



Short Communication

Evaluating seagrass lipid biomarkers as indicator for organic carbon provenance and storage capacity in *Zostera marina* (L.) sediments

Martin Dahl^{a,*}, Maria E. Asplund^b, Mats Björk^c, Sanne Bergman^d, Sara Braun^a, Sara C. Forsberg^a, Petter Hällberg^e, Elin Löfgren^c, Rienk Smittenberg^{e,f}, J. Robin Svensson^g, Martin Gullström^a

^a School of Natural Sciences, Technology and Environmental Studies, Södertörn University, Huddinge, Sweden

^b Department of Biological and Environmental Sciences, University of Gothenburg, Kristineberg Center, Fiskebäckskil, Sweden

^c Department of Ecology, Environment and Plant Sciences, Stockholm University, Stockholm, Sweden

^d The Arctic University Museum of Norway, UiT – The Arctic University of Norway, Tromsø, Norway

^e Department of Geological Sciences, Stockholm University, Stockholm, Sweden

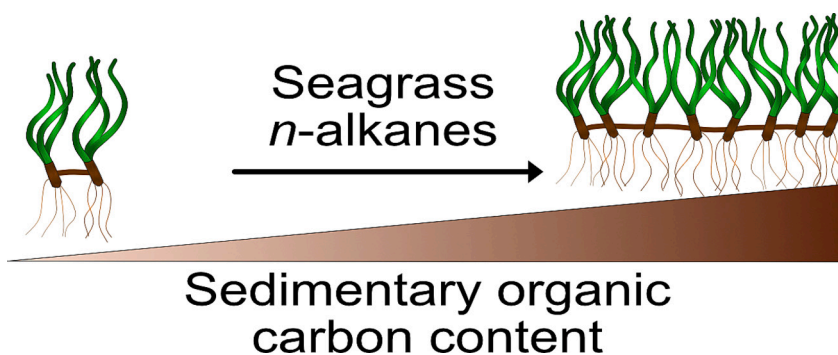
^f Swiss Federal Institute for Forest, Snow and Landscape Research, Birmensdorf, Switzerland

^g Department of Marine Sciences, University of Gothenburg, Gothenburg, Sweden

HIGHLIGHTS

- *Zostera n*-alkanes were clearly correlated to OC in the sediment.
- *n*-Alkanes can be used for fingerprinting seagrass-derived sedimentary OC.
- The presence of seagrass-derived OC increases blue carbon accumulation.

GRAPHICAL ABSTRACT



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ABSTRACT

Seagrass meadows are vital blue carbon habitats, with sedimentary organic carbon (OC) originating from both the seagrass itself and external sources. In this study, lipid biomarkers (*n*-alkanes), a well-known proxy for tracing OC sources, were used to indicate seagrass presence in sediment records and to correlate with sedimentary OC in cold-temperate seagrass (*Zostera marina*) sediments. We calculated a *Zostera*-ratio (seagrass/algae and terrestrial plants-ratio) using identified seagrass biomass *n*-alkanes (C₁₅, C₁₇, C₁₉, C₂₁, C₂₃) as a fingerprint for seagrass-derived OC. Based on the presence or absence of seagrass plant remains in sediments, we confirmed an overall significant positive correlation ($R^2 = 0.49$, with significant sites ranging from 0.66 to 0.81; $p < 0.001$) between the *Zostera*-ratio and OC in sediment profiles down to 2 m depth. The *Zostera*-ratio ranged from 0.0006 to 0.35 with higher values indicating seagrass plant material. The findings show that *n*-alkanes can serve as proxies for both seagrass presence and total OC levels in the sediment.

* Corresponding author.

E-mail address: martin.dahl@sh.se (M. Dahl).

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1. Introduction

Lipid biomarkers can be used as a proxy to trace organic carbon (OC) sources and for determining past plant communities, as different primary producers contain different alkane chain lengths (McClymont et al., 2023; Hällberg et al., 2024). Specifically, photosynthetic organisms produce, mostly with odd-numbered, mid- and long-chain *n*-alkanes. Algae and bacteria typically contain relatively short *n*-alkanes (C₁₅–C₁₉), aquatic plants range from C₂₁ to C₂₅, while vascular terrestrial plants are dominated by the longest alkanes (C₂₇–C₃₅) (McClymont et al., 2023; Aichner et al., 2010). Seagrass plants contain short to medium chain length *n*-alkanes, including C₁₇, C₁₉, C₂₁, C₂₃ and C₂₅ (Chevalier et al., 2015). Therefore, *n*-alkanes have been used to determine the contribution of various OC sources to the sedimentary OC pool in blue carbon (BC) ecosystems (Dahl et al., 2024; Geraldi et al., 2019).

Seagrass meadows are considered a key BC habitat with high capacity for long-term carbon storage (Macreadie et al., 2021). The sedimentary OC accumulated in seagrass meadows is derived from multiple sources, including the foundation habitat itself and organic matter from for example terrestrial and macroalgae habitat (Kennedy et al., 2010; Ortega et al., 2020). Several methods to assess provenance of OC and shifts in plant community composition have been used in BC science. The most common method has been the use of stable isotopes (i.e. $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$). However, the isotopic signal of many of the OC sources (e.g., marine macrophytes and phytoplankton) are overlapping, which results in a low resolution when distinguishing between OC sources. Therefore, several other more detailed fingerprinting techniques have been applied in seagrass sediment analysis (Geraldi et al., 2019), including environmental DNA (Foster et al., 2024; Ortega et al., 2020; Reef et al., 2017), pyrolysis (Kaal et al., 2020a, 2020b), and compound-specific stable isotopes (Kaal et al., 2022). So far, few seagrass studies have used *n*-alkanes as a proxy for seagrass plant biomass (but see Dahl et al., 2024; Kaal et al., 2022), although *n*-alkanes have been shown to distinguish between multiple OC sources in coastal sediments (Sikes et al., 2009; Zhang et al., 2024) and is known to remain stable in the sediment with high resistance to degradation (Ranjan et al., 2015), and therefore can serve as a long-term proxy for OC sources in sediments (Meyers, 2003). To assess the contribution of seagrass plant material to sedimentary OC storage, we used specific seagrass biomass *n*-alkanes as a proxy for seagrass-derived OC and assessed the relationship between a calculated *Zostera*-ratio (seagrass/algae and terrestrial plants-ratio) and %OC in cold-temperate *Zostera marina* meadow sediments. Similar ratios have successfully been used to separate specific OC sources in coastal sediments (Chevalier et al., 2015; Mead et al., 2005), but have not been applied to *Z. marina* sediment for exploring the BC storage in relation to OC derived from the foundation species. In cold-temperate environments, *Z. marina* is the dominant seagrass species and is found in shallow coastal areas across the Northern Hemisphere (Short et al., 2007), where it plays a vital role in coastal BC storage (Röhr et al., 2018) and can store sedimentary OC for millennia (Dahl et al., 2024).

2. Methods

Sediment sampling was conducted in five *Z. marina* meadows on the Swedish Skagerrak coast. In each meadow, one sediment core (except for in Kristineberg where two cores were sampled) was collected using SCUBA and 2 m long PVC-corers. Details regarding study sites and sampling procedure can be found in Dahl et al. (2023, 2024). The OC content was measured with a CN elemental analyzer coupled with a mass spectrometer (Carlo Erba NC2500). The samples were homogenized using a mixing mill and treated with 1 M HCl (direct addition) to remove inorganic carbon prior to analysis of OC content (expressed as % dry weight, DW) (Dahl et al., 2016, 2023). Above- and belowground biomass of *Z. marina* ($n = 3$ for each biomass part) was also analyzed to determine the seagrass biomass *n*-alkanes' signatures. For lipid extraction, dichloromethane (DCM) and methanol (MeOH) (9:1 v/v) were

added and placed in a sonic bath for 15 min (Poynter and Eglinton, 1990) and centrifuged (for more details on the lipid extraction process, see Dahl et al., 2024). Sedimentary and biomass *n*-alkanes were assessed in the non-polar lipid fraction by gas chromatography–mass spectrometry (GC–MS) on a Shimadzu GCMS-QP2010 Ultra, equipped with an AOC-20i autosampler and a split-splitless injector. For separation, a Zebron ZB-5HT Inferno GC column (30 m × 0.25 mm × 0.25 μm) was used and a standard mixture of *n*-alkanes of known concentrations was applied for quantification of *n*-alkanes in the sediment and biomass. After extraction, the total lipid extracts were dried under a stream of N₂ at 30 °C. To avoid evaporation of the volatile short chain *n*-alkanes (mainly C₁₅, and to some extent C₁₇), the N₂ flow was kept to a very low rate. The seagrass biomass was dominated by C₁₉, while there were lower contents of other short and mid-chained *n*-alkanes (odd C₁₅–C₂₃) (Dahl et al., 2024; Fig. 1). Based on this finding and following a similar approach as Chevalier et al. (2015), a *Zostera*-ratio was calculated as:

$$\text{Zostera-ratio} = \frac{\text{C}_{15} \times 0.02 + \text{C}_{17} \times 0.21 + \text{C}_{19} \times 0.61 + \text{C}_{21} \times 0.11 + \text{C}_{23} \times 0.05}{\sum (\text{odd C}_{15} - \text{C}_{35})}$$

where the values of each seagrass *n*-alkane is the weighted proportion based on the quantity of the pooled above- and belowground seagrass biomass (Fig. 1).

To test the site-specific relationship between *Zostera*-ratio and %OC content, logarithmic regression analysis was conducted in R (v.3.2.1). Partial least squares (PLS) regression analysis was performed in SIMCA (v. 18) to test the general influence of *n*-alkane fractional abundance compositions at all sites on the sedimentary %OC. Prior to the analysis, the data was $\log_{10}(x + 1)$ transformed.

3. Results

The *Zostera*-ratio confirmed the visual inspection of seagrass plant debris in the sediment cores (Fig. 2), where high values (up to 0.35) indicated seagrass plant material and low values (down to 0.0006) showed absence of seagrass (Fig. 3). There was a clear and similar trend for %OC and *Zostera*-ratio along the sediment depth profiles, except in Getevik and Västra Korsvik (Fig. 3). We found an overall positive relationship between %OC and *Zostera*-ratio ($R^2 = 0.49$, $p < 0.001$; Fig. 4A), which was even clearer at site-level ($R^2 = 0.66$ to 0.81 ; $p < 0.001$; Fig. 4B). In addition, two dominant seagrass *n*-alkanes (i.e. C₁₉ and C₂₁) displayed strong correlations to %OC when assessed individually for the different cores ($R^2 = 0.39$ to 0.80). The PLS regression was summarized in a biplot where the two components together significantly ($Q^2_{\text{cum}} =$

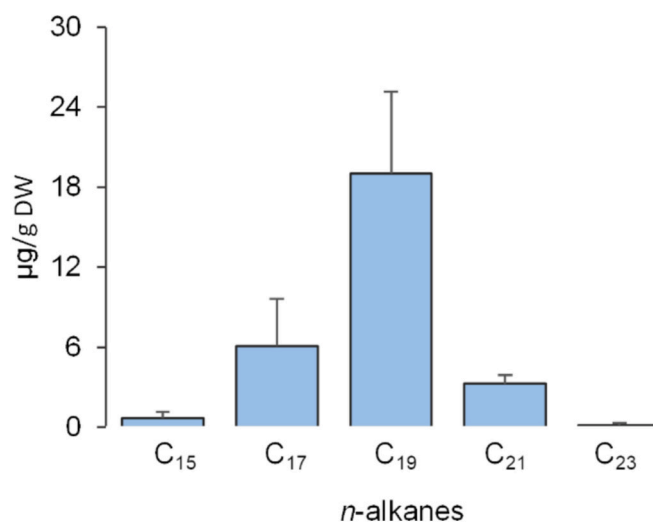


Fig. 1. Frequency distribution of mean ($\pm$ SE) *n*-alkanes in *Z. marina* biomass based on pooled above- and belowground biomass samples.

0.429) explained 57 % (R^2_{cum}) of the cross-validated variation in %OC (Fig. 5). The n -alkanes C_{27} , C_{19} , C_{21} and C_{23} contributed significantly to the model (ranked in order of Variables of Importance (VIP) for VIP-values over 1), whereof C_{19} and C_{21} were positively correlated to the %OC. Component 1 (x-axis) explained most (45 %) of the variation, while component 2 (y-axis) explained 12 %.

4. Discussion

Our results demonstrate that seagrass-derived n -alkanes were present in the sediment depth profiles in a pattern consistent with the confirmed presence of seagrass biomass remains (mainly rhizomes). A clear correlation was observed between the concentration of seagrass-derived n -alkanes and sedimentary OC content in *Z. marina* sediments, indicating that n -alkanes can be used as a proxy for *Z. marina* biomass, and thus, that the seagrass plant material increases the total OC burial in the sediment. This highlights the function of seagrasses as foundation species for BC storage in coastal environments.

The n -alkanes were analyzed as a (*Zostera*) ratio between seagrass-derived n -alkanes (odd C_{15} - C_{23}) and all n -alkanes (odd C_{15} - C_{35}) present in the sediment layers. Ratios are commonly used for interpretation of n -alkanes data; for example, P_{aq} and TAR_{HC} have been used as proxies for aquatic and terrestrial sources (Ficken et al., 2000; Silliman et al., 1996), while other studies have used an n -alkane index calculated on the average chain length (ACL) of all n -alkanes combined (Hällberg, 2024; Aichner et al., 2018). There is also a partial overlap in n -alkane patterns between groups of primary producers (i.e., macroalgae and seagrass that both contain the short-chain n -alkanes C_{15} and C_{17} ; Chevalier et al. 2009; Mead et al., 2005) and by combining all n -alkanes identified in the seagrass biomass the accuracy of the proxy improved. Furthermore, as n -alkanes are resistant to degradation processes they can remain stable in the sediment for long time (Meyers, 2003). Indeed, the *Zostera*-ratio was consistent with the presence of seagrass remains from the scanned and visually inspected sediment at all depths. The positive relationship between %OC and *Zostera*-ratio was seen in sediments with a wide range of

Zostera-ratios (Getevik and Västra Korsvik had limited ranges) showing that n -alkanes can be a tracer for OC sources in seagrass sediments. When considering all cores combined the explanatory power of the *Zostera*-ratio was lower (i.e. ~50 %) compared to the levels for the specific sites where we found a significant relationship between %OC and *Zostera*-ratio (66 to 81 %). The reason for this was that two of the six sites showed no significant correlative relationship between %OC and *Zostera*-ratio, which reduced the explanatory power when considering all cores. This is likely driven by that the sedimentary OC content is influenced by site-specific characteristics, such as sediment properties, hydrodynamic exposure and primary productivity shown in previous studies (Dahl et al., 2023, 2020b, 2020a). The clear relationship between *Zostera*-ratio and OC content highlights that the presence of seagrass plant material in the sediment matrix (at all depths) promotes higher OC storage and permanence, which is likely due to the high re-fractory material, such as lignin, of the seagrass plant biomass (Trevathan-Tackett et al., 2017, 2020). The belowground seagrass plant material has a higher content of lignin compounds in comparison to the leaf structures (Klap et al., 2000). Interestingly, when assessing specific n -alkanes separately, C_{19} and C_{21} had a significant positive correlation to the %OC in the sediment, and were also the n -alkanes with the highest concentrations in the belowground seagrass biomass (Dahl et al., 2024). This indicates that OC derived from *Z. marina* roots and rhizomes have a higher stability and make up most of the seagrass-derived OC stored in the sediment.

At the Kristineberg site, the OC content and *Zostera*-ratio displayed an oscillating pattern clearly visible in the scanned images of the cores, and possibly reflecting a fluctuating seagrass area distribution with declines and re-establishments at this site. The distribution of *Z. marina* can vary extensively, both in space and over time (Frederiksen et al., 2004a) and large meadow changes in areal cover may occur depending on factors such as ice cover, storms and stochastic events (Frederiksen et al., 2004b; Krause-Jensen et al., 2003), which could potentially explain the variation in *Zostera*-ratio and OC concentrations in the sediment. At the Gåsö sites, the seagrass-associated n -alkanes appeared

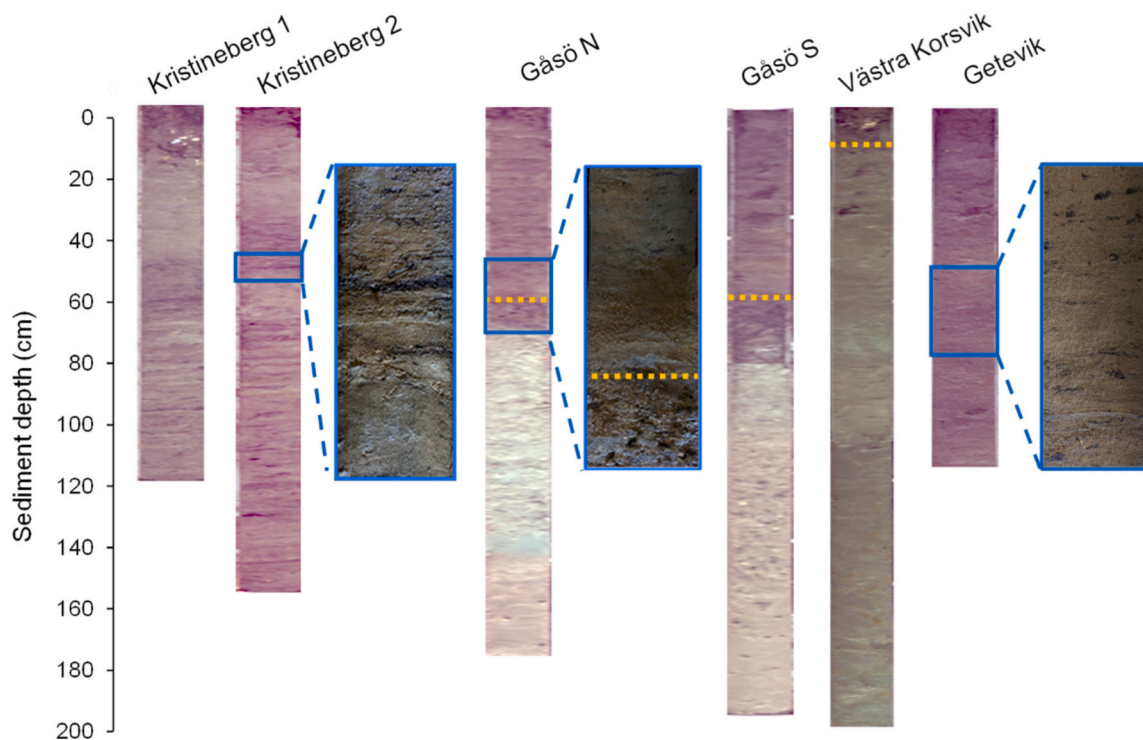


Fig. 2. Scanned images and photos of the sediment cores. The darker bands in the scanned images show remains of seagrass biomass, which is also illustrated in the zoomed pictures (blue boxes). The layers in gray colors show clay and sand deposits. The dashed yellow lines in the Gåsö sites and Västra Korsvik indicate the first appearance of the seagrass in the sediment record, with the deeper part of the sediment composed of layers of post-glacial clays.

around 60 cm down in the sediment depth profile, which has in a previous study been dated to approximately 2000 years ago (Dahl et al., 2024) and demonstrates the millennial scale permanence of *Z. marina* carbon sinks. In Getevik, the OC content remained consistently high (approximately 8–10 %) throughout the sediment profile while at the same time showing large variations in *Zostera*-ratio (varying between 0.001 and 0.32), indicating differences in the OC source composition along the sediment profile. The sediment at Getevik is muddy, with high OC content and low density (e.g. six times lower sediment density compared to Kristineberg; Dahl et al., 2020a) and a seagrass sediment thickness that extends over 2 m of depth (Dahl et al., 2023). These sediment characteristics are usually associated with oxygen deficiency and high preservation of organic matter, independent of OC quality (Schmidt et al., 2011). This could result in larger proportions of labile organic matter being stored, which could explain the high OC content

and the lack of pattern with the *Zostera*-ratio. In contrast, at Västra Korsvik, the seagrass sediment layer was only 11 cm deep (Dahl et al., 2023) and exhibited very low concentrations of both seagrass-derived *n*-alkanes and OC, missing the higher OC and *n*-alkane peaks (with a maximum *Zostera*-ratio of 0.014 and OC content of 1.4 %) observed elsewhere, indicating less influence of seagrass-derived OC and more terrestrial OC in the sediment as seen in the PLS biplot.

The input of both allochthonous and autochthonous OC is important for the seagrass carbon sink function and understanding OC provenance is also vital for assessing BC storage in relation to natural and anthropogenic impacts in the coastal environment (Gerald et al., 2019). While the PLS biplot shows that the OC accumulation in *Z. marina* sediments is complex, involving multiple OC sources, the *Zostera*-ratio is shown to be a valuable tool for understanding BC dynamics in *Z. marina* meadows. Lipid biomarkers (*n*-alkanes) show promise for deciphering the complex

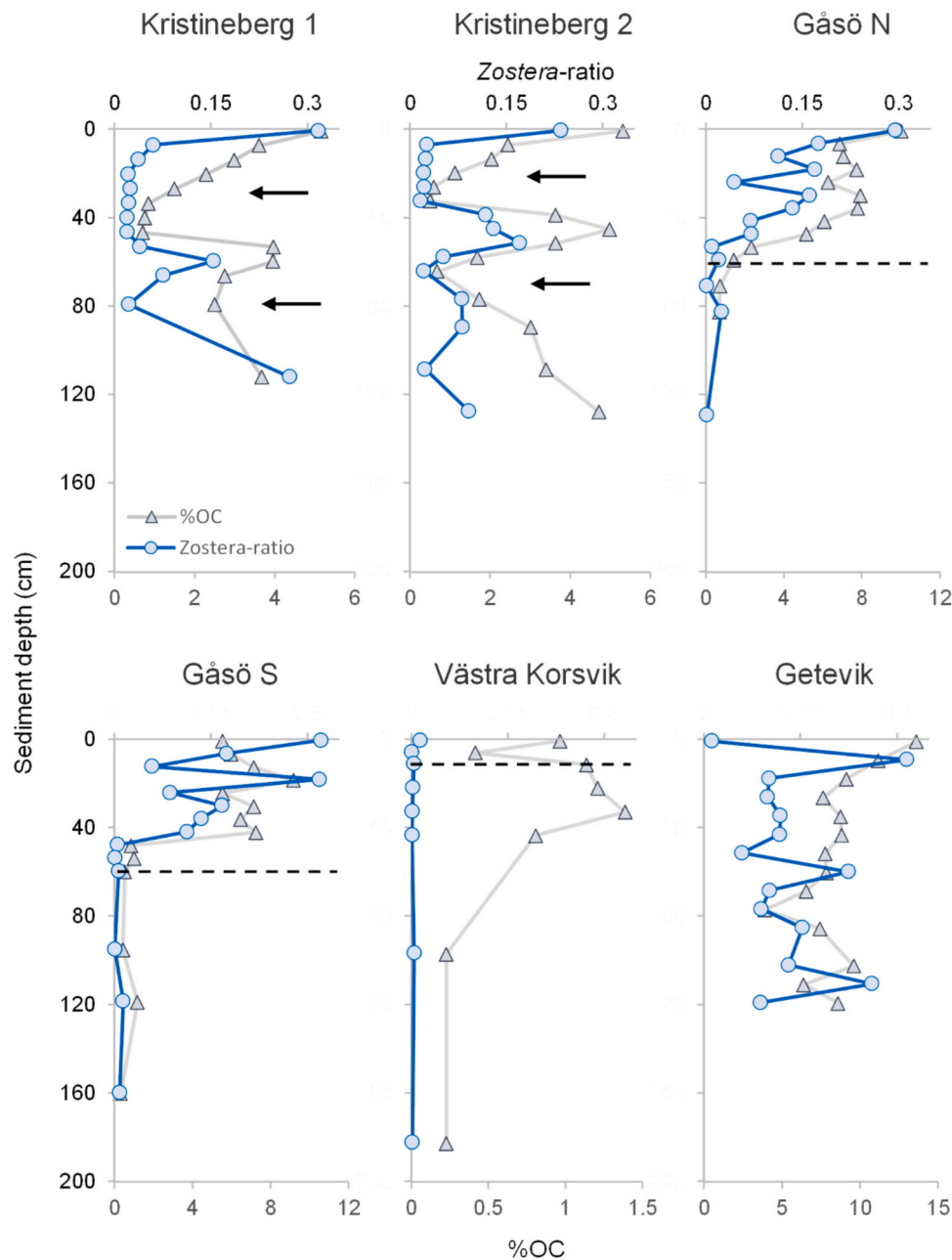


Fig. 3. The %OC and *Zostera*-ratio across sediment depths for the individual cores. The dashed lines indicate the maximum depth of seagrass sediment found at Gåsö and Västra Korsvik (based on the presence of seagrass plant material along the cores; Fig. 1; Dahl et al., 2023). For Getevik and Kristineberg, the seagrass sediment extended the entire core length. Arrows indicate potential seagrass biomass decline. Note the difference in scale for %OC.

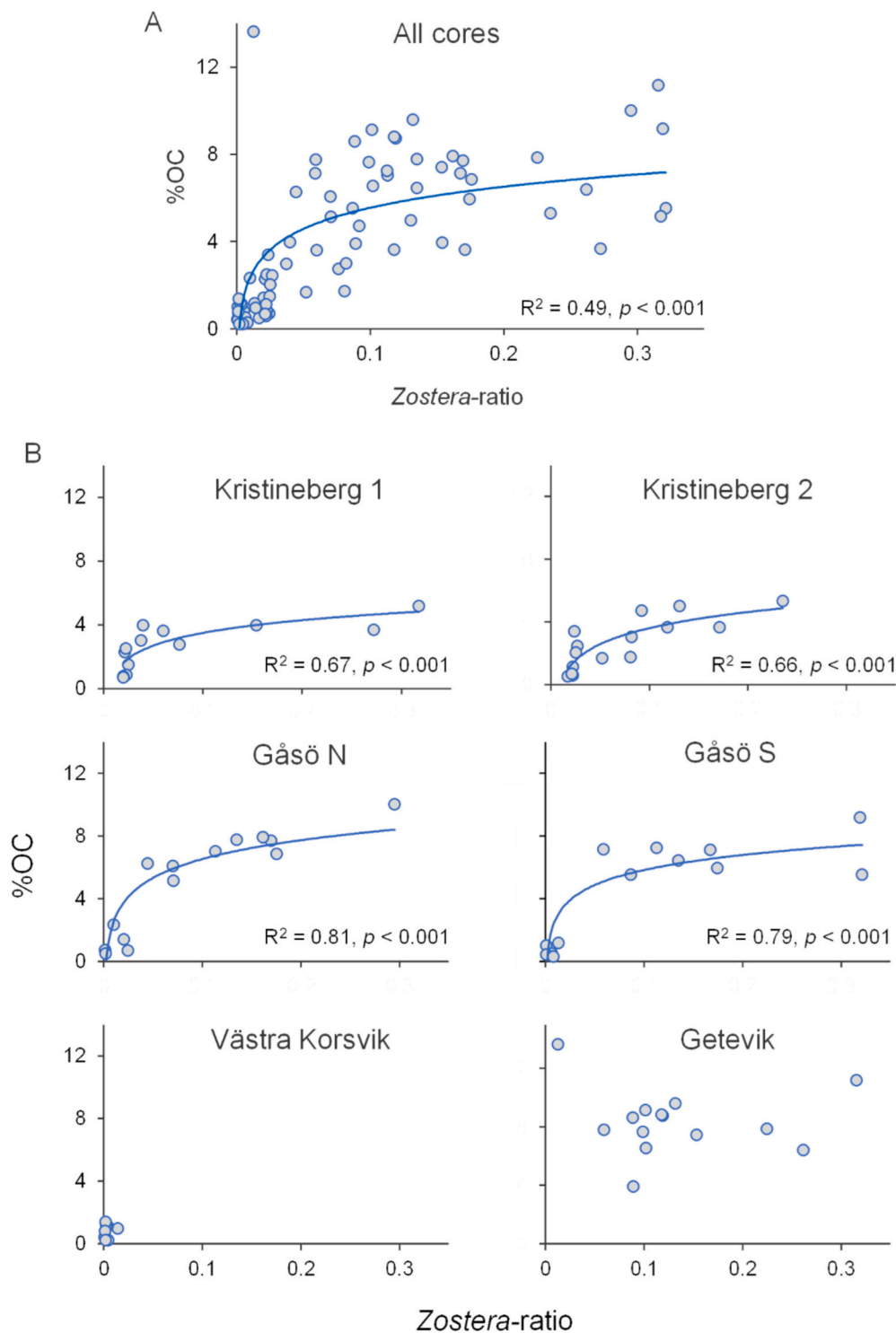


Fig. 4. The relationship between %OC and *Zostera*-ratio for all cores combined (A) and individual cores (B). In Getevik and Västra Korsvik, no correlation was seen.

matrix of sediment OC sources and for linking total sediment OC with seagrass plant debris accumulation, but we encourage further studies that use multiple proxies and techniques to assess OC source composition in BC ecosystems.

CRediT authorship contribution statement

Martin Dahl: Writing – original draft, Visualization, Investigation, Funding acquisition, Formal analysis, Conceptualization. **Maria E. Asplund:** Writing – review & editing, Visualization, Investigation,

Funding acquisition, Formal analysis, Conceptualization. **Mats Björk:** Writing – review & editing, Investigation, Funding acquisition, Conceptualization. **Sanne Bergman:** Writing – review & editing, Formal analysis. **Sara Braun:** Writing – review & editing, Formal analysis. **Sara C. Forsberg:** Writing – review & editing, Visualization. **Petter Hällberg:** Writing – review & editing, Formal analysis. **Elin Löfgren:** Writing – review & editing, Formal analysis. **Rienk Smittenberg:** Writing – review & editing, Formal analysis. **J. Robin Svensson:** Writing – review & editing, Investigation. **Martin Gullström:** Writing – review & editing, Investigation, Funding acquisition, Formal analysis,

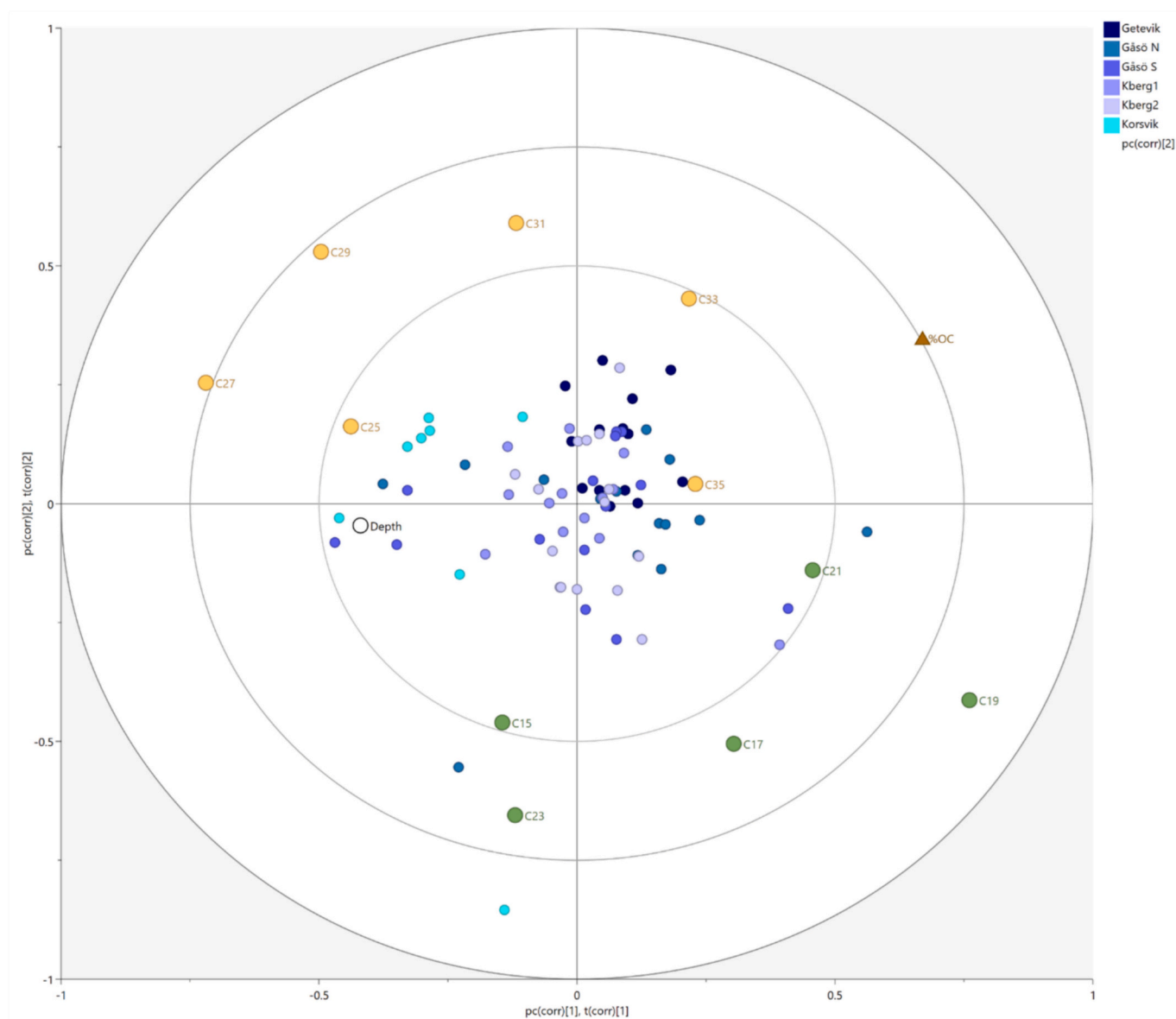


Fig. 5. Partial least squares (PLS) biplot showing the fractional composition of the *n*-alkanes (odd C₁₅–C₃₅) at all sediment depths in the cores from each site (shown in different colors), and in relation to the % sedimentary OC as the response variable. The *n*-alkanes expected to be related to the presence of OC from *Zostera marina* biomass are labeled in green. Depth is representing the sediment profile depth as a predictor variable.

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.

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Data availability

Data will be made available on request.

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