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Glycan purification reveals persistence of algal fucoidan in millennia-old marine sediments

Aman Akeerath Mundanatt[1,2], Silvia Vidal-Melgosa[1,2], Leonard Rößler[1,2], Kevin W. Becker[1], Juliane Müller[3], & Jan-Hendrik Hehemann[1,2]

[1] MARUM - Center for Marine Environmental Sciences & Faculty of Biology/Chemistry, University of Bremen, 28359, Bremen, Germany.
[2] Max Planck Institute for Marine Microbiology, 28359, Bremen, Germany.
[3]Alfred Wegener Institute, Helmholtz Centre for Polar and Marine Research, Bremerhaven, Germany.

Correspondence to: Jan-Hendrik Hehemann (jhhehemann@marum.de)

Abstract:

Marine sediments are an important sink for the carbon fixed by photosynthetic algae in the sunlit ocean. Glycans represent a substantial fraction to the organic carbon buried globally in marine sediments. However, assigning the origin and contribution of specific glycans remains challenging with commonly used methods that are designed to measure the total glycan carbon content. Glycan-specific detection using monoclonal antibodies previously revealed diatom- and brown algae-derived fucoidans in marine sediments of various ages. These complex anionic glycans may contribute to long-term carbon sequestration, while their quantitative significance remains unknown. Here, we combined anion exchange chromatography with glycan-specific monoclonal antibodies to isolate and detect fucoidans from marine sediments. Applying this method to a sediment core from the Bransfield Strait in the Southern Ocean revealed that fucoidan was buried and persisted for the extent of the Holocene (11.8 ka). Our results highlight that glycan purification from sediments can help to resolve the importance of different algal glycans to the sequestration of carbon in the ocean.

1 Introduction:

Marine sediment is the largest long-term reservoir of organic carbon, sequestering carbon over geological timescales (Burdige, 2007; Li et al., 2023). Processes like the biological carbon pump transport organic carbon fixed in the sunlit ocean to the sediments in form of aggregates, faecal pellets, and other particles (Eppley and Peterson, 1979; Cavan et al., 2015; Le Moigne, 2019). The particles reaching the seafloor are compositionally diverse, originating from multiple sources and undergoing various transformations in the water column (Duarte and Cebrián, 1996; Aluwihare et al., 2002; Dittmar et al., 2021; Hedges et al., 2001; Chin et al., 1998; Engel et al., 2004). From this mixture of organic molecules, specific biomolecules have been targeted to reconstruct past climate, ecological dynamics, and carbon cycling processes (Lee et al., 2016; Salmeán et al., 2022; Vorrath et al., 2023a).

Glycans (polymeric carbohydrates) of unidentified origin contribute 5-30% of organic carbon in marine sediments (Burdige, 2007; Miyajima et al., 2001; Vidal-Melgosa et al., 2022). Previously used methods were designed to answer questions about total glycan carbon concentrations and bulk monosaccharide compositions (Burdige et al., 2000; Taylor et al., 1999; Vidal-Melgosa et al., 2022). While certain glycans are enriched in unique monomers specific to certain algal phyla, most monosaccharides are shared across different phyla as building blocks for diverse glycans (Arnosti et al., 2021). Therefore, quantifying monosaccharides or ratios of monosaccharides as

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attempted in earlier studies (Cowie and Hedges, 1984; Klok et al., 1984; Miyajima et al., 2001), may not resolve for specific glycan types or reveal the source of the glycans. To gain more molecular resolution, recent studies have used structure-specific monoclonal antibody-based approaches (Hellige et al., 2026; Salmeán et al., 2022; Vidal-Melgosa et al., 2022). These studies semi-quantitatively revealed that brown algal- and diatom-derived fucoidans persist in sediment for various periods of time, indicating the potential roles of these complex anionic glycans towards long-term carbon sequestration. However, the quantification of these glycans is necessary to understand their exact contributions to the various components of the biological carbon pump and sedimentary organic matter.

Other than the limitations of the available analytical methods, glycan quantification in the sediments is further complicated by the presence of interfering salts, humic compounds and other contaminants. Alginate, an anionic brown algal glycan, was recently quantified in marine sediments using alginate lyases and other colorimetric assays (Nakazato et al., 2026). This was only possible after a multi-step extraction and clean-up protocol that involved the removal of phenolic compounds, other glycans like pectin, and other pigments. The quantification of the purified alginate highlights the potential of brown algal glycans in carbon sequestration (Nakazato et al., 2026). Similarly, coccolith-associated polysaccharides were extracted and isolated from coccolith fossils in the sediment using anion exchange chromatography (Lee et al., 2016). The purification step enabled quantification of uronic acid content in the specific polysaccharides. It was observed that the uronic acid content in the coccolith-associated polysaccharides correlates with the internal saturation state of the coccolith vesicle indicative of past environmental pCO_2 (Lee et al., 2016). These studies highlight that the extraction and purification of specific glycans from complex mixtures enable their quantification and use as proxies for carbon sequestration and/or environmental conditions involved in their synthesis and deposition. We considered that similar approaches may apply to fucoidans. Our aim was to extract and isolate fucoidans from millennia-old marine sediments from the diatom dominated Bransfield Strait.

2 Materials and Methods

2.1 Study site and sample procurement

Sediment samples from the Bransfield Strait were provided as subsamples of sediment sections obtained from a multi corer (PS97/72-2) and piston corer (PS97/72-1) during the *RV Polarstern* expedition *PS97*, both taken at the same station (Latitude: -62.0065, Longitude: -56.0647, see Fig. 1). A total of ten sections, corresponding to ten depths ranging from 2 to 868 cm (see Table 1) were analysed. Sediments from this region are characterized as silt-bearing diatomaceous clay, with up to 40% comprising diatom assemblages i.e., 31.49×10^6 valves per gram (Cárdenas et al., 2019; Lamy, 2016). Resting spores of *Chaetoceros sp.* were the dominant contributors (Cárdenas et al., 2019). Previous radiocarbon measurements indicated that the sediment core spanned the extent of the Holocene i.e., deepest depth (868 cm) is 11.8 ka old (Vorrath et al., 2023b, a). The sediment sections were freeze-dried and then homogenized thoroughly with a mortar and pestle before all further analysis. For negative control, combusted sand was used (450 °C for 4 h).

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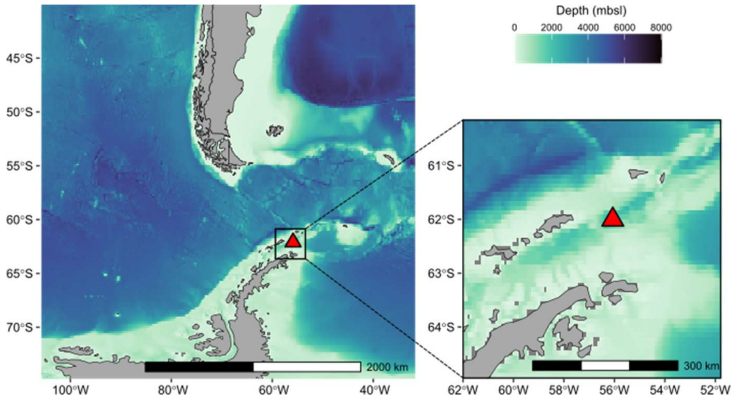

Figure 1: Location of sampling station in the Bransfield Strait. The background colours indicate bathymetry (mbsl i.e., meters below sea level) obtained from the NOAA using the 'getNOAA.bathy()' function in the 'marmap' package in R (version 4.2.1). The larger map on the left is shown at a spatial resolution of 10 arc-minutes, while the inset is at a spatial resolution of 5 arc-minutes.

2.2 Total organic carbon

Total organic carbon was measured as described earlier (Müller et al., 2025). Depending on sample availability, approximately 0.1 g of the homogenized sediment samples was decalcified by treatment with 12.5% hydrochloric acid and dried on a hot plate. Samples of known weight was then combusted at 1800° C in a stream of oxygen. Total organic carbon was quantified by measuring the released CO_2 with a LecoCS744 elemental analyser. The total organic carbon values are given as carbon weight (mg) per gram dry sediment.

2.3 Sequential glycan extraction

The glycans were extracted using a modified sequential extraction protocol (Hellige et al., 2026; Vidal-Melgosa et al., 2022). For every 10 mg of freeze-dried and homogenized sediment, 200 µL of the first solvent i.e., MilliQ water was added, and the sediment slurry was vortexed thoroughly. The slurry was then sonicated for 1 h in a sonication bath and centrifuged at 4000x g for 20 minutes. The supernatant was considered the MilliQ extract. The protocol was repeated for the pellet with same volumes of second solvent i.e., EDTA (0.3 M, pH 7.5), and the final solvent i.e., NaOH (4 M) + $NaBH_4$ (0.1% w/v). All extracts were stored at -20°C until further processing.

2.4 Extracted carbohydrate concentrations

Extracted carbohydrate concentrations were obtained by the phenol sulfuric assay (DuBois et al., 1956). 200 µL of the sequential extracts were mixed with 200 µL of 5% (v/v) Phenol and 1 mL of concentrated sulfuric acid (> 95%) was slowly added and mixed. The tubes were incubated at room temperature for 10 minutes and at 30 °C for 20 minutes to ensure completion of the reaction. After incubation, 200 µL was taken wells of a 96 well-plate. The absorbance was measured at 490 nm using a plate reader. Samples were referenced to increasing concentrations of D-glucose standards for quantification.

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2.5 Anion exchange chromatography

MilliQ and EDTA extracts were pooled together and filtered through a 0.22 µm syringe filter. Two HiTrap ANX FF (high sub) columns (column volume = 1mL) were connected in series to an Äkta start purification system. The top column served as a guard column to trap any particles, pigments, and gas bubbles. Once the columns were washed of any preservatives, they were equilibrated first with 10 column volumes (CV) of an equilibration buffer (20 mM Tris-HCl, pH 7.5). Depending on the sample availabilities, the filtered samples were applied onto the anion exchange column i.e. 8 mL for 11 cm and 464 cm, and 15 mL for the rest. 10 CV of the equilibration buffer was then passed again through the column to wash any unbound molecules. The flow-through and the wash fractions were collected together. A salt gradient spanning 20 CV starting with the equilibration buffer and ending at the elution buffer (20 mM Tris-HCl, 5 M NaCl, pH 7.5) was applied for the elution of the bound molecules. Additionally, 10 CV of the elution buffer was passed to elute any tightly bound molecules. All the elution steps were collected as 1 mL fractions. In between the chromatography runs, the columns were washed with 0.1 M NaOH. After every 4 runs, the columns were extensively cleaned with 1 M NaOH. A blank chromatography run was also performed and the resultant fractions were used for background subtraction during all subsequent analysis.

2.6 Enzyme-linked immunosorbent assay (ELISA)

ELISA protocol was followed as previously described (Cornuault et al., 2014; Vidal-Melgosa et al., 2021). The monoclonal antibody BAM1 (SeaProbes) was used as a primary antibody to detect fucoidans (Torode et al., 2015). Anti-rat antibody conjugated to horseradish peroxidase enzyme (IgG; Sigma-Aldrich) was used as the secondary antibody. After the addition of the substrate (Tetramethylbenzidine, Slow kinetic form, Sigma-Aldrich), the plates were incubated in dark until few samples had a strong colour development. The reaction was stopped with same development time for all samples by adding 1 M HCl. The absorbance was measured at 450 nm.

2.7 Deoxyhexose quantification assay (L-Cysteine assay)

The deoxyhexose concentrations were estimated using a modified deoxyhexose quantification assay (Dische and Shettles, 1948). 100 µL of sample were hydrolysed with 234 µL of concentrated sulfuric acid (>95%) at 99°C for 10 minutes on a heat block. The samples were then cooled rapidly on ice for 10 minutes. Subsequently, 10 µL of 3% (w/v) L-cysteine hydrochloride solution was added to the cool samples. After incubation in the dark for 1.5 hours, 200 µL of the solution was transferred into 96-well plates and the absorbance at 396 nm and 427 nm was measured. Sample measurements were referenced to L-fucose standards in MilliQ water that were run in parallel. The difference in absorbance at 396 nm and 427 nm in the standard curve is proportional to the concentration of deoxyhexoses in the samples.

2.8 Desalting by silica purification

Protocol for desalting was followed as previously described (Schultz-Johansen et al., 2025). 100 µL of the anion exchange fractions were diluted with 1900 µL of absolute ethanol, so that the final concentration of ethanol was 95% (v/v). The diluted sample was then loaded onto a NEB Monarch DNA Cleanup spin column. The samples were spun at 15,000 x g for 5 minutes and the flow-through was discarded. Once all the sample was loaded onto the column, the column was washed twice with 95% ethanol. The samples bound to the silica column were then eluted with MilliQ into a clean collection tube.

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2.9 Monosaccharide quantification by high performance anion exchange chromatography with pulsed amperometric detection (HPAEC-PAD)

Prior to monosaccharide quantification, the samples were either desalted using silica purification (selected fractions) or diluted 10-15 times (MilliQ extracts and EDTA extracts) so that the concentration of salt was low enough for the HPAEC-PAD system. The samples were then acid hydrolysed in 1 M HCl (final conc.) for 24 h at 100 °C. Acid hydrolysed samples were dried in a centrifugal vacuum concentrator for 3 hours. A set of standard mixtures containing known concentrations of monosaccharides in 1 M HCl were dried simultaneously with the samples. The extracts were filtered through a 0.22 µm nylon-spin filter. All other fractions and standards were spun at 21000 g for 10 minutes. 100 µl of the samples and 200 µl of the standard were transferred into HPLC vials with an inlet. The vials were closed with slitted silicone sealing discs and placed in the auto-sampler of the Dionex ICS-5000+ system. The columns used in the system were CarboPac PA10 analytical column (2 x 250 mm) and CarboPac PA10 guard column (2 x 50 mm). After loading the samples onto the columns, the neutral and amino sugars were separated using an isocratic phase of 18 mM NaOH, while the acidic monosaccharides were eluted using a gradient reaching up to 200 mM NaCH3COO. The peaks of the eluted sugars were identified using retention times of the known monosaccharide standards. The peak areas were converted to concentration of the monosaccharides (µg/L) based on the standard curves.

3 Results

3.1 Contribution of carbohydrates to the buried organic carbon

To assess the contribution of carbohydrates to buried organic carbon, we first quantified the total organic carbon in the sediment by elemental analysis after combustion. Organic carbon concentrations ranged between 6.7 mgC. g_{dw}^{-1} (mg carbon per gram dry weight of sediment) at the lowest depth (868 cm) and 10.9 mgC. g_{dw}^{-1} at the uppermost depth (2 cm) (see Table 1).

Carbohydrates extracted sequentially with MilliQ water, EDTA and NaOH were quantified using phenol-sulfuric acid assay. The extraction method was previously found suitable to extract different algae- and plant-derived types of complex glycans from marine sediments (Vidal-Melgosa et al., 2022, Hellige et al., 2026). For example, EDTA chelates cations cross-linked to anionic glycans such as pectin and other uronic acid-containing glycans, while NaOH is required to extract crystalline, insoluble glycans such as cellulose. Because this approach extracts both, free monomers and the ones polymerized in form of glycans, they are collectively described as carbohydrates at this step of the analysis. While the NaOH extracts had the highest carbohydrate concentrations among the three extracts (Fig. S1), they were omitted from the next steps as they are not amicable for the anion exchange chromatography either due to the high pH or due to high salt concentrations after neutralization. The combined carbohydrate carbon concentrations in the MilliQ and EDTA extracts ranged between 0.23 mgC. g_{dw}^{-1} and 1.047 mgC. g_{dw}^{-1} in 192 cm and 4 cm sediment depths, respectively (see Table 1). Carbohydrates in the MilliQ and EDTA extracts constituted 2.45 – 10% of the total organic carbon across the sediment depths.

As fucose is a deoxyhexose sugar and a key constituent of fucoidan, deoxyhexoses were quantified in the MilliQ and EDTA extracts using the L-cysteine assay. Deoxyhexose concentrations ranged between 0.009 mgC. g_{dw}^{-1} and 0.044 mgC. g_{dw}^{-1} in 868 cm depth and 6 cm depth, respectively (see Table 1). Therefore, on average the

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deoxyhexoses contributed 5% of the carbohydrates extracted using MilliQ and EDTA and 0.22% of the total organic carbon.

Table 1: Contribution of carbohydrate carbon to the sedimentary organic carbon pool.

Depth [cm]	Age [ka BP]	Total organic carbon [mgC. g_{dw}^{-1}]	Extracted carbohydrate concentration [mgC. g_{dw}^{-1}]	Deoxyhexose concentration – before AEX [mgC. g_{dw}^{-1}]	Deoxyhexose concentration – after AEX [mgC. g_{dw}^{-1}]
2	-0.05	10.9	0.555	0.024	0.017
4	-0.042	10.2	1.047	0.030	0.016
6	-0.033	9.58	0.545	0.044	0.016
11	-0.015	9.95	0.404	0.027	0.011
21	0.024	7.85	0.240	0.018	0.009
31	0.074	9	0.349	0.018	0.010
192	2.935	9.36	0.230	0.008	0.016
312	4.162	9.37	0.292	0.015	0.009
464	5.766	8.58	0.336	0.016	0.011
868	11.738	6.66	0.335	0.009	0.005

Note: Age models of 2 cm – 31 cm depth intervals were established previously by excess ^{210}Pb dating (Vorrath et al., 2020b, a), and the rest were determined previously by ^{14}C dating (Vorrath et al., 2023b, a).

3.2 Chromatography assisted purification of fucoidans from Bransfield Strait sediments

We aimed to quantify the fucoidan concentrations in sediments from the Bransfield Strait. As we had limited quantities of sediment samples from the Bransfield Strait, we used sediments from the Wadden Sea to test and establish methodologies used in this study (see Fig. S2, Fig. S3). The established method, i.e. anion exchange chromatography, was then used to isolate fucoidans from the bulk glycans extracted (MilliQ and EDTA extracts) from Bransfield Strait. Epitope detection chromatography, a method described in previous studies uses specific monoclonal antibodies for the detection of glycan epitopes after anion exchange purification (Cornuault et al., 2014; Vidal-Melgosa et al., 2021). Similarly, we tested the chromatographic fractions for fucoidans using the specific monoclonal antibody BAM1. Additionally, the deoxyhexose concentrations (as an estimate for L-fucose) in the fractions were measured as a proxy for fucoidans. The concentrations of deoxyhexoses and the antibody signals both peaked in the same elution window (see Fig. 2). Summed deoxyhexose concentrations in this peak ranged between 0.005 mgC. g_{dw}^{-1} to 0.017 mgC. g_{dw}^{-1} in sediment depths 868 cm and 2 cm, respectively (see Table 1). Except for depth 192 cm, 35-70% of the deoxyhexose in the MilliQ and EDTA extracts were recovered using anion exchange chromatography (see Fig. S4). At depth 192 cm, a 200% recovery was observed, indicating possible matrix effects causing underestimation of the crude extracts or overestimation in the purified samples.

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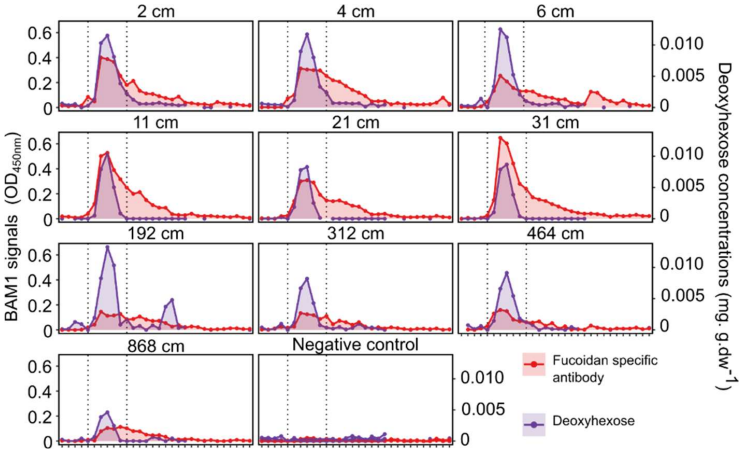

Figure 2: Chromatographic purification of fucoidans from marine sediments confirmed by different analyses. Chromatographic fractions (x-axis) were probed for fucoidans using the monoclonal antibody BAM1, and deoxyhexose concentrations were measured with the L-cysteine assay. The monoclonal antibody signals (OD_{450nm}) in each fraction are shown in red, while the deoxyhexose concentrations are shown in purple. The region where the relative antibody signals and the deoxyhexose concentrations peak and overlap are indicated by the vertical dotted lines in each facet. This region signifies the fucoidans isolated from the corresponding depth.

3.3 Monosaccharide composition before and after anion exchange chromatography

Monosaccharide composition was quantified in the pooled MilliQ and EDTA extracts and also in the pooled fractions from the elution window using HPAEC-PAD. Galactose was the primary monosaccharide in both the crude extracted carbohydrates (average relative abundance of 22.9%) and in the isolated fucoidans (average relative abundance 28%). Fucose, galactose, glucose, xylose, galacturonic acid, and glucuronic acid have higher relative abundances in the isolated fucoidans in comparison to the crude extracts (see Fig. 3). Arabinose, rhamnose, and glucosamine show lower relative abundances in the isolated fucoidans. There are notable increases in the relative abundances of xylose and glucose in sediment depths 464 cm and 868 cm, respectively. The differences in monosaccharide compositions before and after anion exchange chromatography indicates the selection of certain monosaccharides and omission of others.

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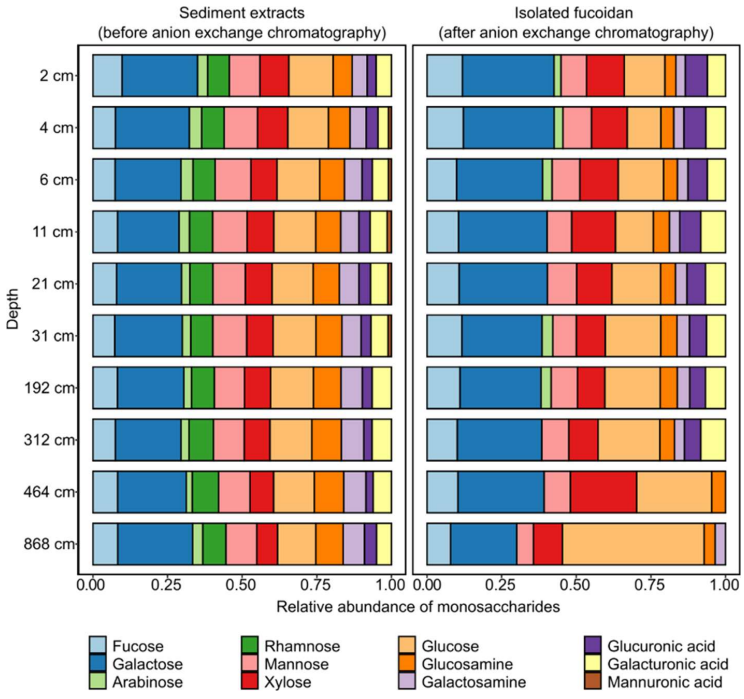

Figure 3: Enrichment of fucoidan monosaccharides after anion exchange chromatography. Relative abundances of monosaccharides before (left) and after (right) anion exchange chromatography are compared. Certain monosaccharides often associated with the building blocks of fucoidan like fucose, galactose, glucose, xylose, and the uronic acids are enriched after anion exchange chromatography. Monosaccharides like rhamnose and arabinose, however, have a lower abundance indicating selection of certain glycans.

4 Discussion

In this study, we estimated the contribution of fucoidans towards carbon sequestration in millennia-old marine sediments. We were able to overcome limitations of existing analytical methods via separation of fucoidans from the sediment matrix using anion exchange chromatography. Our approach was built on previous applications of anion exchange chromatography for quantification and characterization of anionic glycans from diverse biological and environmental sources (Cornuault et al., 2014; Huang et al., 2021; Sichert et al., 2021; Vidal-Melgosa et al., 2021; Buck-Wiese et al., 2023; Krull et al., 2026). Fucoidan-specific monoclonal antibody BAM1 (Torode et al., 2015) also provided support for the isolation of fucoidan from the sediment matrix. While other glycans could have coeluted with the fucoidans, the monosaccharide constituents of the sediment fucoidan corroborated with previously reported fucoidans (Huang et al., 2021; Ponce and Stortz, 2020; Vidal-Melgosa et al., 2021). Future enzyme-based methods could provide additional structure-specific quantification and confirmation of fucoidans (Becker et al., 2017; Buck-Wiese et al., 2023; Nakazato et al., 2026). However, this is limited by the availability of appropriate enzymes, as marine sediments may comprise structurally diverse and poorly characterized fucoidans from multiple sources. The presence of diverse glycans and polyphenols in complex sediment matrices can also obscure the enzymatic quantification of glycans (Nakazato et al., 2026). The necessity of clean-up methods further

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highlights the value of anion exchange chromatography, as used in this study. Therefore, by enabling the isolation of fucoidans, anion exchange chromatography provides a basis for accurately evaluating the roles of these glycans in long-term carbon sequestration.

Fucoidans isolated from the Bransfield Strait likely have a diatomaceous origin. While fucoidans are primarily exuded by both brown algae and diatoms (Buck-Wiese et al., 2023; Huang et al., 2021; Vidal-Melgosa et al., 2021), this region is diatom-dominated with a high proportion of *Chaetoceros* resting spores in the sediment (Cárdenas et al., 2019; Lamy, 2016). However, previous studies also have reported the presence of brown algal detritus (Fischer and Wiencke, 1992; Reichardt, 1987). Similar monosaccharide compositions, with high percentages of galactose have been observed in fucoidans isolated from both diatoms and brown algae (Huang et al., 2021; Ponce and Stortz, 2020; Vidal-Melgosa et al., 2021). Hence, unambiguous assignment of the origin of fucoidan would require a higher structural resolution. Recently, oligosaccharide fingerprints obtained by MALDI-MS analysis of fucoidan hydrolysates have been shown to distinguish the different biological origins (Reyes-Weiss et al., 2024). In the future, oligosaccharide fingerprints of fucoidans from the sediment can be compared to fingerprints of various micro- and macroalgal fucoidans, to better understand their origins. Overall, our study demonstrates that isolation of glycans from marine sedimentary records using anion exchange chromatography provides the foundation for resolving their origins and assessing the roles of various algae in carbon sequestration.

Fucoidan sequesters carbon for climate-relevant timescales. Assuming a constant rate of fucoidan deposition, we find that at least 30% of the fucoidan at the uppermost depth (0.017 mgC. g_{dw}^{-1}) was sequestered for the entire extent of the Holocene (i.e., 0.005 mgC. g_{dw}^{-1}). The binding of fucoidans to the anion exchange column also suggest that they remain sufficiently intact in millennia-old sediments, because low molecular weight molecules are washed away (Buck-Wiese et al., 2023). The preservation of fucoidan carbon has also been semi-quantitatively observed in centuries- to millennia-old sediments (Vidal-Melgosa et al., 2022; Salmeán et al., 2022). These studies were unable to discern if the preservation was attributed to the recalcitrance of fucoidan or the harsh depositional environments like hyper-salinity and anoxia (in the Red Sea), and periodic anoxia (in the Koljö Fjord). However, our findings indicate that fucoidan resists bacterial degradation, as it is transported to the sediment in a 2000 m deep oxic water column. Other than the direct contribution to carbon sequestration, fucoidan also transports other molecules to the sediment by forming aggregates (Vidal-Melgosa et al., 2021). The presence of fucoidan in sinking particles could protect labile organic carbon from bacterial degradation, analogous to their proposed roles in the extracellular matrix of diatoms and brown algae (Bligh et al., 2022) and similar to the shielding effects of mineral associations (Keil et al., 1994). Therefore, fucoidans are important components of the biological carbon pump and may contribute to long-term carbon sequestration through different mechanisms.

5 Outlook

The cultivation of macroalgae is increasingly being considered as a potential climate mitigation strategy. Evidence of algae detritus in marine sediments or the increased accumulation of organic carbon in sediment near algae farms point to carbon sequestration potential of brown algae (Fischer and Wiencke, 1992; Reichardt, 1987; Krause-Jensen and Duarte, 2016; Duarte et al., 2025). However, little is known about the far-field carbon sequestration efficiency of algae farms, due to the lack of stable long-term proxies that can be specifically attributed to the brown algal input. Our study provides a framework for the quantification of fucoidans in sediments, thereby enabling

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their use as proxies to assess carbon sequestration. This approach therefore may facilitate the long-term monitoring of brown algal carbon sequestration beyond the immediate vicinity of cultivation sites.

Data availability

Data reported in this paper will be submitted to the online data archive PANGAEA, and will be made accessible to the public at the time of publication.

Author contributions

AAM, and JHH designed research with contributions from all authors. SVM and JHH supervised the project. AAM performed all laboratory methods. LR developed and validated the modified L-cysteine assay (manuscript in prep). JM collected and provided sediment samples from the Bransfield Strait. AAM, KWB, and JHH led the interpretation and discussion of data and manuscript preparation, with inputs from all authors.

Competing interests

The authors have declared no competing interest.

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