



First assessment of blue carbon stocks, sequestration rates and potential sources since 1900 at Arguin Island (Mauritania)

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Abstract

Global blue carbon assessments are hindered by a lack of data from understudied seagrass regions, such as those of Western Africa. This study reports the first in situ records of organic carbon (OC) stocks and burial rates for seagrass beds at Arguin Island, Banc d'Arguin (Mauritania), Western Africa, measured in intertidal *Zostera noltei* and subtidal *Cymodocea nodosa* meadows. The major blue carbon sources in seagrass meadows since 1900 were assessed using sedimentary environmental DNA (eDNA) and chronostratigraphy. The OC stocks in the top 50 cm of the sediment cores were not significantly different between the beds of the two seagrass species and averaged 27.8 ± 7.14 Mg C ha⁻¹, which is 5 times higher than that in adjacent unvegetated sediments. The OC sequestration rate for the past 100 years was 10.3 ± 1.4 g C m⁻² year⁻¹ in *C. nodosa* sediments and 12.3 ± 5.9 g C m⁻² year⁻¹ in *Z. noltei* sediments. Sedimentary eDNA analysis revealed that the major OC source within the *C. nodosa* and *Z. noltei* sediments has been the seagrass species itself, with low contributions from allochthonous eDNA reads. Carbon sources in *Z. noltei* meadows were more diverse than those in *C. nodosa* meadows. In bare sediment, diatoms were the major carbon source. The present study demonstrates the potential of sedimentary eDNA to reveal the major sources of organic matter in blue carbon ecosystems, improving our understanding of the provenance of sedimentary OC and thus carbon cycling processes. Additionally, it provides new OC stock and sequestration rate measurements from a region of the world that remains underrepresented in global blue carbon assessments.

Keywords Blue carbon · Sedimentary environmental DNA · Organic carbon stocks · Carbon sequestration rates · Mauritania · Seagrass

Introduction

Seagrass meadows provide many benefits for human wellbeing (de los Santos et al. 2020 and references therein), such as their ability to remove CO₂ from the atmosphere and store it as organic carbon (OC) in their sediments. This type of captured carbon is known as blue carbon (Nellemann et al. 2009). The global role of seagrasses as carbon sinks is well recognized (Duarte et al. 2013a, b), but there are still uncertainties in regard to quantifying their capacity to store and sequester carbon on a global scale and about the area they cover globally. The most up-to-date estimates show that, despite covering less than 300,000 km² globally (McKenzie et al. 2020), seagrass meadows have an average global OC

sequestration capacity of 24 g C m⁻² year⁻¹ (Arias-Ortiz 2019) and a global OC stock of 30 Pg C (Macreadie et al. 2021). Their conservation is thus relevant for climate change mitigation (Duarte et al. 2013b).

Global assessments of blue carbon stocks and sequestration rates have increased in number over the last decades (Krause et al. 2025). However, global estimates suffer from an overrepresentation of data from Western Europe, the Mediterranean, the Caribbean, Australia, and North America (Duarte De Paula Costa and Macreadie 2022), while many other regions of the planet remain understudied (Krause et al. 2025). The United Nations Environmental Programme (UNEP) has recently recommended investing in and prioritizing the quantification of seagrass ecosystem services, including blue carbon sequestration, in underrepresented regions of the world (UNEP 2020).

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The western coast of Africa is one of the most understudied regions of the world in terms of seagrass blue carbon (UNEP 2020). Seagrasses have been reported along most of the African coastline (Green and Short 2003), but research has focused mostly on the Indian Ocean along the East African coast (Bandeira and Bjork 2001; Githaiga et al. 2017). Seagrasses in Western Africa have only very recently been the focus of research publications (e.g., El-Hacen et al. 2020; Chefaoui et al. 2021; de los Santos et al. 2022; Sidi Cheikh et al. 2022; Tavares et al. 2022). Thus, there is a general paucity of information on the blue carbon budgets and flows of seagrasses of Africa, especially for sedimentary carbon stocks and sequestration rates (Githaiga et al. 2017; Gullström et al. 2021), and blue carbon studies are virtually absent for the West African coast. Recent studies of blue carbon storage along the African coast have yielded a rough estimate of 673 Tg C stored, with an estimated seagrass area of about 5000 km², based on a single generalized value of seagrass carbon storage (Bryan et al. 2020). However, the calculation of this estimate did not include data from Mauritania, which has one of the largest pristine seagrass areas in the world, in the National Park of Banc D'Arguin (Parc National du Banc d'Arguin; PNBA).

The high capacity of seagrass meadows to sequester and store OC, especially in their sediments, is due to a combination of biological traits, ecological functions, and environmental characteristics (Duarte et al. 2013b). These include their high CO₂ uptake, their ability to trap and store suspended particulate matter in the sediment by promoting sedimentation and reducing resuspension, the low oxygen conditions in their sediment that slow down organic matter decomposition, and their role in promoting the vertical accretion of sediment (Hendriks et al. 2008; Serrano et al. 2016; Potouroglou et al. 2017). Even though there are reports of allochthonous sources accounting for more than 50% of the accumulated carbon (Kennedy et al. 2010), the identification of sources is still a challenge (Kennedy et al. 2010; Geraldi et al. 2019). In fact, this is one of the top-ten pending research questions in blue carbon science (Macreadie et al. 2019). It is important to characterize and quantify the allochthonous fraction of blue carbon sources to avoid the double-counting of carbon from adjacent ecosystems (Macreadie et al. 2019; Williamson and Gattuso 2022). OC provenance analyses have mostly relied on bulk stable isotope mixing models, but differentiation between organic matter sources is hindered by similar or highly variable isotopic signatures (Geraldi et al. 2019; Kelleway et al. 2022).

Techniques based on environmental DNA (eDNA) metabarcoding are promising tools for improving the discrimination of OC sources in blue carbon ecosystems. Although the application of eDNA analysis in these environments is still at an early stage, several studies have successfully used it to identify the main macrophytes, particularly macroalgae,

contributing to sedimentary OC (Geraldi et al. 2019; Reef et al. 2017; Ortega et al. 2020a). The power of such techniques is their ability to achieve taxonomic resolution, with the 18S2 and 18S-Euka02 barcodes performing strongly at detecting and distinguishing marine macrophytes (Ortega et al. 2020b). While most blue carbon studies to date have focused on surface sediments, eDNA metabarcoding has also been proven to be effective at revealing temporal changes in species composition in deeper, and therefore older, sedimentary layers (Wesselman et al. 2021). However, such applications remain relatively uncommon for deeper sediments and need further exploration.

The blue carbon stocks at the PNBA were estimated to be more than 109 Tg C [Trégarot et al. 2018; United Nations Educational, Scientific and Cultural Organization (UNESCO) (2020)]. However, these estimates were based on literature values from elsewhere and not on in situ measures, which are needed to quantify local OC stocks and sequestration rates. Also, the sources of the OC sequestered in the sediments of the Banc d'Arguin have yet to be explored. Such a large shallow hypertrophic ecosystem enriched by iron-rich desert dust from the east and by upwelling from the west is believed to support high primary productivity (Cropper et al. 2014; Jickells et al. 2005). However, the relative contributions of different primary producers to sedimentary OC stocks in this area have yet to be investigated.

Our aim was to provide the first in situ estimates of blue carbon sedimentary stocks (in the top 50 cm) and carbon sequestration rates over the past 100 years within the Banc d'Arguin (Mauritania). Although based on samples from a single study site (Arguin Island), the results of our study offer insights into spatial variability by comparing the OC stocks and sequestration rates of three distinct habitats found there—bare sediment (subtidal, without marine vegetation), *Zostera noltei* meadows (intertidal), and *Cymodocea nodosa* meadows (subtidal). This makes this study a significant step forward in improving estimates of the ecosystem services of this site, which have previously been based only on estimates for other species and regions (Trégarot et al. 2018). Additionally, we used sedimentary eDNA to identify the main sources of organic matter contributing to blue carbon within each habitat. We expected the seagrass meadow sites to hold more OC than the unvegetated site, and high contributions from both seagrass tissue and macroalgae tissue to the sedimentary OC.

Materials and methods

Site description and sampling

The PNBA, which is situated in Western Africa, covers an area of about 12,000 km² of tidal flats and shallow inshore

waters, and borders the Sahara (Fig. 1A, B). It is a UNESCO World Heritage Site, Ramsar wetland, and Gift to the Earth (World Wide Fund for Nature) due to its major importance for migration and as breeding grounds for several species of birds (Wolff and Smith 1990) and fish and as a major feeding ground for green turtles. It was also recently recognized as an important blue carbon hotspot (UNESCO 2020). Blue carbon ecosystems at the PNBA include small areas of mangroves (0.1 km²) and saltmarshes (23 km²) and major areas of intertidal (353 km²) and subtidal (419 km²) seagrass meadows, which are dominated by the species *Z. noltei* and *C. nodosa*, respectively (Pottier et al. 2021). Offshore from Cape Blanc, just south of the PNBA ecosystem, there is an upwelling zone which provides nutrients and phytoplankton to the shallow areas of the Banc d'Arguin. Primary productivity is additionally increased by windblown dust rich in iron, which supports extensive seagrass meadows and filter-feeder populations (Cropper et al. 2014; Jickells et al. 2005). The inner part of the Banc d'Arguin system is dominated by

a detritus-based benthic food web in which seagrasses are the principal primary producers (Wolf et al. 1993).

Sampling took place on 15 February 2020, on the eastern coast of Arguin Island, located in the northeastern part of the Banc d'Arguin (Fig. 1C). During low tide, three PVC core samplers (150 cm length, 4.6 cm internal diameter) were manually hammered into the sediment in each of three different habitats: an intertidal seagrass bed of *Z. noltei*, a subtidal *C. nodosa* bed, and an area of subtidal bare sediment. Both seagrass sites were monospecific meadows, and minimum and maximum distances between sampling sites were 11 and 33 m, respectively. Sediment sampling depths ranged from 44 to 53 cm in bare sediment, 60–64 cm in *C. nodosa*, and 108–120 cm in *Z. noltei* meadows (Table S1). Sediment compaction during coring was measured as the difference in surface sediment elevation inside and outside the sampler. This ranged from 17 to 36% and was used to correct the data to decompressed sediment depths, assuming linear compaction (Glew et al. 2001).

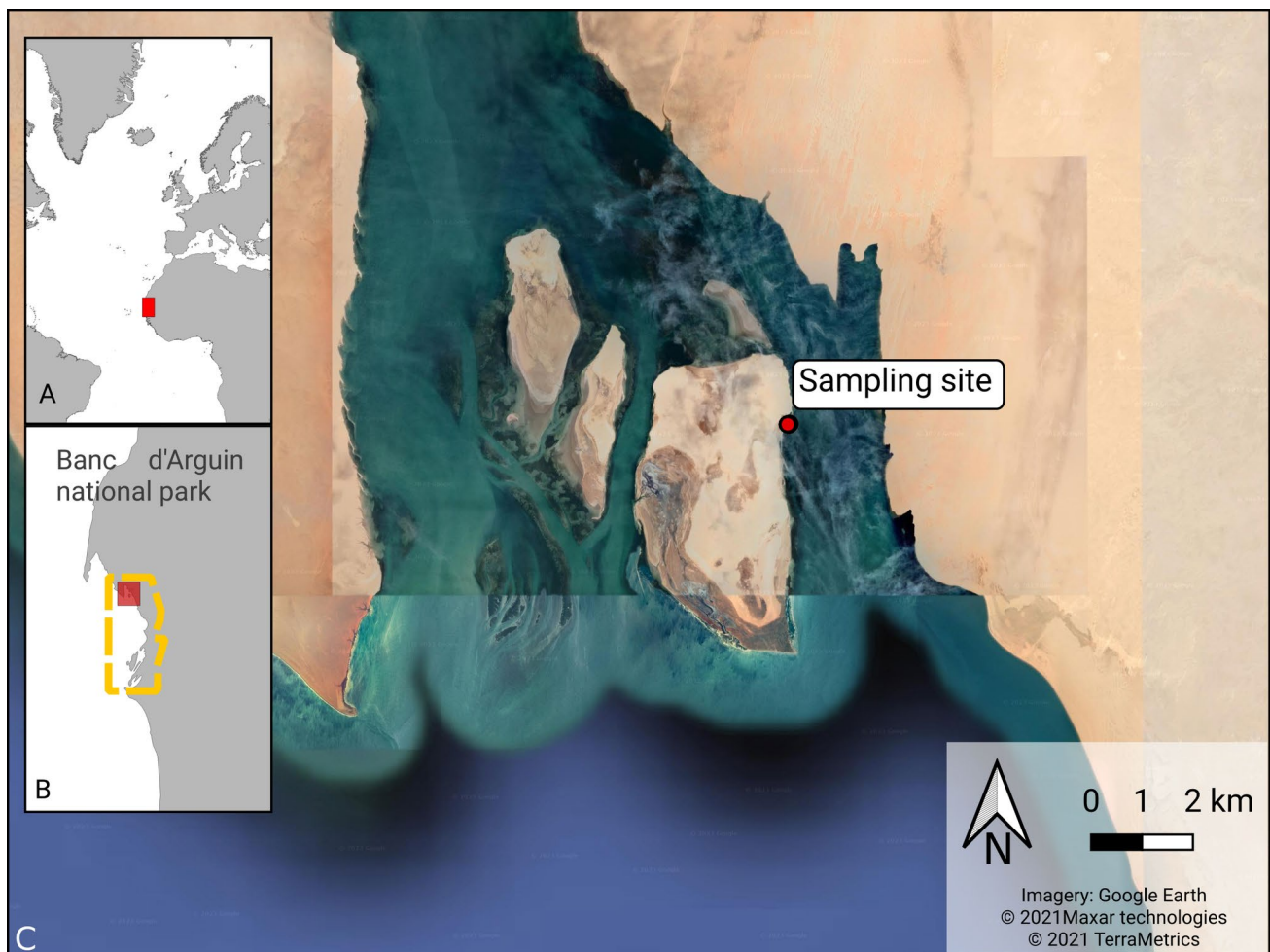


Fig. 1 Location of Mauritania [red rectangle (A)], the sampling area [red rectangle (B)] at the Banc d'Arguin National Park (PNBA; delimited by the orange dashed line), and the sediment cores sampling site [red dot (C)]

The samplers were sealed with a rubber plug, slowly retrieved, stabilized internally with Styrofoam plugs, and sealed at both ends with PVC caps. Cores were transported sealed, at room temperature, to Portugal within 48 h and immediately frozen at $-20\text{ }^{\circ}\text{C}$ upon arrival until they were processed. In the laboratory, the cores were thawed at room temperature and halved longitudinally. One of the cores from each habitat was selected for full analysis (OC, granulometry, chronostratigraphy), while the others were only used for OC analysis. For OC and granulometry, one half of the core was sliced every 2 cm. A sediment sample for eDNA analysis was taken from the top of every other slice, while avoiding sediment from the halving plane and in contact with the PVC sampler to prevent contamination due to material transported during the coring process. The other half of the core was used for chronostratigraphy.

Chronology

The chronology of sediment cores obtained in the vegetated habitats was based on the analysis of the activity of the natural radionuclide ^{210}Pb and of the artificial radionuclide ^{137}Ce , combined with accelerator mass spectrometry (AMS) ^{14}C dates. The bare sediment core did not allow the construction of a depth-age model due to the low levels of ^{210}Pb measured along the core. The activities of ^{137}Ce and ^{210}Pb in the vegetated cores were measured via gamma analysis on 18 samples at GAU–Radioanalytical Laboratories (Table S2). As excess ^{210}Pb profiles did not follow the expected quasi-exponential decline in activity with depth in either core, commonly used ^{210}Pb dating models could not be applied (Sanchez-Cabeza and Ruiz-Fernández 2012). As an alternative, we used the depth at which excess ^{210}Pb reached zero as a dating point. Based on ^{210}Pb 's half-life of 22.3 years, we expected the levels of excess ^{210}Pb to reach zero after 100–130 years (Appleby and Oldfield 1978). Based on this information, GAU–Radioanalytical Laboratories estimated that the depth at which excess ^{210}Pb in our cores reached zero should correspond to approximately 1900 [calendar ages are reported here as years Common Era (McKim 1996)]. A ^{137}Ce peak was found in the *Z. noltei* core and was dated as corresponding to the nuclear weapon testing carried out in 1954 (Ritchie and McHenry 1990).

AMS ^{14}C analysis was performed on the most well-preserved biological calcareous structures found, i.e., two bivalve shells in living position, analyzed at the Leibniz-Laboratory for Radiometric and Stable Isotope Research of University of Kiel, and six benthic foraminifera samples, analyzed at Keck Carbon Cycle AMS Facility of the Earth System Science Department, University of California Irvine (Table S3). Raw AMS ^{14}C dates were converted to calendar ages using the Marine20 calibration curve of INTCAL20 (Reimer et al. 2020).

Age-depth models were constructed using the previously dated depths. For the *C. nodosa* core (M09), a constant sedimentation rate was calculated by linear regression of the age of the top sediment (0 cm corresponding to 2019) and the end of excess ^{210}Pb activity (24 cm—1900). For the *Z. noltei* core (M10), we calculated two separate sedimentation rates: one for the surface of the core using the surface (0 cm—2019), the middle point of the layer with ^{137}Cs activity (10.2 cm—1954), and the end of excess ^{210}Pb activity (19.5 cm—1900). A different sedimentation rate was estimated for the bottom of the core with the three AMS ^{14}C dates.

Sedimentation rates were calculated for the past 100 years as:

$$\text{SR (mm yr}^{-1}\text{)} = \text{Depth at 100 years (mm)} / 100$$

with depth at 100 years determined from the age-depth models.

OC and granulometry

OC was estimated via loss on ignition, using an adaptation of the methods described in Howard et al. (2014). For the top 50 cm of the sediment core, OC was determined in every other 2-cm slice. Below 50 cm, where OC variability is usually lower, we reduced the sampling resolution, with samples selected to ensure that all the different sediment layers were represented (Howard et al. 2014). Root tissue was manually removed, the sediment samples were oven-dried ($60\text{ }^{\circ}\text{C}$) until constant weight, homogenized using a mortar and pestle, and subjected to loss-on-ignition analysis ($450\text{ }^{\circ}\text{C}$, 4 h). The sample dry weight and volume were used to estimate dry bulk density ($\text{g dry weight cm}^{-3}$) and the weight loss during loss-on-ignition was used to determine organic matter content (OM) in percentage of dry weight (% dw). The OC content of the sediment, as a percentage of the dry weight, was estimated by linear regression, using the relationship between OC (% dw) and organic matter from similar ecosystems in southern Portugal [data from Martins et al. (2022), with additional samples; Figure S1]:

$$\text{OC (\% dw)} = 0.297 \times \text{OM (\% dw)}$$

$$(F_{1,164} = 4199, p < 0.001, R^2 = 0.96)$$

Finally, dry bulk density was multiplied by OC content to obtain the sedimentary OC concentration (g C cm^{-3}). To estimate the OC stocks per area (Mg C ha^{-1}), OC concentration was integrated over depth up to 50 cm, assuming a linear change between consecutive samples. For the purpose of comparing our estimates with those of previous works, we also calculated the OC stocks for up to 1 m by extrapolating

the deepest measured value as constant down to 100 cm. OC sequestration rates were calculated for the past 100 years (1920–2020), as:

$$\text{OC sequestration rate (g C m}^{-2}\text{yr}^{-1}) = \text{OC stock}_{100 \text{ years}}/100,$$

where OC stock_{100 years} corresponds to the OC stock integrated up to the depth with an estimated age of 100 years. OC sequestration rates were calculated for all cores in seagrass meadows by assuming that sedimentation rates were the same in all cores of the same habitat.

Sample granulometry was determined by wet sieving after digesting the organic matter with hydrogen peroxide (30% weight/weight). The grain size of the sediment is presented in Krumbein phi (ϕ), which is defined as $\phi = \log_2(d/d_0)$, where d is the particle diameter in millimeters and d_0 is the reference particle diameter (1 mm). Each sample was wet sieved through a 0.062-mm sieve to separate the coarse (i.e., sand and gravel) and fine (i.e., clay and silt) fractions using distilled water. Then, the grain size analysis of the coarse sediment fraction was done by mechanical sieving, with sieve sizes ranging from -2.00ϕ (4 mm) to 4.00ϕ (0.062 mm) at $0.5\text{-}\phi$ intervals. The fine sediment fraction ($>4.00 \phi$) was determined based on a pipette method (Gee and Bauder 1986), performed at $1\text{-}\phi$ intervals, after the addition of 0.5% sodium hexametaphosphate solution as the dispersant. The method of moments was applied to determine mean grain size (first moment; ϕ units) (Friedman and Sanders 1978).

Sedimentary eDNA analysis

The sources of sedimentary organic matter were determined by eDNA analysis. Sediment samples (2 mL) were preserved in DNA/RNA shield buffer (ZymeResearch) and stored at -20°C until extraction. DNA was extracted with the DNeasy PowerSoil® Isolation Kit (QIAGEN) from 0.25 g sediment, following the Vortex Adapter protocol, under strict sterile conditions in a dedicated laboratory, with two blank controls. The variable 18S region of the rRNA gene was used as a genetic marker to characterize the organic matter in the sediments, using the Euka02 primers 5'-TTTGTC TGSTTAATTSCG-3' and 5'-CACAGACCTGTTATTGC-3' (Ortega et al. 2020b). DNA extracts were sent on dry ice to MR DNA (<http://www.mrdnalab.com>; Shallowater, TX), where two replicate PCRs were performed, per sample, using the HotStarTaq Plus Master Mix Kit (Qiagen, USA) under the following conditions: 95°C for 5 min, followed by 35 cycles of 95°C for 30 s, 53°C for 40 s and 72°C for 1 min, after which a final elongation step at 72°C for 10 min was performed. Afterwards, replicate PCRs were pooled and used as such in the library preparation.

PCR products were multiplexed using unique dual indices and pooled together in equal proportions based on their molecular weight (calculated based on the size of the amplicon) and DNA concentrations (using Qubit™; Invitrogen®, Carlsbad, CA), and they were purified using calibrated Agencourt® AMPure® XP beads. DNA libraries were prepared by following Illumina TruSeq DNA library preparation protocol and paired-end (2×250 bp) sequencing was performed in a single run at MR DNA on a MiSeq following the manufacturer's guidelines.

The Q25 sequence data derived from the sequencing process were processed using the MR DNA ribosomal and functional gene analysis pipeline (www.mrdnalab.com, MR DNA, Shallowater, TX). Sequences were joined, primers removed, and then sequences of <80 base pairs (bp) and sequences with ambiguous base calls were removed. Sequences were quality filtered using a maximum expected error threshold of 1 bp and dereplicated. The dereplicated or unique sequences were denoised; unique sequences identified with sequencing or PCR point errors were removed, followed by chimera removal, thereby providing a denoised sequence or zero-radius operational taxonomic unit. Final zero-radius operational taxonomic unit were taxonomically classified using the nucleotide Basic Local Alignment Search Tool against a curated database derived from the National Center for Biotechnology Information (2020) database. After reads were reduced to those representing only primary producers (see Table S4 for groupings), the read numbers ranged between 9360 and 34,701 per sample. The data were rarefied to 9360 reads per sample to normalize the library size. Sedimentary eDNA compositions were expressed in relative abundances, with the focus on the top five most common groups: *Z. noltei*, *C. nodosa*, crop plants, benthic diatoms, and planktonic diatoms. All of the remaining taxa were grouped into "Others."

Data analysis

Values are reported as mean \pm SD, or as minimum–maximum when reporting ranges. Granulometric (ϕ) differences among habitats (fixed factor—*C. nodosa*, *Z. noltei*, and bare sediment) were tested using type-3 analysis of covariance, which also included depth (fixed factor, continuous) and habitat:depth interactions. OC stock and sequestration rate differences were tested with type-3 ANOVA, using habitat as a fixed factor. Normality and homoscedasticity of the data were tested by the Shapiro–Wilk test and visual inspection of the residual plot, respectively. If significant differences were found, pair-wise comparisons were performed with the R package emmeans (Lenth 2022), using Tukey honest significant difference post hoc tests for multiple comparisons adjustment. Differences with α lower than 0.05 were

considered significant. All of the data analysis was performed in R version 4.1.3 (R Core Team 2022).

Results

Chronostratigraphy

The excess ^{210}Pb profile for the dated *C. nodosa* core did not follow the expected quasi-exponential decline of activity with depth. However, excess ^{210}Pb activity was limited to the upper 24 cm, which suggests that this section of the core was deposited between 1900 and the present day, and it yielded an approximate sediment deposition rate of 2 mm year^{-1} (Fig. 2).

The excess ^{210}Pb profile along the *Z. noltei* core did not follow a quasi-exponential decline of activity with depth either. However, values fell to near zero at 19.5-cm depth. Additionally, this core showed detectable ^{137}Cs levels at 10.2 cm. These dated depths yielded an average sedimentation rate of 1.6 mm year^{-1} for the top of the core. The sediment sequences of both *C. nodosa* and *Z. noltei* had a discontinuity between 25 and 43 cm and between 37 and 58 cm, respectively. The dated shells in these layers were older than those of the sediments below (gray and green bands; Fig. 2) and the layers were characterized by coarse sediments, the presence of large and broken shells, the disappearance of siliceous microfossils and the occurrence of planktonic foraminifera. This suggests the occurrence of a high-energy event which transported older sediments from elsewhere and instantaneously deposited them

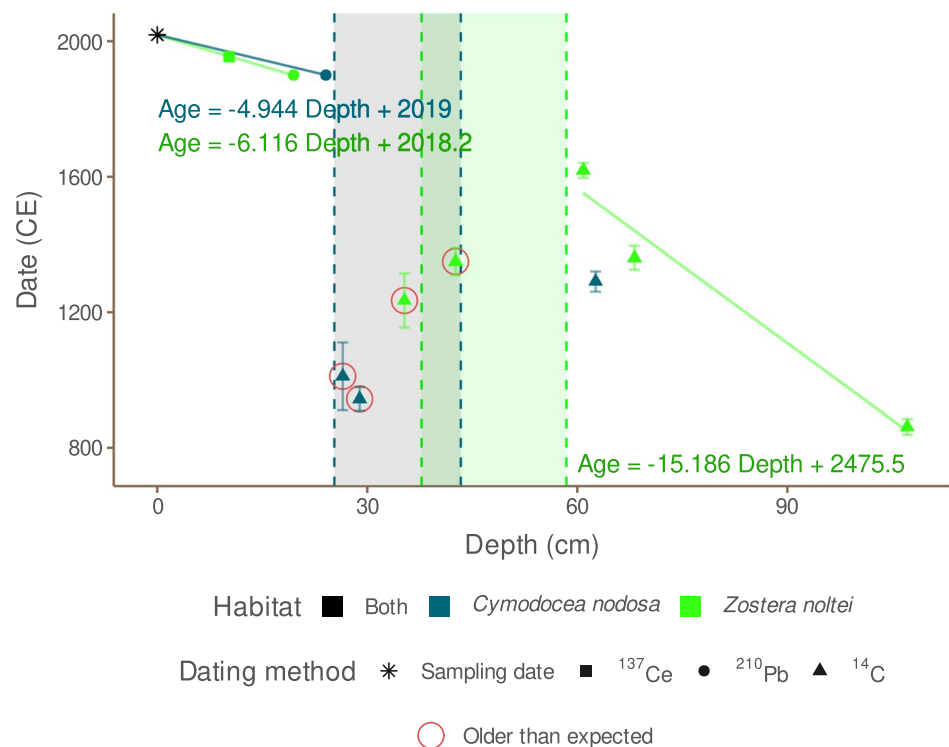
at these sites. The age–depth relationship above the discontinuity was similar in both habitats (Fig. 2). In the *C. nodosa* core, only one sample was viable for ^{14}C dating below the discontinuity, which is insufficient to establish an age–depth relationship. The final age–depth models used for each core are given in Table S5.

Granulometry and OC profiles

Overall, sand was the most abundant grain size category with depth for the three habitats (Fig. 3), yet the granulometric results (ϕ) were significantly different between all three habitats ($F_{2,33}=46.196$, $p<0.001$; Table S6.1). The bare sediment site had a higher average particle size (i.e., lower ϕ) than the vegetated habitats ($p<0.001$; Table S6.2), being composed mostly of sand particles, with mud contents (4–11%) only being of relevance in the sediment layers deeper than 35 cm (Fig. 3). The granulometric results did not differ significantly between vegetated habitats ($p=0.9$; Table S6.2). The average mud content in vegetated habitats was around 30%, with higher variability observed for the *Z. noltei* bed, where mud peaked at about 50% at depths of 6 cm and 76–88 cm (Fig. 3).

In all the sampled cores, seagrass meadow sediments had significantly higher OC contents than bare sediment ($F_{5,106}=20.87$, $p<0.001$; Tables S7.1, S7. 2, Figure S2). In the top 10 cm of the intertidal *Z. noltei* meadow, the OC content was higher than within the subtidal *C. nodosa* meadow.

Fig. 2 Age–depth model for the sediment of *Cymodocea nodosa* and *Zostera noltei* habitats. The points show depths dated by ^{210}Pb , ^{137}Cs or AMS ^{14}C methods (error bars are SDs of the ages estimated by ^{14}C dating). For each habitat, the age-at-depth equations are presented for above and below the sediment layer, with age inversion. The colored bands depict the presence of older material transported from elsewhere and likely to have been instantaneously deposited (blue for *C. nodosa* and green for *Z. noltei*). CE Common Era



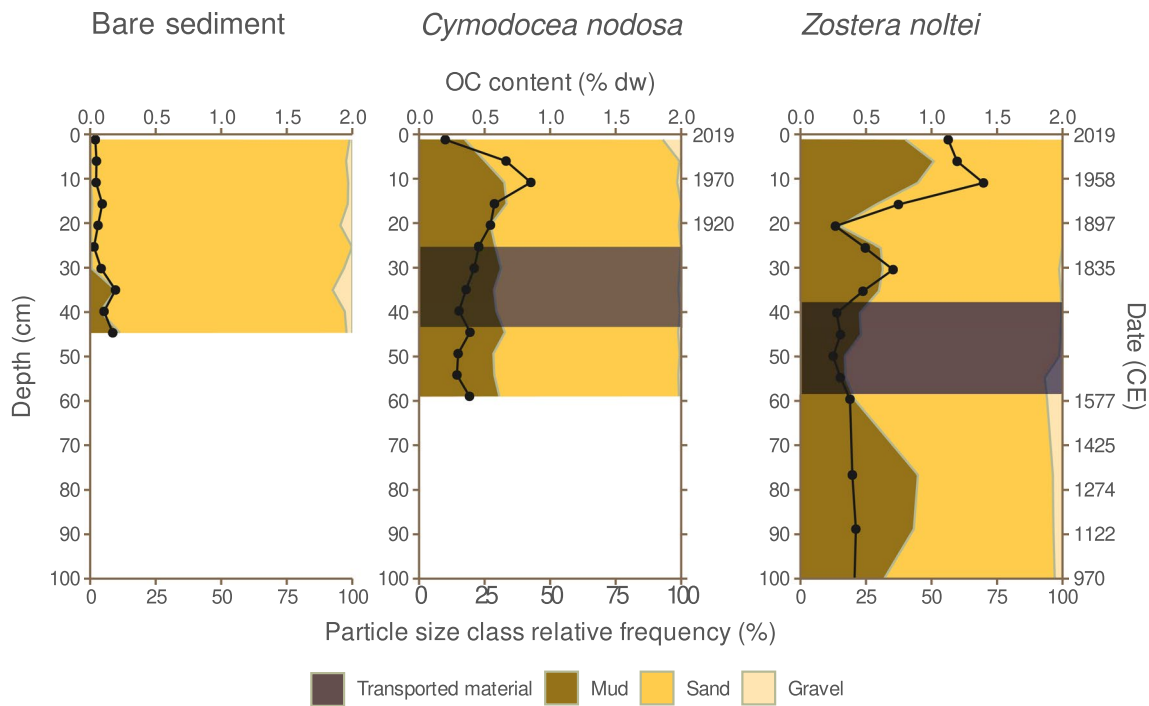


Fig. 3 Profiles of mud, sand, and gravel (percentages; colored areas) and organic carbon (OC) content (black lines) along the dated cores of bare sediment, *C. nodosa* and *Z. noltei* habitats. The blue band depicts the presence of older material transported from elsewhere and

likely to have been suddenly deposited. The OC profile is from the core subjected to granulometry (OC profiles of all sampled cores are shown in Figure S2)

In both habitats the OC content stabilized at around 0.5% in deeper layers below 25 cm (Figure S2).

OC stocks and burial rates

The sedimentary OC stocks in the top 50 cm were significantly different across habitats ($F_{2,6} = 12.77$, $p = 0.007$; Table S8.1), but not between seagrass habitats ($29.7 \pm 10.7 \text{ Mg ha}^{-1}$ in intertidal *Z. noltei* and $25.9 \pm 1.46 \text{ Mg ha}^{-1}$ in subtidal *C. nodosa*, $p = 0.75$; Table S8.2). Bare sediment OC stocks were statistically different from seagrass OC stocks, being about fivefold lower than the latter ($5.59 \pm 1.24 \text{ Mg ha}^{-1}$; Fig. 4; $p < 0.02$; Table S8.2). The average OC stock stored in the top 50 cm of the seagrass sediments was $27.8 \pm 7.14 \text{ Mg ha}^{-1}$. In the dated cores, the OC stocks in the top 50 cm were also estimated after excluding the sediment intrusion layer, to assess how the sediment that originated from elsewhere and was deposited at the site by an extreme event may have influenced the estimation of the OC stocks. The corrected stocks were 35.5 Mg ha^{-1} for *Z. noltei* and 25.9 Mg ha^{-1} for *C. nodosa*, indicating that the *Z. noltei* OC stocks, but not the *C. nodosa* OC stocks, reported above may be underestimates.

The average sedimentation and carbon sequestration rates for the past 100 years, i.e., down to 24 cm in the *C. nodosa* bed and to 19.5 cm in the *Z. noltei* bed, were higher in *C.*

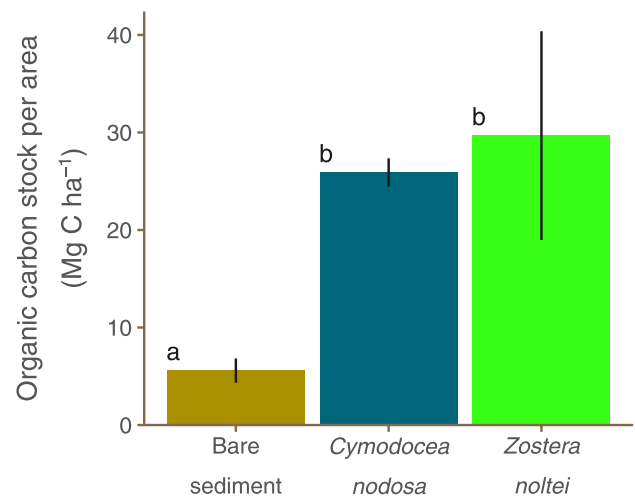


Fig. 4 OC stocks in the top 50 cm of sediment in the three habitats. Bars with the same letter are not significantly different. Data are shown as mean \pm SD

nodosa (2 mm year^{-1}) than in *Z. noltei* (1.6 mm year^{-1}). However, the carbon sequestration rates were not significantly different ($12.3 \pm 5.9 \text{ g C m}^{-2} \text{ year}^{-1}$ in *Z. noltei* and $10.3 \pm 1.4 \text{ g C m}^{-2} \text{ year}^{-1}$ in *C. nodosa*; $F_{1,4} = 0.330$, $p = 0.6$).

Sedimentary eDNA analysis

Sedimentary eDNA metabarcoding showed that the major contributor to *C. nodosa* sediment was the seagrass itself (96–100%, average $99 \pm 1\%$ of DNA reads; Fig. 5), excluding the surface layer, which was dominated by diatoms (98% of DNA reads). The bare sediment profile was dominated by diatoms (92–99% of DNA reads), with minor contributions by microalgae and *C. nodosa* (Fig. 5; Table S4). In contrast, the sequences in the sediment of the *Z. noltei* habitat had a higher diversity of sources (Fig. 5), even though the most important contributor was still the autochthonous species itself (*Z. noltei*, 31–96%, average $66 \pm 22\%$ of DNA reads). DNA from *C. nodosa* was detected in the sediment of *Z. noltei*, mostly at depths of 40 cm (25%), 87 cm (28%) and 97 cm (24%), but little contribution from *Z. noltei* was observed in the *C. nodosa* sediments (< 1% of DNA reads). The only seagrass DNA found in bare sediment was assigned as *C. nodosa*, at a depth of 38 cm, which coincided with the increase in mud and organic matter contents (Figs. 3, 5). Crop plants were important contributors (11–33% of DNA reads) to the *Z. noltei* sediment below a depth of 68 cm. Macroalgae did not contribute significantly to the sedimentary eDNA in any of the sediment cores, and only a small contribution of 0.1% was observed in one sample of the *C. nodosa* bed. Most of the diatoms identified were benthic diatoms (Table S4).

Discussion

OC stocks and burial rates

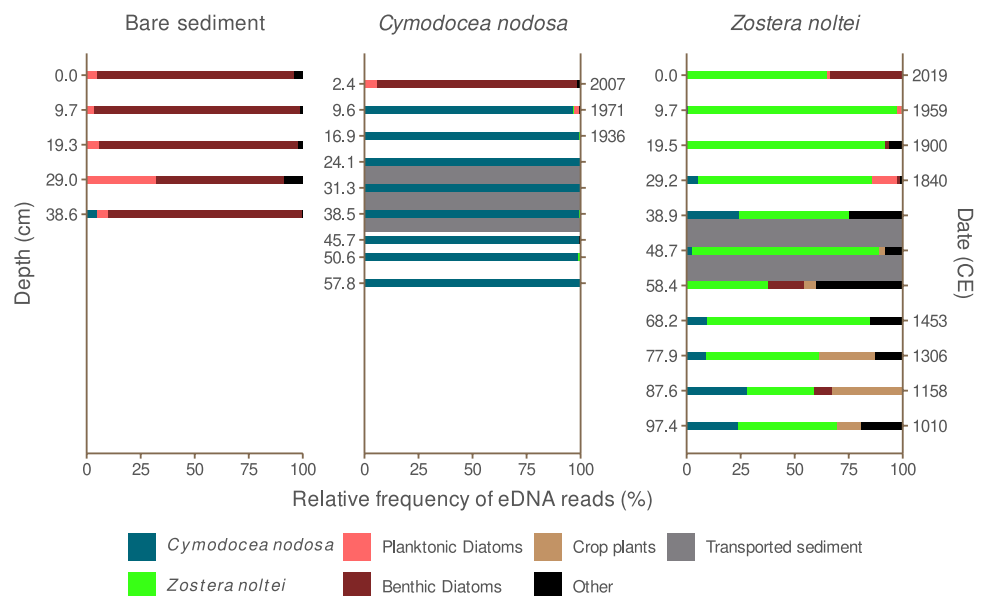
This study reports, to the best of our knowledge, the first in situ measurements of the sedimentary OC stocks and

sequestration rates for seagrass habitats of Western Africa, a region of the globe for which there is a severe lack of data on blue carbon sequestration. This study is a first step towards improving the accuracy of estimates of the local ecosystem services of seagrass beds in the Banc d'Arguin, which have previously been assessed using OC estimates from other seagrass species and regions (Trégarot et al. 2018). However, more extensive sampling over a wider area is needed for further improvement of these estimates. The intertidal and subtidal seagrass meadows at the sampling site in Arguin Island had similar OC stocks in the top 50 cm of sediment (average $27.8 \pm 7.14 \text{ Mg ha}^{-1}$), which were fivefold higher than in an adjacent area of bare sediment ($5.59 \pm 1.24 \text{ Mg ha}^{-1}$). The estimated OC stock of the *C. nodosa* bed at a depth of 50 cm ($25.9 \pm 1.46 \text{ Mg ha}^{-1}$) is at the lower end of the range estimated for *Cymodocea* spp. meadows on the East African coasts of Mozambique and Tanzania (from 20.8 ± 4.3 to $48.9 \pm 8.4 \text{ Mg ha}^{-1}$) (Gullström et al. 2021).

To allow further comparisons, we extrapolated our estimates of OC stocks to estimate that of the top meter of the sedimentary column (Table S1). Extrapolated top meter OC stocks were $45.9 \pm 5.14 \text{ Mg C ha}^{-1}$ for *C. nodosa* and $51.0 \pm 15.5 \text{ Mg C ha}^{-1}$ for *Z. noltei* beds, i.e., approximately threefold higher than those of adjacent areas of bare sediment ($14.8 \pm 4.0 \text{ Mg C ha}^{-1}$).

The blue carbon sink capacity of the Ria Formosa lagoon, southern Portugal, which has a similar species composition to the one at the sampling site in Arguin Island, has been well studied (Dahl et al. 2016; Santos et al. 2019; Fernández 2021; Martins et al. 2022; de los Santos et al. 2022b). The OC stock of the *C. nodosa* bed (top meter) measured here in Arguin Island was about double the levels reported for subtidal mixed meadows of *C. nodosa* and *Z. marina* in

Fig. 5 Profiles of the relative composition of primary producers found in sedimentary environmental DNA (eDNA) in the three habitats. Colored bars represent the relative composition of eDNA reads (%) of the main groups of primary producers. The gray band depicts the presence of older material transported from elsewhere and likely to have been instantaneously deposited



Ria Formosa lagoon (Dahl et al. 2016; de los Santos et al., unpublished; Herrero-Fernández 2021). In contrast, the OC stock of the intertidal seagrass *Z. noltei* bed at Arguin Island ($51.0 \pm 15.5 \text{ Mg C ha}^{-1}$) was similar to that of a high hydrodynamic energy site at Ria Formosa (47 Mg C ha^{-1}) and lower than that of the site at the same location with the lowest hydrodynamic energy (99 Mg C ha^{-1}) (Martins et al. 2022).

The present study provides, to the best of our knowledge, the first assessment of blue carbon sequestration rates in Western Africa, and thus contributes much needed data from this region for the calculation of global estimates of carbon burial by seagrasses, which has thus far been achieved by using global sequestration estimates for seagrasses (Duarte et al. 2013a, b; Bertram et al. 2021). OC sequestration rates were higher for the intertidal seagrass *Z. noltei* bed ($12.3 \pm 5.9 \text{ g C m}^{-2} \text{ year}^{-1}$) than for the subtidal *C. nodosa* bed ($9.2 \pm 1.5 \text{ g C m}^{-2} \text{ year}^{-1}$). These values are lower than those reported for Cadiz Bay, Spain, where the sequestration rate of *Z. noltei* was $44 \pm 15 \text{ g C m}^{-2} \text{ year}^{-1}$ and that of *C. nodosa* was $39 \pm 6 \text{ g C m}^{-2} \text{ year}^{-1}$ (de los Santos et al. 2022a), although the latter study showed a similar trend of vertical distribution to ours. However, de los Santos et al. (2022b) found that intertidal OC stocks and net deposition-resuspension rates of organic matter decreased with intertidal elevation, following the vertical decrease of the hydroperiod. Understanding the interaction of multiple environmental drivers is needed to assess the spatial variability of blue carbon in seagrass ecosystems (Ricart et al. 2020; de los Santos et al. 2022b).

Carbon sources

The sedimentary eDNA data suggested major differences in the sources of organic matter among the sampled sites. In the bare sediment site, the main contributors to organic matter were diatoms, with some minor contributions from dinoflagellates and other microalgae. There was no sequestration of organic matter from macrophytes, which can be explained by the lack of physical barriers and stabilization structures, which favor low deposition rates, as well as high re-suspension rates of deposited material (Hendriks et al. 2008). However, the bare sediment site showed a 5% relative frequency of *C. nodosa* eDNA reads at 39 cm, which coincided with an increase in mud and OC contents (Fig. 3), typical of seagrass sediments. This simultaneous change in sedimentary properties suggests a temporary period of colonization of the bare sediment site by *C. nodosa*.

The main contributor of sedimentary OC in the *C. nodosa* site throughout the entire core was that of the autochthonous seagrass species itself. In contrast, the *Z. noltei* sediment had a much higher variety of organic matter sources, and a higher contribution from allochthonous sources. Contributions

from benthic diatoms may also be of relevance, particularly in superficial seagrass sediments and bare sediments, but as these develop within the seagrass meadows they may be considered an autochthonous source (Williamson and Gattuso 2022). The contribution of diatoms is particularly interesting in the top of the sample of the *C. nodosa* bed, where it dominated the eDNA signal. The lack of seagrass eDNA sequences was also accompanied by low OC contents, which suggests that aerial biomass is being exported offsite. Contrary to what was expected, phytoplankton, the productivity of which is high due to upwelling (Fischer et al. 2019) and nutrient enrichment from the Sahara (e.g., Bristow et al. 2010; Pabortsava et al. 2017), was not a relevant source of sedimentary OC in the studied area.

The analysis of sedimentary eDNA can help to identify the main sources of coastal blue carbon, which are a mixture of autochthonous sources, such as seagrass tissue, and allochthonous sources (Williamson and Gattuso 2022). Our data suggest that seagrass OC stocks in Arguin Island are more dependent on autochthonous seagrass material than on allochthonous contributions. The application of the novel eDNA metabarcoding method to quantify carbon contributions is a growing field but has its limitations. First, taxon identification depends on the availability of reference databases for local species. This was not a problem in our study because our reference database enabled identification to the taxonomic level required for our objectives. Second, accurate quantification requires the use of quantitative PCR. The metabarcoding approach used in this work is only useful to examine relative contributions as qualitative ranks across taxa for sedimentary organic carbon contributions, with low reliability for quantitative analysis (Ortega et al. 2020a, b). Additionally, while eDNA metabarcoding has been successfully used to study changes in the species composition of seagrass meadows over time (e.g., Wesselman et al. 2021), we expect errors to increase with sediment age (i.e., with depth). Differences in degradation rates of DNA sequences from different organisms (Boere et al. 2011) and differences in rates of adsorption to the surface of minerals (Lorenz and Wackernagel 1987) are likely to lead to post-sequestration changes in the relative frequency of sequestered eDNA. For example, the importance of diatoms is likely to be overstated due their resilient structures providing protection from degradation (Boere et al. 2011). This supports the reliability of our results in which diatoms were most frequent in recent rather than ancient sediments in cores with seagrass present. Last, future studies should aim for species identification beyond that of only species of seagrasses, by developing specific DNA barcodes for the identification of local macrophyte species (i.e., for macroalgae most of all, as these have a much higher species diversity than seagrass species). This is important for determining sedimentary carbon

contributions at species level, which we did not attempt in this study beyond that of the two seagrass species that occurred locally.

For both seagrass meadows, chronostratigraphic data revealed a sediment discontinuity and the occurrence of a layer characterized by the reversal of sediment ages and the intrusion of older sediments from elsewhere that had been suddenly deposited. These findings may reflect the effects of high energy events such as the tsunamis of 1531 and 1755 that occurred in the northeast Atlantic. The transatlantic tsunami of 1755, which was particularly strong, having been observed all along North Atlantic coasts and in Central and South America, devastated the Iberian and North Morocco coasts (Baptista and Miranda 2009), and generated similar sediment patterns to those observed here in Portuguese shallow shelf sediments (Abrantes et al. 2005, 2008), the Canary Islands, in front of the Banc d'Arguin (Costa et al. 2021), and in El Jadida in Morocco (Mellas et al. 2012). However, despite the similarity between the date of this event and those estimated here, this is only a hypothesis, as it is difficult to differentiate the sedimentologic effects of tsunamis from those of other extreme-wave events, such as storm surges and waves (Costa et al. 2021), and more sediment cores need to be sampled across a larger area to investigate this further.

Carbon sequestration potential of the PNBA

UNESCO (2020) estimated the total OC stock of seagrass at the Banc d'Arguin to be 109,340,000 Mg, considering an average OC stock of 140 Mg C ha⁻¹ and a seagrass area of 781,000 ha. We believe that both the assumed seagrass area and the OC stock values in that report are likely to be substantial overestimates. Recent studies estimated that the total area suitable for seagrass meadows in the PNBA is 270,908 ha (modified from Chefaoui et al. 2021), which is lower than the estimate used by UNESCO (2020). Other recent studies estimated approximately 67,400 ha for intertidal meadows (Trégarot et al. 2021) and a total of 77,200 ha for beds of both subtidal and intertidal seagrasses (Pottier et al. 2021). In addition, the OC stock values used in the UNESCO report were not measured in situ and are almost 3 times higher than those we measured at Arguin Island. To illustrate the potential magnitude of overestimation by UNESCO (2020), we used our measured OC stocks and sequestration rates to produce a very rough estimate of the blue carbon potential for a seagrass area of 77,200 ha estimated by Pottier et al. (2021), acknowledging that this involves significant assumptions regarding spatial variation and a limited core dataset. Based on our approach, the top meter of seagrass sediments in the PNBA could store about 3,800,000 ± 830,000 Mg of OC, with an additional 3800 Mg and 4300 Mg of OC being sequestered every year

by the intertidal and subtidal seagrass meadows, respectively. These values suggest that the OC stock sizes in this area were likely overestimated by up to 30 times in previous reports. We emphasize the need for more extensive spatial sampling to more accurately assess the blue carbon stocks and fluxes within the PNBA.

Curiously, Bertram et al. (2021), who estimated the wealth created globally by blue carbon sequestration, reported that Mauritania had the smallest blue carbon sequestration potential of any country with blue carbon ecosystems. However, that work considered only mangroves, which cover a small area in comparison to the large area of seagrasses (Pottier et al. 2021). If we include the OC stocks estimated in this work, plus those of the saltmarsh and mangrove areas estimated by Pottier et al. (2021), Mauritania moves up to position number 73 out of 166, when considering only the PNBA area. This may assist decision-makers in promoting conservation measures, as well as in obtaining external funding to finance these efforts (Bryan et al. 2020; Wylie et al. 2016).

We conclude that seagrass meadows are significant carbon sinks at Arguin Island compared to non-vegetated areas, with the main contributors to their sedimentary carbon being of autochthonous origin. While our work in the PNBA was limited in spatial extent, it provides the first in situ measurements of the carbon sink capacity of this World Heritage Site. Protection of the seagrass beds of Mauritania would provide an opportunity to preserve their OC stocks and ensure their continued carbon sequestration and storage. Their protection would also benefit fisheries and biodiversity support, sanitation and water purification, and coastal protection.

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Data availability The analyzed data are available in the supplementary materials. The raw data are available at <https://doi.org/https://doi.org/10.5281/zenodo.7085073>.

Declarations

Conflict of interest The authors declare that they have no competing interests.

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