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High Seasonal Variability in Sediment Carbon Stocks of Cold-Temperate Seagrass Meadows

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Key Points:
- There is a large within-year variation in carbon storage in the topmost 30 cm of sediment for cold-temperate *Zostera marina* meadows
- A significant proportion of the sedimentary organic carbon stocks is not stable but recycled within the year
- Sampling of sedimentary organic carbon stocks within one season might result in unrepresentative carbon stock estimates

Supporting Information:
- Supporting Information S1

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Abstract Seagrass meadows have a high ability to capture and store atmospheric CO_2 in the plant biomass and underlying sediment and thereby function as efficient carbon sinks. The seagrass *Zostera marina* is a common species in the temperate Northern Hemisphere, a region with strong seasonal variations in climate. How seasonality affects carbon storage capacity in seagrass meadows is largely unknown, and therefore, in this study, we aimed to assess variations in sedimentary total organic carbon (TOC) content over a 1-year cycle in seagrass meadows on the Swedish west coast. The TOC was measured in two *Z. marina* sites, one wave exposed and one sheltered, and at two depths (1.5 and 4 m) within each site, every second month from August 2015 to June 2016. We found a strong seasonal variation in carbon density, with a peak in early summer (June), and that the TOC was negatively correlated to the net community production of the meadows, presumably related to organic matter degradation. There was seasonal variation in TOC content at all sediment sections, indicating that the carbon content down to 30 cm is unstable on a seasonal scale and therefore likely not a long-term carbon sink. The yearly mean carbon stocks were substantially higher in the sheltered meadow (3,965 and 3,465 g m^{-2}) compared to the exposed one (2,712 and 1,054 g m^{-2}) with similar seasonal variation. Due to the large intra-annual variability in TOC content, seasonal variation should be considered in carbon stock assessments and management for cold-temperate seagrass meadows.

1. Introduction

Seagrass meadows have the ability to accrete thick sediment layers and efficiently accumulate belowground carbon deposits (Fourqurean et al., 2012; Mcleod et al., 2011), but not all seagrass areas can be considered carbon sinks (Belshe et al., 2018; Dahl, 2017; Enríquez et al., 2019; Morse et al., 1987). The seagrass *Zostera marina* is a common species in the temperate zone of the Northern Hemisphere, creating meadows with a high carbon storage potential where the seagrass areas in the Skagerrak-Kattegat strait and in the Mediterranean show particularly large carbon stocks, exceeding the stocks found in many terrestrial environments (Mcleod et al., 2011; Röhr et al., 2018). There is, however, a large variation in carbon storage efficiency among *Z. marina* habitats (Dahl, 2017; Green et al., 2018; Kindeberg et al., 2018; Röhr et al., 2016, 2018), which is mainly related to the location of the meadow, where water depth, salinity, and exposure to hydrodynamic forces are regulating the sedimentary carbon accumulation (Dahl, Deyanova, Gütschow, et al., 2016; Prentice et al., 2019; Röhr et al., 2018). Understanding this variability is a key issue for conservation and protection of these important carbon sinks as some areas are deemed to have a lower accumulation of carbon than others, such as in the Baltic Sea, where *Z. marina* is mainly found in less sheltered sites compared to the Skagerrak area (Dahl, Deyanova, Gütschow, et al., 2016; Jankowska et al., 2016; Röhr et al., 2016).

1.1. Seasonal Variation in Cold-Temperate Seagrass Ecosystems

In the cold-temperate zone of the Swedish west coast, there is a strong seasonality with water temperatures ranging from icy conditions during winter to mild summers with up to 25 °C in the water (Baden & Boström,

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2001) and with increased light insolation during the summer. This seasonality regulates the growth and productivity of vegetation in the marine environment (Orth & Moore, 1986; Sand-Jensen, 1975; Watanabe et al., 2005) and on the Swedish west coast the growth season stretches from May through November with a peak in August (Baden & Pihl, 1984). During the summer, the *Z. marina* biomass, shoot density, and canopy height increases (Boström et al., 2003), and as the temperature and light insolation decrease during autumn and winter the seagrass acclimatizes by reducing the aboveground biomass through shedding of leaves, whereas the root-rhizome biomass still remains in the sediment and uses carbohydrate reserves stored in the belowground parts of the plant (Baden & Pihl, 1984; Burke et al., 1996). As the water temperature is considerably lower during the winter, the microbial activity in the sediment is reduced, potentially leading to less degradation and remineralization of organic carbon (Arnosti et al., 1998). The hydrodynamic conditions also change with season, with higher frequency of storms during the autumn and winter (Swedish Meterological and Hydrological Institute, 2002). During a storm event, there is a sudden increase in hydrodynamic forcing, leading to resuspension and erosion of sedimentary carbon (Dahl et al., 2018). The meadow canopy can, however, decrease the effect by attenuating the water velocity (Fonseca & Cahalan, 1992; Fonseca & Fisher, 1986; Infantes et al., 2012) and stabilizing the sediment (Chen et al., 2007; Luhar et al., 2008), while during periods with low meadow canopy and shoot density, as seen in the winter season, the seagrasses ability to reduce the water flow becomes reduced or impaired (Adhitya et al., 2014; Lawson et al., 2012). Thus, a strong seasonality has the potential to influence (in a negative or positive way) the sedimentary total organic carbon (TOC) stocks in *Z. marina* meadows. However, most studies assessing seagrass carbon storage in temperate regions have been performed during the summer and to our knowledge only two studies have examined TOC stock variation across seasons in seagrass meadows. These studies were performed in subtropical or warm-temperate seagrass meadows and revealed only minor to moderate variation in sedimentary carbon stocks (Samper-Villarreal et al., 2018; Sousa et al., 2019). However, as seasonality is stronger in cold-temperate areas with larger seasonal variation in environmental conditions, the influence on the carbon stocks will likely be stronger compared to the subtropical and warm-temperate regions, where the seasonal variation in seagrass growth and productivity, although existing, is not as pronounced (Pérez et al., 2006; Sousa et al., 2019; Thorhaug & Roessler, 1977). In this study, we measured the sedimentary TOC content during the course of a year in two *Z. marina* meadows (in both the shallow and deeper parts of the meadow within each site) to examine the effect of seasonality on the carbon storage capacity. With regard to the strong seasonality in cold-temperate regions, the specific aims were to (1) assess seasonal variations in carbon storage, (2) compare the seasonal variation in carbon stocks of the two hydrodynamically different sites and at the different water depths, and (3) examine the relationship between sedimentary TOC and seasonal variation in environmental factors (i.e., light intensity and water temperature), seagrass biomass, and net community production (NCP).

2. Method

2.1. Study Sites

The study was conducted in the Gullmar Fjord on the Swedish west coast (Figure 1). Two *Z. marina* meadows, located in Getevik (58°16′26″N, 11°30′19″E) and at Kristineberg (58°14′55″N, 11°26′54″E), were selected and within each site two sampling areas were determined, one shallow (1.5 m) and one deep (4 m). The two sites were selected based on their difference in exposure level to wind and waves and represent a variation of hydrodynamic conditions in which *Z. marina* meadows are commonly found on the Swedish west coast. The Getevik site is sheltered from hydrodynamics and mostly surrounded by land, and the sediment has a muddy low-density composition, while the Kristineberg site is more exposed to waves and wind events with courser sediment in the shallow parts of the meadow and which becomes finer with depth (Figure 1). The meadow at Kristineberg grew from c. 1- to 6-m depth, while in Getevik the meadow extended from c. 0.5- down to 5-m depth. To characterize the hydrodynamic exposure at both sites, waves and currents were recorded between the 2 and 25 of October 2015. A storm with wind speeds of ~30 knots was recorded on the 6 to 8 of October. At each site, one acoustic Doppler velocimeter (Vector, Nortek) was deployed at 1-m depth and used to record the wave and orbital velocity data. The instrument was placed 15 cm above the seabed, and measurements were taken in bursts every 1 hr, for 4,096 records at 8 Hz (Infantes et al., 2012). To identify flow conditions during average conditions as

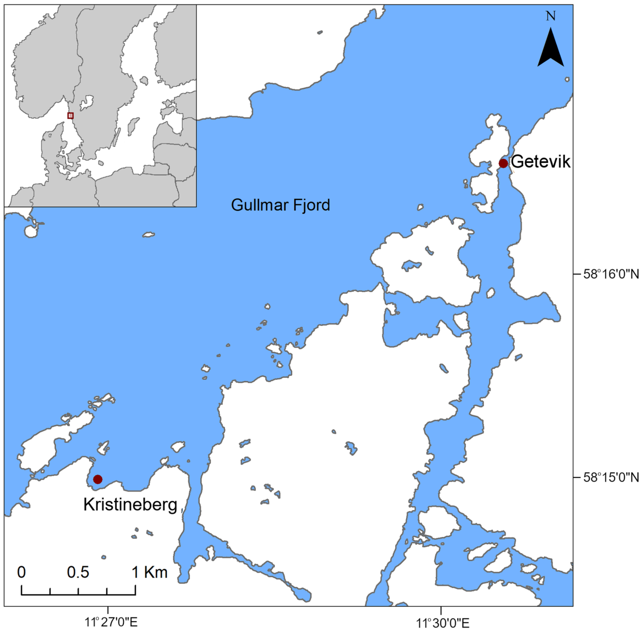

Figure 1. Map of the two study sites in the Gullmar Fjord. The site in Getevik is wave-sheltered compared to the open bay of Kristineberg. In each site, a shallow (1.5 m) and a deep (4 m) area of the *Zostera marina* meadows were sampled.

well as during a storm event, the mean wave heights and orbital flow velocities were calculated for the whole period of deployment, and the maximum wave heights and maximum orbital velocities were calculated for the storm event (Table 1).

2.2. Sediment Sampling

Sediment sampling was conducted in each site at both shallow (1.5 m) and deep (4 m) water depths every second month from August 2015 to June 2016 (making a total of six sampling periods) using SCUBA. For each sampling occasion, three sediment cores ($n = 3$) were collected using a push-corer ($h = 50$ cm, ø = 8 cm) at each site and water depth within each site, rendering a total of 72 cores for the whole year. The push-corer was sharpened at the edge to reduce core shortening (either through compaction of the sediment or friction between the sediment and the core) and to make it easier to shred the seagrass roots and rhizomes when pressing down the corer. The compression of the sediment, which might influence the carbon density estimates (Glew et al., 2001), was recorded ($n = 3$) at each site and water depth by measuring and comparing the inner and outer length of the corer when placed in the sediment. The corers were stored vertically and the total lengths of the sediment cores were measured before dividing them into depth slice intervals. Each core was then sliced at a maximum of six depth intervals, including 0–2.5, 2.5–5, 5–12.5, 12–25, 25–37.5, and 37.5–50 cm. Most of the cores only reached the 25 to 37.5-cm interval layer due to core shortening or difficulties in pressing down the cores.

2.3. Measurements of Environmental and Biological Variables

In order to explore the influence of explanatory factors on TOC stock variability, several environmental and biological variables were measured in close vicinity of the sediment sampling at both deep and shallow parts of the two sites. Seagrass biomass was collected ($n = 3$) from a 0.16 × 0.16-m frame and dried at 60 °C for approximately 48 hr for estimates of above- and belowground biomass dry weight (DW). Photosynthetic active radiation (PAR; Odyssey, New Zealand) and water temperature loggers (HOBO Water Temperature Pro v2 Data Logger - U22-001, ONSET, USA) were deployed in the seagrass canopy in August 2015, with a log interval of 30 min. Every second month, when sediment cores and biomass data were collected, the loggers were cleaned from epiphytes, and the data were downloaded. For measurements of NCP, semi-rigid benthic chambers ($n = 3$; Dahl, Deyanova, Lyimo, et al., 2016) with a known volume were deployed every second month with start in August 2015. Water samples to measure dissolved oxygen were collected through a vial in the chamber before and after the incubation using a 50-ml syringe. The dissolved oxygen concentration was measured immediately after sampling with a multimeter (Multi 3430, WTW) connected to an oxygen sensor (FDO 925). In April to October, the NCP incubations were performed three times during a 24-hr cycle (morning, afternoon, and night), while in December and February, the incubation took place only two times (midday and night) due to the short days and few hours of daylight during the winter season. The timespan for each incubation lasted approximately for 2 hr, and the exact time was recorded. In between the measurements, the chambers were completely opened to allow for natural light and water conditions.

Table 1
Hydrodynamic Conditions (i.e., Wave Heights and Bottom Orbital Velocities) Were Measured at Kristineberg and in Getevik in October 2015

Hydrodynamic property	Kristineberg	Getevik
Mean wave height (m)	0.25	0.10
Max. wave heights (m)	0.35	0.15
Mean orbital velocity (cm s^{-1})	6	2
Max. orbital velocities (cm s^{-1})	10	3

2.4. Sedimentary Carbon Analysis

The sediment samples were cleaned from seagrass roots and rhizomes, large shells, and stones prior to drying. The sediment was dried at 60 °C for approximately 48 hr until constant weight and subsequently ground to a fine powder using a mixing mill (Retch 400). The carbon and nitrogen content (percent of dry weight sediment, % DW) was analyzed using a Carbon Nitrogen elemental analyzer (Flash 2000, Thermo Fisher Scientific). Prior to TOC analysis, the sediment samples were treated with 1-M HCl to remove inorganic carbon and dried for 24 hr. The TOC content was calculated based on the bulk weight of the sediment prior to the HCl treatment. A smaller subset ($n = 33$) was used to assess total inorganic carbon (TIC), which is assumed to be low in cold-temperate *Z. marina* meadows, presumably due to low abundances of epiphytic calcifying algae (Mazarrasa et al., 2015). Sediment organic carbon density ($g{\cdot}C{\cdot}cm^{-3}$) was calculated from the weight of the sample after removing larger shells, stones, and biomass (which affected the weight marginally) divided by the volume of the sliced core and multiplied by the percent organic carbon.

2.5. Statistical Analysis

Prior to all analyses, the sediment data were corrected for core compression as well as checked for normal distribution and homogenous variances, and if these assumptions were not met, log-transformation (log10) was used. All statistical analyses were conducted in R (version 2.15.3) except for the partial least square (PLS) modeling, which was performed using the SIMCA (version 15.0.2) software (UMETRICS). To assess and compare sedimentary TOC variation across months and differences between sites, a nested linear mixed-model analysis was conducted (lme4 package). In the comparison of TOC content among months, sediment slice depth (excluding the deepest section, i.e., 37.5–50 cm, because it was missing in several cores) was nested in core, and core nested in site (deep and shallow parts of the meadow at the two sites) and for the analysis of differences between sites sediment slice depth was nested in core. Where there were significant differences, Tukey's test was performed to determine which months and sites that were significantly different from each other. Effects in TOC density with sediment depths among months were compared using a generalized additive mixed model (gamm, mgcv package) with sediment slice depths nested in site. The k value for the curves was set to 3, which is at least two curvatures less than the unique data points of the profiles. Relationships between the TOC stocks (0–25 cm) and seagrass biomass (i.e., above/belowground biomass, total biomass, and above-/belowground-ratio), NCP, and environmental variables (i.e., light intensity [PAR] and water temperature) were tested using a PLS regression, which takes into account multicollinearity (Wold et al., 2001). In order to compare the variation in sediment carbon density along the sediment depth profiles, the precision (coefficient of variation [CV]) of the different months was calculated as a function of the months' standard deviation (SD) divided by the yearly mean. The CV value shows the deviation from the mean (with lower values having larger deviation), which in this case was used to assess the stability of the sedimentary carbon density along the depth profiles throughout the year.

3. Results

3.1. Seasonal Variation in Sedimentary TOC Content

When comparing mean TOC densities ($g\ cm^{-3}$), based on pooled sediment core depths (0 to 37.5 cm from the sediment surface) over the year, we found an increase from winter to summer with June having significantly higher levels compared to all other months and a TOC density in October that was higher than in August (Tukey's honestly significant difference, $p < 0.05$; Figure 2). The station which remained most stable in TOC content over the year was the deep area in Getevik, with only a decrease in August (Figure 3). In the two depths in Getevik, TOC densities in April were the most similar to the yearly average (Figure 3a), while in the two depths at Kristineberg, December and October had the highest resemblance (Figure 3b). The TOC densities in the depth profiles of February and June differed significantly across the different depth sections ($df = 5$, $F = 4.3$, $p < 0.001$), with a general decrease in TOC content with depth, while the other months showed more stable TOC content with depth (Figure 4). There was no clear difference in precision (CV) among the different depth segments in the sediment profiles (down to 30 cm) over the year (Figure 5), which indicates a similar instability of the carbon density for all depth sections across the different seasons. The TOC stocks ($g\ m^{-2}$) varied among seasons with a reduction of the carbon content during the winter months (December and February) and a buildup from spring (April) to autumn (October; Figure 6).

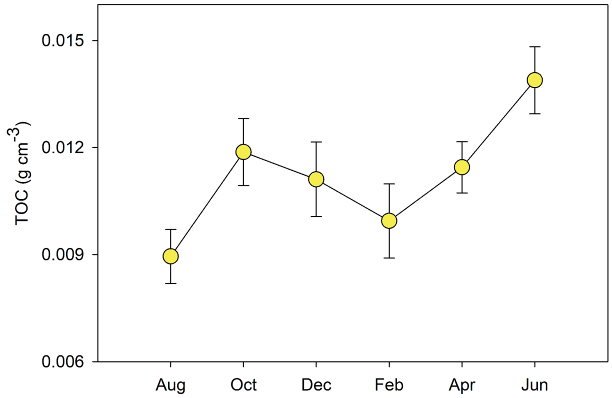

Figure 2. The mean (±standard error) total organic carbon density (g cm^{-3}) from August 2015 to June 2016 for both sites and water depths pooled (i.e., Getevik and Kristineberg and with both water depths, 1.5 and 4 m) shown for the whole sediment cores (0–37.5 cm). TOC = total organic carbon.

3.2. Relationship Between TOC Stock and Predictor Variables

NCP, seagrass biomass, water temperature, and light intensity were used to predict the TOC stock variability and are presented in supporting information, Figure S1. The PLS model was significant (>0.05 cross-validated variance; Q2 statistics), although the cumulative explanation of all the variables combined was low (14%). The NCP (g·C·m^{-2}·day^{-1}) explained most of the variation in TOC stocks (0–25 cm, g m^{-2}) in the PLS model and was the only predictor with a variable influence on the projection value >1 (Figure 7). The correlation between NCP and TOC stock was negative (Figure 7).

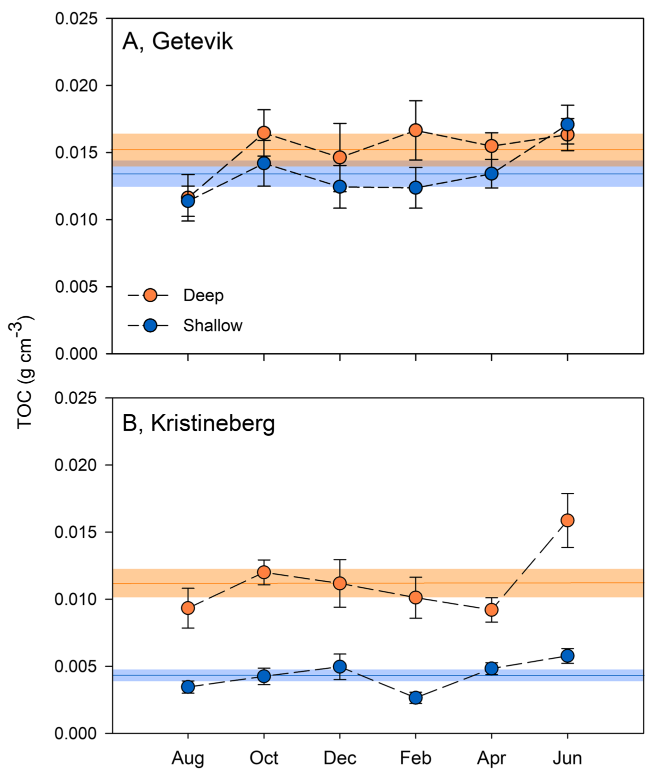

Figure 3. The mean (±standard error) total organic carbon (TOC) density (g cm^{-3}) from August 2015 to June 2016 for (a) Getevik and (b) Kristineberg. The horizontal line represents the yearly TOC average for the two different water depths (shallow, 1.5 m; deep, 4 m) with the shaded area being the confidence interval (± 95%).

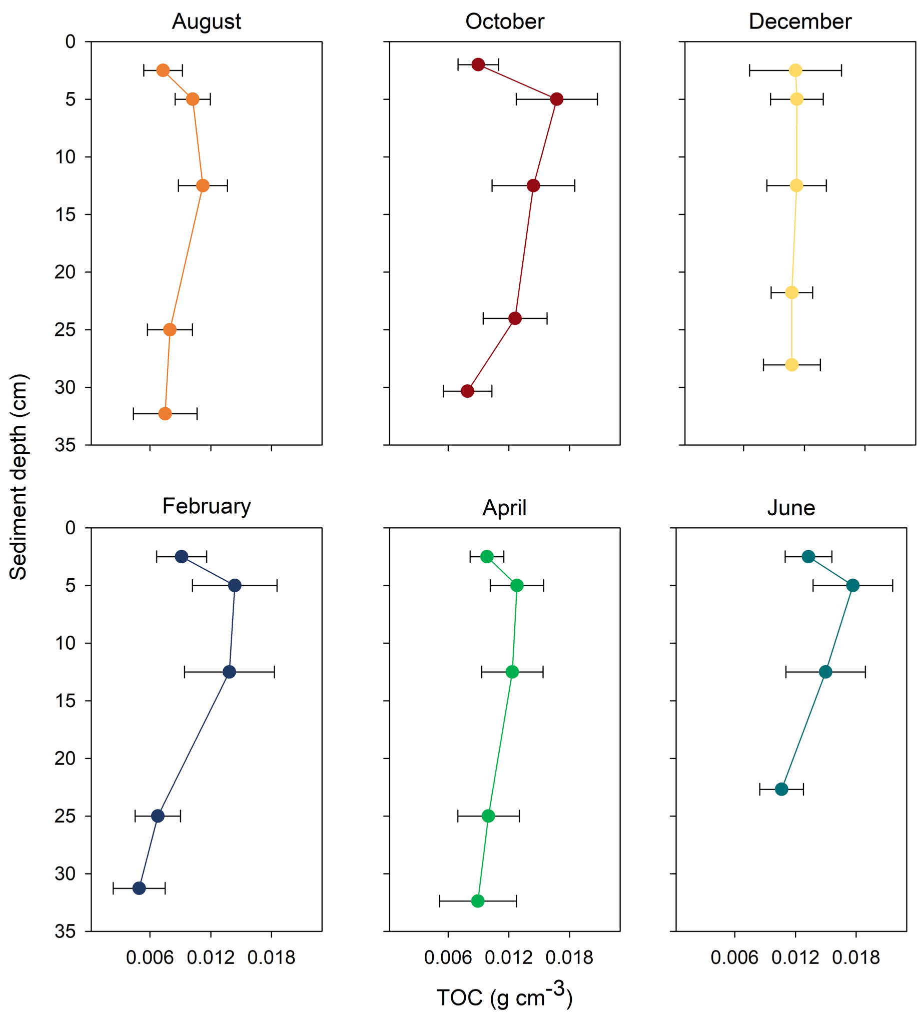

Figure 4. The mean (± standard error) total organic carbon density (g cm^{-3}) for the different sediment depth segments from August 2015 to June 2016 with both sites combined (Getevik and Kristineberg) and including both shallow and deep water depths (i.e., 1.5 and 4 m, $n = 12$). Sediment depths were corrected for core shortening. TOC = total organic carbon.

3.3. Variability in Sedimentary Carbon Stocks Among and Within Sites

There was a significant difference in TOC density (g m^{-2}) among the four stations (i.e., the two water depths at the two sites; Tukey's honestly significant difference, $p < 0.01$), except between the shallow and deep areas at Getevik (Figure 8). The highest TOC stock was found in the deep (4 m) water depth of Getevik and the lowest was found in Kristineberg's shallow (1.5 m) water depth (Figure 8; Table 2). In comparison to the findings of Röhr et al. (2018), both water depths at the Getevik site had a higher TOC stock than the average *Z. marina* meadows of the Northern Hemisphere, but lower than other *Z. marina* meadows in the Kattegatt-Skagerrak region (Table 2). The deeper (4 m) area of Kristineberg had a similar TOC stock to the average *Z. marina* meadows in the Northern Hemisphere, while the shallow water depth had a lower TOC stock (Table 2). The TIC density (g m^{-2}) was similar in all four stations and low in comparison to the TOC concentrations (Table 2).

4. Discussion

In this within-year comparison, there was a high fluctuation in sediment carbon content down to 30 cm, with the highest carbon content during early summer (in June). This variation introduces an additional uncertainty for carbon storage assessments in *Z. marina* meadows as it indicates that a large proportion of the sedimentary carbon is not stable over the year and might result in significantly different carbon

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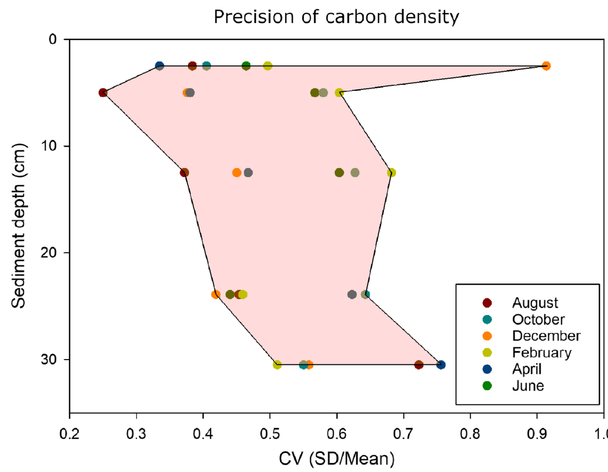

Figure 5. The shape of the precision (coefficient of variation [CV]) of carbon density over the year for the different sediment depths along the profiles (0–30 cm). The "straight" shape of the precision area shows that there is no major difference in the variation of sedimentary carbon density in the sediment sections. Mean = yearly average, SD = standard deviation of the months.

storage estimates depending on when the sampling occurs. Given that most sampling campaigns take place only once, and usually during the summer period (June to August in the northern temperate region), we suggest that sampling in northern *Z. marina* meadows in spring (April) or autumn (October) would result in more representative carbon measures, with less deviation from the yearly mean, compared to the summer and winter periods, or that sampling is repeated for more than one season.

4.1. Seasonal Variation of Sedimentary Carbon

During spring to autumn (April to October), the sediment generally had a high carbon density, except for August, with a significant peak in June. The increasing level of carbon accumulation from spring to autumn indicates a buildup of organic matter that coincides with an increase of seagrass biomass production and trapping of allochthonous material during the temperate growth season (Baden & Pihl, 1984). This might lead to a gradual increase in accumulated detritus and belowground deposits of organic material, which is highest when the biomass production ceases at the end of the growing period in the autumn, and as the water temperature decreases during October, the decomposition of organic matter is likely reduced (Arnosti et al., 1998; Waksman & Renn, 1936). Although interannual variability was not examined in this study, the low TOC stocks in August might be due to a generally less productive year (in 2015) as this month was the first

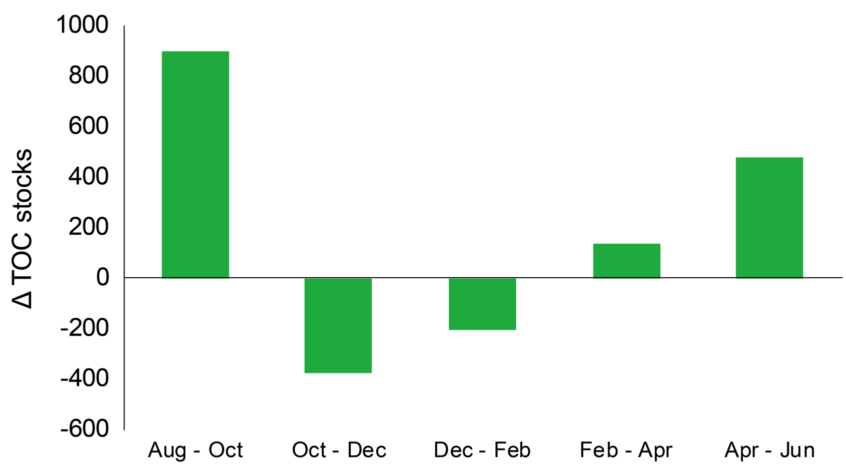

Figure 6. Changes in TOC stocks (0–25 cm, g m^{-2}) between the different months from August 2015 to June 2016. TOC = total organic carbon.

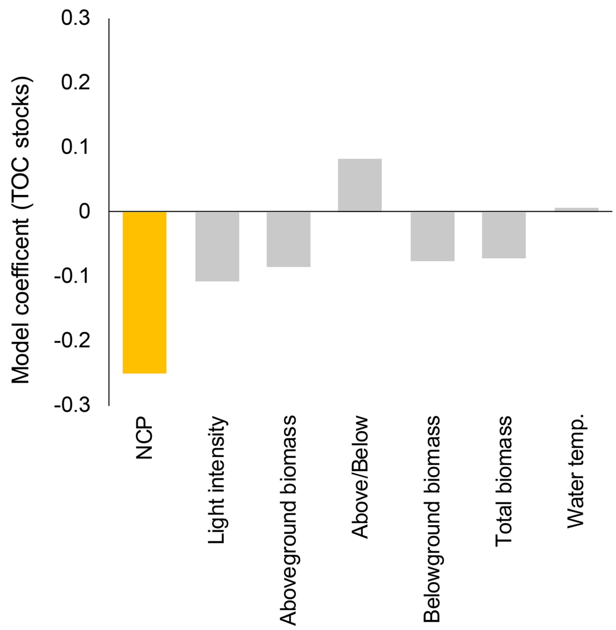

Figure 7. Partial least square (PLS) coefficient plot showing the relationship between TOC stock (0–25 cm, g m^{-2}) and different explanatory (predictor) variables. The different predictors are sorted after level of importance (left to right), and the yellow bar color indicates the only variable with a variable influence on the projection value >1 (and thereby contributing more than average to the model). NCP = net community production (g·C·m^{-2}·day^{-1}), Light intensity = photosynthetic active radiation (μmol·e^{-}·m^{-2}·24hr^{-1}), Above/below = above- and belowground seagrass biomass-ratio, Total biomass = above- and belowground biomass combined. The seagrass biomass predictors were calculated as g·DW·m^{-2} and water temperature as °C. See supporting information, Figure S1 for the data of the explanatory variables used in the modeling. TOC = total organic carbon.

period of measurement in this study. However, monitoring data from an oceanographic (Moored) buoy near Kristineberg marine research station show no differences in sea temperature, PAR, precipitation, and wind speed between 2014 and 2017, indicating that the time period of the study is representative for the general conditions and gives no indications that 2015 was less productive than 2016 (supporting information, Figure S2). The carbon density depth profiles in June and February showed a different pattern compared to the profiles taken the other months, which had straighter curvatures, with an increase in carbon content in the middle followed by a downward decline towards the end of the profile. In June, with its high accumulation of carbon, there was likely a faster build-up of organic matter in the surface layers due to high seagrass plant production and turnover, and input of allochthonous carbon, compared to the deeper sediment sections causing the more humped depth profile. However, this cannot explain the similar trend in February, which was the only month with extensive ice cover (lasting for 3 weeks, personal observation) that might have reduced the hydrodynamic conditions resulting in less erosion at the sediment surface, but it could also be related to an increased die-off of aboveground seagrass biomass in the autumn and winter (Baden & Pihl, 1984), potentially resulting in less accumulation of sedimentary carbon. Between the months, there were also differences at all levels of the sediment depth profiles, with a strong seasonal variability present down to at least 30 cm into the sediment, showing that the carbon stocks within this system is not stable but subjected to an internal cycling visible within a timespan of months. The upper most sediment (0–2.5 cm), however, showed the highest variability over the year, which was expected, as it is more oxic and likely contains more labile carbon and detritus material affected by degradation (Eldridge & Morse, 2000) as well as being more exposed to hydrodynamic processes than deeper sediment. The larger variation in the sediment surface was primarily due to the high CV value in December, which was the month with the most stable carbon content along the depth profile.

4.2. The Influence of Seasonality on Sedimentary TOC

The carbon stock variability was negatively linked to the net community production and although this seems contradictory, the high biomass production in summer and autumn (Baden & Pihl, 1984) and the associated

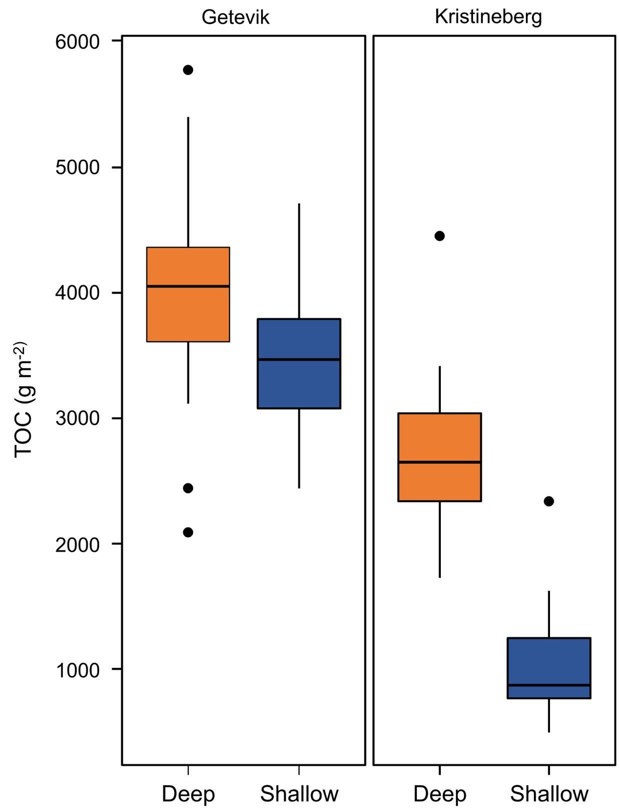

Figure 8. The total organic carbon stocks (0–25 cm, g m^{-2}) in *Zostera marina* meadows of Getevik and Kristineberg separated into deep (4 m) and shallow (1.5 m) water depths (n = 18 at each water depth). The horizontal lines show the median values, the boxes represent the first and third quartiles, the whiskers show the minimum and maximum values, and the black dots (•) are outliers. TOC = total organic carbon.

build-up of autochthonous and allochthonous organic matter will cause a high detritus pool subjected to an internal cycling by the microbial community (Trevathan-Tackett et al., 2017), resulting in higher respiration rates and hence a low or negative NCP. This might explain the negative correlation between NCP and TOC stocks as the increased sedimentary TOC during summer and autumn is a consequence of the high detritus formation, which to a large extent has been consumed by the microbial community, leading to both a negative NCP and high organic matter accumulation. However, a large part of the TOC variability was not explained in our model, and therefore, other factors might be of importance. The carbon accumulated in seagrass sediments is not in a steady state but subjected to various subsurface processes (e.g., seagrass production and exudation from roots and rhizomes, microbial decomposition of organic matter, and bioturbation by benthic organisms) working on different time scales (Belshe et al., 2017). The cycling of carbon and the subsurface processes are in turn influenced by seasonal variations and could contribute to the variability in carbon content at all depth layers found in this study. For instance, the belowground seagrass biomass can contribute a large part to the sedimentary carbon pool (Serrano et al., 2012), and the transport of carbon from the seagrass leaves to the belowground biomass can be substantial, with 6% to 17% of the production being released into the sediment as root and rhizome exudates (Moriarty et al., 1986), causing a continuous release of carbon to the deeper sediment layers. The production and turnover rate of roots and rhizomes are high in short-lived seagrass species, such as *Z. marina* (Duarte & Chiscano, 1999), and these processes may likely be enhanced during the growing season (May to November). The summer period has likely a faster decomposition of organic matter by the microbial community due to warmer temperatures (Arnosti et al., 1998; Waksman & Renn, 1936), and although the degradation is certainly highest in the oxygenated upper sediment layers (Sahm et al., 1999), remineralization is also affecting the deeper carbon deposits, causing a reduction of carbon in the lower sediment layers, although to a lesser degree (Mateo et al., 1997; Trevathan-Tackett et al., 2017). Oxygenation of the sediment varies over the season with higher oxygen release from the roots- and rhizomes during summer (August; Caffrey

Table 2
Summary of Carbon and Nitrogen Content (Yearly Mean ± Standard Error) for the Seagrass Sites Divided Into Shallow and Deep Areas, and in Comparison to Global and Regional Zostera marina Sedimentary Carbon Average Values

Site	TOC (%)	TOC density (g cm^{-3})	TOC stock (g m^{-2})	TIC density (g cm^{-3})	C: N	TON (%)
Getevik						
Deep	9.7 ± 0.10	0.0152 ± 0.0008	3965 ± 214	0.0020 ± 0.0007	10.1 ± 0.7	0.94 ± 0.014
Shallow	9.9 ± 0.25	0.0135 ± 0.0006	3465 ± 154	0.0010 ± 0.0004	9.7 ± 0.6	0.97 ± 0.022
Kristineberg						
Deep	2.2 ± 0.18	0.0112 ± 0.0006	2712 ± 146	0.0019 ± 0.0014	9.9 ± 0.7	0.24 ± 0.021
Shallow	0.3 ± 0.02	0.0042 ± 0.0003	1053 ± 108	0.0015 ± 0.0015	9.0 ± 1.3	0.03 ± 0.002
Comparison with Röhr et al. (2018)						
Z. marina (Northern temperate zone)			2721 ± 989			
Z. marina (Kattegatt-Skagerrak)			4862 ± 741			

Note. TOC: TON-ratio (%).
Abbreviations: C = carbon, N = nitrogen, TIC = total inorganic carbon, TOC = total organic carbon, TON = total organic nitrogen.

& Kemp, 1991), which could affect the organic matter degradation. Similarly, bioturbation can increase remineralization deeper down in the sediment through redox oscillation and reexposure to oxygen resulting in continuous decomposition (Aller, 1994) as well as a downward transport of labile organic matter (Kristensen & Holmer, 2001). These processes can hence both increase and decrease the carbon content and explain the within-year fluctuations in TOC at deeper sediment layers seen in this study.

4.3. Hydrodynamic Exposure

The main source sedimentary carbon in seagrass meadows in the Gullmar Fjord is of pelagic origin with a low contribution from autochthonous organic matter (Röhr et al., 2018), suggesting that trapping of carbon within the seagrass canopy by reducing the water velocity (Fonseca & Cahalan, 1992; Fonseca & Fisher, 1986) is of importance, which should likely be most efficient towards the end of the summer when the seagrass plants are at maximum height and density (Baden & Pihl, 1984). The winter season then allows for a lower accumulation rate as exposure to hydrodynamics increases, with less protection from the aboveground biomass (Adhitya et al., 2014; Lawson et al., 2012) due to the seasonal reduction in seagrass shoot density (Baden & Pihl, 1984), and with more frequent storms during late autumn and winter (Swedish Meterological and Hydrological Institute, 2002). The protection from wind- and wave actions in the deep area of Getevik might also explain the low seasonal variation in TOC as it is situated deeper (4 m compared to 1.5 m for the shallower site) and in a sheltered bay with less hydrodynamic forcing acting on the sediment, which otherwise could cause sedimentary erosion and export of organic matter (Dahl et al., 2018; Fourqurean & Rutten, 2004; Infantes et al., 2011). The exported carbon could be transported to adjacent shallow habitats and/or to the deep sea, where it can either be remineralized or contribute to the carbon storage in these environments (Duarte & Krause-Jensen, 2017). The low exposure to wind and waves, as seen in this study, likely also favors the accumulation of TOC in both deep and shallow areas in Getevik as the more exposed site of Kristineberg had overall lower carbon stocks, where the shallow part was the lowest of the two and the only site in this study with carbon stocks below the average of *Z. marina* meadows in the Northern Hemisphere (2721 ± 989 g m^{-2}; Röhr et al., 2018).

4.4. Inorganic Carbon and Nutrient Content

The TIC content was generally much lower in comparison to the global estimates for seagrass meadows (Mazarrasa et al., 2015), and the low inorganic carbon content in these cold-temperate seagrass systems is likely related to less epiphytic- and free-living calcifying algae growing in these meadows compared to warm-temperate and tropical regions (Mazarrasa et al., 2015; Semesi et al., 2009). Some tropical seagrass species can, for instance, be a direct source of inorganic carbon to the sediment by formation of aragonite crystals in the leaves (Enríquez & Schubert, 2014); this has, however, not been seen in any temperate seagrass species. The C: N ratio was similar to previous studies on the Swedish west coast (Dahl, Deyanova, Gütschow, et al., 2016; Pihl et al., 1999) and elsewhere in the region (Kindeberg et al., 2019), with low nitrogen content in relation to organic carbon levels, which is also commonly found in other seagrass areas (Gullström et al., 2018; Santos et al., 2019). The highest nitrogen content was found in the carbon-rich, sheltered site of Getevik, as the nitrogen content is known to positively correlate to both carbon- and silt-clay content (Kindeberg et al., 2018).

5. Conclusion

This study highlights the within-year dynamics of sedimentary carbon content and the influence of seasonality on carbon stock levels in cold-temperate seagrass meadows. Not only does *Z. marina* meadows display a large spatial variation in carbon storage (Dahl, Deyanova, Gütschow, et al., 2016; Green et al., 2018; Kindeberg et al., 2019; Röhr et al., 2018), but as shown in this study, there is also a high seasonal variability (at all sediment depth layers down to at least 30 cm) where sedimentary carbon levels both increased and decreased over the year. Our findings show a peak carbon density in June (0.0139 ± 0.0009 g cm^{-3}) and the lowest in August (0.0089 ± 0.0008 g cm^{-3}), and the PLS model indicated that there was a negative correlation between TOC stocks and NCP. However, as a large part of the variation in the PLS analysis could not be explained by the model, other factors, such as seasonal variability in internal cycling of carbon and decomposition rates (related to changes in water temperature) as well as hydrodynamic conditions, may also influence the TOC variation seen in this study. The carbon density over the year was generally variable throughout the sediment depth profiles (0–30 cm), which suggests that seasonality influences the temporal stability of the carbon content deeper down into the sediment. In comparison, the more sheltered site (Getevik) had higher carbon stock levels than Kristineberg, likely due to the difference in hydrodynamic exposure. At both shallow and deep areas in Getevik, the mean carbon stocks (3,465 and 3,965 g m^{-2}, repectivley) were exceeding the average estimates for *Z. marina* in the Northern hemisphere. We can conclude that the large seasonal variation may significantly affect the carbon sink function in cold-temperate areas as a substantial part of the carbon is subjected to intra-annual recycling processes and not stable throughout the year. To further strengthen this statement studies on carbon accumulation rates and using deeper (>1 m) sediment cores are needed. We emphasis that estimations of carbon budgets or stock assessments to, for example, quantify the carbon storage potential in cold-temperate *Z. marina* meadows should be based on data incorporating the intra-annual variation in sedimentary carbon content.

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