0.000$), while Zone D was significantly deeper than zone A ($p = 0.00$) and zone C ($p = 0.00$).

Table 1. Environmental factors in the four zones in the subtidal area of Gazi Bay (mean ± SD).

Area	Depth (m)	Temp (°C)	Salinity (ppt)	pH	TDS (mg/L)
Zone A	2.2 ± 0.6	28.9 ± 0.4	35.8 ± 0.5	7.8 ± 0.1	35,340.5 ± 370
Zone B	3.9 ± 0.9	28.7 ± 0.3	35.6 ± 0.2	7.8 ± 0.1	35,062.9 ± 163
Zone C	2.9 ± 1.2	28.5 ± 0.3	35.3 ± 0.2	7.8 ± 0.1	34,877.9 ± 185
Zone D	4.9 ± 1.3	28.2 ± 0.4	35.1 ± 0.1	7.7 ± 0.1	34,661.3 ± 46

Temperature varied significantly among the four zones ($F (3, 40) = 5.852$, $p < 0.05$). Temperature was statistically significantly higher in Zone A compared to Zone D ($p = 0.002$). Temperature was also significantly higher in Zone B compared to Zone D ($p = 0.013$).

Salinity varied significantly among the four zones in the subtidal area ($F (3, 40) = 11.381$, $p < 0.05$). Salinity was significantly higher in Zone A than Zone C ($p = 0.002$) and Zone D ($p = 0.00$). Zone B had significantly higher salinity levels that Zone D ($p = 0.001$).

pH also varied significantly among the four zones in the subtidal area ($F (3, 40) = 5.304$, $p < 0.05$). Zone A was significantly higher in pH concentration than Zone D ($p = 0.019$). Zone B was also significantly higher than Zone D ($p = 0.01$), and Zone C was also higher than Zone D ($p = 0.004$).

TDS varied significantly among the four zones in the subtidal area ($F (3, 40) = 15.654$, $p <.05$). Zone A was significantly more turbid than Zone B ($p = 0.022$), Zone C ($p < 0.00$) and Zone D ($p = 0.00$). Zone B was significantly more turbid than Zone D (0.001), while zone D was significantly less turbid than Zone A ($p = 0.000$) and B ($p = 0.001$). (Table 1).

3.2. Subtidal Seagrass Species Composition, Distribution and Structure within Gazi Bay

3.2.1. Seagrass Species Composition

Nine seagrass species that belong to three families, namely Zosteracea, Hydrocharetacea and Cymodoceaceae, were identified in the subtidal area of Gazi Bay. These include *C. rotundata* Asch. & Schweig, *C. serrulata* (Braun) Asch. & Magnus, *E. acoroides* (L.f.) Royle, *H. uninervis* (Forssk.) Asch, *H. ovalis* (Braun) Hooker, *H. stipulacea* (Forssk.) Asch., *S. isoetifolium* (Asch.) Dandy, *T. hemprichii* (Ehrenb.) Asch., and *T. ciliatum* (Forssk.) den Hartog.

3.2.2. Seagrass Species Distribution

C. serrulata was found in three zones, whereas *E. acoroides* and *C. rotundata* were only found in Zone B. *T. ciliatum* was found in deeper Zones C and D (Table 2).

Table 2. Distribution of seagrass species in the subtidal zone, + = presence, - = absence.

Species	Zone A	Zone B	Zone C	Zone D
C. serrulata	+	-	+	+
T. hemprichii	+	+	-	-
C. rotundata	-	+	-	-
H. uninervis	-	+	+	-
E. acoroides	-	+	-	-
S. isoetifolium	-	+	+	-
H. stipulacea	-	-	+	+
H. ovalis	-	-	+	-
Thalassodendron ciliatum	-	-	+	+

T. hemprichii, *T. ciliatum* and *C. serrulata* had the highest frequency of occurrence, while *E. acoroides* and *H. ovalis* had the lowest frequency in the subtidal zone (Table 3).

Table 3. Frequency of occurrence of seagrass species within plots in the subtidal area of Gazi Bay.

Species	Frequency	% Frequency
C. rotundata	5	6.3
C. serrulata	12	15
E. acoroides	2	2.5
H. uninervis	8	10
H. ovalis	1	1.3
H. stipulacea	7	8.8
S. isoetifolium	8	10
T. hemprichii	23	28.7
T. ciliatum	14	17.4

3.2.3. Seagrass Meadow Structure

The average percentage canopy cover across the subtidal area was 57.2 ± 2.2%, with a range of 40–90%, while the mean canopy height was 20.4 ± 1.9 cm, ranging between 5.0 cm and 61.4 cm. Additionally, the mean seagrass density was 666 ± 61 shoots per m^2, with a range of 16–1792 shoots per m^2. *E. acoroides* had the highest canopy height (49.2 ± 0.4 cm), followed by *T. ciliatum* (41.8 ± 0.8 cm). *H. ovalis and H. stipulacea* had the lowest canopy height, with 5.0 ± 0.1 cm and 4.8 ± 0.1 cm, respectively (Table 4).

Table 4. Mean shoot density, canopy height and canopy cover for seagrass species in the subtidal area (±SE).

Species	Density/m^2	Canopy Height (cm)	% Cover
C. rotundata	794 ± 42.9	16.5 ± 0.2	66.3
C. serrulata	523 ± 14.3	19.4 ± 0.1	55.4
E. acoroides	344 ± 19	49.2 ± 0.4	55.0
H. uninervis	758 ± 19.7	11.3 ± 0.1	65.0
H. ovalis	164 ± 31	5.0 ± 0.1	60.0
H. stipulacea	464 ± 30.9	4.7 ± 0.1	48.4
S. isoetifolium	580 ± 26.4	20.6 ± 0.1	64.3
T. hemprichii	611 ± 10.1	15.6 ± 0.1	53.8
T. ciliatum	350 ± 11	41.8 ± 0.8	53.5

C. rotundata had the highest % cover (66.3%), followed by *H. uninervis* (65%), while *T. ciliatum* had the lowest (53.5%). *C. rotundata* (793.6 ± 42.9 m^2) and *H. uninervis* (758 ± 19.7 m^2) recorded the highest densities, while *H. ovalis* recorded the lowest density (164 ± 0.3).

In comparing shoot density among the four dominant species within the subtidal zone, *S. isoetifolium* recorded the highest shoot density at 1021 ± 69 shoots/m^2, while *T. ciliatum* recorded the lowest shoot density at 286 ± 72 shoots/m^2. Variation in shoot density among the dominant species was statistically significant (F (3, 16) = 24.708, $p < 0.05$). Shoot height also varied among the dominant species in the subtidal area (F (3, 16) = 13.592, $p < 0.05$), with *T. ciliatum* recording 41.8 ± 1 cm, while *T. hemprichii* recorded the lowest height at 15.6 ± 0.1 cm. Canopy cover was highest in *S. isoetifolium* at 64.3% and lowest in *T. hemprichii* at 53.8%. There was no statistically significant difference in canopy cover among the four dominant species in the subtidal area (F (3, 16) = 2.13, $p < 0.05$).

3.3. Vegetation Carbon Stocks of the Seagrasses

3.3.1. Above Ground Carbon of the Seagrasses

Mean above ground vegetation carbon stock in subtidal seagrass meadows was 0.5 ± 0.1 Mg C ha^{-1} and ranged between 0.2 and 2.1 Mg C ha^{-1} (Table 5).

Table 5. Above ground carbon of dominant seagrass species in subtidal zone.

Species	AGC Mg C ha^{-1} (Mean ± SE)	AGC Mg C ha^{-1} (Range)
C. serrulata	0.48 ± 0.2	0.19–0.7
S. isoetifolium	0.42 ± 0.3	0.25–0.7
T. hemprichii	0.35 ± 0.2	0.22–0.7
T. ciliatum	1.04 ± 0.4	0.63–2.1

There was no significant variation in above ground biomass among the zones (F (3, 38) = 1.685, $p > 0.05$), while there was a significant difference among the species (*S. isoetifolium*, *C. serrulata*, *T. hemprichii* and *T. ciliatum*) (F (3, 16) = 4.967, $p < 0.05$). The Tukey HSD test showed that AGB in *T. ciliatum* meadows was significantly higher than that of *T. hemprichii* meadows ($p = 0.013$).

3.3.2. Belowground Carbon of the Seagrasses

Mean below ground vegetation carbon concentration in subtidal seagrass meadows was 5.1 ± 0.7 Mg C ha^{-1}, with a range of (0.51–23.16 Mg C ha^{-1}).

Belowground biomass among the zones in the subtidal area was not significantly different (F (3, 38) = 1.952, $p > 0.05$). Similarly, the belowground carbon among the four dominant species in the subtidal area showed no significant difference (F (3, 16) = 1.108, $p > 0.05$).

Belowground carbon stocks were significantly higher than aboveground carbon stocks in the subtidal seagrass meadows of the Bay (t (43) = −6.817, $p < 0.05$); (Figure 3). The mean total vegetation carbon in the subtidal area was 5.6 ± 0.7 Mg C ha^{-1} (range: 0.8–23.9 Mg C ha^{-1}), giving a total vegetation carbon of seagrasses in the bay of 2631 Mg C.

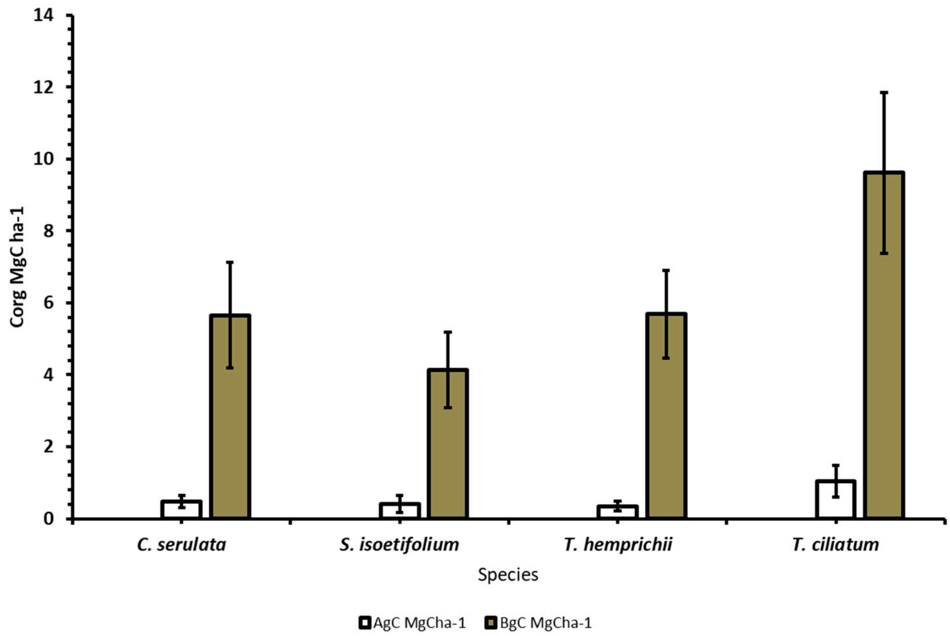

Figure 3. Vegetation aboveground (Agc) and belowground (Bgc) carbon stocks of dominant species reported to a maximum depth of 50 cm. Below ground carbon (Bgc) does not include sediment carbon.

3.4. Sediment Carbon of Seagrass Species

The mean sediment carbon stock across the subtidal seagrass areas was 113 ± 8 Mg C ha^{-1}. Carbon values ranged between 20.1 and 193.1 Mg C ha^{-1}, with no significant differences (t = −8.73; $p = 0.237$) between monospecific (S. *isoetifolium*, *C. serrulata*, *T. hemprichii*, *H. uninervis*, *T. ciliatum*, *H. ovalis*) and mixed (*S. isoetifolium* and *T. hemprichii*; *H. uninervis* and *T. hemprichii*; *C. serrulata* and *T. hemprichii*; *E. acoroides*, *T. hemprichii* and *S. isoetifolium*; *T. hemprichii*, *S. isoetifolium* and *C. rotundata*) seagrass meadows.

There was no significant difference in sediment carbon among the zones in the subtidal area (F (3, 39) = 0.35, $p = 7.90$). Sediment carbon stocks in *S. isoetifolium* meadows were the highest at 134 ± 63.2 Mg C ha^{-1}, with a range of 28.3–188.8 and lowest in *T. ciliatum* meadows with a value of 98.2 ± 43.7 Mg C ha^{-1}, with a range of 36.4–152.3 Mg C ha^{-1} (Figure 4). However, variation in sediment carbon stocks among the four dominant seagrass species in the subtidal area was not statistically significant (F (3, 16) = 0.958, $p = 0.437$).

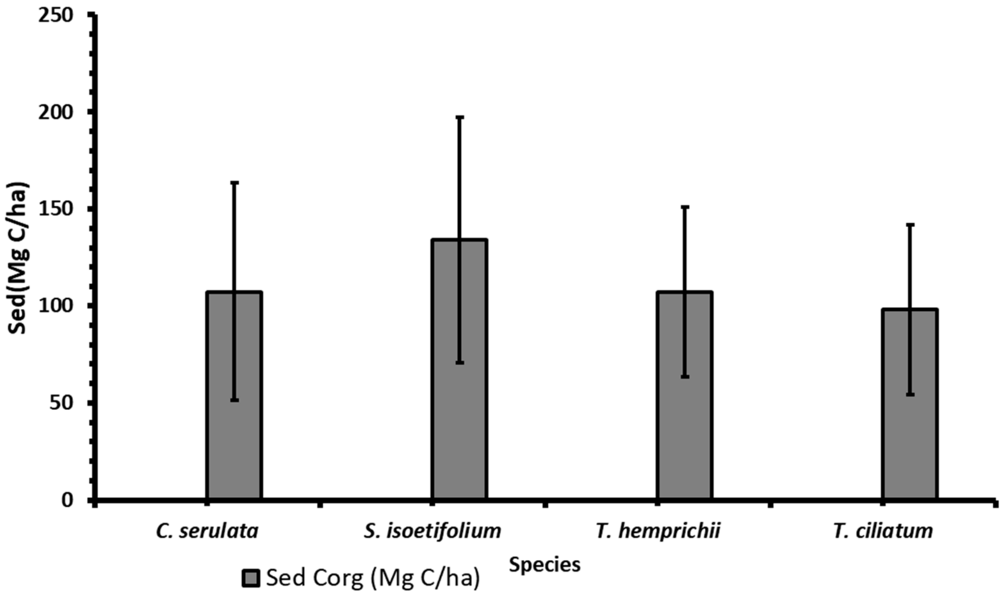

Figure 4. Corg stock in top 50 cm in sediments of dominant seagrass species in subtidal area.

The depth profile showed that on average, carbon concentrations in the sediment were relatively higher in the first 10 cm and then decreased with depth (Figure 5). Total sediment carbon stored in the subtidal areas of Gazi Bay was estimated at 53,100 Mg C.

3.5. Total Carbon Stocks of the Subtidal Seagrass Meadows in Gazi Bay, Kenya

The total carbon stock from the subtidal seagrass meadows that cover approximately 470 ha of the bay is about 55,742 Mg C. Sediment carbon contributes 97% of the total ecosystem carbon pool. This is followed by belowground carbon (2%) and lastly, the aboveground carbon component, which comprises only 1% of the total ecosystem carbon (Table 6).

Table 6. Total carbon stocks in Subtidal seagrass meadows of Gazi Bay, Kenya.

Habitat	Area (ha)	Aboveground Carbon (Mg C ha^{-1})	Belowground Carbon (Mg C ha^{-1})	Sediment Carbon (Mg C ha^{-1})	Total Ecosystem Carbon Mg C
Subtidal	470	0.54 ± 0.1(1%)	5.06 ± 0.7(2%)	113 ± 8(97%)	55,742

3.6. Relationship between Biomass and Meadow Structure Parameters

There was a significant positive relationship between canopy height and aboveground biomass ($r_{(38)} = 0.71$, $p < 0.001$), as well as between belowground biomass and total biomass ($r_{(38)} = 0.98$, $p < 0.001$). Conversely, shoot density and canopy height were negatively correlated ($r_{(38)} = -0.34$, $p = 0.036$).

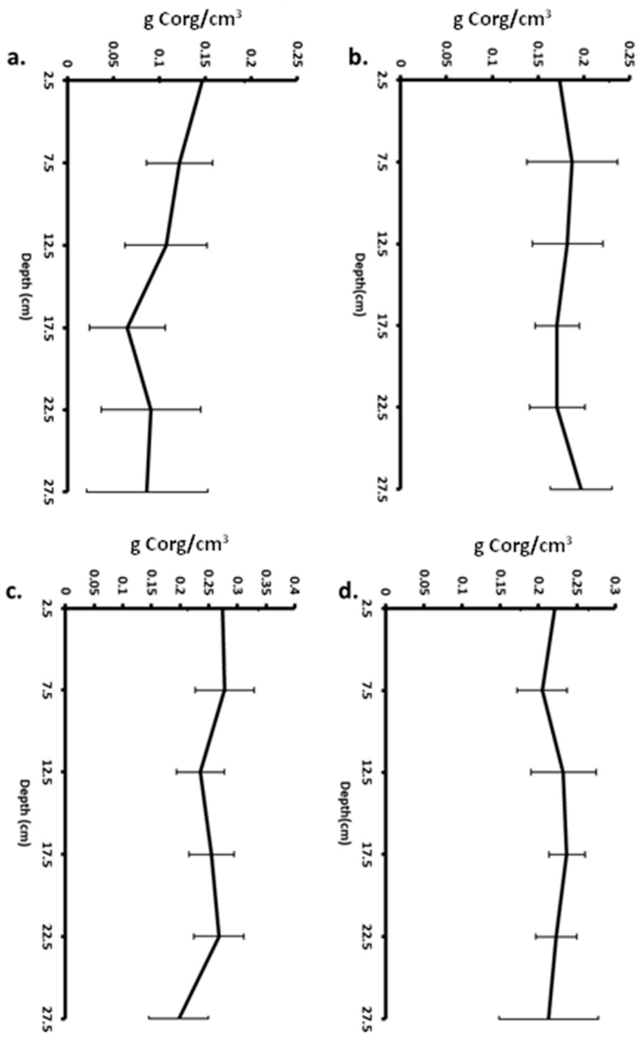

Figure 5. Depth profile in top 30 cm in meadows of (**a**). *S. isoetifolium* (**b**) *C. serrulata* (**c**) *T. hemprichii* and (**d**) *T. ciliatum*.

4. Discussion

4.1. Physico-Chemical Properties in the Sub Tidal Area

Gazi is a shallow bay, with subtidal depths ranging from 1.2 to 7.4 m at low spring tide. Differences in zones are caused by the gradient associated with the continental shelf. Zone A is the shallowest within the littoral zone, whereas Zone D is the deepest and closest to the open ocean. However, Gazi Bay is shallow in comparison to Ungwana Bay in Northern Kenya (range 12 m–100 m at 1.5 nm and 7 nm, respectively) [44]. The decreasing gradient in temperature with depth across the zones is due to differences in irradiation and evaporation. Higher temperatures in Zone A can be attributed to greater heat absorption in shallow depths versus deeper areas [16,18,45]. Gazi Bay's average water temperature is typical of tropical bays and comparable to the Bay of Bengal in Bangladesh, 28.02 $\pm$ 2.49 [46]. Salinity was also high in shallow zones of the bay compared to deep zones. This is due to the influx of fresh water from R. Mkurumudzi into the southern part of the bay [29]. The salinity in Gazi Bay is higher than in the Bay of Bengal, at 28.18 $\pm$ 3.72. This could be due to differences in hydrology and fresh water sources. Unlike Gazi, which has only two seasonal sources of fresh water, the Bay of Bengal has many rivers flowing into it [46]. Gazi bay's PH levels are suitable for supporting life because they are more alkaline. These measurements were obtained once during the entire sampling period and due to seasonal variability, they present only a snapshot.

4.2. Species Composition Distribution and Abundance of Seagrasses

This study confirmed the presence of nine seagrass species within the subtidal zone of Gazi Bay. These were found to occur either as single or mixed species stands. Previous studies [14,15,30] reported 12 species of seagrass species in the intertidal areas of the bay. *Halodule wrightii*, *Halophila minor* and *Zostera capensis* were not encountered in our study, although their presence was recorded in the intertidal area of the bay in previous studies [14,15]. The distribution of seagrasses in the bay follows the typical distribution observed along the East African coast [47], which is mainly attributed to variation in substrate type and water quality parameters, mainly salinity and water depth [47]. Additionally, the presence of multi-species formations in the subtidal area is also a common occurrence in tropical seagrass meadows [48]. Seagrass communities in the bay are dominated by *T. ciliatum*, *T. hemprichi*, *E. acoroides* and *S. isoetifolium* [14]. These species are slow growing, have high above ground to belowground biomass ratios and possess large roots and rhizomes. This makes them efficient in accumulating allochthonous material, stabilizing sediments and minimizing resuspension by reducing water motion, thus inhibiting erosion and promoting deposition [14,18,22,49]. Small pioneering species, on the other hand, are generally shallow rooted, have small diameter rhizomes, lower biomass and have higher turnover rates than climax communities [50]. Human or biological disturbance to aquatic communities is known to cause dominance of pioneering species. This shift in species composition is beneficial, as it allows for succession and meadow re-establishment for large and perennial species. However, shifts can sometimes lead to permanent loss of seagrass and subsequently, the loss of seagrass ecosystem services and functions that enhance the biophysical functioning of sediments [51]. This could further affect both primary and secondary productivity, sediment stability and ultimately compromise the capacity of seagrass meadows to act as long-term carbon sinks [51]. Effects of disturbance in tropical seagrass meadows have been reported by [52], and [49], who highlighted that seagrass loss due to grazing and shading leads to the loss of associated fauna and carbon stocks, respectively.

4.3. Seagrass above Ground Carbon

The mean vegetation carbon for subtidal seagrasses within Gazi Bay estimated from this study was (5.60 $\pm$ 0.66 Mg C ha^{-1}), which is above the global value (2.51 $\pm$ 0.49 Mg C ha^{-1}), as reported by [5]. The difference in aboveground biomass observed among species is likely due to differences in species traits, which affect photosynthesis, productivity and biomass accumulation rates [6,14,22,28]. Therefore, large sized species, such as *E. acoroides* and *T. hemprichii*, tend to have higher biomass when compared to smaller species [50]. Similarly, species that form high canopy and or dense canopies can accumulate more biomass and organic matter [18]. This was confirmed by the positive correlation between above-ground biomass and canopy height, as found in this study. *Thallasondedron ciliatum* had the highest above-ground biomass and also the greatest canopy height. On the other hand, there was no significant difference in aboveground carbon among the four zones in the subtidal area; this possibly indicates a relatively homogenous environment, owing to the relatively small spatial extent of the subtidal area. Differences in aboveground carbon among the species observed in our study is comparable to previous studies in the WIO region where the large sized species *T. ciliatum* had the highest AGC stocks, 1.06 $\pm$0.09 Mg C ha^{-1}, followed by *S. isoetifolium*, 0.84 $\pm$ 0.30 Mg C ha^{-1} [20]. Smaller sized species, on the other hand, recorded the lowest mean ABG stocks, i.e., *H. ovalis*, 0.16 $\pm$ 0.02 Mg C ha^{-1}; *Z. capensis*, 0.08 $\pm$ 0.01 Mg C ha^{-1}, and *H. wrightii*, 0.03 $\pm$ 0.01 Mg C ha^{-1} [20]. Our values, however, are lower than previous studies in Kenya, 0.89 $\pm$ 0.13 Mg C ha^{-1} [14] and Seychelles, 0.76 $\pm$ 0.04 Mg C ha^{-1} [20], but higher than Madagascar, 0.06 Mg C ha^{-1} [20]. The observed differences in aboveground carbon could be attributed to sample size and species composition.

4.4. Belowground Carbon of Subtidal Seagrasses

Belowground organic carbon of seagrasses in the subtidal zone of the bay did not show significant differences among the species and zones. Variation among habitats is often attributed to differences in environmental conditions that influence seagrass growth, such as light, temperature and nutrient supply [6,22,53,54]. The lack of significant variation observed in this study could be an indicator that the biophysical setting in the subtidal area is homogenous and that the species in the subtidal zone do not exhibit large differences in productivity or accumulation of belowground biomass. On the other hand, this could indicate the general absence of herbivory of belowground biomass.

Belowground organic carbon was significantly higher than aboveground carbon and is consistent with observations from previous studies in the region [12,14,15] and across the globe [9,20,48,50]. Large differences in AGB and BGB are often observed in the literature and attributed to greater disturbance of above ground biomass and pressure, such as grazing, higher turnover rates in AGB and higher content of refractory matter in belowground biomass [50,55]. Refs. [11,49] reported a significant relationship between belowground biomass and sediment carbon in the seagrass meadows of Zanzibar, mainland Tanzania and Mozambique. This suggests that belowground biomass often dominates total biomass and ensures inflow of decay resistant organic matter, rich in lignin, into the sedimentary carbon pool [16,38]. These BGC stocks are higher than those reported from other studies in Tanzania, 1.92 $\pm$ 0.20 Mg C ha^{-1}; Mozambique, 1.58 $\pm$ 0.24 Mg C ha^{-1} and Mauritius, 0.78 $\pm$ 0.02 Mg C ha^{-1} [11,20].

4.5. Sediment Organic Carbon Stocks in the Subtidal Area of Gazi Bay

Sediment C_{org} from subtidal seagrasses in the bay yielded a mean of 113 $\pm$ 8 Mg C ha^{-1}. This is just below the global range of 115.5–829.2 Mg C ha^{-1} [5]. Available information from a global database [5] revealed that the carbon storage capacity within one meter depth of sediment of seagrasses was 19.9 Pg, with an average of 137.7 Mg C ha^{-1}, although with large variation globally [5]. The Mediterranean bioregion had the highest C stock at 372 $\pm$ 74.52 Mg C ha^{-1}, while the lowest was in the Indo-pacific bioregion at 23.6 $\pm$ 8.32 Mg C ha^{-1} [5]. Similar variability has also been observed on regional, meadow, landscape scales and across species around the world, where there was an 18-fold difference in C stocks [6]. Much of this carbon may be allochthonous, given the relatively low standing biomass; further supporting export of organic matter into the subtidal areas from the mangrove forests and intertidal area through tidal action and flushing by the two channels [31,34,36].

Seagrasses in the subtidal zone are mostly submerged, and with reduced photosynthetic activities [16], culminating in low biomass increments. However, through the allocthonous process, the sedimentary carbon pool in subtidal seagrass meadows can be enriched by organic carbon from the nearby mangroves and other terrestrial ecosystems [20,35,36]. Typically, the transport of organic matter and fine sediment from mangrove forest reduces with increased distance from the mangrove fringed creeks [56]. This is supported by the relatively higher turbidity in Zone A closer to the intertidal areas and relatively low turbidity observed in meadows in Zone D. This might have an implication on the subtidal area, as the gradient is already reduced. The absence of significant differences in sedimentary organic carbon stocks across the four subtidal zones supports this hypothesis. It also further indicates a fairly homogenous sedimentary substrate and almost equal capacity of seagrass meadows to filter and facilitate the deposition of organic matter, regardless of the meadow type. This is also supported by the lack of significant differences in sedimentary carbon among species and between meadow type (mixed or monospecific). Similar results were reported by [6], who did not find significant differences between the soil C_{org} stocks in seagrass meadows that occur in shallow and deep subtidal habitats in Australia. This was also the case for [12], who found no evidence of a decreasing gradient in carbon stock with depth in Lizard Island within the Great Barrier Reef. However, small scale spatial variation has been shown to exist in seagrass meadows by [17,24]. Their studies showed a fourfold decrease in C_{org} stocks from shallow to deep meadows of *Posidonia sinuosa* in Australia (averaging 7.0 and 1.8 kg m^2, respectively; top meter of sediment) and a 14-fold to 16-fold decrease from shallow (2 m) to deep (32 m) *Posidonia oceanica* meadows in Spain (200 and 19 kg m^2 average, respectively; top 2.7 m of sediment).

Additionally, [21], in a study conducted in four distinct areas of Europe, i.e., Gullmar Fjord on the Swedish Skagerrak coast, Askö in the Baltic Sea, Sozopol in the Black Sea and Ria Formosa in southern Portugal, also reported that sediment characteristics (dry bulk density, grain size, porosity) and water depth affect Corg storage.

The OC stocks in the top 50 cm of sediment in the subtidal area of Gazi Bay is lower than those in the Mediterranean bioregion, 372 ± 74.5 2 Mg C ha^{-1} [5], temperate Northern hemisphere region [9], and the global average for all seagrass species [5]. The Gazi Bay stocks is also lower than those of the United Kingdom (140 ± 73.32 Mg C h^{-1} [10]). However, it is higher than the Arabian Peninsula, 49.1 ± 7.0 Mg C ha^{-1} [7], and the Pacific Northwest region (71.68 Mg C ha^{-1}) [8]. The 50 cm stocks in Gazi Bay (113 ± 8 Mg C ha^{-1}) were similar to the mean 1 m stocks from WIO (116 ± 24.1 Mg C ha^{-1}; [20]); however, compared to country-based assessments, Gazi Bay carbon stocks are comparatively higher than Zanzibar at 33.9 ± 7.7 Mg C ha^{-1} [57], Mozambique at 28.99 ± 13.70 tonnes C ha^{-1} and Tanzania at 40.14 ± 3.45 tonnes C ha^{-1} [12,20] and lower than Kenya at 236 ± 24 Mg C ha^{-1} [14] in the WIO region. Our values are also higher than most studies that report shallow cores (25 cm), e.g., Denmark, Baltic Sea, North Sea, 43.25 ± 11.88 Mg C ha^{-1} [9]; UK, English Channel, 33.71 ± 16.26 Mg C ha^{-1} [10]; Sweden, Baltic Sea, 20 ± 21.21 Mg C ha^{-1} [58]; Portugal, North Atlantic, 10 ± 1.20 Mg C ha^{-1} [58]; Finland, Baltic Sea, 627.00 ± 25.00 Mg C ha^{-1} [9]; Bulgaria, Black Sea, 500.00 ± 50.00 Mg C ha^{-1} [59].Organic matter content in the sediment was higher in the top layer, representing the accumulation of organic matter in the surface sediments. The subsequent decrease in organic carbon content with depth is attributed to remineralization or breakdown of organic matter by anaerobes [7,24,36,45]. While we acknowledge that the scaling-up approach recommended in the Blue Carbon Manual [39] can, under some circumstances, overestimate carbon stocks [60,61], the absence of data on environmental covariates in Gazi Bay means that modelling is not currently a viable alternative approach but one to consider for future studies. Conversely, while uncertainties caused by extrapolation of sediment up to 1 m depth have been avoided, there is a possibility that the Gazi Bay estimate has been underestimated. Due to the shallow cores obtained in most areas during sampling, we only considered the top 50 cm depth in the subtidal area. Other areas may have deeper sediment and are, thus, more likely to harbor larger stocks. Future research at Gazi Bay should aim to identify areas with deeper subtidal soils, and also quantify the sediment accumulation rate and the inorganic carbon within the subtidal area.

4.6. Total Carbon Stocks of the Seagrass Meadows in Gazi Bay

The mean carbon density for the 470 ha of subtidal seagrass meadows in Gazi Bay was 118.6 ± 6 Mg C ha^{-1}, giving a total stock of 55,742 Mg C, with the sediment organic carbon pool contributing 97% of the total ecosystem carbon stocks. Similar carbon allocations have been obtained in previous research conducted within the intertidal meadows, as well as seagrasses in creeks, where the sediment carbon pool was larger than the biomass at 97% and 3%, respectively [14,15]. This highlights the significance of the sediment carbon pool in seagrass ecosystems, as the organic carbon in sediment is more stable and can be stored for millennia, in contrast to that stored in living biomass [5,39]. The proximity of mangrove forest and seagrass meadows, combined with hydrodynamic and geomorphologic forcing, necessitates the inclusion of allochthonous material in the sediment of the seagrass ecosystem [36,56]. However, this study did not assess the sources of carbon within the subtidal area, which can be an important influencing factor that determines carbon stocks [10,27].

Previous estimates of the total carbon stored by seagrass meadows within the bay by [14] was 168,642 Mg C. However, this study arrived at the estimate by using values obtained from the intertidal seagrass meadows only, excluding sub-tidal and creek seagrasses, and thus is certain to have underestimated the total carbon stored by seagrasses across the entire bay. Combining the subtidal carbon stocks with the open intertidal [14] and mangrove fringed creeks [15] provides a better and more robust estimate of the total carbon stocks in seagrass ecosystems within the bay. By pooling stocks from the three zones, the total carbon stored in seagrass meadows of the bay is now estimated to be 196,721 Mg C (Table 7). The Intergovernmental Panel on Climate Change (IPCC) and other studies provide a range of possible fates for 'near-surface carbon' upon conversion from 25% to 100% emissions to the atmosphere, depending on land use types [40]. Using the low-end figure of 25% emissions, the potential carbon loss from seagrasses in Gazi Bay is estimated at 9216 Mg C ha^{-1}, equivalent to 33,822.72 Mg CO_2e yr^{-1}.

Table 7. Estimates of total ecosystem carbon stocks of seagrass meadows in Gazi Bay.

Habitat	Area (ha)	Vegetation Carbon	Sediment Carbon	Total Ecosystem Carbon	Source
		(Mg C h^{-1})	(Mg C ha^{-1})	Mg C	
Eastern creek	50	10.2 ± 0.6	258 ± 90	13,420 (7%)	[15]
Western creek	70	4.3 ± 0.3	107 ± 21	7769 ± (4%)	[15]
Intertidal	495	5.9 ± 0.9	236 ± 24	119,790 (61%)	[14]
Subtidal	470	5.6 ± 0.7	118 ± 6	55,742 (28%)	This study
Total				196,721	This study

5. Conclusions

This study confirms that subtidal seagrass meadows store a substantial proportion of the carbon stocks and contribute significantly to its total seagrass ecosystem carbon stocks. This should strongly encourage targeted evaluations of subtidal seagrass meadows when estimating total carbon stocks in any carbon accounting frameworks, especially in regions where this information is limited (e.g., those in which resources and water quality have historically restricted subtidal sampling). Sediment carbon was the largest carbon pool (97%), followed by belowground biomass at (2%) and above ground biomass, making up the remaining fraction (1%). Even though different species have different capacities to sequester carbon, as evidenced by differences in their biomass, sediment carbon appears to be relatively homogenous. It is likely that species composition is not a major factor influencing the accumulation and storage of carbon in the subtidal sediments of Gazi Bay.

This study builds on previous studies [11,14,15,49] and provides information crucial to facilitate expansion of carbon offset projects that include seagrass meadows. Furthermore, these findings add to the growing database of carbon inventories, demonstrating the significance of subtidal and deep-water seagrasses as blue carbon sinks [58]. These trends emphasize the importance of obtaining local values for carbon sequestration and storage in coastal habitats, particularly in the context of carbon credits and offset schemes. Finally, we highlight the risks of basing total ecosystem carbon on intertidal meadows alone, as this is likely to underestimate the total stocks. Seagrass ecosystems provide numerous goods and services, and their role as active carbon sinks presents a nature-based solution to mitigate climate change. As a result, improving and maintaining the integrity of seagrass ecosystems is critical for improving livelihoods, conserving biodiversity, and regulating climate.

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References

1. Macreadie, P.I.; Costa, M.D.; Atwood, T.B.; Friess, D.A.; Kelleway, J.J.; Kennedy, H.; Lovelock, C.E.; Serrano, O.; Duarte, C.M. Blue carbon as a natural climate solution. *Nat. Rev. Earth Environ.* **2021**, *2*, 826–839. [CrossRef]
2. Mcleod, E.; Chmura, G.L.; Bouillon, S.; Salm, R.; Björk, M.; Duarte, C.M.; Lovelock, C.E.; Schlesinger, W.H.; Silliman, B.R. A blueprint for blue carbon: Toward an improved understanding of the role of vegetated coastal habitats in sequestering CO_2. *Front. Ecol. Environ.* **2011**, *9*, 552–560. [CrossRef]
3. Nellemann, C.; Corcoran, E. (Eds.) *Blue Carbon: The Role of Healthy Oceans in Binding Carbon: A Rapid Response Assessment*; UNEP/Earthprint: Nairobi, Kenya, 2009.
4. Duarte, C.M. *The Role of Seagrass in Climate Change Mitigation and Adaptation*; The University of Western Australia and Spanish National Research Council: Bonn, Germany, 2013.
5. 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.; et al. Seagrass ecosystems as a globally significant carbon stock. *Nat. Geosci.* **2012**, *5*, 505–509. [CrossRef]
6. Lavery, P.S.; Mateo, M.Á.; Serrano, O.; Rozaimi, M. Variability in the carbon storage of seagrass habitats and its implications for global estimates of blue carbon ecosystem service. *PLoS ONE* **2013**, *8*, e73748. [CrossRef] [PubMed]
7. Campbell, J.E.; Lacey, E.A.; Decker, R.A.; Crooks, S.; Fourqurean, J.W. Carbon storage in seagrass beds of Abu Dhabi, United Arab Emirates. *Estuaries Coasts* **2015**, *38*, 242–251. [CrossRef]
8. Prentice, C.; Poppe, K.L.; Lutz, M.; Murray, E.; Stephens, T.A.; Spooner, A.; Hessing-Lewis, M.; Sanders-Smith, R.; Rybczyk, J.M.; Apple, J.; et al. A synthesis of blue carbon stocks, sources, and accumulation rates in eelgrass (*Zostera marina*) meadows in the Northeast Pacific. *Glob. Biogeochem. Cycles* **2020**, *34*, e2019GB006345. [CrossRef]
9. Röhr, M.E.; Holmer, M.; Baum, J.K.; Björk, M.; Boyer, K.; Chin, D.; Chalifour, L.; Cimon, S.; Cusson, M.; Dahl, M.; et al. Blue carbon storage capacity of temperate eelgrass (*Zostera marina*) meadows. *Glob. Biogeochem. Cycles* **2018**, *32*, 1457–1475. [CrossRef]
10. Green, A.; Chadwick, M.A.; Jones, P.J. Variability of UK seagrass sediment carbon: Implications for blue carbon estimates and marine conservation management. *PLoS ONE* **2018**, *13*, e0204431. [CrossRef]
11. Gullström, M.; Lyimo, L.D.; Dahl, M.; Samuelsson, G.S.; Eggertsen, M.; Anderberg, E.; Rasmusson, L.M.; Linderholm, H.W.; Knudby, A.; Bandeira, S.; et al. 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* **2018**, *21*, 551–566. [CrossRef]
12. York, P.H.; Macreadie, P.I.; Rasheed, M.A. Blue Carbon stocks of Great Barrier Reef deep-water seagrasses. *Biol. Lett.* **2018**, *14*, 20180529. [CrossRef]
13. Vanderklift, M.A.; Gorman, D.; Steven, A.D. Blue carbon in the Indian Ocean: A review and research agenda. *J. Indian Ocean Reg.* **2019**, *15*, 129–138. [CrossRef]
14. Githaiga, M.N.; Kairo, J.G.; Gilpin, L.; Huxham, M. Carbon storage in the seagrass meadows of Gazi Bay, Kenya. *PLoS ONE* **2017**, *12*, e0177001. [CrossRef] [PubMed]
15. Juma, G.A.; Magana, A.M.; Michael, G.N.; Kairo, J.G. Variation in seagrass carbon stocks between tropical estuarine and marine mangrove-fringed creeks. *Front. Mar. Sci.* **2020**, *7*, 696. [CrossRef]
16. Serrano, O.; Lavery, P.S.; Rozaimi, M.; Mateo, M.Á. Influence of water depth on the carbon sequestration capacity of seagrasses. *Glob. Biogeochem. Cycles* **2014**, *28*, 950–961. [CrossRef]
17. Serrano, O.; Ricart, A.M.; Lavery, P.S.; Mateo, M.A.; Arias-Ortiz, A.; Masque, P.; Rozaimi, M.; Steven, A.; Duarte, C.M. Key biogeochemical factors affecting soil carbon storage in Posidonia meadows. *Biogeosciences* **2016**, *13*, 4581–4594. [CrossRef]
18. Mazarrasa, I.; Samper-Villarreal, J.; Serrano, O.; Lavery, P.S.; Lovelock, C.E.; Marbà, N.; Duarte, C.M.; Cortés, J. Habitat characteristics provide insights of carbon storage in seagrass meadows. *Mar. Pollut. Bull.* **2018**, *134*, 106–117. [CrossRef]
19. Koch, E.W.; Sanford, L.P.; Chen, S.N.; Shafer, D.J.; Smith, J.M. Waves in Seagrass Systems: Review and Technical Recommendations. 2006. Available online: https://apps.dtic.mil/sti/pdfs/ADA458760.pdf (accessed on 7 August 2022).

20. Palacios, M.M.; Waryszak, P.; de Paula Costa, M.D.; Wartman, M.; Ebrahim, A.; Macreadie, P.I. Literature Review: Blue Carbon Research in the Tropical Western Indian Ocean. 2021. Available online: https://seyccat.org/wp-content/uploads/2020/01/BlueCarbonLab_LitReport_Seychelles_20210301_final.pdf (accessed on 7 August 2022).
21. Dahl, M.; Deyanova, D.; Gütschow, S.; Asplund, M.E.; Lyimo, L.D.; Karamfilov, V.; Santos, R.; Björk, M.; Gullström, M. Sediment properties as important predictors of carbon storage in *Zostera marina* meadows: A comparison of four European areas. *PLoS ONE* **2016**, *11*, e0167493.
22. Mateo, M.; Cebrián, J.; Dunton, K.; Mutchler, T. Carbon Flux in Seagrass Ecosystems. In *Seagrasses: Biology, Ecology and Conservation*; Springer: Berlin/Heidelberg, Germany, 2006; pp. 159–192.
23. Serrano, O.; Lavery, P.S.; Duarte, C.M.; Kendrick, G.A.; Calafat, A.; York, P.H.; Steven, A.; Macreadie, P.I. Can mud (silt and clay) concentration be used to predict soil organic carbon content within seagrass ecosystems? *Biogeosciences* **2016**, *13*, 4915–4926. [CrossRef]
24. Kennedy, H.; Beggins, J.; Duarte, C.M.; Fourqurean, J.W.; Holmer, M.; Marbà, N.; Middelburg, J.J. Seagrass sediments as a global carbon sink: Isotopic constraints. *Glob. Biogeochem. Cycles* **2010**, *24*, 2010GB003848. [CrossRef]
25. Orth, R.J.; Carruthers, T.J.; Dennison, W.C.; Duarte, C.M.; Fourqurean, J.W.; Heck, K.L.; Hughes, A.R.; Kendrick, G.A.; Kenworthy, W.J.; Olyarnik, S.; et al. A global crisis for seagrass ecosystems. *Bioscience* **2006**, *56*, 987–996. [CrossRef]
26. Pendleton, L.; Donato, D.C.; Murray, B.C.; Crooks, S.; Jenkins, W.A.; Sifleet, S.; Craft, C.; Fourqurean, J.W.; Kauffman, J.B.; Marba, N.; et al. Estimating global "blue carbon" emissions from conversion and degradation of vegetated coastal ecosystems. *PLoS ONE* **2012**, *7*, e43542. [CrossRef]
27. Macreadie, P.I.; Baird, M.E.; Trevathan-Tackett, S.M.; Larkum, A.W.D.; Ralph, P.J. Quantifying and model-ling the carbon sequestration capacity of seagrass meadows–a critical assessment. *Mar. Pollut. Bull.* **2014**, *83*, 430–439. [CrossRef]
28. Githaiga, M.N.; Gilpin, L.; Kairo, J.G.; Huxham, M. Biomass and productivity of seagrasses in Africa. *Bot. Mar.* **2016**, *59*, 173–186. [CrossRef]
29. Kitheka, J.U. Water circulation and coastal trapping of brackish water in a tropical mangrove-dominated bay in Kenya. *Limnol. Oceanogr.* **1996**, *41*, 169–176. [CrossRef]
30. Coppejans, E.; Beeckman, H.; de Wit, M. The Seagrass and Associated Macroalgal Vegetation of Gazi Bay (Kenya). In *The Ecology of Mangrove and Related Ecosystems*; Springer: Dordrecht, The Netherlands, 1992; pp. 59–75.
31. Bouillon, S.; Dehairs, F.; Velimirov, B.; Abril, G.; Borges, A.V. Dynamics of organic and inorganic carbon across contiguous mangrove and seagrass systems (Gazi Bay, Kenya). *J. Geophys. Res. Biogeosci.* **2007**, *112*, G02018. [CrossRef]
32. Peel, M.C.; Finlayson, B.L.; McMahon, T.A. Updated world map of the Köppen-Geiger climate classification. *Hydrol. Earth Syst. Sci.* **2007**, *11*, 1633–1644. [CrossRef]
33. McClanahan, T.R. Seasonality in East Africa's Coastal Waters. 1988. Available online: https://www.int-res.com/articles/meps/44/m044p191.pdf (accessed on 7 August 2022).
34. Hemminga, M.A.; Slim, F.; Kazungu, J.; Ganssen, G.M.; Nieuwenhuize, J.; Kruyt, N.M. Carbon outwelling from a mangrove forest with adjacent seagrass beds and coral reefs (Gazi Bay, Kenya). *Mar. Ecol. Prog. Ser.* **1994**, *106*, 291–301. [CrossRef]
35. Signa, G.; Mazzola, A.; Kairo, J.; Vizzini, S. Small-scale variability in geomorphological settings influences mangrove-derived organic matter export in a tropical bay. *Biogeosciences* **2017**, *14*, 617–629. [CrossRef]
36. Bouillon, S.; Dehairs, F.; Abril, G.; Borges, A. Distribution and Sources of Organic Carbon in a Mangrove Seagrass Ecosystem (Gazi Bay, Kenya). 2005. Available online: https://orbi.uliege.be/bitstream/2268/246507/1/EGU05-J-01904.pdf (accessed on 7 August 2022).
37. Musembi, P.; Fulanda, B.; Kairo, J.; Githaiga, M. Species composition, abundance and fishing methods of small-scale fisheries in the seagrass meadows of Gazi Bay, Kenya. *J. Indian Ocean. Reg.* **2019**, *15*, 139–156. [CrossRef]
38. Harcourt, W.D.; Briers, R.A.; Huxham, M. The thin (ning) green line? Investigating changes in Kenya's seagrass coverage. *Biol. Lett.* **2018**, *14*, 20180227. [CrossRef]
39. Howard, J.; Hoyt, S.; Isensee, K.; Telszewski, M.; Pidgeon, E. Coastal Blue Carbon: Methods for Assessing Carbon Stocks and Emissions Factors in Mangroves, Tidal Salt Marshes, and Seagrasses. 2014. Available online: https://www.cifor.org/publications/pdf_files/Books/BMurdiyarso1401.pdf (accessed on 7 August 2022).
40. Intergovernmental Panel on Climate Change. *Supplement to the 2006 IPCC Guidelines for National Greenhouse Gas Inventories: Wetlands*; IPCC: Geneva, Switzerland, 2014.
41. Short, F.T.; Koch, E.W.; Creed, J.C.; Magalhaes, K.M.; Fernandez, E.; Gaeckle, J.L. SeagrassNet monitoring across the Americas: Case studies of seagrass decline. *Mar. Ecol.* **2006**, *27*, 277–289. [CrossRef]
42. Waycott, M.; McMahon, K.; Mellors, J.; Calladine, A.; Kleine, D. *A Guide to Tropical Seagrasses of the Indo-West Pacific*; James Cook University: Townsville, Australia, 2004.
43. Duarte, C.M. Seagrass nutrient content. *Mar. Ecol. Prog. Ser.* **1990**, *6*, 201–207. [CrossRef]
44. Marine, K. *Current Status of Trawl Fishery of Malindi-Ungwana Bay Final Report December 2002*; Kenya Marine and Fisheries Research Institute: Mombasa, Kenya, 2002.
45. Serrano, O.; Almahasheer, H.; Duarte, C.M.; Irigoien, X. Carbon stocks and accumulation rates in Red Sea seagrass meadows. *Sci. Rep.* **2018**, *8*, 15037. [CrossRef]
46. Pai, I.K.; Govekar, K. An Extensive Study on Physico-Chemical Parameters of Bay of Bengal and Central Indian Ocean Basin. 2016. Available online: http://medcraveonline.com/JAMB/JAMB-04-00097.pdf (accessed on 7 August 2022).

47. Gullström, M.; de la Torre Castro, M.; Bandeira, S.O.; Björk, M.; Dahlberg, M.; Kautsky, N.; Rönnbäck, P.; Öhman, M.C. Seagrass ecosystems in the western Indian Ocean. *AMBIO* **2002**, *31*, 588–596. [CrossRef]
48. Aller, E.A.; Eklöf, J.S.; Gullström, M.; Kloiber, U.; Linderholm, H.W.; Nordlund, L.M. Temporal variability of a protected multispecific tropical seagrass meadow in response to environmental change. *Environ. Monit. Assess.* **2019**, *191*, 774. [CrossRef]
49. Dahl, M.; Deyanova, D.; Lyimo, L.D.; Näslund, J.; Samuelsson, G.S.; Mtolera, M.S.; Björk, M.; Gullström, M. Effects of shading and simulated grazing on carbon sequestration in a tropical seagrass meadow. *J. Ecol.* **2016**, *104*, 654–664. [CrossRef]
50. Duarte, C.M.; Chiscano, C.L. Seagrass biomass and production: A reassessment. *Aquat. Bot.* **1999**, *65*, 159–174. [CrossRef]
51. Bourque, A.S.; Kenworthy, W.J.; Fourqurean, J.W. Impacts of physical disturbance on ecosystem structure in subtropical seagrass meadows. *Mar. Ecol. Prog. Ser.* **2015**, *540*, 27–41. [CrossRef]
52. Githaiga, M.N.; Frouws, A.M.; Kairo, J.G.; Huxham, M. Seagrass removal leads to rapid changes in fauna and loss of carbon. *Front. Ecol. Evol.* **2019**, *7*, 62. [CrossRef]
53. Thom, R.M.; Borde, A.B.; Rumrill, S.; Woodruff, D.L.; Williams, G.D.; Southard, J.A.; Sargeant, S.L. Factors influencing spatial and annual variability in eelgrass (*Zostera marina* L.) meadows in Willapa Bay, Washington, and Coos Bay, Oregon, estuaries. *Estuaries* **2003**, *26*, 1117–1129. [CrossRef]
54. Miyajima, T.; Hori, M.; Hamaguchi, M.; Shimabukuro, H.; Adachi, H.; Yamano, H.; Nakaoka, M. Geographic variability in organic carbon stock and accumulation rate in sediments of East and Southeast Asian seagrass meadows. *Glob. Biogeochem. Cycles* **2015**, *29*, 397–415. [CrossRef]
55. Govindasamy, C.; Arulpriya, M.; Anantharaj, K.; Ruban, P.; Srinivasan, R. Seasonal variations in seagrass biomass and productivity in Palk Bay, Bay of Bengal, India. *Int. J. Biodivers. Conserv.* **2013**, *5*, 408–417.
56. Huxham, M.; Whitlock, D.; Githaiga, M.; Dencer-Brown, A. Carbon in the coastal seascape: How interactions between mangrove forests, seagrass meadows and tidal marshes influence carbon storage. *Curr. For. Rep.* **2018**, *4*, 101–110. [CrossRef]
57. Belshe, E.F.; Hoeijmakers, D.; Herran, N.; Mtolera, M.; Teichberg, M. Seagrass community-level controls over organic carbon storage are constrained by geophysical attributes within meadows of Zanzibar, Tanzania. *Biogeosciences* **2018**, *15*, 4609–4626. [CrossRef]
58. Jankowska, E.; Michel, L.N.; Zaborska, A.; Włodarska-Kowalczuk, M. Sediment carbon sink in low-density temperate eelgrass meadows (Baltic Sea). *J. Geophys. Res. Biogeosciences* **2016**, *121*, 2918–2934. [CrossRef]
59. Garcias-Bonet, N.; Delgado-Huertas, A.; Carrillo-de-Albornoz, P.; Anton, A.; Almahasheer, H.; Marbà, N.; Hendriks, I.E.; Krause-Jensen, D.; Duarte, C.M. Carbon and nitrogen concentrations, stocks, and isotopic compositions in Red Sea seagrass and mangrove sediments. *Front. Mar. Sci.* **2019**, *6*, 267. [CrossRef]
60. Gorman, D.; Sumida, P.Y.; Figueira, R.C.; Turra, A. Improving soil carbon estimates of mudflats in Araçá Bay using spatial models that consider riverine input, wave exposure and biogeochemistry. *Estuar. Coast. Shelf Sci.* **2020**, *238*, 106734. [CrossRef]
61. Asplund, M.E.; Dahl, M.; Ismail, R.O.; Arias-Ortiz, A.; Deyanova, D.; Franco, J.N.; Hammar, L.; Hoamby, A.I.; Linderholm, H.W.; Lyimo, L.D.; et al. Dynamics and fate of blue carbon in a mangrove–seagrass seascape: Influence of landscape configuration and land-use change. *Landsc. Ecol.* **2021**, *36*, 1489–1509. [CrossRef]