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JGR Biogeosciences

RESEARCH ARTICLE
10.1029/2024JG008163

Patterns of Carbon and Nitrogen Accumulation in Seagrass (*Posidonia oceanica*) Meadows of the Eastern Mediterranean Sea

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Key Points:

- Seagrass (*Posidonia oceanica*) meadows of the South Aegean Sea (Greece) represent important natural sinks for organic carbon, nitrogen, and carbonate.
- The accumulation pattern of organic carbon, nitrogen, and carbonate in the underlying seagrass sediments was mainly driven by sediment characteristics, followed by seagrass traits and environmental conditions.
- Fine-scale assessments are crucial for understanding the local factors shaping the storage capacity of seagrass meadows to support management decisions.

Supporting Information:

Supporting Information may be found in the online version of this article.

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Citation:

Apostolaki, E. T., Lavery, P. S., Litsi-Mizan, V., Serrano, E., Inostroza, K., Gerakaris, V., et al. (2024). Patterns of carbon and nitrogen accumulation in seagrass (*Posidonia oceanica*) meadows of the Eastern Mediterranean Sea. *Journal of Geophysical Research: Biogeosciences*, *129*, e2024JG008163. https://doi.org/10.1029/2024JG008163

Received 29 MAR 2024
Accepted 27 NOV 2024

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Abstract

The variability in stocks and accumulation rates of organic carbon (C_{org}), nitrogen (N), and carbonate ($CaCO_3$) was studied in fifteen *Posidonia oceanica* meadows spread throughout the South Aegean Sea (Greece). In addition, the abiotic and biotic drivers determining the pattern of variability in the accumulation rates were assessed by exploring the influence of sediment characteristics, seagrass traits, and environmental settings. The meadows supported on average (±STDEV) 14.6 ± 5.0 kg C_{org} m^{-2}, 0.47 ± 0.17 kg N m^{-2}, and 249 ± 210 kg $CaCO_3$ m^{-2} in the top meter of their sediments, with mean accumulation rates over the last 500 years of 33.6 ± 23.6 g C_{org} m^{-2} yr^{-1}, 1.00 ± 0.62 g N m^{-2} yr^{-1}, and 405 ± 336 g $CaCO_3$ m^{-2} yr^{-1} across sites. A redundancy analysis (RDA) explained 70% of the variation in C_{org}, N, and $CaCO_3$ accumulation rates, with three sediment characteristics (i.e., sediment C_{org}:N and C_{org}:C_{inorg} ratios and *P. oceanica* contribution to the sediment C_{org} pool) emerging as the primary set of factors shaping the accumulation of matter, followed by seagrass traits (i.e., leaf biomass and rhizome elongation) and environmental variables (i.e., suspended organic matter). The high degree of variability within the region emphasizes the need for fine-scale assessments to understand the local conditions influencing sequestration. Our findings underscored the critical role of seagrass meadows in carbon and nitrogen sequestration in the region, urging conservation efforts to protect these ecosystems and prevent potential losses of stored carbon and nitrogen following seagrass degradation.

Plain Language Summary

In the present study, we explored the abiotic and biotic factors influencing the accumulation patterns of carbon, nitrogen, and carbonate in 15 seagrass (*Posidonia oceanica*) meadows across the South Aegean Sea (Greece). Sediment characteristics (i.e., sediment C_{org}:N and C_{org}:C_{inorg} ratios and *P. ocenica* contribution to the sediment C_{org} pool) mainly drove the pattern of carbon, nitrogen, and carbonate accumulation, with seagrass traits (i.e., leaf biomass and rhizome elongation) and environmental conditions (i.e., suspended organic matter) contributing to a lesser extent. Overall, seagrass meadows play a crucial role in storing carbon and nitrogen in the studied region, serving as important natural sinks, and thus, protecting these ecosystems is important to prevent the loss of these stored elements. Additionally, understanding the factors that shape the variability in *Posidonia oceanica* storage capacity is crucial for management and conservation efforts.

1. Introduction

The significant role of seagrass ecosystems in storing elements over millennia, namely carbon and nitrogen, has been documented several decades ago (Mateo et al., 1997; Romero et al., 1994; Smith, 1981). However, it is within the last decade that a plethora of information has accumulated (Costa et al., 2022) to highlight how that role could contribute toward combating climate change (Macreadie et al., 2021). Seagrass meadows have been shown to store 115.3–829.2 Mg ha^{-1} of organic carbon (C_{org}) (Fourqurean, Kendrick, et al., 2012; Fourqurean, Duarte, et al., 2012) and 3–1,660 Mg ha^{-1} of inorganic carbon (C_{inorg}) (Mazarrasa et al., 2015) within 1-m thick deposits, and as such, they rank among the most effective natural carbon sinks on Earth. Lately, the significant role of seagrass ecosystems as nitrogen (N) filters has emerged (Aoki et al., 2020), highlighting their potential role in

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mitigating coastal eutrophication (McGlathery et al., 2007, 2012; Reynolds et al., 2016). Seagrass ecosystems owe their high biogeochemical storage capacity to their intense metabolism (Duarte et al., 2010) and their ability to trap allochthonous organic and inorganic particles from adjacent ecosystems including terrestrial ones (Gacia et al., 2002), and to the preservation of matter in their underlying sediments (Duarte, Kennedy, et al., 2013) which is favored by the subsurface anoxic conditions and, especially, the recalcitrant nature of seagrass detritus (Kaal et al., 2019).

The size of the sink of each element exhibits high variability across seagrass habitats and species. The cycling of matter in seagrass ecosystems involves an endless fixation and loss of elements through complex and cooccurring biogeochemical processes, which result in high spatial and temporal heterogeneity in carbon and nitrogen pools in seagrass sediments. A series of processes (e.g., metabolism, mineralization, calcification, carbonate dissolution, denitrification) operate between the water and sediment interface (Barrón et al., 2014; Garcias-Bonet et al., 2018), mediated by the biota (i.e., the seagrass itself and the associated flora, fauna, and microbes (Eyre et al., 2016; Trevathan-Tackett et al., 2019), and influenced by the geochemical and environmental context (Spivak et al., 2019). Some of these processes are highly interrelated; for instance, the CO_2 release from the metabolism of the community or the mineralization of organic matter could fuel carbonate ($CaCO_3$) dissolution in the upper sediment layer, whereas high production of $CaCO_3$ could increase C_{org} preservation (Macreadie et al., 2017). Furthermore, the contribution of each set of factors regulating those processes may differ depending on the element under study; variability in environmental settings, such as water column nutrients, for example, should have a greater influence on the C_{org} and N (Kindeberg et al., 2018; Lima et al., 2020) than the $CaCO_3$ accumulation, as both C_{org} and N represent more labile pools that often show a parallel pattern in accumulation (Apostolaki et al., 2022; Fourqurean, Kendrick, et al., 2012; Fourqurean, Duarte, et al., 2012; Leiva-Dueñas et al., 2023), than the $CaCO_3$ that has larger permanence and may also include inputs of lithogenic provenance (Saderne et al., 2019). Therefore, the magnitude of each sink depends on multiple abiotic (i.e., sediment characteristics and environmental settings) and biotic (i.e., seagrass traits) factors acting in concert at several spatiotemporal scales, and C_{org}, N and $CaCO_3$ assessments, when conducted in parallel, could enhance our understanding of the variability in the capacity of seagrass meadows for elemental sequestration.

However, previous studies have explored the main factors driving this variability separately for each element, rather than in parallel. Available information shows that storage for each element varies with environmental settings (e.g., water depth, hydrodynamics), sediment characteristics (e.g., grain size, OM availability, biochemical composition and origin), and seagrass traits (e.g., production, structure), but the amount of relevant information is largely biased toward C_{org} (e.g., Kennedy et al., 2022; Lavery et al., 2013; Lima et al., 2020; Mazarrasa et al., 2021; Novak et al., 2020; Ricart et al., 2020; Röhr et al., 2016; Samper-Villarreal et al., 2016; Serrano, Lavery, López-Merino, et al., 2016) compared to N (Kindeberg et al., 2018; Leiva-Dueñas et al., 2023; Prystay et al., 2023) or $CaCO_3$ (Gullström et al., 2018). In addition, the available studies have investigated the factors determining the accumulation along a certain thickness of sediment (usually the top 1 m), and not during a given time period. The sediment accretion rate may differ significantly among sites (Serrano, Lavery, López-Merino, et al., 2016) due to sediment supply dynamics and local environmental factors resulting in deposits that cover a period from several years to centuries or even millennia in some species (Monnier et al., 2021). Therefore, in such assessments, it is also important to consider the period of accumulation and not only the sediment thickness to improve our understanding of the timescales of elemental sequestration.

The iconic seagrass meadows of the Mediterranean, *Posidonia oceanica*, rank among the most important natural carbon sinks across the terrestrial and coastal realm (Röhr et al., 2018). However, available estimates show remarkable variability in stocks and accumulation rates of C_{org}, N, and $CaCO_3$ in the western Mediterranean (Apostolaki et al., 2022; Mazarrasa et al., 2017a; Monnier et al., 2022; Serrano, Lavery, López-Merino, et al., 2016) compared to the Eastern basin (Apostolaki et al., 2019). Although recent studies have shown that *P. oceanica* traits have a crucial contribution in shaping the significant capacity of the species to store C_{org} compared to other seagrass species (Kennedy et al., 2022), we still lack a robust explanation of the seagrass environmental and geochemical factors that determine the high C_{org} storing capacity of the species at local scales. Furthermore, a limited understanding exists regarding the factors driving the accumulation of N and $CaCO_3$. Therefore, fine-scale assessments are important to understand the patterns of variability across *P. oceanica* meadows and eventually allow us to identify hotspots for the implementation of blue carbon projects toward climate change mitigation.

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Here, we studied the variability of carbon and nitrogen sequestration in *P. oceanica* meadows of the eastern Mediterranean Sea. We estimated the stocks and accumulation rates of C_{org}, N, and $CaCO_3$ in 15 meadows expanding along the South Aegean Sea (Greece). In addition, we assessed the abiotic and biotic drivers that determine the pattern of variability among the accumulation of C_{org}, N, and $CaCO_3$ by exploring the influence of sediment characteristics, seagrass traits, and environmental settings.

2. Materials and Methods

2.1. Study Area and Sampling

The study was conducted in the South Aegean Sea. The study included 15 monospecific *P. oceanica* meadows extending over sedimentary, metamorphic, and volcanic sediments (IGME, 1983) along approx. 3,500 km of coastline (Figure 1). The area is characterized by steep rocky cliffs, sandy shores, low precipitation, and the absence of major riverine inflow.

Within 100 m^2 of each meadow, the number of *P. oceanica* shoots was counted in triplicates using a 50 × 50 cm quadrat randomly tossed over the meadow. All shoots present within each quadrat were collected by hand, and leaves were separated and weighed. Fifteen *P. oceanica* shoots were randomly sampled from the site Gouves to calculate a mean dry weight: fresh weight ratio (DW:FW) and allow the estimation of leaf DW biomass in all 15 sites. We assumed that water content in seagrass leaves did not vary significantly among the study sites. Therefore, we used the mean DW:FW value and the fresh weight of leaves per site to estimate leaf biomass at each site. Ten orthotropic shoots were also collected at each site to allow reconstruction of rhizome elongation. The presence of seagrass species other than *P. oceanica* (e.g., *Cymodocea nodosa*) or macroalgae (e.g., *Caulerpa prolifera*) was recorded by visual census.

At each site, triplicate cores were randomly collected using manual percussion and rotation. One replicate core was sampled using a PVC pipe (2.2 m long and 7.5 cm inner diameter), while the other two replicate cores were sampled using aluminum pipes (1.5-m long and 8-cm inner diameter) with 3 cm-wide holes predrilled at 3-cm intervals along the pipe. The aluminum pipes were predrilled to effectively subsample to sediments inside the pipes in the field, a method commonly used in blue carbon science (e.g., Fourqurean, Kendrick, et al., 2012; Fourqurean, Duarte, et al., 2012). The degree of compaction was similar between PVC and aluminum pipes (23 ± 10% and 29 ± 8%, respectively). The porewater content does not have any effect on the dry bulk density calculations run to estimate carbon stocks. Potential C_{org} remineralization was not relevant considering the short period between sampling and processing of the cores (i.e., a few hours for the aluminum cores and a few days for the PVC cores) and the age of the carbon samples (i.e., from years to centuries).

The cores were inserted down to 1 m of sediment or deeper (up to 202 cm) (Table S1). The inner, outer, and total length of each core were measured after coring to allow the estimation of sediment compression, which ranged between 1.6% and 39.6% (mean ± SD = 24 ± 9% Table S1).

2.2. Laboratory Analysis

Fresh leaves from shoots collected at the Gouves site were weighed, dried at 60°C for 48–72 hr, and weighed again, yielding a DW:FW ratio of 0.24. Rhizome elongation was reconstructed using the lepidochronology analysis, based on the cyclic variation in sheath thickness along the rhizome (Pergent-Martini & Pergent, 1994). The thickness of each sheath per shoot was measured using a caliper. The period between two consecutive minima in sheath thickness corresponded to one lepidochronological year and, by convention, to one calendar year. The length of each rhizome segment per shoot and year was measured using a caliper.

The PVC cores were cut lengthwise, and the sediments were sliced into 1 cm-thick intervals. A subsample of sediment was collected from each hole of the aluminum cores using a modified 60-mL syringe with the end cut off. All samples were dried at 70°C until constant weight and then divided by quartering for subsequent analyses. Bulk subsamples were used for the determination of grain size, after digestion of organic matter with hydrogen peroxide (30%). Samples were sieved using 1-mm sieves, and the fractions >1 mm and <1 mm were weighed. The fraction <1 mm was analyzed using a laser diffraction particle analyzer (Mastersizer 2,000; Malvern Instruments Ltd., UK). The grain size fractions were classified as very coarse sand (>1 mm), coarse sand (0.5–1 mm), medium sand (0.25–0.5 mm), fine sand (0.063–0.25 mm), and silt/clay (<0.063 mm). Other subsamples of sediment were milled to fine powder and were used for the determination of organic carbon (C_{org}), nitrogen

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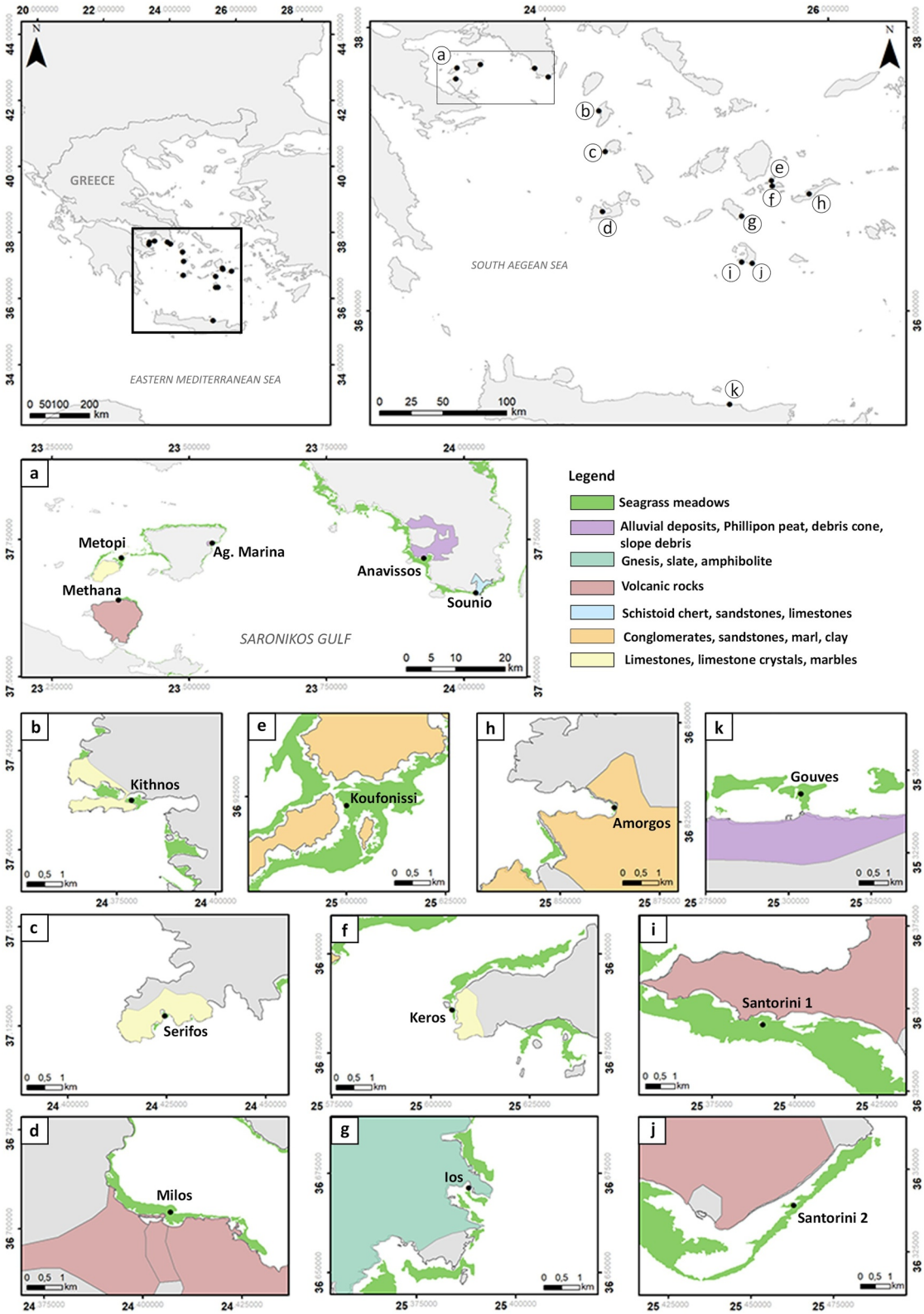

Figure 1. Map of the study area in the South Aegean Sea and sites sampled (a–k). The extent of *P. oceanica* meadows at each site was obtained from Panayotidis et al. (2022). The lithology of the catchments was obtained from IGME (1983).

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(N), and carbonate ($CaCO_3$) contents, and the stable organic carbon isotopic composition ($\delta^{13}C$) of sediment. The determination of C_{org}, $\delta^{13}C$, and N was done using a Costech 4010 elemental analyzer coupled to a Thermo Delta V Advantage isotope ratio mass spectrometer (UH Hilo Analytical Laboratory) at the University of Hawaii at Hilo. Prior to analysis, 50-mg powder samples were acidified in silver capsules with 4% hydrochloric acid (HCl) to remove inorganic carbon (Kennedy et al., 2005). Isotope ratios were expressed as δ values in parts per thousand (‰) relative to the Vienna Peedee Belemnite standard ($\delta^{13}C$), using US Geological Survey standards 40 and 41. Replicate assays and standards (NIST 8704) indicated measurement errors of 0.01% for C_{org} and N contents, and 0.2‰ for $\delta^{13}C$. The $CaCO_3$ content was determined using a calcimeter (Pressure Gauge Model 432 (Fann®); ASTM D 4373-84 Standard) by adding 10% HCl to the powder sample in a sealed reaction cell. The pressure built up due to the CO_2 was measured with a bourdon tube pressure gauge that was precalibrated with reagent-grade calcium carbonate.

Three to five samples of *P. oceanica* sheaths from one replicate core per site were radiocarbon-dated at the Direct AMS Radiocarbon Business Unit (Accium BioSciences, USA) following standard procedures (Stuiver & Polach, 1977) (Table S2).

2.3. Calculations and Data Analysis

Shoot density (shoots m^{-2}) was estimated as the number of shoots per unit area at each site. Leaf biomass (g DW m^{-2}) at each site was estimated as the product of fresh weight of leaves at the given site and the mean DW:FW ratio per unit area. Rhizome elongation (mm $shoot^{-1}$ yr^{-1}) at each site was estimated as the mean of annual elongation during the reconstructed period for the given site. The temporal period of reconstruction corresponded to years 1995–2016 across sites, with a maximum year span of 22 years (at Gouves) and a mean shoot age of 9.9 ± 3 years. Rhizome segments corresponding to the two most recent lepidochronological years of each shoot were excluded from the analysis, as the lepidochronological cycles may have not been complete at the time of sampling (Peirano, 2002).

The dry bulk density (DBD, g cm^{-3}) of each slice was estimated by dividing the DW of sediment by the volume of the corresponding wet sample. The elemental content (% DW) was measured in alternate slices, whereas in the remaining slices, the contents were estimated as the mean content of the slices immediately above and below the slice in question. The mass of C_{org}, $CaCO_3$, and N (g element cm^{-2}) at each slice was estimated by multiplying the DBD with the corresponding elemental content and the decompressed sediment slice thickness (in cm).

Stocks of C_{org}, N, and $CaCO_3$ (kg element m^{-2}) were estimated as the cumulative mass of the corresponding element and were standardized to 1 m of sediment thickness. In cases where the length of sediment sampled was less than 1 m (in 19 out of 45 cores, Table S1), we fitted a linear regression to the downcore trends in cumulative stocks to estimate the 1-m stocks. To validate this approach, data from the cores with at least 1-m depth were used to estimate the correlation between extrapolated stocks to 1-m thickness and measured stocks in 1-m cores (Table S6), with significant correlations for C_{org} stock ($R^2 = 0.85$ and $P < 0.001$), N stock ($R^2 = 0.94$ and $P < 0.001$), and $CaCO_3$ stock ($R^2 = 0.97$ and $P < 0.001$) (Figure S1 in Supporting Information S1).

The radiocarbon ages (yr BP; Table S2) were used to produce age-depth models using the R routine "Bacon" (Blaauw & Christen, 2011), after calibration using the Marine13 Radiocarbon Age calibration curve, considering a local delta R of 110 ± 38 years (Reimer & McCormac, 2002), and assuming that the top of the core corresponded to the year of sampling (Table S1). Age-depth models for cores that only had one ^{14}C dating were obtained by fitting a linear regression between the calibrated ^{14}C age and the top of the core assuming that it corresponded to the year of sampling. In four cores, the ^{14}C ages obtained were too modern to be calibrated, and therefore, we assumed that the first ^{14}C-dated sample corresponded to 1,800 cal AD and fitted a linear regression assuming that the top of the core corresponded to the year of sampling to obtain approximate accumulation rates. This assumption is conservative and relies on the raw radiocarbon ages obtained in these four cores (ranging from 261 to 375 years BP; Table S2), which correspond to about half of the radiocarbon ages adjusted for Delta R that can be calibrated using postbomb curves (i.e., calibrated 700 years BP would render about 1,700–1,900 cal AD at our study sites (Stuiver & Reimer, 1993)). All ^{14} C ages reported are expressed as radiocarbon-calibrated years (cal yr BP; before present corresponding to 2018). The sediment accretion rate (SAR, cm yr^{-1}) per core was estimated from the ^{14}C age-depth model and was standardized for the last 500 years whenever possible. In cases where the age of the core was less than 500 years (Table S1), the SAR was standardized to the oldest age possible. The SARs of the two replicate cores per site that were not radiocarbon-dated were assumed to equal the SAR in

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the replicate core dated. Accumulation rates of C_{org}, N, and $CaCO_3$ (g element m^{-2} yr^{-1}) of each core were derived by multiplying the corresponding cumulative mass of each element accumulated over 500 years by the corresponding SAR of the core.

2.4. Statistical Analysis

Statistical analyses were done using the accumulation rates rather than the stocks to ensure meaningful comparisons among sites. The top meter of sediment thickness, which is commonly used to assess the blue carbon storage capacity across sites, corresponded to very diverse periods of accumulation across sites, ranging from 238 years at Serifos to 2,152 years at Anavissos (Table S1). Nevertheless, we report data on C_{org}, N, and $CaCO_3$ stocks at the top meter (Table S1) to facilitate comparisons among other studies.

One-way analysis of variance (ANOVA) was used to test possible significant differences in accumulation rates among sites. Normality and homogeneity of variance were checked before analysis using the Shapiro-Wilk and Levene's tests, respectively. When these assumptions were not met, data were $\log_{10}$-transformed. If significant differences occurred ($P < 0.05$), Tukey's post hoc test was used to identify which sites differed.

A multivariate analysis was used to explore the abiotic and biotic factors influencing the accumulation rates across the South Aegean Sea. In particular, a redundancy analysis (RDA) was used, which performs multiple linear regression (MLR) of response variables on explanatory variables and then conducts a principal component analysis (PCA) to the matrix of fitted values of all response variables generated through the MLR. Therefore, the RDA produces two ordinations in space, one defined by the matrix of response variables and another defined by the matrix of explanatory variables. The analysis provides the total variance of the data set, partitioned into constrained variance, thereby showing how much variation in the response matrix can be explained by the matrix of explanatory variables, and unconstrained variance. In our data set, the response variables were the C_{org}, N, and $CaCO_3$ accumulation rates, and the explanatory variables were composed of three sets of variables that described the sediment characteristics, seagrass traits, and environmental settings.

Sediment characteristics included the mean values of grain size fractions, C_{org}, $CaCO_3$, and N contents, the contribution of *P. oceanica* detritus to the sediment C_{org} pool during the last 500 years, and the lithology of the sites. We did not use C_{org}, N, and $CaCO_3$ contents in the RDA to avoid any potential numerical influence they might have had on the response matrix due to their interference in the mathematical calculation of the C_{org}, N, and $CaCO_3$ accumulation rates, respectively. Instead, we used the C_{org}:N and C_{org}:C_{inorg} ratios, considering a mass ratio of 12% C_{inorg} in $CaCO_3$. For determining the contribution of *P. oceanica* in the C_{org} pool, stable isotope mixing models were run for each core in R ("simmr" and "rjags" packages; (Parnell et al., 2013)). The $\delta^{13}C$ of each slice along the 500-year profile from each core was used. We acknowledge that the $\delta^{13}C$ values of *P. oceanica* detritus in the deeper sediment layers may have been altered during decomposition. However, very few studies have determined the $\delta^{13}C$ fractionation of seagrass species during decomposition, and their results show considerable variability, with fractionation ranging from negligible to changes up to 4‰ (Kelleway et al., 2022). In addition, to the best of our knowledge, none of the studies have focused on *P. oceanica*. Lastly, available decomposition studies assess the change of $\delta^{13}C$ in shorter timescales (months to a few years), while blue carbon studies refer to centennial scales. Therefore, no fractionation correlation factor between the $\delta^{13}C$ and the timeframe of our study was available. Lastly, for the multivariate statistical analysis, we used the mean values of the 500-year profile for all the geochemical variables, to integrate the variability along the profile. For the sake of comparison, using the $\delta^{13}C$ signatures along the profile rather than the ones of the superficial sediment was chosen. Potential end-members considered were as follows: "*P. oceanica* leaves," "Other macrophytes," and "seston and terrestrial material." "Other macrophytes" included seagrass species other than *P. oceanica* (i.e., *C. nodosa* and *H. stipulacea*) and macroalgae. Other seagrass species had limited presence, and macroalgae had low coverage, so they were pooled together in one group by calculating the mean value of their $\delta^{13}C$ signatures (Table S3 in Supporting Information S1). Mean $\delta^{13}C$ signatures for each source were obtained from our own unpublished data or the literature (Table S3 in Supporting Information S1). Possible differences in $\delta^{13}C$ among end-members were assessed through *t*-tests. Other macrophytes and seston had similar ($P > 0.05$) $\delta^{13}C$ signatures and were grouped to decrease uncertainty in the model outcome. The simmr_mcmc() function was used to generate the potential contribution of different sources by applying a Markov chain Monte Carlo (MCMC) (Parnell et al., 2010, 2013). In total of 10,000 iterations were conducted, from which 1,000 burn-initial iterations were discarded. The remaining samples were used to construct the posterior distribution. The convergence of each

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model for each site was assessed through model diagnostics, which indicated that R-hat values in all cases were close to 1, suggesting effective convergence (Vehtari et al., 2019). Finally, the lithology of each site was included as a nominal binary variable of karstic/nonkarstic mineral matrix, which served as an indication of the biogenic or lithogenic origin, respectively, of $CaCO_3$ in the sediments.

The seagrass variables considered were the mean shoot density, leaf biomass, and rhizome elongation measured at each site. The environmental variables taken into consideration were water depth, the concentration of chlorophyll *a* (Chl *a*) in the water column as a proxy for the nutrient regime, Secchi depth as a proxy of water transparency, and suspended particulate matter (SPM) as a proxy for turbidity. Data of Chl *a*, Secchi depth, and SPM were satellite data downloaded from the Copernicus Marine database (https://marine.copernicus.eu/). We used L4 optimally interpolated data at 4 × 4 km resolution (OCEANCOLOUR GLO BGC L4 MY 009 104). The "nearest neighbor" with available satellite data for each site was selected in MATLAB v. R2018a software. The distance between our sites and their "nearest neighbor" was on average 2.66 ± 1.73 km. Only in the cases of Amorgos and Milos, did the available "nearest neighbors" extend beyond the 4 × 4-km grid, but they were at a maximum distance of 6 km from the sampling sites. We retrieved all available data for each variable (on diel resolution in case of Chl *a* and monthly resolution in case of Secchi depth and SPM) from the earliest measurement available (i.e., 1997) until the year of sampling. The mean value of each variable across the whole timescale available per site was used for the analysis. We acknowledge that environmental and seagrass variables referred to a shorter temporal scale than that covered by sediment variables. However, these variables were used as indicative of the environmental and seagrass context, assuming that they are representative of the period of accumulation.

Before running the RDA, possible multicollinearity among explanatory variables was assessed. First, a PCA was performed on the correlation matrix of the grain size fractions, after data were transformed using centered log ratio (Aitchison, 1986). The principal component 1 (PC1) explained 94% of the variability in grain size distribution among sites, and therefore, the PC1 scores were used in further statistical analysis (Figure S2 in Supporting Information S1). Then, a Pearson correlation was performed, and highly correlated variables (Pearson's $|r| > 0.7$) were removed (i.e., Chl *a*). The final data set included the following explanatory variables: PC1 scores of grain size fractions, C_{org}:N and C_{org}:C_{inorg} ratios, *P. oceanica* contribution to sediment C_{org}, lithology, shoot density, leaf biomass, rhizome elongation, water depth, Secchi depth, and SPM. The explanatory variables were examined for normality, using the Shapiro-Wilk test, and transformed with $\log_{10}$ or square root to achieve normality, if necessary. All variables were subsequently standardized using z-scores.

An initial RDA model was run, and its significance was assessed by Monte Carlo permutation test (999 permutations). Then, the most parsimonious RDA model was selected by identifying the explanatory variables that most significantly ($P < 0.05$) contributed to the variance of the response matrix through the Monte Carlo permutation test (backward selection, 999 permutations). A final RDA was run with those explanatory variables and tested by Monte Carlo permutation test (999 permutations) for its significance. A correlation plot (Type II scaling) was used to show the relation among the three response variables and between each response variable and each of the backward selected explanatory variables. In such plots, the relation between each pair of variables is equal to the cosine of the angle between them (i.e., a right angle describing no correlation as cos (90°) = 0, an acute angle, a positive correlation, and an obtuse angle, a negative correlation). Unique and shared variations among sets of variables were identified through variation partitioning (based on R^2 adjusted) and visualized in a Venn diagram.

All analyses were performed in R version 4.0.5 (R Core Team, 2021), using the vegan package (Oksanen et al., 2022).

3. Results

3.1. Variability of C_{org}, N, and $CaCO_3$ Stocks and Accumulation Rates

C_{org} stock at the top meter of sediment ranged from 7.7 ± 0.4 kg m^{-2} at Metopi to 23.2 ± 7.8 kg m^{-2} at Santorini 2, with a mean ± STDEV of 14.6 ± 5.0 kg m^{-2} across all sites (Table S1). The range of N stock was 0.29 ± 0.09–0.81 ± 0.02 kg m^{-2} among sites, and the mean was 0.47 ± 0.17 kg m^{-2}. The variability of $CaCO_3$ stocks between sites was high, ranging from 16.6 ± 8.7 kg m^{-2} at Santorini 2 to 663 ± 55 kg m^{-2} at Koufonisi, having a mean value of 249 ± 210 kg m^{-2}.

Sediment accretion rates in the last 500 years varied from 0.05 to 0.41 cm yr^{-1}, with a mean of 0.22 ± 0.01 cm yr^{-1} among the sites studied (Table S1). C_{org} accumulation rates over the last 500 years ranged

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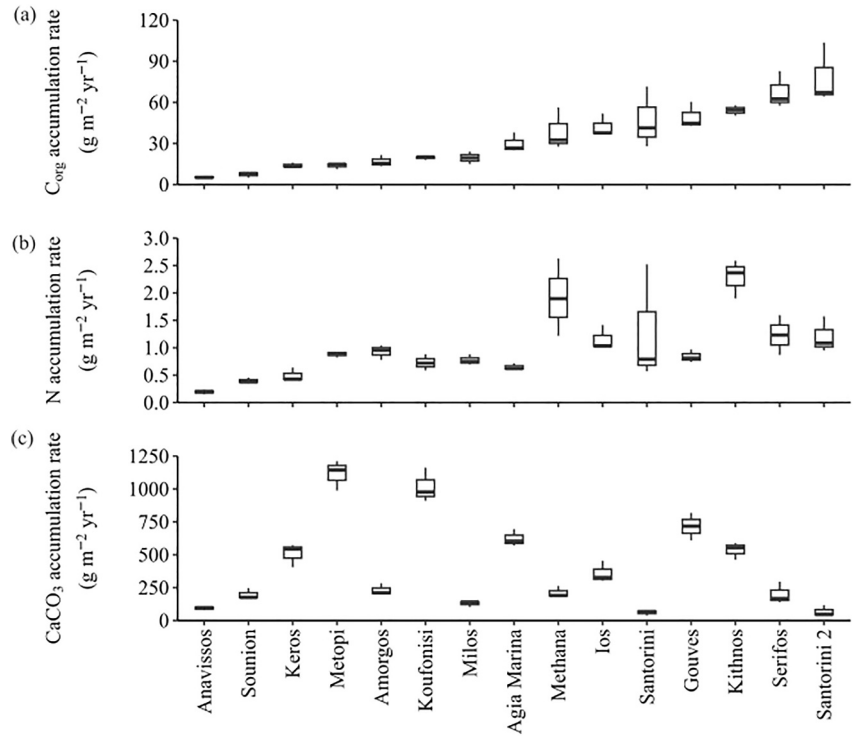

Figure 2. Boxplots of (a) organic carbon (C_{org}), (b) nitrogen (N), and (c) carbonate ($CaCO_3$) accumulation rates over the last 500 years at each site. Each box encompasses the 25% and 75% quantiles, and the horizontal dash indicates the median. Boxplots are sorted by the mean value from the lowest to the highest value of the C_{org} accumulation rate.

from 5.4 ± 0.8 g C_{org} m^{-2} yr^{-1} at Anavissos to 78.4 ± 22.0 g C_{org} m^{-2} yr^{-1} at Santorini 2, with a mean of 33.6 ± 23.6 g C_{org} m^{-2} yr^{-1} across all sites (Figure 2a). Significantly higher C_{org} accumulation rates were measured at Methana, Ios, Santorini, Gouves, Kithnos, Serifos and Santorini 2 than at the remaining sites (Table S5). The N accumulation rate ranged between 0.19 ± 0.04 at g N m^{-2} yr^{-1} at Anavissos and 2.29 ± 0.35 g N m^{-2} yr^{-1} at Kithnos, with a mean across all sites of 1.00 ± 0.62 g N m^{-2} yr^{-1} (Figure 2b). Overall, the N accumulation rate was higher at the sites having had also the highest C_{org} accumulation rates (i.e., Methana, Ios, Santorini, Gouves, Kithnos, Serifos, and Santorini 2), although the difference of N accumulation rates at those sites was not always significant from the rest of the sites. The accumulation rates of $CaCO_3$ ranged from 61 ± 21 g $CaCO_3$ m^{-2} yr^{-1} at Santorini to 1,115 ± 115 g $CaCO_3$ m^{-2} yr^{-1} at Metopi, with a mean value of 405 ± 336 g $CaCO_3$ m^{-2} yr^{-1} across all sites and significantly higher rates at Metopi, Keros, Koufonisi, Agia Marina, and Gouves than those measured at the sites with high C_{org} accumulation rates (Figure 2c). Anavissos and Sounion had significantly lower accumulation rates than the rest of the sites for all studied elements.

3.2. Drivers of Variability in C_{org}, N, and $CaCO_3$ Accumulation Rates

The temporal distribution of sediment variables in the last 500 years showed low variability at all sites (Table S1). Sediments were mainly sandy, with a high percentage of very coarse (mean ± SE in the last 500 years across sites of 10.3 ± 0.5%), coarse (5.9 ± 0.4%), medium (18.4 ± 0.5%), and fine (47.4 ± 0.6%) sands, and silt/clay (18.0 ± 0.7%) contents (Figure 3). Mean DBD in the last 500 years ranged between 0.52 ± 0.01 and 1.06 ± 0.02 g cm^{-3} across sites, with an average of 0.86 ± 0.01 g cm^{-3} for our study area (Figure 4a). The change of C_{org} and N contents with time followed similar patterns at each site (Table S1). The mean C_{org} content in the last 500 years varied from 1.08 ± 0.15 to 4.35 ± 0.76% among sites, and it was on average 2.24 ± 0.09% (Figure 4b). The range in the mean N content in the last 500 years among sites was 0.036 ± 0.006–0.138 ± 0.004%, and the mean for the study was 0.069 ± 0.002% (Figure 4c). The mean $CaCO_3$ content in the last 500 years showed considerable variability among sites, with a range of 1.9 ± 0.3–74.5 ± 1.4% and an average of 28.1 ± 1.2% for the study area (Figure 4d). The mean $\delta^{13}C$ signature across sites in the last 500 years ranged from −19.0 ± 0.4 to −15.3 ± 0.2‰ and was on average −17.3 ± 0.1‰ (Figure 5a).

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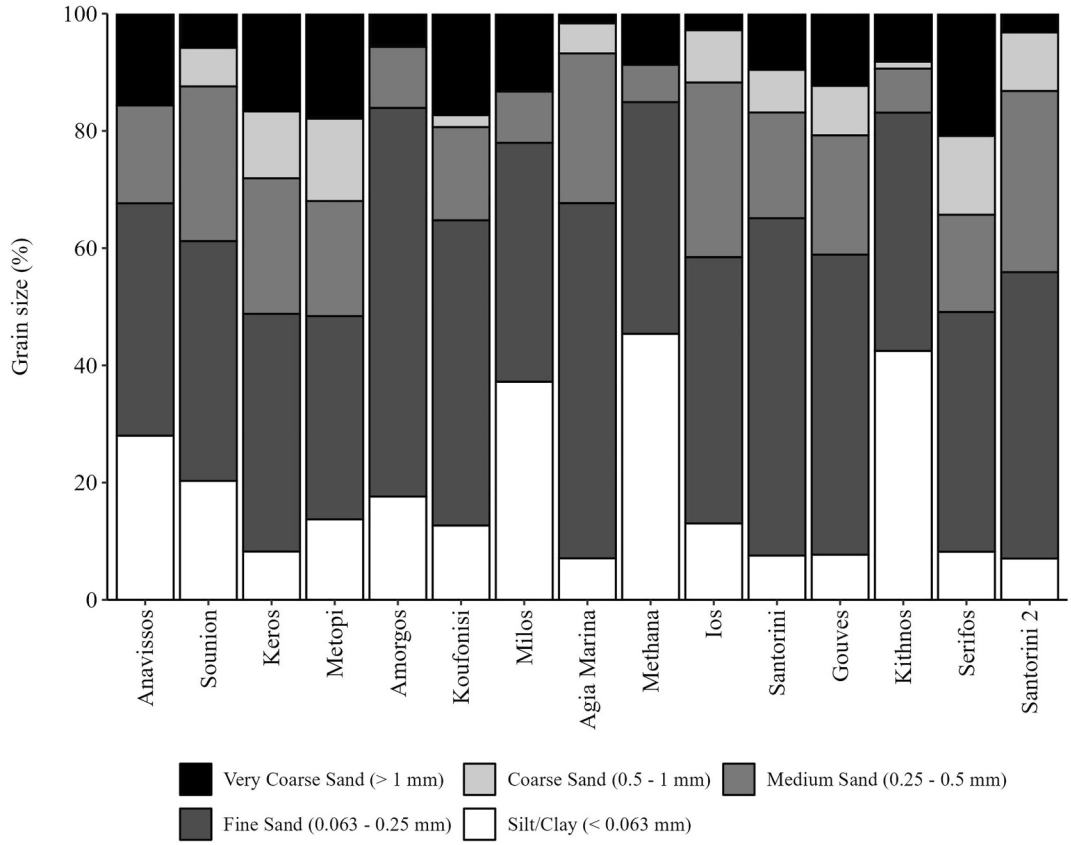

Figure 3. Mean value of cumulative grain size fractions (%) accumulated over the last 500 years at each site.

The contribution of *P. oceanica* detritus to the sediment C_{org} pool ranged from 42 ± 11% to 74 ± 4%, being on average 60 ± 10% across sites (Figure 5b). The contribution of other macrophytes and seston was on average (±STDEV) 22 ± 7%, with a range of 17 ± 3 to 32 ± 13% among sites. Terrestrial material had the lowest contribution to the sediment C_{org} pool, with a mean and range of 18 ± 5% and 8 ± 1–27 ± 2%, respectively.

Data on seagrass traits and environmental settings at the study sites are shown in Table S4. The shoot density range was 160 ± 18–505 ± 52 shoots m^{-2} across sites, with a mean ± STDEV of 388 ± 125 shoots m^{-2}. Leaf biomass ranged between 627 ± 171 and 2,278 ± 629 g DW m^{-2} and rhizome elongation between 4.8 ± 0.1 and 12.5 ± 0.6 mm yr^{-1}, with mean values of 1,374 ± 532 g DW m^{-2} and 8.6 ± 2.3 mm yr^{-1}, respectively. Water depth ranged between 3 and 14 m with a mean ± STDEV of 8 ± 3 m and Secchi depth between 15 and 28 m with a mean of 24 ± 3 m. The concentration of Chl *a* was on average 0.18 ± 0.06 mg m^{-3}, varying from 0.12 ± 0.01 to 0.37 ± 0.07 mg m^{-3}, and SPM was on average 0.52 ± 0.17 g m^{-3}, ranging from 0.38 ± 0.08 to 1.04 ± 0.08 g m^{-3} across sites.

The RDA model explained 70% of the variation in the pattern of C_{org}, N, and $CaCO_3$ accumulation rates, considering all the explanatory variables tested. The explanatory variables that most significantly influenced that variability were the C_{org}:N and C_{org}:C_{inorg} ratios, *P. oceanica* contribution to sediment C_{org}, leaf biomass, rhizome elongation, and SPM (Table 1). C_{org} and N accumulation rates had a strong positive correlation, and both negatively correlated with the $CaCO_3$ accumulation rate. C_{org} and N accumulation rates were positively correlated with C_{org}:N and C_{org}:C_{inorg} ratios, *P. oceanica* contribution to the sediment C_{org} pool, leaf biomass, and rhizome elongation (Figure 6). The $CaCO_3$ accumulation rate had a positive correlation with SPM. In total, the greatest part of the variation in the response variables was explained by sediment characteristics (40%), followed by environmental settings (5%) and seagrass traits (2%) (Figure 6).

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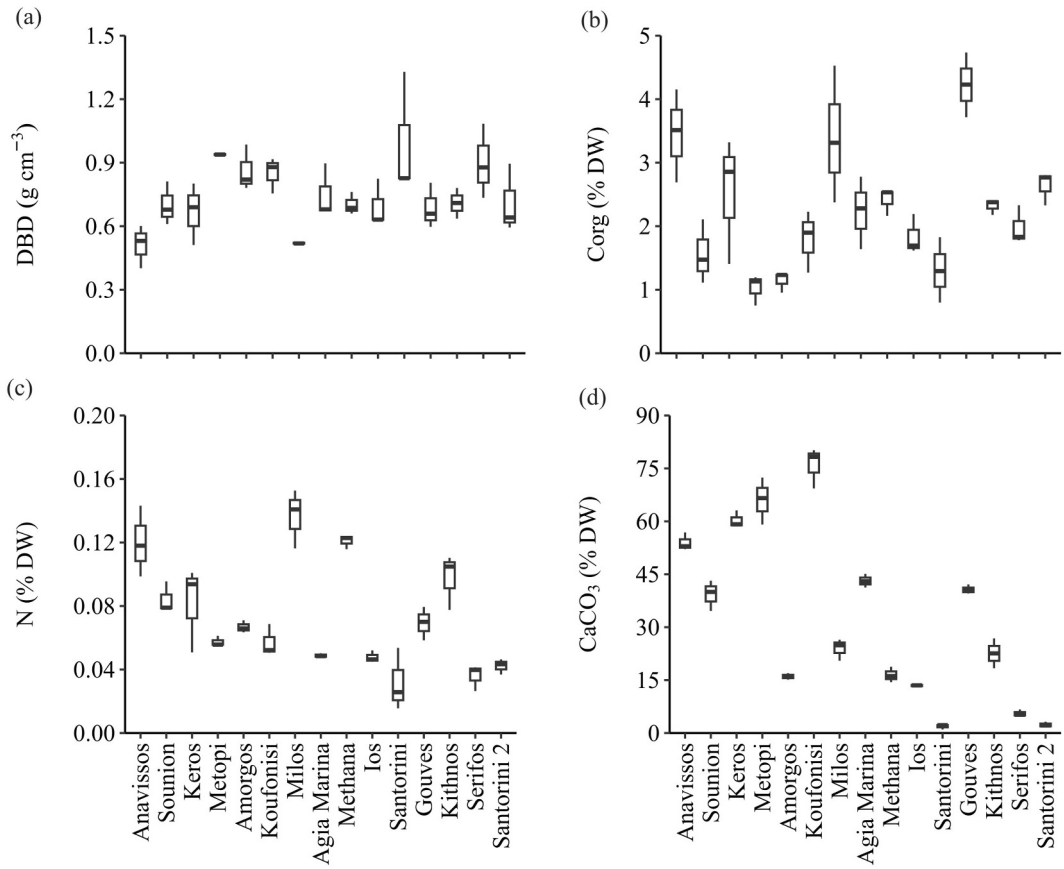

Figure 4. Boxplots of the mean (a) dry bulk density (DBD), (b) C_{org} content, (c) N content, and (d) $CaCO_3$ content over the last 500 years at each site. Each box encompasses the 25% and 75% quantiles, and the horizontal dash indicates the median.

4. Discussion

This study revealed that *P. oceanica* meadows of the South Aegean Sea rank among the most effective carbon and nitrogen sinks reported for seagrasses worldwide. The low variability in habitat geomorphology across the area of study, with all meadows being near the shore (70–450 m from the nearest coast) and away from river mouths or streams (even ephemeral ones), allowed us to understand the influence of the local biogeochemical and environmental context on the differences between organic and inorganic accumulation. Sediment characteristics shaped the pattern of accumulation, contributing the most to explaining the variability among the accumulation of the different elements, followed by the influence of seagrass traits and environmental regime. The large contribution of *P. oceanica* C_{org} into the sedimentary pool reinforces the role of seagrasses as natural blue carbon sinks.

4.1. C_{org}, N, and $CaCO_3$ Accumulation Rates in *P. oceanica* Meadows From the South Aegean Sea

Despite the significant increase in research efforts around BC in seagrass ecosystems (Costa et al., 2022), surprisingly we still lack a global robust estimate of the C_{org} accumulation rate in seagrass meadows, apart from early estimations based on a few species (Kennedy et al., 2010; Mcleod et al., 2011) which may render the current value ambiguous. Generally, assessments of C_{org} accumulation rates are undertaken at a local or, at best, at a national level based on very limited data. Comparison with estimates of the long-term C_{org} accumulation rate of seagrass species from other parts of the world shows that our mean value over the last 500 years (33.6 ± 23.6 g C_{org} m^{-2} yr^{-1}) lies on the higher end of the range reported for the taxa so far in the Red and Caribbean Seas, as well as the Indian, Pacific, and Southern Oceans (Fu et al., 2023; Lafratta et al., 2020; Miyajima et al., 2022; Rozaimi et al., 2016; Serrano et al., 2018, 2021). The mean C_{org} accumulation rate in this study was lower than the mean value reported for *P. oceanica* meadows in Italy, Spain, and Malta (84 ± 20 g C_{org} m^{-2} yr^{-1}) (Serrano,

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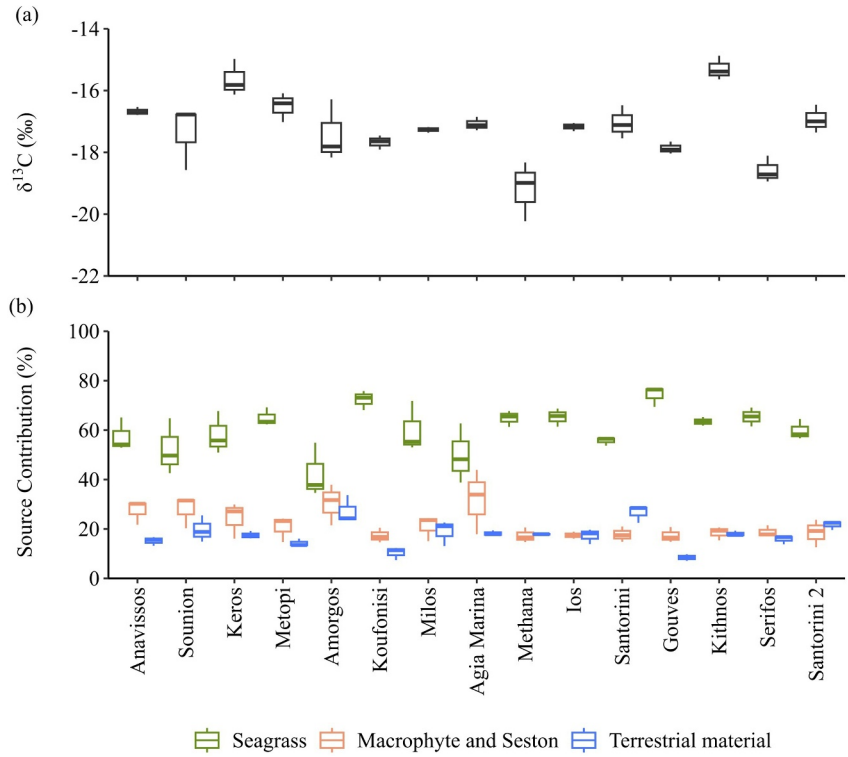

Figure 5. Boxplots of the mean (a) $\delta^{13}C$ composition and (b) contribution of end-members to sediment C_{org} over the last 500 years at each site. Each box encompasses the 25% and 75% quantiles, and the horizontal dash indicates the median.

Lavery, López-Merino, et al., 2016). However, Serrano, Lavery, López-Merino, et al. (2016) reported data for hotspots of C_{org} accumulation in shallow meadows where organic-rich escarpments of several meters in thickness were present and thereby, likely provided an overestimate of C_{org} accumulation in *P. oceanica* meadows. When compared with data from other studies, our mean C_{org} accumulation rate fell close to the mean rate for the species in Spain (27 ± 16 g C_{org} m^{-2} yr^{-1}, Mateo et al., 2019), or even higher than the short-term C_{org} accumulation rate (~100–120 years based on ^{210}Pb dating) measured in Spain (26 ± 15 g C_{org} m^{-2} yr^{-1} (Mazarrasa et al., 2017a), Italy (24 ± 4 g C_{org} m^{-2} yr^{-1} (Apostolaki et al., 2022), and Cyprus (14 ± 4 g C_{org} m^{-2} yr^{-1} (Wesselmann et al., 2021)). It is important to note, however, that the aforementioned C_{org} accumulation rates corresponded to very different timeframes; the mean in Serrano, Lavery, López-Merino, et al. (2016) was standardized for a 2-m sediment thickness corresponding to 400 to 3,300 years, while in Mateo et al. (2019) corresponded to 355 to 9,422 years, suggesting that they should be recalculated to 500 years to deliver robust comparisons. In addition, comparisons with short-term accumulation rates should be made with caution, as ^{14}C-based SAR is usually lower than the SAR derived from excess ^{210}Pb, further highlighting the importance of incorporating timescales in BC assessments. Standardizing the timeframe, along with establishing precise chronologies and sedimentation rates are crucial for determining the capacity of seagrass to sequester carbon over meaningful timescales for blue carbon science and related management interventions such as identifying hotspots for blue carbon projects. Given the potential of *P. oceanica* for climate mitigation in the Mediterranean (Pergent-Martini et al., 2021), a coordinated effort to summarize and standardize the available knowledge should be undertaken soon to provide a spatially explicit estimation of the C_{org} accumulation rate for the region, following similar initiatives in the Nordic region (Krause-Jensen et al., 2022), and inform the implementation of blue carbon crediting accounting frameworks.

The mean N accumulation rate of *P. oceanica* in the South Aegean Sea (1.00 ± 0.62 g N m^{-2} yr^{-1}) was higher than the mean long-term mean rates reported for the species in Spain (0.59 ± 0.35 g N m^{-2} yr^{-1}, with a range of 0.16–1.03 g N m^{-2} yr^{-1}) (Mateo et al., 1997) and the short-term N accumulation rate reported in Italy (0.6 ± 0.1 g N m^{-2} yr^{-1}) (Apostolaki et al., 2022). It also fell inside the range reported for several other seagrass

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Table 1
Summary Table of Redundancy Analysis (RDA) and Statistics Between the Response Variables (C_{org}, N and $CaCO_3$ Accumulation Rates) and the Explanatory Variables

Monte Carlo permutation test for the initial RDA model (999 permutations) with all the explanatory variables tested (PC1 scores of grain size fractions, C_{org}:N and C_{org}:C_{inorg} ratios, P. oceanica contribution to sediment C_{org}, lithology, shoot density, leaf biomass, rhizome elongation, water depth, Secchi depth, and SPM)						
	df	Variance	F	p-value		
Model	11	2.10	7.0	0.001		
Residuals	33	0.90				
R^2	0.70					
R^2 adjusted	0.60					
Monte Carlo Permutation test with backward selection in constrained ordination (999 permutations)						
	df	F	p-value			
C_{org}:N	1	5.16	0.006			
C_{org}:C_{inorg}	1	31.07	0.001			
P. oceanica contribution	1	4.77	0.008			
Leaf biomass	1	3.59	0.021			
Rhizome elongation	1	4.10	0.017			
Suspended matter (SPM)	1	6.60	0.002			
RDA model with backward selected explanatory variables						
Partitioning of variance						
Constrained	0.65					
Unconstrained	0.35					
	RDA1	RDA2	RDA3	PC1	PC2	PC3
Importance of components:						
Eigenvalue	1.30	0.44	0.22	0.90	0.09	0.05
Proportion explained	0.43	0.15	0.07	0.30	0.03	0.02
Cumulative proportion explained	0.43	0.58	0.65	0.95	0.98	1.00
Monte Carlo Permutation test for the final RDA model with the backward selected explanatory variables (999 permutations)						
	df	Variance	F	p-value		
Model	6	1.96	11.9	0.001		
Residuals	38	1.04				
R^2	0.65					
R^2 adjusted	0.60					

species globally (Aoki et al., 2020; Apostolaki et al., 2019; Eyre et al., 2016; Leiva-Dueñas et al., 2023; Martins et al., 2022; Saderne et al., 2018; de los Santos et al., 2023). These comparisons across sites or species should be made with caution, as in the case of comparing the C_{org} accumulation rates, due to the different timescales involved. Nevertheless, the available information on N accumulation rates in seagrass ecosystems remains extremely scarce, despite the recognized role of these ecosystems as coastal filters (McGlathery et al., 2007). Although assessing the pathways of N cycling was outside the scope of this study, research on *Z. marina* indicates that burial dominates the N-removal processes, serving as the main mechanism by which seagrasses achieve their N-filtering function (Aoki et al., 2020). In this sense, *P. oceanica* meadows are expected to significantly contribute to nitrogen filtration along the eastern Mediterranean coasts, where eutrophication events, although usually localized, can occasionally become a significant source of coastal contamination (Simboura et al., 2016). Eutrophication threatens the integrity of seagrasses, possibly compromising the capacity of the latter to support effective actions against the former. The variety of biogeochemical processes involved in fixing and releasing N (Eyre et al., 2016; Prystay et al., 2023; Risgaard-Petersen & Ottosen, 2000), which

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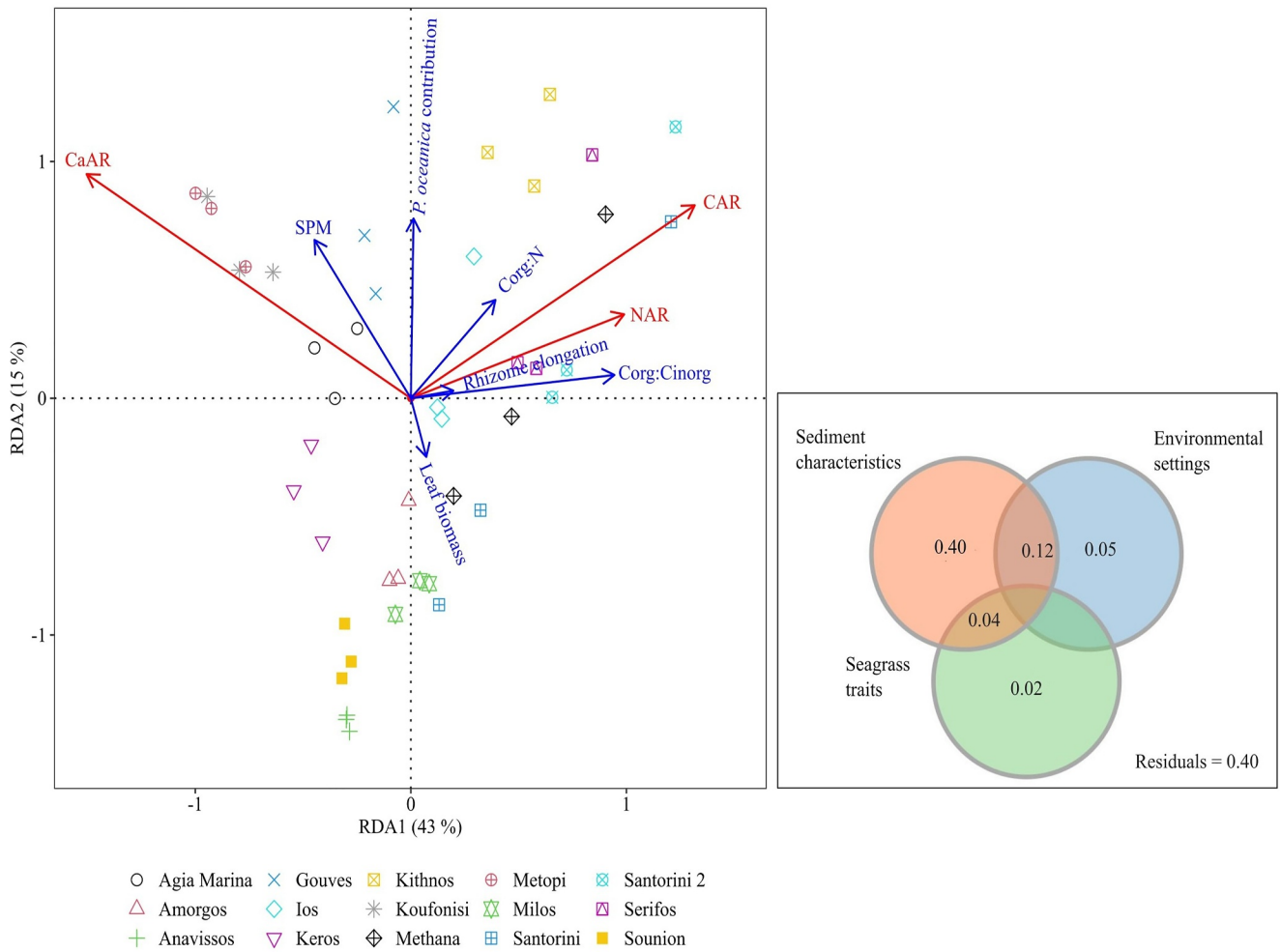

Figure 6. Redundancy analysis (RDA) correlation plot (Type II scaling) showing the pattern in the response variables (red vectors) and the backward selected explanatory variables (blue vectors) that mostly drove that variation. CAR, NAR, and CaAR indicate C_{org}, N, and $CaCO_3$ accumulation rates, respectively. A Venn diagram shows the unique and shared variation (R^2 adjusted) explained by the most significant variables of each set of variables (sediment characteristics (i.e., C_{org}:N and C_{org}:C_{inorg} ratios and *P. oceanica* contribution to the sediment C_{org} pool), seagrass traits (i.e., leaf biomass and rhizome elongation), and environmental settings (i.e., suspended matter, SPM)).

ultimately determine the magnitude of N burial in the sediments, can vary significantly across biogeochemical and environmental gradients. This variability may disrupt the balance between N input and burial, potentially leading to a decline in N burial due to eutrophication (McGlathery et al., 2007). However, further studies are needed to draw reliable conclusions about how seagrass degradation may impact its capacity to remove N, and thereby, aid the development of N credits and markets.

Compared with other *P. oceanica* meadows, the mean $CaCO_3$ accumulation rate in this study (405 ± 336 g $CaCO_3$ m^{-2} yr^{-1}) was 7-fold higher than estimates from *P. oceanica* in Spain (54.3 ± 1.9 g $CaCO_3$ m^{-2} yr^{-1}) (Serrano et al., 2012). Considering a mass ratio of 12% C_{inorg} in $CaCO_3$, the recorded values (7–134 g C_{inorg} m^{-2} yr^{-1}) fall within the range reported for other seagrass species (Rozaimi et al., 2016; Saderne et al., 2018). Overall, our mean C_{inorg} accumulation rate (49 ± 40 g C_{inorg} m^{-2} yr^{-1}) ranged considerably lower than the short-term global mean (182 ± 94 g C_{inorg} m^{-2} yr^{-1}) calculated for seagrasses (Saderne et al., 2019). Again, the different timescales in those studies may add some uncertainty to the comparisons, but, generally, seagrass sediments are shown to support considerable, albeit variable, carbonate stocks (Mazarrasa et al., 2015). This variability is often seen across seagrass species, geomorphologies, and environmental gradients, as these factors affect the calcification by seagrass-associated biota, the trapping of carbonate particles, and the balance between carbonate production and dissolution in seagrass sediments (Saderne et al., 2019). The results obtained highlight the exceptional role of seagrasses in carbonate production, which is comparable to other benthic habitats

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including maerl and coralligenous habitats (Canals & Ballesteros, 1997). This reinforces the hypothesis that seagrass meadows contribute to climate change adaptation by generating carbonated sands that help protect against coastal erosion and sea level rise (Duarte, Losada, et al., 2013). On the other hand, the production of $CaCO_3$, which is enhanced by the 3D habitat provided by seagrass meadows for calcifying organisms, results in net CO_2 emissions and thereby, withdrawing on the net CO_2 sequestration by C_{org} burial (Macreadie et al., 2017). However, carbonate production and dissolution processes in seagrass meadows are complex and poorly understood. This, together with uncertainties regarding the net effect of carbonate accumulation on C_{org} preservation and accumulation, the export of alkalinity as a net carbon sink pathway, or the potential allochthonous origin of carbonates buried in the meadows, among others (Howard et al., 2018; van Dam et al., 2021), have precluded the inclusion of carbonates in carbon accounting. Therefore, further research is required to fully understand the implications of carbonates in the carbon cycle both within and beyond seagrass habitats.

4.2. Biotic and Abiotic Drivers of Variability in C_{org}, N, and $CaCO_3$ Accumulation Rates Across the South Aegean Sea

The relations identified by statistical analysis between the C_{org} and N accumulation rates and the abiotic and biotic explanatory variables (i.e., sedimentary C_{org}:N and C_{org}:C_{inorg} ratios, *P. oceanica* contribution to the C_{org} pool, leaf biomass, rhizome elongation and SPM) suggest that the accumulation of organic matter tended to be higher in inorganic carbon-poor sediments where seagrasses were the main contributors of organic matter, which in turn was the result of healthy meadows that extended in clear waters. The positive associations of C_{org} and N accumulation rates with C_{org} and N contents in the sediment have been widely shown to drive the storage of C_{org} and N, respectively (Kindeberg et al., 2018; Leiva-Dueñas et al., 2023). In several studies of *P. oceanica* and other seagrass species, C_{org} and N contents usually show a covariation along the sediment profiles (Apostolaki et al., 2022; Fourqurean, Kendrick, et al., 2012; Fourqurean, Duarte, et al., 2012; Leiva-Dueñas et al., 2023). This is possibly due to the similar timescales in the sequestration and decomposition of these elements that drive the stabilization of organic matter. Underlying sediments in seagrass meadows are typically enriched in C_{org}:N due to seagrass tissue having higher C_{org}:N than phytoplankton (Mazarrasa et al., 2017b). It is also indicative of large seagrass species, which could be attributed primarily to their elevated biomass and production (Mazarrasa et al., 2018). This is particularly true for *P. oceanica*, which has relatively recalcitrant tissue when compared to other seagrass species (Kaal et al., 2018). This recalcitrance slows down the mineralization, resulting in detritus enriched in C_{org}.

Accordingly, the results of mixing models indicated that the accumulation of organic matter was driven by the input of *P. oceanica*. The C_{org} pool was a mixture of C_{org} deriving mainly from *P. oceanica* and to a lesser extent from allochthonous sources. We acknowledge that deeper layers may have undergone postdepositional diagenesis, potentially modifying the $\delta^{13}C$ signatures, so the results of the models should be interpreted with caution. However, there is still limited knowledge about the potential shifts in $\delta^{13}C$ signals during decomposition, especially over large periods (Kelleway et al., 2022). This has led to similar studies in blue carbon science applying the mixing models either in the first cm of sediment (e.g., 5 cm in Apostolaki et al., 2022) or along the whole sediment profile (e.g., 60 cm in Serrano et al., 2018). All the above suggests that further studies are needed before disentangling the relation between decomposition and $\delta^{13}C$ over meaningful timescales for blue carbon assessments. In any case, potential variability in $\delta^{13}C$ signatures is expected to decrease with sediment depth, following the decrease in the decomposition rate with time (i.e., downcore). In this study, temporal variability of $\delta^{13}C$ along the 500-year profile was small. Given that the meadows were monospecific and extended in the ultraoligotrophic conditions of the eastern Mediterranean, far from any significant terrestrial input, it is reasonable to expect that the contribution of *P. oceanica* detritus in the sedimentary C_{org} pool would be considerable.

Leaf biomass and rhizome elongation had a positive influence on C_{org} and N accumulation rates. The importance of diverse seagrass traits (e.g., shoot density, above- and/or below-ground biomass, and plant elemental content) in driving the storage of C_{org} and, to a lesser extent, N has been shown primarily for *Zostera* spp. (Kim et al., 2022; Lima et al., 2020; Novak et al., 2020; Ricart et al., 2020; Röhr et al., 2016). To our knowledge, this is the first study to examine the effect of seagrass traits on the accumulation rates in *P. oceanica* meadows. This species has been demonstrated to influence the sequestration capacity in multiple species comparisons, owing to its particular traits that drive the variability of C_{org} stocks across all seagrass species, even over large-scale factors such as geomorphology (Kennedy et al., 2022). *P. oceanica* is a long-lived large species, reaching high biomass and production (Duarte et al., 2010). The positive correlation between organic matter accumulation and leaf biomass

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and rhizome elongation, which is a proxy for seagrass growth, shows that good seagrass status results in a considerable input of seagrass-derived organic matter in the underlying sediments, thereby directly influencing storage. Contemporarily, *P. oceanica* has long leaves and forms structurally complex meadows, which modify water flow, increase particle sedimentation, and decrease resuspension, enhancing trapping of allochthonous organic matter (Hendriks et al., 2009) and therefore accumulation in the underlying sediments. Among the traits tested, shoot density did not affect the pattern of accumulation, similar to other studies (Gullström et al., 2018; Kim et al., 2022; Röhr et al., 2016). Shoot density is a generic indicator with a slow response time (Roca et al., 2016). This is particularly true for the long-lived, large seagrass species, like *P. oceanica* studied here, which can sustain high environmental stress, at least until reaching a tipping point. Any change in the environmental conditions is more likely to be first reflected in a physiological variable (e.g., seagrass nutrient content), or like in this case, a morphological one (i.e., growth), eventually affecting the meadow structure. The sampling area included sites in relatively unaffected conditions, with only a few ones situated close to coastal developed areas. As a result, shoot density is not expected to largely differ to the extent that it would interfere with the capacity of the shoots to trap organic particles. Therefore, the contribution of *P. oceanica* to C_{org} input is mainly through its high biomass and growth, rather than the number of shoots per surface area, as it remains relatively constant over time in healthy meadows like those in this study.

The C_{org} and N accumulation rates were negatively influenced by SPM, suggesting that good environmental status fueled the accumulation of organic matter. Sites with high sediment C_{org} and N accumulation rates (e.g., Santorini, Serifos, and Kithnos) held healthy and extensive meadows from the near-surface down to approximately 30 m depth, probably associated with ample light availability that enhanced photosynthesis (Alcoverro et al., 2001) allowing the formation of productive meadows. In contrast, sites with low C_{org} and N accumulation rates (e.g., Anavissos, Sounion, and Metopi) were located near coastal developed areas. Poor environmental conditions, likely due to anthropogenic activities, may have weakened the blue carbon potential of the underlying seagrass sediments due to the accumulation of more labile, allochthonous carbon (Kindeberg et al., 2018; Liu et al., 2023; Mazarrasa et al., 2017b; Novak et al., 2020; Samper-Villarreal et al., 2018). Besides, the negative relation of SPM with C_{org} and N accumulation rates confirmed that one of the reasons for the higher accumulation of organic matter in our study was that the main source of carbon in the underlying sediments was autochthonous. This could remove major concerns around the implementation of conservation and restoration blue carbon projects in southern Greece, owing to the relatively low relevance of allochthonous inputs which could otherwise bring uncertainties into the net role of seagrasses as carbon sinks.

Some of the factors usually driving the sequestration of C_{org} and N, such as the mud content (Dahl et al., 2016; Kindeberg et al., 2018; Leiva-Dueñas et al., 2023) or water depth (Serrano et al., 2014), were not important in our multivariate analysis. The sediment texture in our sites was rather homogeneous, with generally limited variation of each grain size fraction across sites, which may explain the lack of influence of granulometry in the pattern of accumulation. Sediments across sites were composed mainly of fine sands (47.4 ± 12.5% on average) with low silt/clay content (18 ± 15% on average). Mud content has been shown to affect positively the accumulation of organic carbon, mostly in cases of small species where the contribution of terrestrial input is usually significant. However, in large species like *P. oceanica*, the expected positive relation may be disrupted by the higher contribution of autochthonous input (Serrano, Lavery, Duarte, et al., 2016), as in this case. For example, meadows in Amorgos and Milos, which had ∼80% fine sand and silt/clay contents, supported 3-fold lower accumulation rates than the meadows with the highest rates (i.e., Methana, Ios, Santorini, Gouves, Kithnos, Serifos and Santorini 2), despite the latter having similar or even lower fine sand and silt/clay contents (52%–85%). Likewise, the depth range of the studied meadows was relatively small (3–14 m) for the bathymetric range of the species in this region, where lush meadows are found at >15 depths, with a mean depth of 17 m for the species in the Greek Seas (Gerakaris et al., 2021). Since the threshold for a decrease in seagrass production in Greece is at depths >14 m (Litsi-Mizan, 2023), a decrease in accumulation may be expected below that value.

The negative correlations between $CaCO_3$ accumulation rates and both C_{org} and N accumulation rates, as well as C_{org}:C_{inorg} and C_{org}:N ratios, suggest that meadows with >40% $CaCO_3$ content are less effective sinks than those growing in $CaCO_3$-poor sediments. Only Gouves, which had one of the highest $CaCO_3$ accumulation rates in our data set showed a high C_{org} accumulation rate and a C_{org}:C_{inorg} of 0.89 (above the global mean of 0.74 (Mazarrasa et al., 2015). This suggests a positive feedback between $CaCO_3$ and C_{org} which possibly resulted in the rapid burial and enhanced preservation of C_{org} at the specific site through high sediment

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accretion and burial (Gattuso et al., 1998). This result should be considered with caution given the different timescales in C_{org} and $CaCO_3$ decay rates and their resulting preservation, and the relative importance of lithogenic carbonates. The variability in the $CaCO_3$ accumulation rate in our data set was considerable, with a coefficient of variation of 83%, likely originating from different lithogenic settings across sites. The sites with volcanoclastic sediments (i.e., Santorini, Santorini 2, Milos and Methana) had significantly lower mean $CaCO_3$ content than sites with karstic, siliciclastic, or mixed karstic/siliciclastic sediments (Kruskal-Wallis test and p-value = 0.02), supporting, on average, 3.4-times lower $CaCO_3$ accumulation rates (118 ± 70 g $CaCO_3$ m^{-2} yr^{-1}) than the mean measured across all sites. Volcanic minerals in the sediments could enhance carbonate dissolution, resulting in lower $CaCO_3$ contents (Vizzini et al., 2019). The remaining sites belonged to the Attico-Cycladic geotectonic zone, which included the sites in the Attica Peninsula, Cyclades archipelago, and northern Crete, where the primary sedimentary rocks were composed of siliciclastic or karstic sediments. Naturally, the seagrass sediments at some of our sites included lithogenic carbonates, yielding high $CaCO_3$ accumulation rates, as observed in Metopi and Keros. However, the partition between karstic and nonkarstic sediments did not affect the accumulation pattern, as not all sites with high $CaCO_3$ accumulation rates had karstic sediments. In fact, meadows at Metopi and Keros (i.e., within karstic sediments) and meadows at Agia Marina, Koufonisi, and Gouves (i.e., within nonkarstic sediments) had up to 2-fold higher $CaCO_3$ accumulation rates than the other counterpart sites surveyed. This implies that the accumulation of carbonates was probably fueled by the calcifying organisms inhabiting the meadow (Frankovich & Fourqurean, 1997). The positive influence of SPM on the $CaCO_3$ accumulation rate suggests that the accumulation of $CaCO_3$ was also driven by the deposition of suspended carbonate-bearing particles from the bottom water above the canopy and the subsequent trapping of the latter within the meadow (Gacia et al., 2003).

We acknowledge that the timescale accounted for the sediment variables was different from that of the environmental and seagrass variables. Yet the temporal variability of geochemical variables over the last 500 years was overall low (Table S1), indicating relatively stable accumulation rates. This could be due to the nature of the seagrass-enriched sediments, which are usually refractory, resulting in low decay rates and high preservation, or a result of stable input. Although an increase in C_{org} and N contents was observed at some sites during the last 50 years (e.g., Keros, Koufonisi, Santorini, and Gouves), this trend does not necessarily reflect an increase in the organic matter availability in recent years, as those sites are away from major human activity. Relevant studies in Greek Seas have indicated that human impacts are restricted to specific areas of the country (close to major cities and/or industrial activities) and mainly since the years following post-World War II development (Hatzianestis et al., 2020; Pappa et al., 2018). Therefore, those downcore decreases most probably indicated an initial decay followed by stabilization, suggesting the preservation of C_{org} and N. It must be noted, however, that the chronology of our sediments was based on ^{14}C dating, which introduces uncertainty when reconstructing the recent past (~50–100 years). To enhance the accuracy of assessing possible changes linked to recent human development in the region, the application of more adequate methods (e.g., ^{210}Pb dating), although with their own limitations (Arias-Ortiz et al., 2018), should be considered.

Overall, the analysis of our data suggested that the *P. oceanica* meadows of the South Aegean Sea represent important natural sinks for carbon and nitrogen. Intriguingly, a significant degree of variability was observed within the region, which prompts the need for fine-scale assessments to decipher the intricacies of local conditions influencing carbon and nitrogen sequestration and support effective seagrass management. In our study, the accumulation of organic matter was driven by the contribution of seagrass matter to the sediments, which in turn was a result of healthy meadows extending in clear waters. The significant contribution of *P. oceanica* material, which is normally recalcitrant, in the sedimentary organic matter indicates that these meadows represent permanent pools of elements. This permanence underscores the critical need for conservation efforts to safeguard these coastal ecosystems and prevent the potential loss of centennial stored carbon and nitrogen following seagrass degradation, which could contribute to accelerate climate change and exacerbate eutrophication.

Data Availability Statement

The data supporting this study are available and hosted in the SEANOE database: https://www.seanoe.org/data/00885/99669 (Apostolaki et al., 2024).

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Acknowledgments
This work was supported by ARC DECRA (DE170101524), PID2020-117639GB-100 funded by MCIN/AEI, DRESSAGE (MIS5045792) through the Operational Program "Competitiveness, Entrepreneurship and Innovation" (EPAnEK 2014–2020, NSRF), and MEDCHANGE funded by the Agencia Española de Investigación. The publication of the article in OA mode was financially supported by HEAL-Link. We thank the reviewers for their constructive comments.

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