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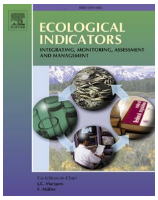

Original Articles

Global patterns in seagrass leaf and sediment carbon isotope fractionation have implications for carbon provenance calculations in blue carbon accreditation

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ABSTRACT

Seagrass carbon sequestration is known to be an accumulative process of both autochthonous and allochthonous carbon sequestration, however, carbon accreditation focuses on increasing autochthonous organic carbon only. In seagrass carbon accreditation methodologies peer-reviewed published data may be utilised as evidence for the deduction of a percentage of allochthonous carbon from the total seagrass sediment organic carbon. These literature-based proxies are often derived from stable isotope mixing models, which utilise seagrass and sediment δ^{13}C values. This study looks at global seagrass sediment and leaf δ^{13}C analyses, and demonstrates that climatic bioregion, geomorphology and seagrass morphological traits explain global patterns in seagrass leaf and sediment isotope δ^{13}C ratios. Multi-factor analysis of mixed data shows a separation between seagrass bioregions and different leaf-size populations, specifically; north temperate regions from tropical and south temperate regions; medium leaf-size individuals to all others. Analysis of variance confirmed a significant difference ($p < 0.001$) in the $\Delta\delta^{13}C_{\text{seagrass-sediment}}$ between bioregions and species sizes classifications. KMeans clustering of the seagrass and sediment δ^{13}C and sediment depth data suggests that three main clusters can be identified (1) small deltas, (2) tidal systems coastlines, (3) an aggregation of lagoons, arheic and fjords coastlines. If proxies are used for blue carbon accreditation, this paper presents an informed criterion to improve the selection of allochthonous sediment organic carbon proxies based on their derivative sediment and seagrass δ^{13}C values. However, proxy values from the literature are not a direct substitute for site specific δ^{13}C seagrass leaf and sediment data, and their use in context dependent mixing models.

1. Introduction

Carbon-oriented management of coastal ecosystems has received considerable interest for its potential to incentivise financial investment into protecting or restoring these habitats, thereby supporting climate change mitigation to achieve a sustainable future (Thomas, 2014). The payments for environmental services (PES) incentivise financial support for goods and services directly provided by nature, due to man-made conservation activities (Wunder 2015; Derissen and Latacz-Lohmann, 2013). Direct finance to support the conservation and restoration of coastal ecosystems to increase their carbon sequestration provision is an example of PES. In this context, blue carbon can be understood as a product or service (Vanderklift et al., 2019), providing the premise for carbon markets, whereby carbon stored in these coastal ecosystems and quantified using scientific methods can be sold as credits (Wylie et al., 2016).

Seagrass ecosystems sequester carbon in two ways: first, *in situ* photosynthetically, when the excess to the metabolic requirement results in net carbon fixation of autochthonous seagrass-derived organic carbon; and second, by sedimentation of organic matter suspended in the water column that originates from outside the ecosystem, which can be marine or terrestrial and is termed allochthonous carbon (Fig. 1.)

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(Kennedy et al., 2010; Greiner et al., 2013). Autochthonous carbon is derived from the long-term retention of seagrass formed via the growth of roots and shoots accumulating in the sedimentary compartment of the seagrass meadow, as dead seagrass matter (Fig. 1B). The capture of allochthonous carbon by seagrasses only represents additional storage or carbon storage providing climate mitigation benefits if such carbon would otherwise remineralise before burial (Johannessen and Macdonald, 2016; Chew and Gallagher, 2018). Therefore, it is only the storage of autochthonous carbon which mitigates the reduction of greenhouse gas (GHG) emissions and reduces existing excess GHG concentrations in the atmosphere (Macreadie et al., 2021).

1.1. Blue carbon offsetting mechanisms and their application to seagrass ecosystems

Carbon credits currently form part of two broad carbon markets: the compliance carbon market and the voluntary carbon market. The compliance market is utilised by those that must reduce emissions as part of a treaty (such as the Kyoto Protocol or the European Union Emissions Trading Scheme); the voluntary market includes buyers who voluntarily buy credits to support broader strategic priorities such as sustainability (Vanderklift et al., 2019; Wylie et al., 2016). Carbon credit mechanisms to support financial investment into blue carbon restoration are supported by the United Nations Framework Convention on Climate Change (UNFCCC) within the compliance market, e.g., the Clean Development Mechanism (CDM) and the Reducing Emissions from Deforestation and Forest Degradation plus (REDD+, plus the role of conservation, sustainable management of forests and enhancement of forest carbon stocks). Because the high costs and administrative requirements of compliance carbon markets favour large-scale and low-cost emission reduction efforts, to date, the voluntary market has been the primary source of finance for blue carbon projects. Carbon credit mechanisms to support financial investment in the voluntary carbon market use carbon credit accounting methodologies like those proposed under schemes such as Plan Vivo or the Verified Carbon Standard (VCS) (Vanderklift et al., 2019; Wylie et al., 2016).

Current blue carbon accreditation projects on the voluntary market have been dominated by those centred on mangrove forests. The route-to-market and accounting methodologies for this habitat aligns closely with established terrestrial afforestation and reforestation activities (Hejnowicz et al., 2015). The comparative lag in formulating methodologies backed by accreditation schemes to quantify the carbon sequestered in seagrass meadows for carbon credits, compared to habitats such as mangrove forests, has resulted in uncertainty in its application, even if accreditation schemes have produced methodologies to quantify seagrass carbon credits (e.g., VCS VM0033 Methodology for Tidal Wetland and Seagrass). Since seagrass restoration projects tend to be minor, carbon credit accreditation through the voluntary carbon market is the most applicable route-to-market for seagrass restoration activities (Needleman et al., 2018; Vanderklift et al., 2019; Wylie et al., 2016). Voluntary carbon markets also pose the most suitable approach for seagrass carbon credit accreditation, since the market audience motivation in wider strategic sustainability means they are likely to take into consideration the co-benefits and location of seagrass restoration projects (Vanderklift et al., 2019; Needleman et al., 2018).

The Verified Carbon Standard (VCS), has created a carbon credit accounting methodology (VM0033) to support a financial crediting mechanism for seagrass habitat restoration activities on the voluntary carbon market (CEC, 2014; Emmer et al., 2015). This VCS GHG accounting methodology has been applied to a seagrass restoration project in principle to prove the positive effect of seagrass restoration on net GHG removal from the atmosphere (Oreska et al., 2020). Seagrass restoration activities are expected to contribute to atmospheric GHG reduction through increased biomass, increased autochthonous sedimentary organic carbon, reduced methane and/or nitrous oxide emissions – due to increased salinity or changing land use, and reduced carbon dioxide emissions – due to avoided sediment carbon loss (Emmer et al., 2015). The focus on increased autochthonous organic carbon in seagrass sediment highlights that carbon fixed outside the project area cannot be attributed to project activities (CEC, 2014) because it raises concerns of double carbon counting across habitats. But also, because carbon accreditation values carbon which represents a reduction of existing excess GHG concentrations in the atmosphere, the focus is therefore to only value carbon stored which is a result of the seagrass habitat for which the accreditation is concerned with.

For carbon credit integrity, in addition to discerning carbon provenance other criteria are required, for example additionality and permanence. Additionality means the restoration activity must

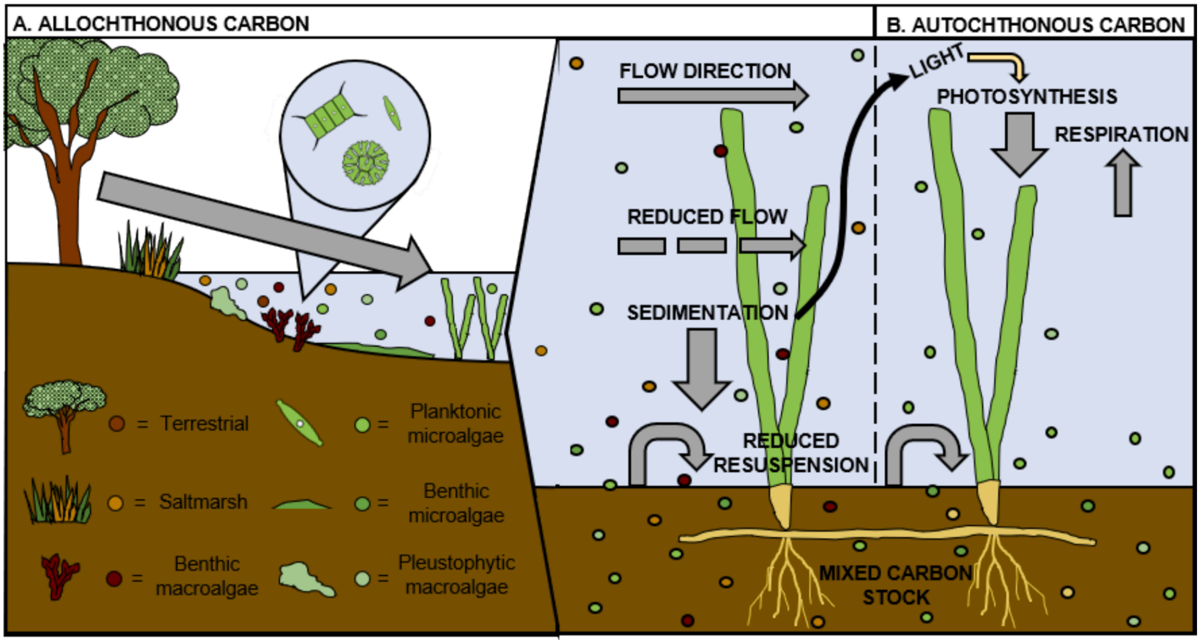


Fig. 1. The organic carbon accumulation routes and mechanisms in a temperate North Atlantic seagrass bed **(A)** Connection to neighbouring coastal habitats, the influx and storage of allochthonous carbon. **(B)** Excess photosynthetic fixation of seagrass-derived autochthonous carbon within seagrass habitat.

demonstrate an additional reduction of GHG emissions, compared to the baseline scenario without the activity intervention. Whilst relative permanence must be demonstrated for carbon stored from a restoration activity to be considered a reduction of CO_2 emissions, namely that the carbon remains stored over long-time scales (Locatelli et al., 2014). There is a trade-off between the stringency of permanence requirements and the ability for a project to participate under such requirements (Ruseva et al., 2020). Literal permanence is rarely obtainable and therefore the long-term 100-year approach allows relative permanence to be integrated into policy and accreditation frameworks, but it also leads to insecurity regarding the 'solution' offsetting truly presents. Further to this there are significant knowledge gaps in the provenance, additionality and permanence of carbon stored in seagrass, limiting uptake and confidence in restoring blue carbon habitats as nature-based solutions (UKBCEP, 2023). This has resulted in the production of carbon codes which aim to recommend a pathway for development and adoption of seagrass restoration for nature-based solutions (Ward et al., 2023).

1.2. Current understanding of carbon provenance within global seagrass sediment

Seagrass isotopic carbon values often differ from plankton, seagrass epiphytes and terrestrial vegetation (Moncreiff and Sullivan, 2001). Through these values it is possible to distinguish the seagrass derived contributions within sedimentary carbon stocks (Moncreiff and Sullivan, 2001; Kennedy et al., 2010). However, carbon contributions to seagrass sediment are not always distinguishable by stable isotopic analysis, and it is key the potential sources of organic carbon must have well constrained isotopic values, with limited to no overlap. Such overlaps include: macroalgae with epiphytic and benthic microalgae (Moncreiff and Sullivan, 2001; Oreska et al., 2018), which can lead to a lack of resolution between these sources. The use of eDNA to determine carbon provenance in seagrass sediment in combination with stable isotopic analysis has been demonstrated to reduce the ambiguity in provenance and suggests that stable isotope analysis may underestimate the contributions of autochthonous carbon (Reef et al., 2017; Ortega et al., 2020). Most recently, within tropical seagrass sediment eDNA discriminated the carbon provenance of macrophyte taxa to species level (Ortega et al., 2020). A well-resolved understanding of carbon provenance to species-level utilising eDNA techniques has yet to be determined for seagrass sediment across the globe, and especially within temperate seagrass meadows. Therefore, the most commonly utilised approach for determining carbon provenance on a global scale is utilising stable isotopic analyses in stable isotope mixing models (SIMMs).

Peer-reviewed published data may be utilised as evidence to generate a value of the percentage of allochthonous carbon to be deducted for carbon credit accounting (Emmer et al., 2015). The requirements for selecting the literature-based proxy are that the value be from a study in the same or similar systems as those in the project area, to account for regional variation of species and ensure like for like comparison (Emmer et al., 2015). Previous analysis of seagrass leaf $\delta^{13}C$ and seagrass sediment $\delta^{13}C$ suggested the global ratio of autochthonous to allochthonous carbon buried in situ in seagrass sediment is 50:50 (Kennedy et al., 2010). Seagrass species often occupy specific climatic regions of the world, as such distinct seagrass bioregions have been identified based on species distributions and provide a useful framework for interpreting ecological, and physiological results collected in specific locations (Short et al., 2007). Further to this the chemical recalcitrance of seagrass tissues can vary across tissue types, taxa, and geography (Trevathan-Tackett et al., 2017). Therefore, the $\delta^{13}C$ seagrass and sediment values noted globally will vary, likely relative to seagrass plant traits and the locations or settings of these plants. Therefore, the climatic species composition will not act as a standalone predictor, but rather interplay with the typical habitat placement within that climatic coastal setting and the subsequent landscape dynamics. When utilising allochthonous carbon proxies the criteria and influencing factors which make the proxy similar to the restoration project should be considered and justified to provide context on the decision process behind the proxy selection.

In the context of determining carbon provenance in coastal sediments SIMMs are formed of the unknown sediment mixture, the representative autochthonous source (e.g., seagrass) and the allochthonous source(s) (e.g., saltmarsh, particulate matter). As the number and type of allochthonous sources utilised in SIMMs will vary dependent on the situational context in question, the constant elements in seagrass carbon provenance SIMMs are the unknown sediment mixtures and the autochthonous seagrass source. This study therefore collates an updated worldwide synthesis of $\delta^{13}C$ data for seagrass sediment and leaves. Given that peer-reviewed published data may be utilised as evidence to generate a value of the percentage of allochthonous sediment organic carbon, typically derived from SIMMs derived in part from $\delta^{13}C$ seagrass and sediment values, this study investigates which influencing factors need to be considered when utilising allochthonous carbon proxies based on their derivative $\delta^{13}C$ seagrass and sediment values from around the globe. It determines the difference between $\delta^{13}C$ seagrass and sediment ($\Delta\delta^{13}C_{\text{seagrass-sediment}}$). It examines the $\delta^{13}C$ seagrass and seagrass sediment values, depending on the climatic setting, according to known seagrass bioregions (Short et al., 2007), in relation to geomorphology (e.g., estuarine, lagoonal) or the subsequent 'typical' seagrass communities, by addressing seagrass morphological traits (i.e., size).

2. Methods

2.1. Compilation of $\delta^{13}C$ dataset

Estimates of $\delta^{13}C$ seagrass sediment, and $\delta^{13}C$ seagrass leaves were compiled from the literature. The search criteria focused on utilising key terms including 'carbon', 'isotope', 'isotopic', 'sediment', 'seagrass' and '$\delta^{13}C$', searches were repeated utilising various combinations of these terms until the literature returned saturated. In total, 52 papers contributing 409 analyses of $\delta^{13}C$ seagrass sediment were utilised (Supplementary 1), in addition to the 219 analyses compiled by Kennedy et al. (2010). Overall, the data set compiled for this study contained 628 analyses of $\delta^{13}C$ seagrass sediment, versus a total of 523 $\delta^{13}C$ seagrass leaves analyses. Data from each seagrass meadow did not always contain values for both $\delta^{13}C$ seagrass leaves and $\delta^{13}C$ seagrass sediment, so the number of data points and the locations that the data represent may differ between parameters. The $\delta^{13}C$ seagrass sediment values were from various subsampled depths, but all were obtained from within the top 30 cm of seagrass sediment (i.e., surface to 30 cm depth). Where in the literature deeper sediment cores were subsampled as smaller depth intervals, an average value of the subsamples within the top 30 cm was utilised. The differences between $\delta^{13}C$ seagrass sediment and $\delta^{13}C$ seagrass leaves were calculated ($\Delta\delta^{13}C_{\text{seagrass-sediment}}$). This dataset includes a total of 500 $\Delta\delta^{13}C_{\text{seagrass-sediment}}$ values. The sample stable carbon isotopic composition (δ_{sample}) was calculated with the following formula (Kennedy et al., 2010):

$$\delta_{sample} = 1000[(R_{sample}/R_{standard}) - 1],$$

where R_{sample} is the ratio between the heavy and the light stable isotope in the sample ($R = {}^{13}C/{}^{12}C$), and R_{standard} is the standard ratio of the same quantities, where standard means Vienna Pee-dee Belemnite (VPDB).

The $\Delta\delta^{13}C_{\text{seagrass-sediment}}$ dataset was initially divided into climatic groups (Temperate or Tropical seagrass habitat); these were further classified into several temperate (North Pacific, North Atlantic, Southern Oceans and Mediterranean) and tropical bioregions (Atlantic and Indo-Pacific) (Short et al., 2007). Moreover, the dataset was grouped by morphological seagrass species size, which aligns with species traits for below-ground biomass allocation (Kilminster et al., 2015; Collier et al.,

2021) (Fig. 2.). Although it is important to note that within localised areas of the seagrass bioregions certain seagrass size classes are considered dominant (Table 1).

2.2. Data Analysis of the $\delta^{13}C$ dataset

The median global $\Delta\delta^{13}C_{\text{seagrass-sediment}}$ compiled in this study was compared to the median global $\Delta\delta^{13}C_{\text{seagrass-sediment}}$ of Kennedy et al. (2010) by Wilcoxon rank sum test with continuity correction. The Shapiro-Wilk test was used to test the normality of the data. Whenever two groups were compared, a Kruskal Wallis test was applied (when normality assumptions were not satisfied) with pairwise Mann-Whitney tests as the appropriate post hoc test. The P values of the Mann-Whitney tests were adjusted by the Bonferroni method to reduce the false positive rate associated with multiple testing (Jafari and Ansari-Pour, 2018). Climatic seagrass bioregion (Temperate: North Pacific, North Atlantic, Southern Oceans and Mediterranean; Tropical: Atlantic and Indo-Pacific) and seagrass size classifications (large, mid-range, small and mixed) were considered as factors in the analysis of $\Delta\delta^{13}C_{\text{seagrass-sediment}}$. Given the small sample size when considering both factors' (<3), the effect of climatic bioregions and size on $\Delta\delta^{13}C_{\text{seagrass-sediment}}$ were initially assessed separately.

Data quality control was performed with the R package *skimr*. The data were checked for inconsistencies (e.g., data with different units or values that are defiinite outliers), and duplicates were removed. Rows with missing data were removed when full details were necessary to analyse the dataset. This implied a reduction to 414 instances from the initial 731. Principal Component Analysis (PCA), Multiple factor analysis (MFDA) and analysis of variance (ANOVA) were performed on the reduced dataset. Multiple pairwise-comparison between the means of different groups were performed with the Tuckey HSD.

3. Results

The $\delta^{13}C$ values of seagrass sediment ranged globally from −28.14 ‰ to −6.38 ‰ (Table 2), whilst the global $\delta^{13}C$ values of seagrass leaves ranged from −19.65 ‰ to −3.85 ‰. Shapiro-Wilk tests confirmed that the overall $\delta^{13}C$ seagrass sediment ($W = 0.99554$, $P > 0.05$) and $\Delta\delta^{13}C_{\text{seagrass-sediment}}$ ($W = 0.99539$, $P > 0.05$) data followed a normal distribution, while that was not the case for the $\delta^{13}C$ seagrass leaves data ($W = 0.96191$, $P < 0.05$). Therefore, it was decided to use the median as the best measure of central tendency across the global dataset (Table 2). On average, the $\delta^{13}C$ values of seagrass leaves were enriched with ^{13}C (Median $\tilde{x} = -9.88$ ‰) compared to those of seagrass sediment (Median $\tilde{x} = -17.20$ ‰). The difference between $\delta^{13}C$ values from seagrass leaf tissue and $\delta^{13}C$ values from seagrass sediment, in those samples where the two types of values were paired, produced a positive global average with a $\Delta\delta^{13}C_{\text{seagrass-sediment}}$ median of 7.36 ‰ (Table 2). The global average in this study (Median $\tilde{x} = 7.36$ ‰) is significantly higher ($W = 43071$, $P < 0.001$) than the global median (Median $\tilde{x} = 6.3$ ‰) reported in the original Kennedy et al. (2010) dataset. The compiled dataset contained analyses from the coastlines of the North-East Pacific, Sub-arctic, Red Sea, Persian Gulf, Bay of Bengal and South Atlantic compared to historic global datasets (Fig. 3A) (Kennedy et al., 2010; Bouillon and Boschker, 2006). However, very limited data were found for the coastlines along the South Atlantic, South-East Pacific and western region of the Indian Ocean.

3.1. Seagrass bioregions

Shapiro-Wilk tests confirmed that when grouped by climate, the temperate ($W = 0.98373$, $P < 0.05$) and tropical ($W = 0.97052$, $P < 0.05$) $\Delta\delta^{13}C_{\text{seagrass-sediment}}$ data were not normally distributed. Overall, there was a significant difference in $\Delta\delta^{13}C_{\text{seagrass-sediment}}$ between temperate and tropical bioregions ($\chi^2_{(1)} = 36.747$, $P < 0.01$), with a higher $\Delta\delta^{13}C_{\text{seagrass-sediment}}$ in temperate seagrass meadows (Median $\tilde{x} = 8.3$ ‰, Range = −5.4 to 19.8 ‰) compared to the tropical ones (Median $\tilde{x} = 6.11$ ‰, Range = −1.0 to 18.8 ‰) (Table 2).

This identifies that a significant difference in the $\Delta\delta^{13}C_{\text{seagrass-sediment}}$ was observed between seagrass bioregions ($\chi^2_{(5)} = 72.752$, $P < 0.01$). The Shapiro-Wilk test confirmed that several groupings did not follow a normal distribution when $\Delta\delta^{13}C_{\text{seagrass-sediment}}$ values were grouped by seagrass bioregion (Supp. 2. Table 1). Pairwise comparisons showed that a significant difference in $\Delta\delta^{13}C_{\text{seagrass-sediment}}$ was only observed between some of the temperate and tropical bioregions (Supp. 2. Table 2). The temperate North Atlantic and North Pacific bioregions though not significantly different from each other, show significantly higher values ($\Delta\delta^{13}C_{\text{seagrass-sediment}}$ median $\tilde{x} = 9.06$ ‰ and median $\tilde{x} = 8.54$ ‰) than all other bioregions (Fig. 3B). Some temperate bioregions $\Delta\delta^{13}C_{\text{seagrass-sediment}}$ were comparable to tropical regions, with the $\Delta\delta^{13}C_{\text{seagrass-sediment}}$ in the Mediterranean (Median $\tilde{x} = 7.21$ ‰) not significantly different from the tropical Indo-Pacific (Median $\tilde{x} = 6.48$ ‰). The bioregions with the lowest $\Delta\delta^{13}C_{\text{seagrass-sediment}}$ were the temperate Southern Oceans (Median $\tilde{x} = 4.20$ ‰) and the tropical Atlantic (Median $\tilde{x} = 5.60$ ‰), which were not significantly different from each other (Fig. 3B).

3.2. Seagrass size classifications

Seagrass habitats with the highest difference between the $\delta^{13}C$ value

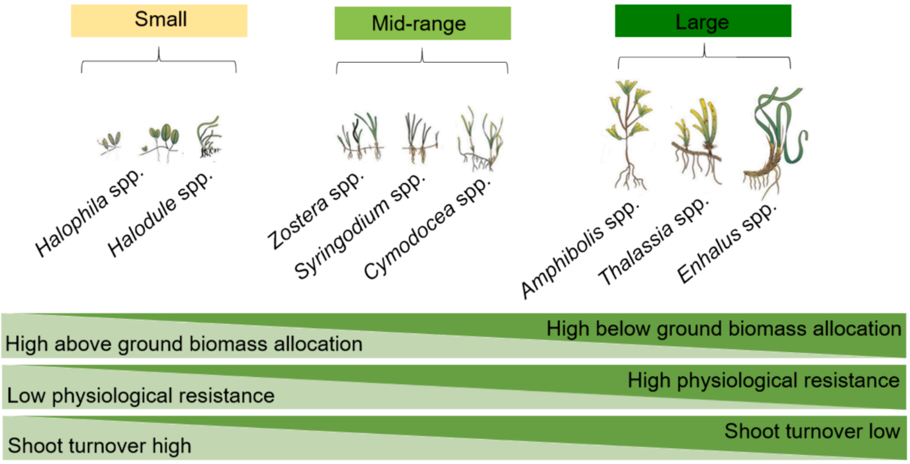


Fig. 2. Classification of seagrass by their morphological size (Figure adapted from Kilminster et al., 2015; Collier et al., 2021).

Table 1
The seagrass size classes and representative genera that occur within specific seagrass bioregions, (modified from; Short et al., 2007). Those in grey are considered the typical dominant genera within localised areas of that bioregion.

Seagrass size classes with representative genera		Seagrass Bioregions					
		Temperate				Tropical	
		North Atlantic	North Pacific	Southern Oceans	Mediterranean	Atlantic	Indo-Pacific
Small	*Halodule* spp.	X	X	X	X	**X**	**X**
	Halophila spp.		X	X	X	X	**X**
Mid-range	*Cymodocea* spp.	X			X		**X**
	Phyllospadix spp.		X				
	Ruppia spp.	X	X	X	X	X	X
	Syringodium spp.			X		**X**	X
	Zostera spp.	**X**	**X**	**X**	X		X
Large	*Amphibolis* spp..			**X**			
	Enhalus spp.						X
	Posidonia spp.			**X**	**X**		
	Thalassia spp.					**X**	**X**
	Thalassodendron spp.			X			**X**

Table 2
Average $\delta^{13}C$ seagrass leaves, $\delta^{13}C$ seagrass sediment and $\Delta\delta^{13}C_{seagrass\text{-}sediment}$ for seagrass habitat across the temperate and tropical seagrass bioregions further grouped according to seagrass size and as such their relative below-ground biomass allocation. The average presented is the median alongside the range. Replication for each classification in italics.

Seagrass bioregion	**Seagrass size**	**$\delta^{13}C_{seagrass}$ (‰)**	**Range**	**n**	**$\delta^{13}C_{sediment}$ (‰)**	**Range**	**n**	**$\Delta\delta^{13}C_{seagrass\text{-}sediment}$ (‰)**	**Range**	**n**
North Atlantic	Mid-range	-9.82	-15.0 to -5.4	*184*	-18.36	-28.1 to -6.4	*171*	*9.06*	-2.6 to 19.8	*165*
	Mixed				-19.50	-19.7 to -19.3	*2*			
	Subtotal	-9.82	-15.0 to -5.4	*184*	-18.45	-28.1 to -6.4	*173*	*9.06*	-2.6 to 19.8	*165*
North Pacific	Mid-range	-9.84	-11.8 to -7.2	*24*	-18.62	-27.5 to -15.2	*29*	8.54	6.1 to 16.3	*28*
Southern Oceans	Large	-10.49	-12.7 to -9.5	*8*	-13.98	-23.3 to -7.3	*45*	4.10	-5.4 to 11.0	*11*
	Mid-range	-10.80	-19.1 to -10.5	*13*	-19.60	-24.6 to -14.6	*15*	5.13	0.3 to 11.4	*13*
	Small	-13.20		*1*	-17.62	-18.5 to -15.6	*5*	2.35		*1*
	Subtotal	-10.78	-19.1 to -9.5	*22*	-14.80	-24.6 to -7.3	*65*	4.20	-5.4 to 11.4	*25*
Mediterranean	Large	-12.4	-15.8 to -8.2	*36*	-18.08	-24.6 to -11.8	*42*	5.55	0.5 to 9.9	*34*
	Mid-range	-9.30	-11.6 to -5.7	*39*	-18.00	-23.9 to -12.6	*37*	7.80	4.3 to 16.9	*37*
	Small	-8.40	-9.3 to -7.8	*3*	-19.50	-19.6 to -18.1	*3*	11.20	8.8 to 11.7	*3*
	Subtotal	-11.59	-15.8 to -5.7	*78*	-18.10	-24.6 to -11.8	*82*	7.21	0.5 to 16.9	*74*
Temperate bioregions		**-10.20**	**-19.1 to -5.4**	***308***	**-18.00**	**-28.1 to -6.4**	***349***	**8.30**	**-5.4 to 19.8**	***292***
Atlantic	Large	-8.65	-11.6 to -6.3	*45*	-13.01	-17.5 to -9.8	*44*	4.12	-1.0 to 11.2	*44*
	Mid-range	-7.10	-9.4 to -4.8	*3*	-17.50	-17.7 to -17.2	*3*	10.1	8.3 to 12.7	*3*
	Small	-9.90	-10.2 to -8.7	*10*	-15.50	-20.8 to -14.4	*9*	5.60	4.5 to 12.1	*9*
	Mixed	-8.99	-15.4 to -6.5	*30*	-15.59	-21.2 to -12.0	*29*	6.69	2.9 to 11.8	*29**
	Subtotal	-8.99	-15.4 to -4.8	*88*	-14.53	-21.2 to -9.8	*85*	5.60	-1.0 to 12.7	*85*
Indo-Pacific	Large	-9.83	-19.7 to -5.9	*60*	-16.30	-26.6 to -9.2	*54*	6.65	2.3 to 18.6	*48*
	Mid-range	-10.38	-18.8 to -3.6	*24*	-20.85	-26.4 to -18.5	*27*	12.00	3.9 to 18.8	*4*
	Small	-8.00	-18.7 to -7.1	*32*	-16.40	-25.9 to -9.0	*63*	7.22	3.9 to 13.4	*29*
	Mixed	-9.52	-9.9 to -5.4	*11*	-13.99	-21.7 to -9.9	*50*	4.55	2.4 to 12.6	*42***
	Subtotal	-9.74	-19.7 to -3.6	*127*	-16.56	-26.6 – 9.0	*194*	6.48	2.3 to 18.8	*123*
Tropical bioregions		**-9.40**	**-19.7 to -3.6**	***215***	**-15.59**	**-26.6 to -9.0**	***279***	**6.11**	**-1.0 to 18.8**	***208***
Global		**-9.88**	**-19.7 to -3.6**	***523***	**-17.20**	**-28.1 to -6.4**	***628***	**7.36**	**-5.4 to 19.8**	***500***

*Mixed community containing large seagrass species n = 27; mixed community with only small or mid-range sized seagrass n = 2.
**Mixed community containing large seagrass species n = 38; mixed community with only small or mid-range sized seagrass n = 4.

of seagrass leaves and sediment were meadows dominated by mid-range seagrass ($\Delta\delta^{13}C_{seagrass\text{-}sediment}$ median $\tilde{x} = 8.73$ ‰) (Fig. 4). Shapiro-Wilk test confirmed that when $\Delta\delta^{13}C_{seagrass\text{-}sediment}$ was grouped by seagrass size, several groupings did not conform to a normal distribution (Supp. 2. Table 3).

Seagrass size was therefore a significant factor for determining the $\Delta\delta^{13}C_{seagrass\text{-}sediment}$ in seagrass meadows ($\chi^2_{(3)} = 79.355$, $P < 0.01$). Pairwise Mann-Whitney tests confirmed that meadows dominated by seagrass from the mid-range size category (e.g., *Zostera* spp., *Cymodocea* spp., *Ruppia* spp. and *Syringodium* spp.) had significantly higher $\Delta\delta^{13}C_{seagrass\text{-}sediment}$ than meadows formed of small, large or mixed seagrass species. However, there is a high variation across the $\Delta\delta^{13}C_{seagrass\text{-}sediment}$ values of mid-range-sized seagrass meadows. The average $\Delta^{13}C_{seagrass\text{-}sediment}$ in meadows dominated by small seagrass species (Median $\tilde{x} = 7.15$ ‰) was significantly lower than the value in mid-range meadows, and significantly higher than the $\Delta^{13}C_{seagrass\text{-}}$

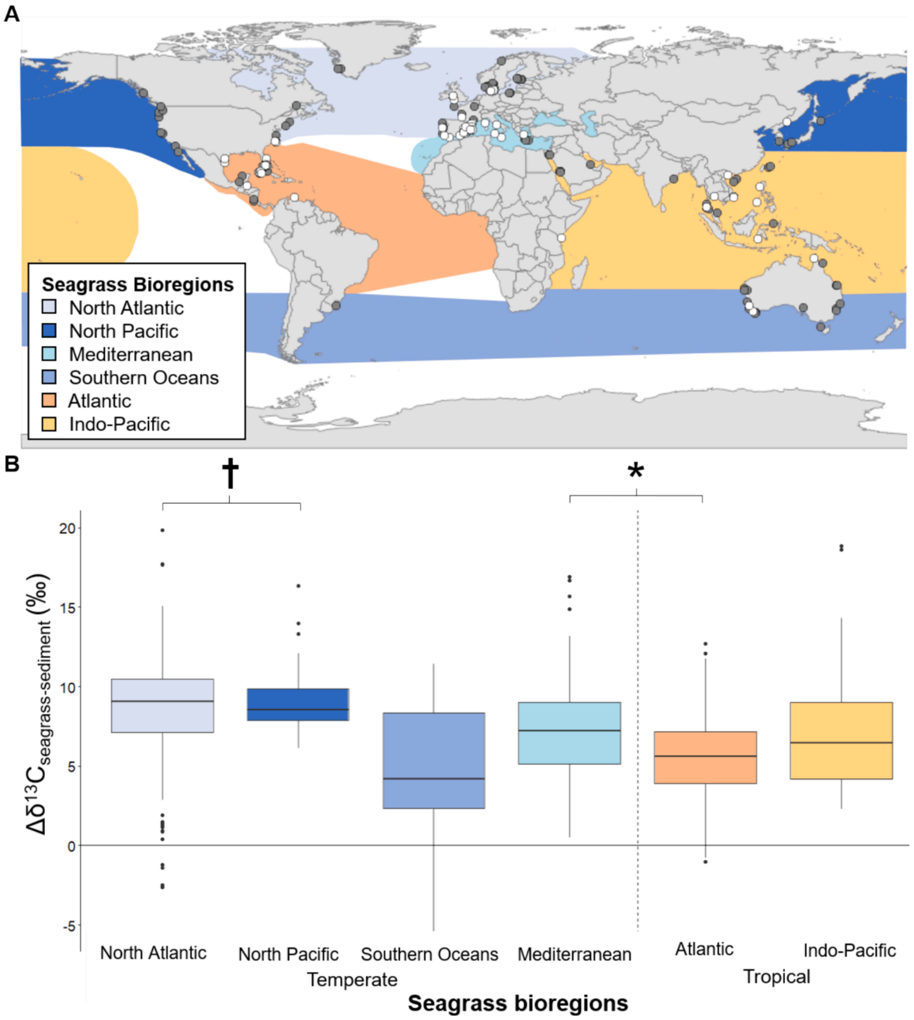


Fig. 3. A Distribution of seagrass meadows where $\delta^{13}C$ sediment has been reported in this study, across global seagrass bioregions (Short et al., 2007). White points are from Kennedy et al. (2010), and grey points are those added by this study (Supplementary 1). World countries base map ©Esri. B The $\Delta\delta^{13}C_{seagrass\text{-}sediment}$ for seagrass habitat across temperate (North Atlantic, North Pacific, Southern Oceans and Mediterranean) and tropical (Atlantic and Indo-Pacific) seagrass bioregions. † = Significantly different from all other regions $P < 0.05$. Other significant pairwise differences * = $P < 0.05$.

$_{sediment}$ measured in meadows dominated by large species (Fig. 4, Supp. 2. Table 4). Therefore, this suggests that within meadows that contain only one seagrass size class, the $\Delta^{13}C_{seagrass\text{-}sediment}$ decreases by seagrass size ($\Delta^{13}C_{seagrass\text{-}sediment}$; Mid-range > Small > Large seagrass species). Seagrass habitats with the lowest $\Delta^{13}C_{seagrass\text{-}sediment}$, were monospecific meadows of large seagrass species (Median $\tilde{x}$ = 5.24 ‰) or mixed meadows (Median $\tilde{x}$ = 5.63 ‰). However, within this dataset the seagrass composition of mixed meadows generally included large seagrass species (Table 2). Thus, it may be concluded that seagrass habitats with the lowest overall $\Delta^{13}C_{seagrass\text{-}sediment}$ are typically monospecific or mixed meadows that house large-bodied seagrass with high below-ground biomass such as *Amphibolis* spp., *Enhalus acoroides.*, *Posidonia* spp., *Thalassia* spp and *Thalassodendron* spp.

3.3. Principle component analysis

All analyses below were performed on 414 samples. Before performing the PCA, the correlation analysis was run between the five variables: latitude, longitude, seagrass $\delta^{13}C$, sediment $\delta^{13}C$ and sediment depth. The analysis showed a significant positive correlation between seagrass $\delta^{13}C$ and sediment $\delta^{13}C$ and a lower significant positive correlation between the sediment depth and both seagrass $\delta^{13}C$ and sediment $\delta^{13}C$. A negative significant correlation was observed between the longitude and all other variables (Fig. 5A). The PCA analysis showed that latitude and seagrass $\delta^{13}C$ explain most of the variation in medium and temperate North Atlantic species (Fig. 5B & C). Sediment $\delta^{13}C$ explains most of the variation in tropical Atlantic species independently of their size, and longitude and sediment depth can explain most of the variation in Tropical Indo-Pacific species.

3.4. Multi-factor analysis of mixed data

Given the structure of the available information, that is, each species is described by a set of quantitative and qualitative variables structured in groups, multi-factor analysis of mixed data in which the categorical variables were considered together with the numerical ones was performed. The representation of individuals (Fig. 6A & B) clearly confirms a separation between seagrass bioregions and different leaf-size populations. The first axis opposes north temperate regions to tropical and south temperate regions, with the Mediterranean region separating the two areas. The first axis also opposes medium leaf-size individuals to all others. The second axis differs tropical Atlantic individuals from all others.

The representation of variables shows that the Seagrass bioregion is the most contributing variable to both factors (Dim1 and Dim2) (Supp. 2. Fig. 3); latitude is closely linked to Dim1, while longitude, sediment

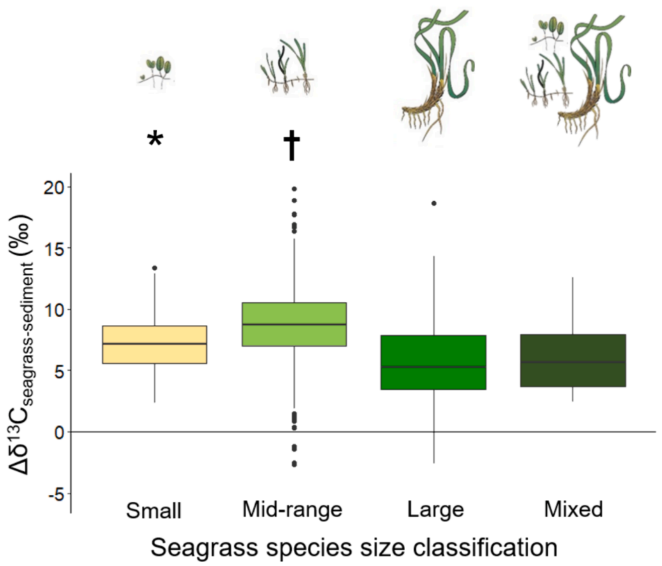


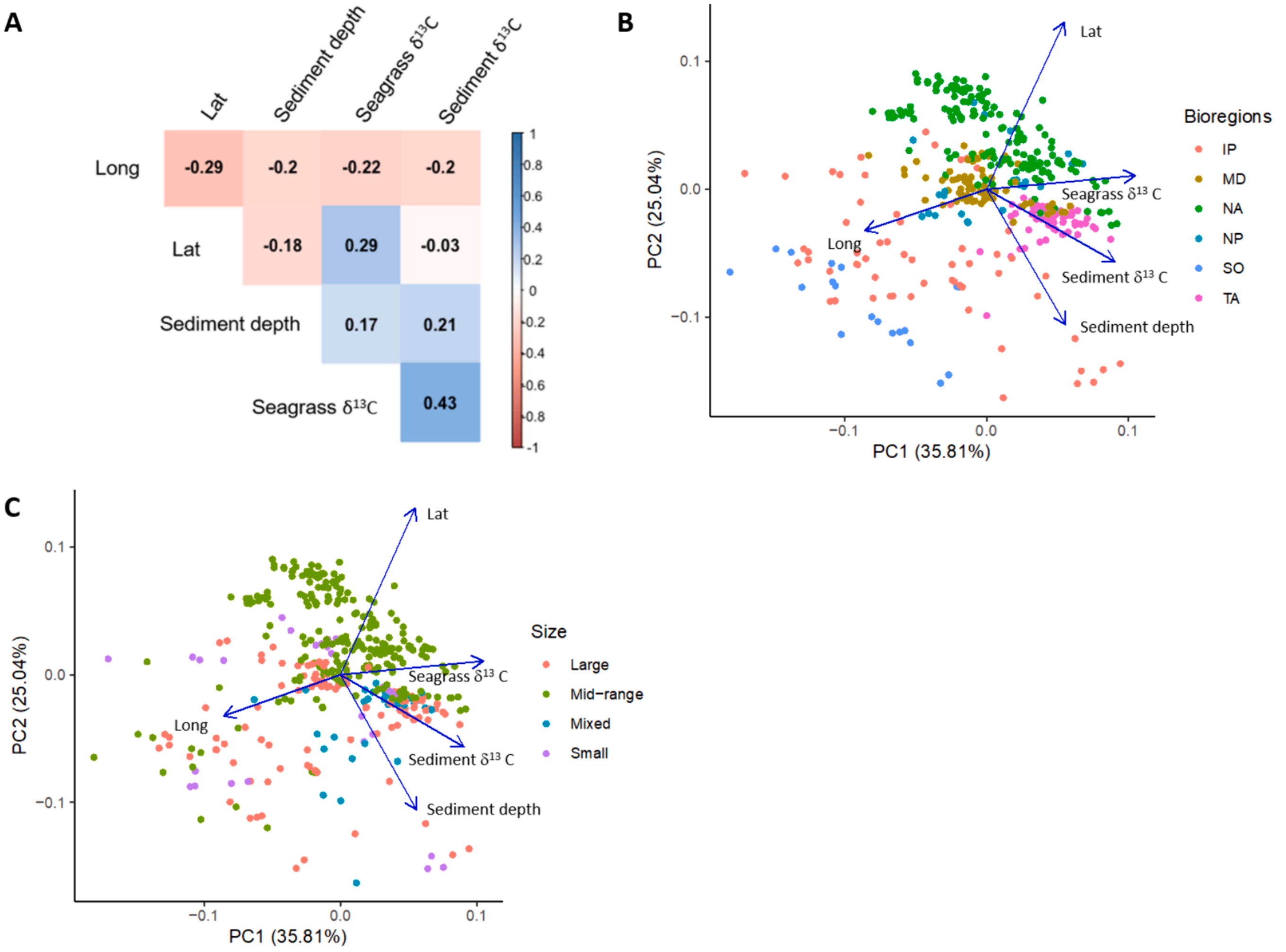
Fig. 4. $\Delta\delta^{13}C_{seagrass\text{-}sediment}$ grouped according to seagrass species size classification. † = Significantly different from all other size classifications $P < 0.05$. * = Significantly different from groups of only one seagrass size class $P < 0.05$. (Seagrass icons from; Kilminster et al., 2015; Collier et al., 2021).

and seagrass $\delta^{13}C$, and sediment depth are linked to Dim2. The percentage of contribution of each variable (numerical and categorical) to the factors is shown in the bar plots (Supp. 2. Fig. 3). The correlation circle specifies the sign of the correlation between variables and dimensions (Fig. 6C). Seagrass $\delta^{13}C$ and latitude correlate negatively with Dim1 and positively with Dim 2, sediment $\delta^{13}C$ and sediment depth correlate positively with both factors and finally, longitude correlates negatively with Dim1 and positively with Dim2.

The analysis of variance was run with the model:

$$\Delta\delta^{13}C_{seagrass-sediment} = Bioregion + Size + Long + Lat + \varepsilon$$

The result strongly agreed with the previous analysis, indicating a significant difference ($p < 0.001$) in the difference between sediment and seagrass $\delta^{13}C$ between bioregions and leaf sizes. A Tukey comparison showed that the most significant difference could be observed between Medium vs Large leaf-size seagrass ($p < 0.001$; Supp. 2. Table 5) and Small vs Large leaf-size seagrass ($p < 0.05$). In terms of bioregions, significant differences ($p < 0.001$) could be observed between Temperate Southern Oceans and Temperate North Atlantic, or Temperate North Pacific; and between Tropical Atlantic and Temperate North Atlantic, or Temperate North Pacific, or Tropical Indo-Pacific.



	Lat	Sediment depth	Seagrass δ¹³C	Sediment δ¹³C
Long	-0.29	-0.2	-0.22	-0.2
Lat		-0.18	0.29	-0.03
Sediment depth			0.17	0.21
Seagrass δ¹³C				0.43

Fig. 5. **(A)** Correlation analysis between the variable's latitude, longitude, seagrass and sediment $\delta^{13}C$ and sediment depth. Principle component analysis with data visualisation focused on distinguishing **(B)** seagrass bioregion (MD=Mediterranean; NA=North Atlantic; NP=North Pacific; SO=Southern Oceans; TA=Tropical Atlantic; IP=Indo- Pacific) and **(C)** seagrass species size classification.

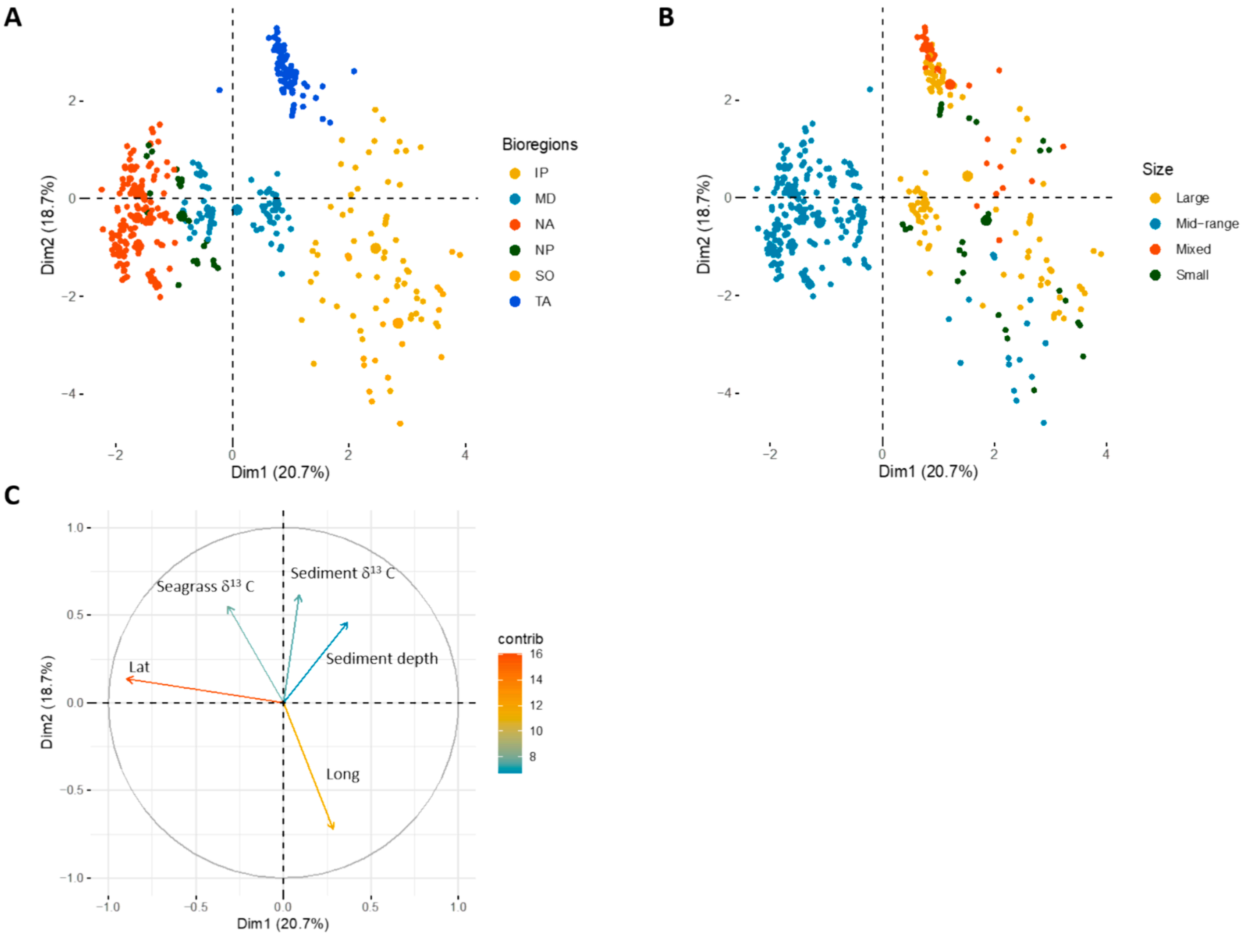


Fig. 6. The individuals presented on a mixed FAMD factor map for **(A)** seagrass bioregions and **(B)** seagrass species size classification **(C)** Correlation between variables and dimensions.

3.5. *Geomorphological trends –Cluster analysis*

KMeans clustering of the seagrass and sediment δ^{13}C and sediment depth data suggested that three main clusters can be identified (Fig. 7A). When reported on the world Global Coastal Typology map (https://doi.org/10.1007/s12237-011-9381-y) it could be observed that the first (red) and the third (green) clusters mostly fall onto small deltas and tidal systems coastlines respectively, while the second cluster (black) mostly corresponds to lagoons, arheic and fjords coastlines (Fig. 7B). It is clear from this analysis that more factors need to be considered in order to

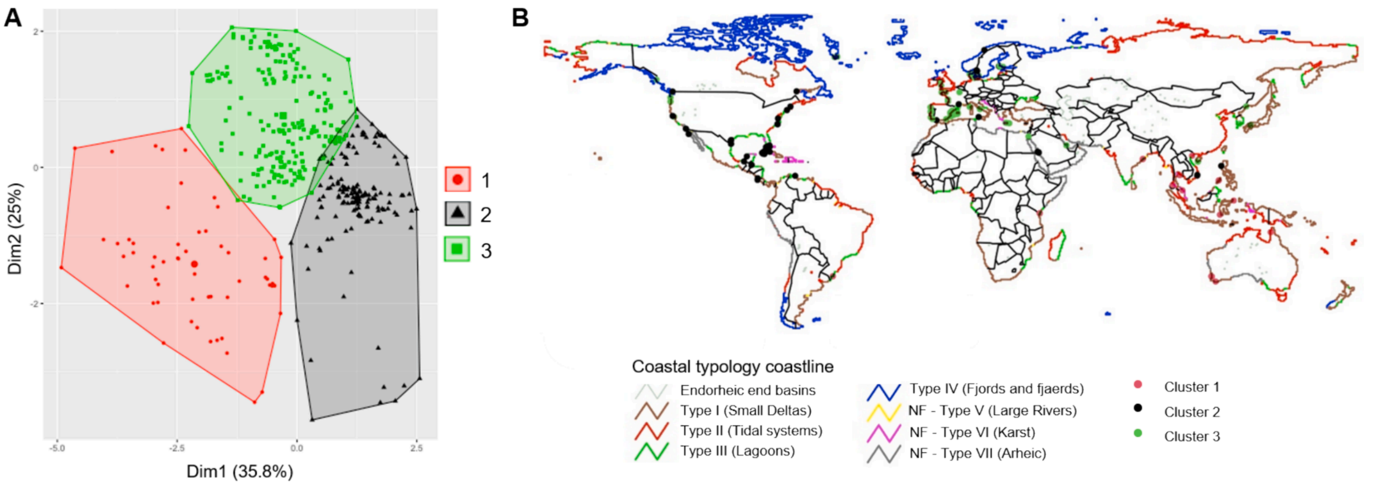


Fig. 7. (A) Cluster plot displaying KMeans clustering of the seagrass and sediment δ^{13}C and sediment depth data **(B)** The three distinct clusters (1 = Red, 2 = Black, 3 = Green). Reported on the world Global Coastal Typology map (https://doi.org/10.1007/s12237-011-9381-y). Cluster 1 and 3 mostly fall onto small deltas and tidal systems coastlines, Cluster 2 corresponds to lagoons, arheic and fjords coastlines. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

obtain a better distinction among the different species. Also, despite considering latitude and longitude in the analysis, these do not seem to have a strong effect on the characterization of the three clusters.

4. Discussion

Blue carbon accreditation typically credits the sediment organic carbon originating or forming in the project area, namely the autochthonous organic carbon (e.g., from vegetation) (Emmer et al., 2015), which is the carbon formed by the target vegetative blue carbon habitat, in this instance seagrass derived carbon. However as demonstrated in this study the presence of allochthonous carbon within seagrass sediment is ubiquitous. The proportion of allochthonous carbon present in seagrass sediment alongside the organic carbon accumulation rate, determines the suitability for a meadow to be managed for carbon benefits. Therefore, the evidence used to generate a percentage of allochthonous sediment organic carbon value to be deducted for carbon accreditation calculations needs to be carefully contemplated. This research indicates that when choosing a percentage of allochthonous sediment organic carbon from existing literature, it is important to evaluate whether the δ^{13}C values used in calculating the proxy accurately reflect the characteristics of the restoration site. Specifically, it is crucial to assess if the isotopic carbon values originate from a site with comparable geomorphology, seagrass plant characteristics (such as size or species), and location, and in certain instances, to what extent they align with the bioregional scale of the restoration area. The consequence of applying inappropriate allochthonous carbon proxies could cause carbon offsets to be overestimated. The sale of carbon offsets for a project that has overestimated its capacity to remove GHG versus its true-realised capacity will result in carbon emissions, i.e., the carbon has been theoretically offset by being sold as a credit and retired, but then the project does not manage to achieve the carbon offset to balance the credits already sold.

4.1. Factors affecting photosynthetic fractionation of seagrass leaves

During photosynthesis and the fixation of CO_2, discrimination between the lighter and heavier carbon isotopes occurs causing isotopic fractionation, such that plants become depleted in the heavier carbon isotope ^{13}C. Therefore, the environmental parameters which influence photosynthesis, have the potential to influence isotopic fractionation and the δ^{13}C values of seagrass tissues. Decreased irradiance leads to increased isotopic discrimination, such that in shaded seagrass the δ^{13}C values of seagrass leaves are isotopically lighter (Durako and Hall, 1992). This means differences in fractionation can occur locally within a seagrass meadow in response to these environmental conditions, associated with reduced irradiance with increased depth (−11 ‰ at 5 m depth, −16.4 ‰ at 35 m depth) (Cooper and DeNiro, 1989). This would also suggest that seawater turbidity, which alters irradiance penetration, could locally influence levels of photosynthetic activity and as such fractionation. This could be a result of the general catchment dynamics (e.g., estuarine flow or sediment loading) or due to pulse events (e.g., storm events, tides and dredging) (Erftemeijer and Robin Lewis, 2006; Longstaff and Dennison, 1999). It could also suggest that fractionation may changes seasonally in seagrass, due to seasonal senescence and decreased plant density over winter, in fact seasonal changes in seagrass leaf fractionation has been documented (Papadimitriou et al., 2006). Ultimately though the change in fractionation associated with irradiance is related to reduced carbon demand at lower irradiances (Lepoint et al., 2003) and carbon-limited photosynthesis in periods of light saturation, which provides a mechanistic link between irradiance, photosynthesis and isotope fractionation (Hu et al., 2012).

Our analysis revealed that latitude and seagrass δ^{13}C explain most of the variation in medium and temperate North Atlantic species. This implies that the changes in environmental light conditions (e.g., decreased light intensity, decreased photoperiod) associated with increased latitude may partly explain the seagrass tissue fractionation pattern within this bioregion. Especially so given other factors such as seagrass species, and the associated seagrass traits, are more negligible within the North Atlantic bioregion which has the lowest seagrass species diversity globally and subsequently reduced seagrass size trait diversity (Short et al., 2007, Table 1). In tropical areas where light is saturated changes in latitude would not explain irradiance driven isotopic fractionation, rather other factors such as sediment δ^{13}C, longitude and sediment depth become increasingly important as seen in our dataset. Hemminga and Mateo (1996) highlighted that the effect of temperature on CO_2 availability in seawater might also offer a plausible explanation for latitudinal trends in seagrass δ^{13}C. Each of these parameters, i.e., temperature, irradiance and photoperiod, change with latitude. Thus, it may be difficult to disentangle these factors, as they likely interact while driving photosynthesis and isotopic fractionation. However, Hemminga and Mateo (1996) highlight that the mechanism for latitudinal change in the North Atlantic bioregion seagrass δ^{13}C is related to latitudinal changes in carbon availability, the subsequent carbon fixation and relative discrimination of ^{12}C and ^{13}C. The North Atlantic bioregion does not have deep coastal seagrass meadows associated with other temperate bioregions (NP, MD and SO) or the back-reef seagrass meadows associated with tropical regions (TA, IP) (Short et al., 2007). Therefore, the North Atlantic bioregion has a reduced variety of coastal settings in which seagrass is found, which makes the seagrass more uniform at the bioregional scale. Akin to the lack in species diversity within the bioregion, the reduced coastal settings in which seagrass is found in this region, likely enhances the clarity of latitudinal trends in seagrass δ^{13}C, as demonstrated in this study. The similarity in species composition and coastal setting experienced across the North Atlantic bioregion result in seagrass δ^{13}C which are distinct at a bioregional scale, particularly in comparison to other bioregions, which have to contend with additional factors such as varied species composition, size traits and coastal settings. Therefore, restoration projects in the temperate Northern Atlantic bioregion must use percentage of allochthonous sediment organic carbon proxies calculated from seagrass δ^{13}C from within the bioregion to represent the project site. However, North Atlantic bioregion values can perhaps be utilised more coarsely with higher confidence than for other bioregions that demonstrate wider variability and need other factors to be considered such as species composition, size traits and coastal settings.

4.2. Seagrass size traits and their biogeographic implications

The fact that the traits of the seagrass species inhabiting a meadow (e.g., seagrass species size classification) influences the sediment and seagrass δ^{13}C has regional consequences when considering the geographical distributions of certain seagrass size classes (Table 1). Our analysis suggested the two north temperate regions (North Atlantic and North Pacific) to be most distinct from the south temperate regions, with the Mediterranean region separating the two areas. The North Atlantic and North Pacific bioregions were represented only by mid-range seagrass species. The temperate North Atlantic and North Pacific dataset also did not contain any monospecific meadows of small or large species, or any mixed meadows containing large seagrass species. Temperate seagrass meadows in the Northern hemisphere are limited in this respect, the only and most notably large seagrass species being *Posidonia oceanica*, which is found in the Mediterranean seagrass bioregion (Table 1). In contrast, the temperate Southern Oceans bioregion have various large seagrass species: *Amphibolis antarctica, A. griffithii, Posidonia angustifolia, P. australis, P. ostenfeldii complex, P. coriacea, P. denhartogii, P. kirkmanii, P. robertsoniae, P. sinuosa, Thalassodendron pachyrhizum* and *T. ciliatum* (Short et al., 2007). Most of these large species in the Southern Oceans proliferate around the coasts of Australia and are typically considered the dominant species there. Regarding the other temperate southern coasts, South Africa has only one large species (*T. ciliatum)* with mid-range *Zostera* spp. considered dominant; while the

South American (Chile and Argentina) and New Zealand coasts have no large species and are dominated by mid-range *Zostera* spp. Therein, temperate Australian seagrass meadows are relatively unique in that they host multiple large seagrass species. The Southern Oceans data analysed in this study are mostly based on $\delta^{13}C$ seagrass leaves and sediment values from Australian coasts, which biases the dataset. Therefore, many other temperate seagrass meadows such as *Zostera mulleri* seagrass in New Zealand (Bulmer et al., 2020) may be akin to seagrass meadows dominated by mid-sized seagrass in the Northern hemisphere. Our study suggests that the temperate Southern Ocean seagrass meadows, which host multiple large seagrass species, and the Mediterranean, which hosts the large seagrass species *P. oceanic* are more distinct from the North Atlantic and North Pacific bioregions. This difference could be related to the bioregions increased diversity of species with different size traits or specifically the presence of localities where large sized seagrasses are dominant (Table 1).

4.3. The complexity of multi-species meadows for allochthonous carbon proxies

In multi-species seagrass communities, several canopies may exist creating a vertically and horizontally heterogeneous landscape; some Indo-Pacific seagrass beds, for example, may have a main canopy formed by *T. hemprichii,* emergent patches of *E. acoroides* (~50 cm), mid canopy of *Cymodocea* spp. and *Syringodium* spp. (~15–30 cm), lower canopies of *Halodule* spp. (~10 cm) and *Halophila* spp. (~5 cm) (Vermaat et al., 1995). As such there may be a difference in fractionation between the leaves in different layers of the canopy due to their relative placement and rate of CO_2 uptake for photosynthesis, related to environmental variables such as light penetration (Durako and Hall, 1992), such as seen in terrestrial closed canopy forests associated with height, light availability and tree species, resulting in low canopy leaves depleted in ^{13}C (Lowry et al., 2021). However, isotope fractionation in terrestrial plants is also linked to their carbon concentrating mechanism (e.g., C_3, C_4 and CAM) for acquiring carbon from the atmosphere in the form of CO_2 from the air, which for C_3 and C_4 plants usually results in two non-overlapping ranges (O'Leary, 1988). In aquatic environments formed of more viscose water opposed to air, slower diffusion of inorganic carbon through thick boundary layers results in greater carbon limitation relative to terrestrial counterparts (Touchette and Burkholder, 2000). As a result, seagrass $\delta^{13}C$ values fall within the range of C_4 plants despite the belief that seagrasses in general have a C_3 type of photosynthetic metabolism (Hemminga and Mateo, 1996), related to carbon limitation from existing in aquatic environment, namely the medium of water. Seagrass have shown species specific differences in structure and diffusive boundary layers (Borum et al., 2016). To complicate this further, there are discrepancies regarding whether seagrass species are C_3, C_4, or are C_3-C_4 intermediates (Touchette and Burkholder, 2000). In addition to this, debate still remains about whether specific seagrass species also utilise, and to what extent, HCO_3^- in addition to dissolved CO_2 (Invers et al., 2001). Ultimately this emphasises that species-specific traits relating to the leaf boundary layers and carbon metabolism pathways would lead to varied isotopic fractionation between species, which may also vary depending on environmental influences on isotopic fractionation.

In both monospecific, but particularly in mixed species meadows there are multiple seagrass derived sources to consider each with potentially different seagrass $\delta^{13}C$ values due to varying isotopic fractionation. Whilst adding more sources into mixing models to determine the percentage of allochthonous sediment organic carbon seems to better mimic complex real situations, adding more sources also increases internal errors and uncertainty (Fry, 2013). Often the stable isotope mixing models applied in mixed species meadows pool the isotopic values of multiple species or utilise only the most dominant species (Kennedy et al., 2004; Wahyudi and Afdal, 2019). Therefore, when selecting proxies, and especially for mixed species meadows, an additional selection criterion would be to assess the stable isotope mixing model decision process for that literature-based value (e.g., what seagrass species are utilised and/or pooled to represent the seagrass source) to ensure any percentage value of allochthonous carbon from these meadows remains representative for the project context. An assessment of the stable isotope mixing model decision process for a literature-based value would complement the informed criterion this *meta*-analysis provides for the selection of $\delta^{13}C$ values according to influencing seagrass traits, biogeography and geomorphological factors.

4.4. Within plant $\delta^{13}C$ variation

This *meta*-analysis focuses on seagrass leaf and sediment $\delta^{13}C$ values, but isotopic difference occurs between pant tissues (e.g. leaves and roots) and plant compounds (e.g. lignin and cellulose) (Hobbie and Werner, 2003). As such it has been suggested post-photosynthetic discriminations occur, leading to isotopic difference between autotrophic and heterotrophic tissues/organs within the same plant. Further research is needed to fully understand the processes leading to post-photosynthetic discriminations such as root respiration; differences in root fractionation processes in different soils/substrate or in differing pH availability. (Ghashghaie and Badeck, 2013). Seagrass leaf and root $\delta^{13}C$ values have been shown to differ with root tissues more ^{13}C-depleted (Cooper, 1989). However, this is not always the case, as *P. oceanica* roots and shoots have shown similar isotopic values at impacted sites versus ^{13}C-depleted roots at pristine sites (Holmer et al., 2004), suggesting the processes determining isotope discrimination and fractionation between plant organs is not a rigid process. This adds further complexity and variation into the utilisation and interpretation of $\delta^{13}C$ values. There may be instances where the utilisation of root $\delta^{13}C$ values is integral such as in large seagrasses with high below-ground mass allocation, as the organic carbon deriving from this seagrass tissue may be more predominantly retained within the sediment. However, large seagrass species do not always have ^{13}C-depleted roots (Holmer et al., 2004), so this should not be assumed. Mixed meadows with increased above ground complexity are also likely to have increased root system complexity below ground (Rattanachot and Prathep, 2015), as such this suggests multiple leaf and root seagrass derived sources could be considered. Utilising root $\delta^{13}C$ values into mixing models to calculate percentage of allochthonous sediment organic carbon proxies nonetheless remains important in order to reflect a seagrass-derived $\delta^{13}C$, that considers multiple tissues, especially if some tissues (e.g., roots and rhizome) are more likely to become buried within the sediment. The uncertainty regarding the processes that determine post-photosynthetic discriminations are greater than what is currently understood for photosynthetic discriminations. Therefore, the focus on seagrass leaf $\delta^{13}C$ values provides a better context to discuss the global pattern in seagrass $\delta^{13}C$ values. Especially as our *meta*-analysis on seagrass leaf and sediment $\delta^{13}C$ values adequately highlights the variation and caution that should be taken when utilising percentage of allochthonous sediment organic carbon proxies and their derivative $\delta^{13}C$ values, in the context of blue carbon accreditation.

4.5. Influence of geomorphology on isotopic fractionation

There is distinct separation within the dataset based on the geomorphology of the seagrass sites, mainly separated into delta, tidal, and collectively lagoons, arheic and fjord coastlines, which suggests connectivity to the sea is driving the differences. Deltas and tidal systems are well connected to the sea, whether that be fully tidally influenced as in tidal systems or the recipient of sediment supplied by tides or waves as typical in a delta (Schwartz, 2005; Dürr et al., 2011). In comparison lagoons, fjords and arheic coastlines are influenced by some form of separation from external water inputs, coastal lagoons being separated from the open ocean by a physical barrier, fjords being separated from the sea by a sill or rise at their mouth, and the arheic coasts of arid regions are characterised by a near-total absence of water inputs. Delta and tidal systems will therefore receive inputs of inorganic carbon from the coastal waters connected to it and/or terrestrial inorganic carbon upstream. The δ^{13}C values of seagrass is related to the isotopic composition of the inorganic carbon source in the environment, such that seagrass tissues may subsequently reflect ^{13}C depleted carbon values of the inorganic sources, for example seagrass leaves grown near to mangroves -12.8 ± 1.1 % versus those far from mangroves -8.3 ± 0.9 % (Lin et al., 1991). This is due to input of ^{13}C depleted inorganic carbon derived from the decomposition of terrestrial and mangrove organic matter, supplied to these seagrass meadows (Lin et al., 1991; Hemminga and Mateo, 1996). In comparison, within the surface layer of the oceans, the dissolved inorganic δ^{13}C values can near zero, such as the 1.5–2 ‰ values recorded in the Pacific Ocean (Quay and Stutsman, 2003). Therefore, the input and sources of inorganic carbon (e.g., coastal, terrestrial or oceanic) to deltas and tidal systems influences the inorganic carbon pool. This inorganic carbon pool is available for photosynthesis by the seagrass and as such influences the isotopic value of the seagrass leaves prior to further ^{13}C fractionation by seagrass photosynthesis. Because lagoons, fjords and arheic coastlines are subject to less water inputs the inorganic carbon pool will be dependent on those sources in their direct locality, and may have a higher potential for recycling in a decomposition loop leading to distinct fractionation values. Therefore, it stands to reasons that the geomorphology of an environment would influence the supply and sources of inorganic carbon, its subsequent retention and remineralisation leading to variation in the isotopic values of the seagrass tissues prior to further ^{13}C fractionation by seagrass photosynthesis. This study did not identify which inorganic carbon sources are of greater importance to seagrass meadows based on their geomorphology, but indicate that the geomorphology of the seagrass sites may influence the isotopic value of the seagrass leaf prior to further ^{13}C fractionation by seagrass photosynthesis.

The geomorphological features of coastlines (e.g., tidal, lagoon) impact the terrestrial-marine import and export of carbon, and therefore the supply and/or source of allochthonous organic carbon directly deposited in the sediment. These differences in the supply and/or source of allochthonous carbon to sediment change the δ^{13}C value of the sediment. Allochthonous sediment organic carbon ratios are typically calculated via mixing models including the potential allochthonous, seagrass and sediment δ^{13}C values. The use of mixing models has its own limitations e.g., the similarity of source and mixture isotopic values (Phillips and Gregg, 2003); need to characterise the δ^{13}C of all potential sources or those that are more likely within each habitat tested (Parnell et al., 2010). Therefore, a literature derived percentage of allochthonous sediment organic carbon proxy is an amalgamation of not only potential allochthonous, seagrass and sediment δ^{13}C values, but the decision process and mathematical solution, the selected mixing model intended for use in that context. As stated prior in this *meta*-analysis this study did not try to determine specific allochthonous sources, nor to test or critique the various mixing models which can be applied, but further highlights that an allochthonous sediment organic carbon proxy is exactly that, a mathematical proxy to a complex process. Given this dataset is derived from the existing literature variation within the dataset could also be due to numerous factors including, that the measurements were taken by different laboratories across the globe, in different years, at different times of the year and may have followed slightly different protocols. Some of this variability is therefore a caveat of handling a globally derived dataset from the literature. In addition, diagenetic processes downcore can alter δ^{13}C signatures post-burial and can be observed within the first 5–10 years (Gälman et al., 2009), which adds complexity to using percentage of allochthonous sediment organic carbon and their derivative δ^{13}C values as a proxy of carbon provenance in sediment. Thereby proxies in blue carbon accreditation need to consider how the derivative δ^{13}C values influence and contribute to the calculated percentage of allochthonous sediment organic carbon and whether the variation or uncertainty in that value is appropriate for its use, in terms of reflecting a different site. Recently the use of eDNA and carbon and nitrogen isotopes of lipids have displayed the potential to alleviate some of the uncertainties associated with stable isotope analysis, but need further validation and wider employment as tools of seagrass carbon provenance (Reef et al., 2017; Geraldi et al. 2019; Arina et al., 2023).

5. Conclusion

Proxy values from the literature are not a direct substitute for site specific δ^{13}C seagrass leaf and sediment data, and their use in context dependent mixing models. Nonetheless given isotopic mass spectrometry analysis can be expensive to undertake peer-reviewed published data as proxies can be useful and potentially an economic necessity. The investment into such analyses and filling the carbon knowledge gaps to achieve accreditation, such as those surrounding carbon provenance, additionality and permanence, often outweigh the future return from accreditation for seagrass restoration projects. In fact, full GHG inventory accounting of a temperate *Zostera marina* seagrass meadow in the USA demonstrated that financial investment through carbon accreditation would have only recovered 10 % of the restoration costs (Oreska et al., 2020). However, caution should be taken if proxies are used for blue carbon accreditation, because there is the potential for carbon offsets to be sold for a project with an overestimated capacity to remove GHG versus its true-realised capacity. This study demonstrates that climatic setting, according to known seagrass bioregions (Short et al., 2007), geomorphology (e.g., estuarine, lagoon) or the subsequent 'typical' seagrass communities and traits (i.e., size), can improve the selection of allochthonous sediment organic carbon proxies based on their derivative sediment and seagrass δ^{13}C values. It also places an emphasis on further developing the use of other methods such as eDNA for carbon provenance analysis. Ultimately proxies are a current necessity for blue carbon accreditation, and as such this paper presents an informed criterion to improve the selection of allochthonous sediment organic carbon proxies based on their derivative sediment and seagrass δ^{13}C values. It is therefore strongly recommended that seagrass morphology and biogeographic context are incorporated into future revisions of carbon credit methodologies as factors that can improve allochthonous carbon proxy selection.

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CRediT authorship contribution statement

Emma A. Ward: Writing – original draft, Visualization, Methodology, Investigation, Formal analysis, Conceptualization. **Marianna Cerasuolo:** Writing – review & editing, Visualization, Methodology, Formal analysis. **Federica Ragazzola:** Writing – review & editing, Supervision. **Sarah E. Reynolds:** Writing – review & editing, Supervision. **Joanne Preston:** Writing – review & editing, Supervision, Project administration, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecolind.2024.112546.

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