Fossilized diatoms as indirect indicators of the origin of carbon stored in intertidal flats

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Coastal systems store enormous carbon quantities in their sediment, which originates from various autochthonous and allochthonous sources. Carbon fluxes in coastal ecosystems have a strong effect on the recipient food-webs and carbon emission offsets. Yet, the relative importance of autochthonous vs. allochthonous C inputs to coastal carbon budget is still challenging to identify. Here, we combine diatoms preserved in the sediment with geochemical analyses to identify the sources of carbon stored in Africa's largest intertidal seagrass beds at Banc d'Arguin, Mauritania. The area lies between an active ocean upwelling and the 'Sahara-dust hotspot' systems. The extensive seagrass beds of the area are thus expected to receive C from these neighboring systems in addition to producing C *in-situ*. Three sediment cores (50 cm) were collected at three intertidal sites with different hydrodynamic regimes, and analyzed for diatom composition, total organic carbon (TOC), total nitrogen (TN), total phosphorus (TP), and carbon isotopic signatures (δ^{13}C). Diatom taxa are grouped into three guilds: (1) benthic (epiphyte, epipelon, and epipsammon), (2) planktonic, and (3) freshwater. Benthic diatoms are considered to be autochthonous, while typical oceanic and freshwater diatoms are considered to be allochthonous. Benthic diatoms are the most diverse and abundant group, while allochthonous freshwater (i.e., dust imported) and typical upwelling (i.e., tidal imported) taxa ranked last in both abundance and species' richness. Structure equation modelling shows that variation in the stored carbon is best explained by the total abundance of diatoms and guild composition. We conclude that the C stored in the intertidal seagrass beds of Banc d'Arguin is predominantly autochthonous. Our method provides an effective way to identify historical carbon sources in coastal systems.

KEYWORDS

Banc d'Arguin-Mauritania, carbon sequestration, global warming, carbon flux, fossils, seagrass (*Zostera*)

Introduction

Coastal systems play a crucial role worldwide as habitats for birds, fish, and other coastal fauna and flora as well as carbon sinks. These coastal systems are supported by organic carbon of different origins (Reef et al., 2017). For instant, iconic intertidal habitats such as seagrass beds, saltmarshes, and mangrove forests are generally characterized by high productivity as well as by high sediment trapping capacity (Phang et al., 2015). Thus, C in these coastal sediments is either locally produced (autochthonous) or comes from elsewhere (allochthonous) by tidal and fluvial transport and atmospheric deposition (Duarte et al., 2013; Hayes et al., 2017). Allochthonous C can contribute significantly to the growth of different trophic levels of the recipient habitats (Polis et al., 1997; Garcia et al., 2019). It is hence not surprising that in a recent review authored by 36 leading scientists in the field of carbon research, the quantification of the sources of carbon sequestration was ranked as one of the ten key fundamental questions in this field that must be urgently addressed (MacReadie et al., 2019).

Vegetated coastal ecosystems such as seagrass, salt marshes, and mangroves are major carbon (C) sinks and play a significant role in buffering global warming. Although these coastal ecosystems occupy less than 2% of the marine biome, they account for 50% of all green carbon burial in marine sediments (Nellemann et al., 2009). The origin of this high carbon sequestration is often from different sources. For instance, the efficiency of seagrass beds at storing carbon is primarily due to their capacity to (1) produce large quantity of C as detritus (leaves, roots, and rhizomes) (Pergent et al., 1994); (2) capture suspended material (sediment and/or carbon) from tidal water with their aboveground biomass (Bouma et al., 2005); (3) stabilize and bury both locally produced and allochthonous captured C with the aid of the usually complex belowground structure and relatively fast rate of sediment accretion (Bos et al., 2007); and (4) preserve buried C within anoxic sediment conditions that reduce its decomposition rate and thus the loss of C (Sun et al., 2020). As a consequence, seagrass beds across the globe store large quantities of both allochthonous and autochthonous C that accumulated in most cases over millennia (Duarte et al., 2010; Fourqurean et al., 2012). However, reliable reconstructions of seagrass presence and their long-term contributions to carbon sequestration remain challenging, as plant material of marine angiosperm generally do not preserve well in the sediment (Tuya et al., 2017), with few exceptions such as the Mediterranean seagrass, *Posidonia oceanica*, that is known to form mats and preserve for thousands of years (López-Merino et al., 2017). Hence, assessment of seagrass in the geological record has typically involved indirect indicators such as geochemical and sediment indexes, i.e., stable isotopes, elemental, lipid biomarkers, and environmental DNA (Reich et al., 2015; Forsey, 2016). Thus, there is a need for novel alternative ways to identify the origin of historical-accumulated carbon sources in seagrass ecosystems.

Carbon isotopes ($\delta^{13}C$) and total carbon to nitrogen (C/N) ratios are the most commonly used techniques for assessing sources of C in the sediment (Phillips and Gregg, 2003). Carbon isotopes have widely been used to differentiate between C_3 and C_4 photosynthetic pathways in plants as well as the fractionation of $\delta^{13}C$ between atmospheric (terrestrial plants) and dissolved sources of CO_2 (plankton and aquatic plants). Most seagrass species belong to C_3 pathway group although some species appear to be C_3–C_4 intermediates (Touchette and Burkholder, 2000). Further, the C/N ratio is also an indicator of the C origin (terrestrial versus marine) in coastal sediments (Lamb et al., 2006). Overall, marine and terrestrial sources have distinct carbon isotopic and elemental signatures (France, 1995). Stable isotopes signatures can be used in Bayesian mixing models to estimate the contributions of different primary producers (Kennedy et al., 2010; Bulmer et al., 2020). The main disadvantage of these methods is the great overlap in isotopic and elemental signatures among species from the same biome, beside that these signatures are known to change with life stages, tissue types, and over seasons (Geraldi et al., 2019). Lipid biomarkers such as fatty acids and alkanes have also been used to infer past and present coastal C sources (Bianchi et al., 2016; Geraldi et al., 2019). For example, the terrestrial-to-aquatic ratio of fatty acid (TAR_{FA}) is useful to evaluate the relative contributions of terrigenous and aquatic C stocks (Geraldi et al., 2019). The main inconvenience of biomarkers is that their concentrations in the sediment may be dependent on the degree of sediment oxygenation (Bianchi et al., 2016). Moreover, some biomarkers originate from both allochthonous and autochthonous sources (Waterson and Canuel, 2008). Finally, the environmental DNA (eDNA) technique has been recently used to accurately assign stored C to its sources (Reef et al., 2017; Ortega et al., 2020). The main drawback of this technique is that eDNA reads depend heavily on the selection of primers. Besides that, DNA of marine plankton origin is known to undergo faster degradation than that of terrestrial origin (Boere et al., 2011).

Seagrass associated organisms, such as a variety of epiphytes including diatoms (Vermaat and Verhagen, 1996), are known to often preserve well in sediment (Vos and de Wolf, 1993). In addition, epiphytic and microphytobenthic algae contribute significantly to seagrass meadow productivity, up to 62 and 54% respectively (Borowitzka et al., 2006; Lebreton et al., 2009). Moreover, it is possible to distinguish 3 diatom guilds representing important carbon sources: (1) benthic locally produced (autochthonous), (2) allochthonous planktonic coming from the open seaward area and (3) allochthonous freshwater coming from the landward area. In this study, we aim to combine fossilized diatoms with geochemical analyses in sediments to backtrack the sources of the stored organic carbon in the intertidal seagrass beds of the Parc National du Banc d'Arguin (Mauritania).

The study was conducted at the Parc National du Banc d'Arguin, protecting a 12,000 km^2 wetland along the coast of

Mauritania (Figure 1). Banc d'Arguin contains the largest intertidal seagrass beds in Africa and is considered among the most pristine in the world (UNESCO, 2020). The dominant intertidal seagrass species in term of biomass and cover, *Zostera noltei*, has been considered the most important primary producer in the area (Clavier et al., 2014), with microphy tobenthos being important on bare mudflats. The park is surrounded by two important systems that can significantly contribute to its carbon budget: (1) the ocean upwelling of Cap Blanc, which is one of the most productive in the world (Wefer and Fischer, 1993) and is characterized by an intense exchange of neritic and pelagic water masses (van Camp et al., 1991; Romero et al., 2020; Romero et al., 2021); (2) the Sahara dust hotspots, which are known to export large quantities of organic carbon and nutrients westwards to regions as far as the Amazon Forest in Brazil (Prospero et al., 1981; Ben-Ami et al., 2010; Barkley et al., 2021). Both the upwelling (Romero et al., 2020) and Saharan dust (Pokras, 1991; Romero et al., 2003; Barkley et al., 2021) are known to transport large quantities of planktonic and freshwater diatoms that are indicators of their origin. The food web of the inner intertidal system of Banc d'Arguin, however, has been suggested to rely predominately on *in-situ* benthic primary production than on transported C sources (Wolff et al., 1993; Carlier et al., 2015). However, these shallow inner intertidal flats represent relatively recent deposition (ca. 800 cal. yr. BP) (Proske et al., 2008), and seagrass stands were found only in the youngest part of these intertidal flats (Proske et al., 2008). The origin of the longer-term carbon sequestration thus remains unknown.

Materials and methods

Sample collection

Sampling locations were chosen to represent different hydrodynamic regimes: exposed, intermediate, and sheltered from wave energy (El-Hacen et al., 2019). At each location (Figure 1), a sediment push core was taken in January 2015. The cores had a length of 50 cm and an inner diameter of 2.5 cm. Each core was divided in slices of 2 cm, resulting in 25 depth samples per core. Each depth sample was oven dried, stored in plastic containers and transported to the Netherlands for further analyses.

Age determination of core sediments

^{210}Pb dating of the core was performed but the unsupported levels of ^{210}Pb were too low, and the data could not be used to determine the age of the sediments. Instead, we estimated the age of our samples using the data of two cores taken in close proximity of our sampling stations and which were dated using ^{14}C (Proske et al., 2008). These ^{14}C ages are based on deep shell layers from the sedimentary succession. Using radiocarbon dates at 239 cm depth in core LV-6 and 248 and 159 cm in core LV-2, sedimentation rates of 0.5 cm/yr. and 0.3-1.1 cm/yr. were obtained for LV-6 and LV-2, respectively (Supplementary 1). The age-depth model (cal. yr. BP, ± 2σ) of core LV-6 was extrapolated to the core collected at the wave
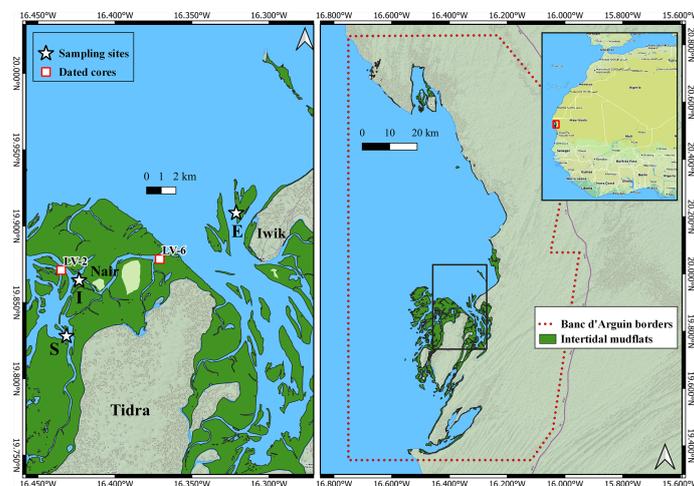
FIGURE 1
Map of the Parc National du Banc d'Arguin, Mauritania, with sampling locations: black stars indicate where cores were taken for carbon, diatom and geochemical analyses; while red squares represent site where dated cores were previously taken. The sampling sites represent three distinct wave action regimes: E = Exposed (19°54′34″ N, 16°19′10″ W), I = Intermediate (19°51′52″ N, 16°25′26″ W) and S = Sheltered (19°49′39″ N, 16°25′54″ W) (El-Hacen et al., 2019).

exposed site due to their proximity and similarity in wave energy index (El-Hacen et al., 2019). Similarly, the age-depth model of core LV-2 was extrapolated to the cores of the intermediate and wave sheltered sites. This extrapolation, however, should be interpreted with caution (transfer from one core to another, sediment compaction, and large confidence interval of the calibrated radiocarbon dates) and will only serve as an indication of the possible time interval represented in our push cores for discussion.

Diatom analyses

Of the 25 depth samples in each push core, fifteen per core were selected for diatom analysis. Subsamples of ± 0.75 g were taken and prepared for siliceous microfossil analysis at the University of Utrecht, The Netherlands. Each subsample was oxidized with 1.5 mL permanganate (KMnO4) to remove organic matter and treated with 3 mL 30% HCL to remove carbonates. Then, the subsamples were rinsed and diluted ten times with distilled water. Diatoms were left to settle on coverslips overnight using Battarbee evaporation trays to optimize random distribution (Battarbee, 1973). The coverslips were then permanently mounted on slides in Naphrax$^®$ (RI = 1.7). A Leica DM2500 microscope was used to count diatoms and photos were taken with a Leica DFC320 and an Olympus DP25. At each depth level, the conventional counting of 300 diatom valves following Schrader & Gersonde (1978) was used. These counts were then used to calculate taxon percentages. The objective was set to 63x and the Optovar to 1.5x. Thus, the eyepiece-micrometer reticule had 1.05 µm divisions and the area counted could be calculated. The diatom relative abundance in valves/g can be calculated as:

$$\frac{\text{\# diatoms} \times \text{area Battarbee tray} \times \text{dilution}}{\text{counted area on slide} \times \text{weight in g dried sediment}}$$

Taxonomical identification was based on well-known bibliographies (Halse and Syvertsen, 1996; Witkowski et al., 2000) and online databases such as algaebase.org, www.diatombase.org and the World Register of Marine Species (WoRMS). In total, 43 specimen-type were identified to the species level, 61 to the genus level, and other twelve-types could not be identified (Table S1, Supplementary 2). In addition, identified diatom species and genera were grouped (Table S1) into three guilds (benthic, planktonic, and freshwater) based on previous studies on diatoms in the region (Margalef, 1975; Sterrenburg and Sterrenburg, 1990; Vos and de Wolf, 1993; Romero et al., 1999; Romero et al., 2003; Bernárdez et al., 2010; Romero and Fischer, 2017; Romero et al., 2020; Romero et al., 2021). Benthic taxa were further divided into two groups: (1) epiphytes that grow attached to seagrass leaves and (2) non-epiphytic that grow on the sediment surface.

Geochemical analyses

Ground sediment subsamples of each depth levels were analyzed at NIOZ, Yerseke, The Netherlands. Total organic carbon (TOC), total nitrogen (TN), and δ^{13}C were measured simultaneously by a CNS analyzer (Vario MACRO CNS) on 5 mg of sediment per subsample (n = 25/core; every 2 cm).

Statistical analyses

All statistical analyses were performed in R (v. 4.0.2) (R Development Core Team, Vienna, Austria) in RStudio environment (v. 1.3.1073) (RStudio Inc., Boston, USA). Changes in the vertical (n = 25) abundances of the most common diatom guilds were evaluated using change point analysis with the 'changepoint' package in R (Killick and Eckley, 2014). Change point analysis identifies statistically significant changes in the mean or variance within series of observations based on likelihood ratios (Killick and Eckley, 2014). Linear regression analysis was used to test if the total diatom abundance as well as the abundances of the different guilds significantly explain the carbon stocks over time. One-way analysis of variance (ANOVA) and *post hoc* Tukey test were used to analyze the effect of site (n = 3) on both sediment carbon isotopes (δ^{13}C) and C/N ratios (n =25) as an indication for the sources of carbon in the system. Parametric assumptions were checked on the residuals.

Additionally, we performed a multi-level piecewise structural equation modelling (piecewise SEM) to simultaneously assess the relative importance of diatom diversity (richness, abundance, and community structure) and environmental conditions (depth and source of carbon) on carbon stocks (n = 75: 25 per site). SEM was conducted in 'piecewiseSEM' R package, which can account for hierarchically structured data by incorporating mixing effect modelling approach (Lefcheck, 2016). *A priori* meta-model was developed, based upon known knowledge on factors controlling C stocks in intertidal systems (Figure S1, Supplementary 3), which was improved by removing non-significant paths using Akaike's information criterion (AICc) (Grace et al., 2010; Lefcheck, 2016). The goodness of fit of the final SEM was assessed using directional separation test (d-separations test) Fisher's C statistic (Shipley, 2013). Homogeneity of variance was checked visually using residuals plots (Figure S2). To characterize diatom community composition, the first two axes of Redundancy analysis (RDA) were used as a proxy. RDA analyses relate trait-environmental relationship at the community level (Lepš and Šmilauer, 2003; Legendre et al., 2011; Legendre et al., 2012). RDA first and second scores describe assemblages in terms of similarities in traits and responses to environmental gradients (Kleyer et al.,

2012; Guillaume Blanchet et al., 2014), and have been used before as a proxy for community composition (Widenfalk et al., 2015; Sgro and Reavie, 2018). RDA analysis was performed using the 'vegan' package on Hellinger distance transformed data, to reduce the influence of the most abundant taxa. Prior RDA procedure, a detrended correspondence analysis (DCA) on diatom abundance data resulted in very short gradient lengths (< 0.2), suggesting that RDA analysis was more appropriate than non-linear approach such as NMDS (Šmilauer and Lepš, 2014).

Results

In total, 76 different diatom taxa were identified at the exposed site, 48 at the intermediate, and 93 at the sheltered site (Supplementary 2). Across sites, the tychopelagic (grows predominantly benthic and is easily lifted into planktonic form) species, *Paralia sulcata*, was by far the most common, accounting for 33, 74, and 36% of the total recovered taxa at the exposed, intermediate, and sheltered sites, respectively. At the wave-exposed site, epiphytic (56-59%) and freshwater (10-25%) taxa were the most abundant in the upper layers (0-4 cm), whereas benthic non-epiphytic (growing on sediment) (34-85%) and planktonic (12-50%) taxa dominated down-core (Figure 2, Figure S3). The intermediate site was barren of diatoms in the lower part (34-50 cm) of the core, and benthic non-epiphytic taxa (73-86%) dominated above 34 cm, with two small peaks of freshwater taxa (10 and 6%, respectively) and a very recent peak of epiphyte taxa (21%) (Figure 2, Figure S3). At the wave-sheltered site, epiphyte (21-42%) and freshwater (7-21%) taxa

were the most abundant in the upper layers (0-14 cm), while the lower part (14-50 cm) was dominated by benthic non-epiphytic (40-73%) taxa. Moreover, there was almost a complete absence of planktonic taxa throughout this core (Figure 2; Figure S3).

Total organic carbon content (%) of the sediment was significantly correlated to total diatom relative abundance (# valves/g) ($R^2 = 0.19$, $F_{1,42} = 10.1$, $p = 0.002$), as well as the relative abundance of benthic non-epiphytic group ($R^2 = 0.1$, $F_{1,42} = 4.8$, $p = 0.034$), but not the other guilds (Figure 2).

Sediment carbon isotopes (δ^{13}C) values significantly differed between the three sites ($F_{2,41} = 48.9$, $p < 0.001$, Figure S4). A *post hoc* Tukey test showed that the δ^{13}C values of the wave-sheltered site (M = -10.5, SE = 0.15) was significantly higher than in the intermediate (M = -11.8, SE = 0.1) and wave-exposed site (M = -12.38, SE = 0.13), indicating a dominance of benthic sources at the sheltered site and more mixed sources at the exposed and intermediate sites (Figure 3). Sediment C/N ratio also significantly differed between the three sites ($F_{2,41} = 4.7$, $p = 0.01$, Figure S4). A *post hoc* Tukey test showed that the C/N ratio of the wave-sheltered site (M = 10.3, SE = 0.5) was significantly higher than in the intermediate (M = 8.9, SE = 0.2) but not different from the ratio of the wave-exposed site (M = 9.6, SE = 0.15), indicating a dominance of seagrass sources at the sheltered site, a microalgae sources at the intermediate site and mixed sources at the exposed site (Figure 3).

The final structural equation model (SEM) yielded a good fit to the data (Fisher's C statistic = 6.1, $p = 0.64$, Table S2), explaining 57% of the variance in sediment TOC (Figure 4). Both diatom relative abundance and species composition (RDA1) had significant and positive effect on sediment TOC
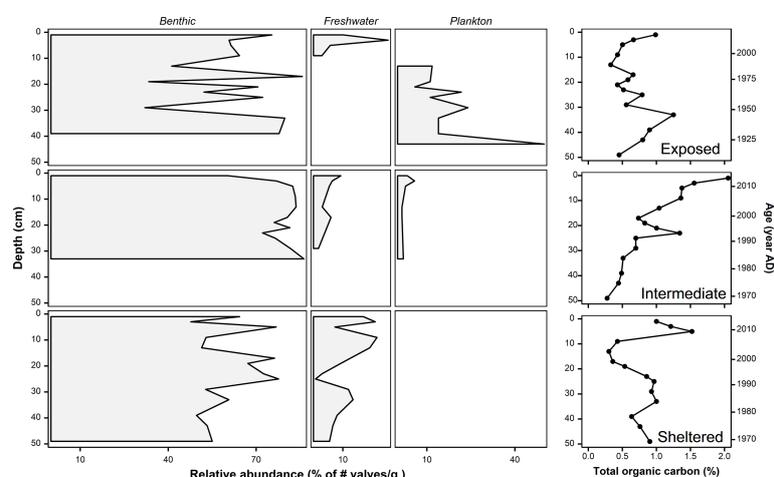

FIGURE 2
A stratigraphic diagram showing the relative abundance (%) of diatom guilds (benthic, freshwater and plankton) as well total organic carbon (%). Samples were analyzed in three cores, 50 cm-long each, at three sites representing different hydrodynamic regime sites: Exposed (top panel), Intermediate (middle panel) and Sheltered (bottom panel). Age estimates (right y-axis) are based on sediment accumulation rates obtained from 14C ages of shells retrieved from nearby cores (Proske et al., 2008).

(Figure 4). The effect of sediment depth on TOC was more complex, including direct and indirect associations: a significant direct negative effect was observed, while we also found a significant indirect negative effect mediated through abundance, plus a significant indirect positive effect mediated through RDA1 (Figure 4). Similarly, δ^{13}C had both positive (via abundance) and negative (via RDA1) indirect significant effects on TOC (Figure 4), and a direct marginally significant positive effect on it. No direct link was identified between diatom species richness, RDA2 and sediment TOC (Figure 4). Overall, the SEM implies that variation in the stored TOC is best explained by the total abundance of diatoms and guild composition.
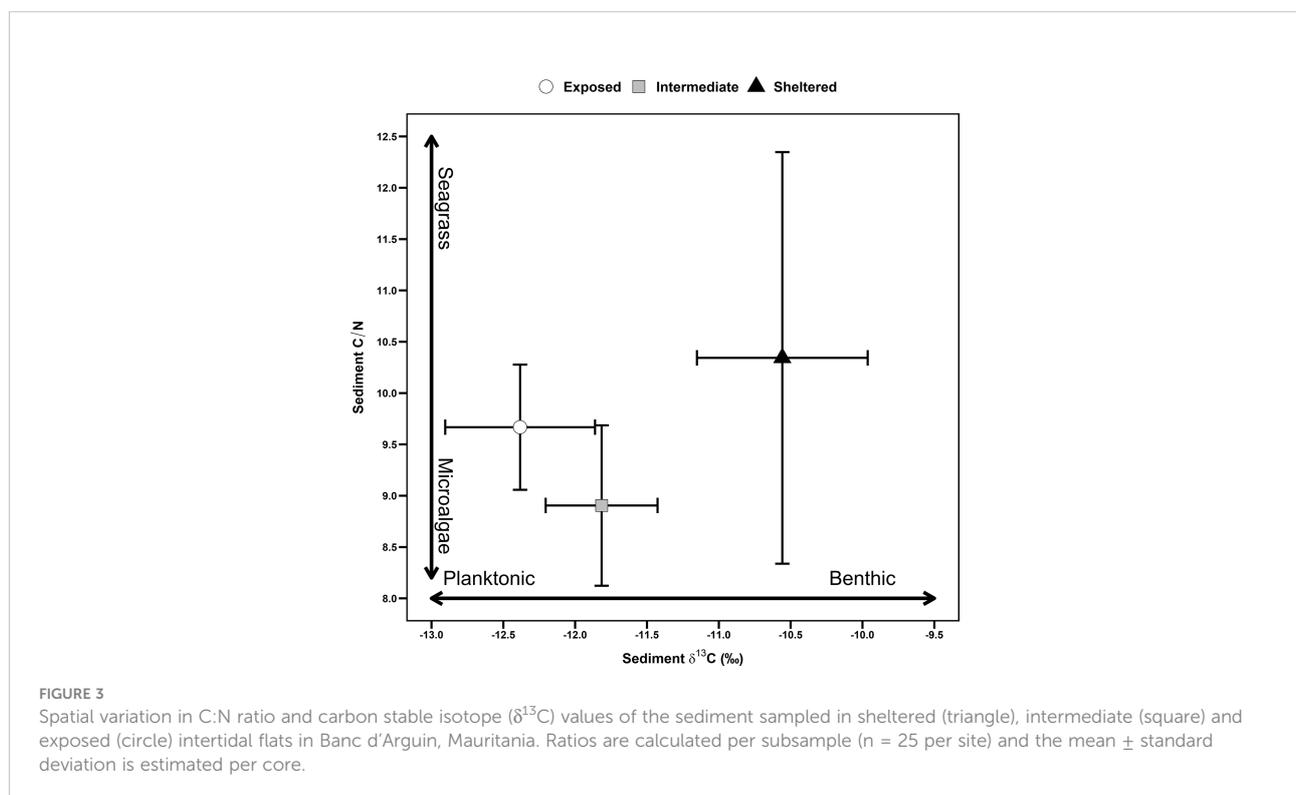
Discussion

Diatom guild and carbon stocks

In this study, we found that the exposed site was dominated by autochthonous benthic diatoms (locally produced) followed by allochthonous planktonic taxa (seaward origin), while the sheltered site was dominated by autochthonous benthic taxa followed by allochthonous freshwater ones (landward origin). The intermediate site was generally poor in abundance and dominated by benthic taxa with compete absence of diatom valves in the lower part of the core. Further, we found that the relative abundance and guild types of preserved diatoms statistically explained a large part of the variation

in the amount of carbon in the intertidal sediments at Banc d'Arguin (Figure 4). Diatom valves from different guilds seem to generally preserve well in the sediment, which confirms that fossilized diatoms are informative on the source of stored C (Reich et al., 2015). In addition, the combination of δ^{13}C and C/N geo-markers showed that the C at the wave-sheltered site was dominated by seagrass signatures, while at the exposed and intermediate-sites the planktonic signatures prevail (Figure 3). The average δ^{13}C and C/N values of the exposed and intermediate sites fall within the ranges reported for planktonic/microphytobenthos sources, while the values of the sheltered site fall within seagrass sources (Meyers, 1994; Machás et al., 2006; Kim et al., 2014; Tuntiprapas et al., 2019). Marine algae usually have lower C/N (<10) ratios compared to seagrass (Meyers, 1994; Tuntiprapas et al., 2019). Similarly, the sediment δ^{13}C values of the sheltered site are similar to the ones generally reported for *Zostera* sp. elsewhere (Machás et al., 2006; Kim et al., 2014). Indeed, the observed δ^{13}C signatures in this site are similar to the signatures of the shoots of *Z. noltei* in our study area (El-Hacen et al., 2019).

An interesting observation that is hard to explain is the shift of dominance over the last century from planktonic to benthic taxa at the exposed site. This could be the result of an increase in seagrass cover as has been documented over the last three decades, particularly in the northern most exposed area in Banc d'Arguin (El-Hacen et al., 2020). Another unexpected observation is the absence of diatom valves in the lowest part of the intermediate core, which coincides with a strong decrease in stored organic matter (Figure 2). It could be that the lowest part of the core consists of a large sand deposition from

FIGURE 3
Spatial variation in C:N ratio and carbon stable isotope (δ^{13}C) values of the sediment sampled in sheltered (triangle), intermediate (square) and exposed (circle) intertidal flats in Banc d'Arguin, Mauritania. Ratios are calculated per subsample (n = 25 per site) and the mean ± standard deviation is estimated per core.

the nearby sandy island, Nair (Figure 1). Occasional extreme storm events have been shown to cause strong morphological changes in the intertidal systems of Banc d'Arguin (Trégarot et al., 2021).

The main challenge that we faced in using fossilized diatoms in tracking sources of C was the lack of detailed knowledge on species composition and characteristics of the different sources. In our study, diatoms were identified mostly at the genus level, and thus species that belonged to the same genus were pulled together although they might have originated from completely different sources. This might be true for many species of *Nitzschia* and *Synedra* that were considered in our study as marine benthic although many of them are known to be planktonic and dust-freshwater species (Romero et al., 1999; Breuning-Madsen and Awadzi, 2005). A best practice would have been to identify in advance the diatom species of the different sources (benthic, pelagic, and dust) contributing to the C pool of our study site.

Origin of the diatom species

Overall, freshwater species were more abundant at the sheltered site. In both the exposed and intermediate sites, freshwater diatoms appeared only in few occasions after 1976 (Figure 2), which is the peak year of the Sahel great drought that was characterized by intense dust storms (Goudie and Middleton, 1992). It is surprising though that a previous diatom survey conducted in Banc d'Arguin in 1988, including sheltered flats, did not encounter freshwater species (Sterrenburg and Sterrenburg, 1990). Nonetheless, a study on fluxes of airborne freshwater diatoms at Cap Blanc (close

proximity to the northern border of Banc d'Arguin), showed also a strong peak in 1988 (Romero et al., 2003). Although, Saharan largest dust source, the Bodélé depression in Chad, is known to consist largely of freshwater diatoms particularly *Aulacoseira*, *Fragilaria* and *Stephanodiscus* species (Gasse, 2002), only *Fragilaria* were present in our cores. However, the input of diatoms *via* Saharan dust seems to vary a lot spatially and temporally (Romero et al., 1999). For instant, it has been shown before that the Saharan wind-transported diatoms deposited in the equatorial Atlantic are dominated by *Melosira* and *Stephanodiscus* species, accounting for approximately 70 and 17% of the assemblage, respectively (Pokras, 1991). Again, both genera were not present in our samples. This spatio-temporal variation in the distribution of Saharan wind-transported diatoms can be explained by the strong seasonality in storms with a maximum in summer and minimum in winter (Prospero et al., 1981; Prospero et al., 2014) as well as the weight and shape of the diatom species (Mallios et al., 2020; Barkley et al., 2021), which will determine where they deposit. In addition, the fragmentation process that happens to many diatom valves during the wind-transport events is likely to lower their recovery in the geological records (Warren et al., 2007). Hence, fully quantifying the contribution of Saharan dust to Banc d'Arguin C stocks and the functioning of its intertidal system requires conducting additional studies including dust flux measurements and identification of the wind-transported diatom species. This study, however, allowed us to gain insight into the spatial distribution as well as the historical dynamic of dust-imported C into Banc d'Arguin intertidal systems.

The most common species that made a significant contribution to the total abundance of fossilized diatoms in all cores was *Paralia*
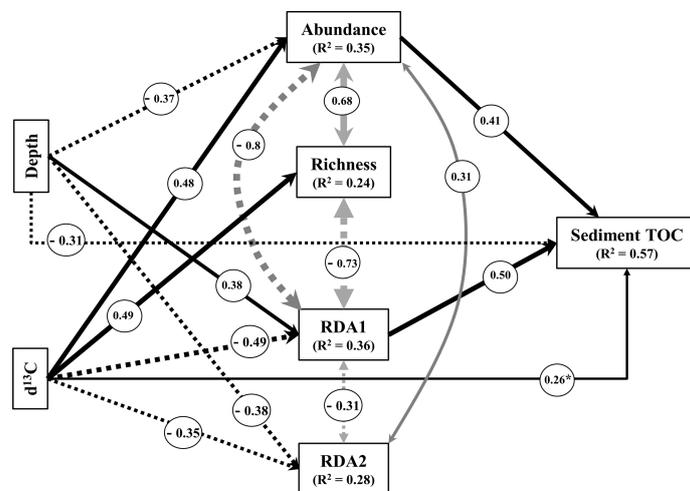

FIGURE 4
Most parsimonious structural equation model (Fisher's C statistic = 6.1, p = 0.64), depicting the causal link between sediment organic carbon, depth and diatom community structure and composition. Black arrows represent unidirectional relationships among variables and grey arrows non-causal correlations. Solid and dashed arrows denote positive and negative relationships, respectively. The thickness of the paths is scaled based on the magnitude of path coefficient (β). The R^2 value indicates the amount of variance explained by the model. The final model included only significant and almost significant R^2 values (0.05 > p< 0.1; indicated by * pathways). RDA = redundancy analysis.

sulcata, a species that grows predominantly benthic and is easily lifted into plankton by strong winds and tidal mixing (Roelofs, 1984; Zong, 1997; McQuoid and Nordberg, 2003). This species has been suggested to adopt a dual benthic-planktonic lifestyle: settles benthic in the growing season (spring) and suspends planktonic in autumn due to the increase of storms (Gebühr, 2011). Although, not considered an upwelling species (Romero et al., 2021), *P. sulcata* has been associated with nutrient rich waters (Gebühr, 2011). The association of *P. sulcata* to seagrass is, to our knowledge, not known and worth further investigation. Further, the rarity of both upwelling and pelagic planktonic species in our cores supports earlier findings showing low allochthonous planktonic biomass in the shallow part of Banc d'Arguin ecosystem (Sevrin-Reyssac, 1977; Sevrin-Reyssac, 1982; Sevrin-Reyssac, 1984). Indeed, the fact that planktonic species were only present in the core of the wave-exposed site is in agreement with the notion that the upwelling of Cap Blanc has only an effect on the northern most exposed area of Banc d'Arguin (Carlier et al., 2015). Thus, consistent with the suggestion by (Wolff et al., 1993), we conclude that the carbon stored in the intertidal system of Banc d'Arguin is dominated by autochthonous benthic products such as seagrass and microphytobenthos; a conclusion that was made before but lacked empirical evidences (Wolff et al., 1993).

Conclusions

The combined use of preserved diatoms in sediment and geochemical analyses allowed us backtrack the main sources of carbon in Banc d'Arguin intertidal system over time. Diatom taxa were divided into three guilds (benthic, freshwater, and pelagic) representing different sources of C: autochthonous benthic taxa and allochthonous freshwater and pelagic taxa. Autochthonous benthic diatom taxa were the most diverse and abundant group, while typical allochthonous freshwater and upwelling taxa ranked last in both abundance and species richness. Carbon stored in the sediment (% TOC) was significantly correlated to the total diatom abundance as species composition (guilds). Further, the $\delta^{13}C$ and C/N ratios, showed a dominance of autochthonous benthic sources at the sheltered site and mixed sources at the wave-exposed site. We conclude that the C supporting the food webs and stored in the inner intertidal flats of Banc d'Arguin are predominantly autochthonous with a significant allochthonous contribution from the planktonic taxa in the wave-exposed and from freshwater taxa in the wave-sheltered zones. Thus, studies of fossilized diatoms along a sediment core will provide a useful estimate of C sources over time.

Data availability statement

The original contributions presented in the study are included in the article/Supplementary Material. Further inquiries can be directed to the corresponding author.

Author contributions

Conceptualization: TB, HO, EE, FS, and TP. Methodology: FS, TB, TM, HO, and EE. Data acquisition and analyses: EE, TM, TB, FS, and SL. Writing (original draft): EE and TM. Supervision: TP, SL, FS, and TB. Funding acquisition: HO, FS, and TP. All authors contributed to the article and approved the submitted version.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fmars.2022.1006847/full#supplementary-material

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