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Key Points:

- Low-density temperate eelgrass beds act as a low end-member carbon sink
- Sediment organic matter content depends on eelgrass vegetation and environmental features
- Global estimates of carbon storage in seagrass beds should be revisited

Supporting Information:

- Table S1

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Sediment carbon sink in low-density temperate eelgrass meadows (Baltic Sea)

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Abstract Seagrass meadows are highly productive habitats that can act as "blue carbon sinks" in coastal ecosystems by facilitating sedimentation and trapping particles. However, the magnitude and occurrence of these effects may be species and density dependent. The present study is the first estimation of seagrass sediment carbon sink in the temperate *Zostera marina* beds in the Baltic Sea. Several descriptors of organic matter characteristics, along with possible organic matter sources in the sediment were compared at vegetated and unvegetated bottoms. The ^{210}Pb dating of the sediment has been used for accumulation rate assessment. The photopigments and POC concentrations in sediments were higher in vegetated bottoms. The SIAR (Stable Isotopes in R) mixing model based on nitrogen and carbon stable isotope values, indicated that higher percentages of organic matter originated from seagrass production in vegetated sediments (40–45%) compared to unvegetated ones (5–21%). The carbon stock in the upper 10 cm of the vegetated sediments ranged from 50.2 ± 2.2 to 228.0 ± 11.6 (g m^{-2}), whereas the annual C accumulation amount from 0.84 ± 0.2 to 3.85 ± 1.2 (g m^{-2} yr^{-1}). Our study shows that even the relatively weakly developed vegetation of the small temperate seagrass species enhance organic carbon concentration in the sediments. Estimated carbon stock was much lower than those reported for most of the seagrass meadows elsewhere, and the carbon burial rate was the lowest ever reported. Evidently, the global calculations of sediment carbon stock should be reconsidered by taking into account density and species-related variability.

1. Introduction

Seagrass meadows rank among the most productive habitats in the world, providing many goods and services [*Hemminga and Duarte*, 2000]. Mostly growing on sandy bottoms and structuring densely vegetated habitats, seagrasses have the ability to change the surrounding environment as ecosystem engineers—by facilitating sedimentation, reducing resuspension, and trapping seagrass-derived detritus and other particles. Moreover, these plants create three-dimensional habitats that, together with enhanced food supplies, support high biodiversity in associated benthic communities [*Green and Short*, 2003; *Włodarska-Kowalczuk et al.*, 2014]. The ability of underwater meadows to change sedimentary environments depends on the characteristics of the vegetation (e.g., canopy heights and shoot density, [*Gacia et al.*, 1999]), original sediment characteristics, and local hydrodynamic regime [*van Katwijk et al.*, 2010]. Hence, ecosystem engineering effects largely vary among different coastal localities and seagrass species [*Bos et al.*, 2007; *Herkul and Kotta*, 2009].

Seagrass meadows are regarded as blue carbon sinks [*Nellemann et al.*, 2009]. This term refers to natural marine habitats that are able to capture and store carbon for long periods (centuries or millennia, [*Murray et al.*, 2011]). Recent reports of considerable increases in the carbon dioxide concentration in the atmosphere over the last century [*Ciais et al.*, 2013] have fueled intensive research into the mechanisms and efficiency of natural processes that are able to mitigate these changes. In seagrass beds, mineral carbon is photosynthetically fixed as organic matter in plant tissues and part of it is allocated to belowground tissues (roots and rhizomes). Particulate organic carbon suspended in the water can also be trapped by seagrass and buried into the sediments due to vegetation-induced reductions in water flow and wave action [*Koch et al.*, 2006]. Then, it can remain stored in the seagrass meadow sediments over millenary time scales [*Mateo et al.*, 1997].

The estimated global seagrass meadows carbon storage amounts to 19,900 Tg [*Fourqurean et al.*, 2012], whereas annual rate of carbon accumulation provided by other global studies exceeds 83 g C m^{-2} yr^{-1} [*Duarte et al.*, 2005] or 27–44 Tg C yr^{-1} [*Kennedy et al.*, 2010]. Global estimations of the sediment carbon stock within seagrasses were performed using available data concerning the organic carbon amounts and accumulation rate in the vegetated sediments [*Fourqurean et al.*, 2012]. A recent study of Australian seagrass meadows indicated a strong variability in the seagrass sediments' organic carbon storage among different plant species and habitats (18-fold difference across a range of explored sites [*Lavery et al.*, 2013]). The local environmental conditions can also control carbon storage—*Lavery et al.* [2013] showed that sediments vegetated by large seagrass species (*Posidonia australis*) trapped lower amounts of carbon in some places than those populated by much smaller species, such as *Halophila ovalis*. This phenomenon was explained by the differences in the local hydrological regimes—*Posidonia* sites were located in the exposed area, whereas *Halophila* beds were situated in a sheltered bay with high inputs of allochthonous matter [*Lavery et al.*, 2013]. In addition, the heterogeneity of seagrass meadows may cause considerable differences in the amount of stored carbon [*Ricart et al.*, 2015]. Study done on Australian seagrass species *Zostera muelleri* shows that much less carbon is stored within the edges than in the center of the meadows [*Ricart et al.*, 2015]. *Marbà et al.* [2015] demonstrated that loss of seagrass can result in loss of sediment carbon stocks and that revegetation projects effectively restore seagrass carbon sequestration capacity. All of those factors as well as many not yet studied may cause a high variation in organic matter content in the sediments under seagrass meadows—ranging from 0.1 wt % to 11.0 wt % [*Kennedy et al.*, 2010]. *Z. marina* is a relatively small species, with potentially much lower capability to modify the surrounding abiotic environment than bigger species such as Posidonia. Moreover, studies performed in warmer waters (mostly in the Mediterranean Sea) with relatively weak seasonal variability in the environmental conditions (compared to the Baltic Sea) are by no means comparable to the one from the higher latitudes as the higher year-round water temperatures may cause higher rates of carbon remineralization [*Lavery et al.*, 2013]. The large variability in the factors controlling the carbon storage calls for more detailed (i.e., considering the effects of different species and the regional and local environmental regimes) assessments of seagrass sediment sink capacities to update the present global estimates [*Macreadie et al.*, 2014]. One of the current limitations in assessing the capacity of seagrass meadows for carbon burial is the lack of knowledge on the driving mechanisms conducive to high carbon sink capacity and the rates of carbon burial [*Duarte et al.*, 2010].

Here we present the first assessment of seagrass sediment carbon sink storage in temperate *Zostera marina* beds in the Baltic Sea. The global estimations of seagrass importance as a carbon stock by *Fourqurean et al.* [2012] did not consider data from the Baltic Sea at all, even if the recent estimation of seagrass areal coverage in the Baltic Sea (1480 km^2) [*Böstrom et al.*, 2014] indicates the considerable potential to impact carbon storage. The study was performed in the Gulf of Gdańsk in the southern Baltic Sea. The seagrass beds' presence and aerial coverage in these waters declined dramatically within the last century. Recently, the natural recovery of *Zostera* meadows took place in the area. The areal coverage of the seagrass beds increased rapidly, but the density and biomass of the plant tissues remained low compared to other European *Z. marina* meadows [*Jankowska et al.*, 2014], which may result from both the recent history of these habitats and the relatively severe environmental conditions (strong seasonality, low temperatures, severe storms in autumn, and ice cover in winter). The documented effects of the Gulf of Gdańsk's seagrass vegetation on the other components of benthic system (bacteria, meiofauna, and macrofauna) were relatively weak and/or season dependent but statistically significant; e.g., in case of bacteria and macrofauna, higher abundance in vegetated habitat was observed [*Jankowska et al.*, 2014, 2015; *Włodarska-Kowalczuk et al.*, 2014]. Here we hypothesized that the Southern Baltic Sea *Z. marina* meadows, despite their low density, were able to significantly modify the environments of shallow coastal waters and act as sediment blue carbon sinks. We estimated the sediment carbon storage capacities (Cstock (g m^{-2}) and Caccumulation (g m^{-2} yr^{-1})) in the studied seagrass meadows. Moreover, we compared the sediment characteristics (grain size), organic matter quantity and quality (particulate organic matter concentration and ratio to total nitrogen, carbon and nitrogen stable isotopes signatures, and photosynthetic pigments), and sources (assessed using the Stable Isotopes Mixing Models in R SIAR (Stable Isotopes in R), [*Parnell et al.*, 2010] applied to stable isotope ratios of organic carbon and nitrogen) in the vegetated and unvegetated bottoms at three locations of different seagrass density and hydrodynamics.

2. Materials and Methods

2.1. Study Site

The Gulf of Gdańsk is located in the southern Baltic Sea off the Polish coast. A considerable part of the gulf is the Puck Bay, separated from the open sea by the Hel Peninsula. The Ryf Mew sandbank (8 km long) divides

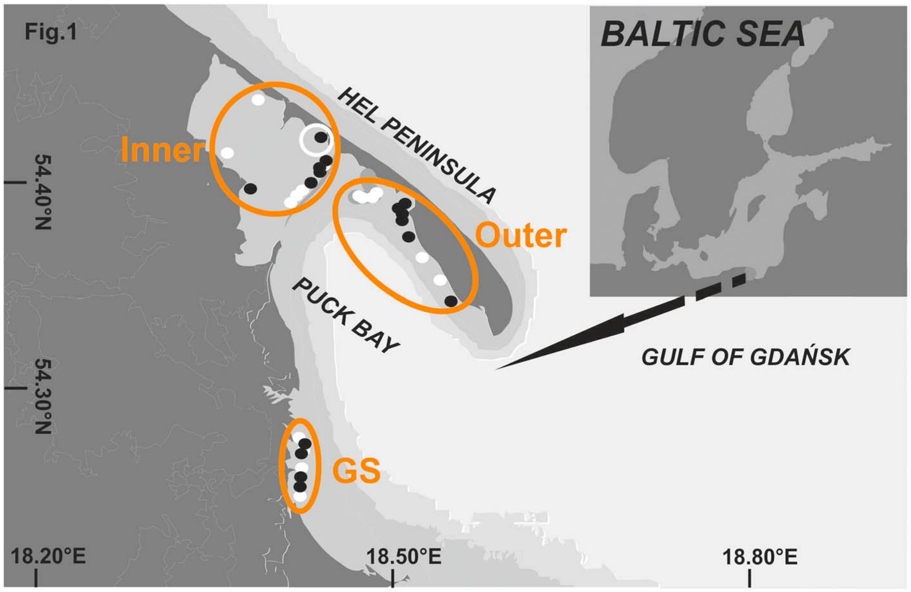

Figure 1. Map of the sampling area with the locations and sampling points marked: GS, Gdańsk-Sopot; Inner, Inner Puck Bay; Outer, Outer Puck Bay. The white circle in the Inner area represents the location where long sediment cores were collected.

the bay into two parts: the notably deeper outer Puck Bay (with an average depth of 20 m) and the shallower inner part called the Puck Lagoon (3 m on average). The sandbank forms a shallow dam of average depth 1 m with only two depth channels (4 up to 7 m depth) and causes significant reduction of water exchange between inner part of the Bay and open waters of the outer Bay. It was documented that the water can be exchanged for not more than 17% of the year (*Nowacki*, 1993). The inner part of the Bay is surrounded by the land from each side so that it is protected from the impact of open sea storms. The average wave height measured during wind blowing from all directions is greatly higher for the outer and shallow area of the Gulf of Gdańsk (maximum 4, minimum 0.2 m), than the inner Bay (maximum 1.5, minimum 0.1 m) [*Jarosz and Kowalewski*, 1993]. The present study was therefore conducted at three locations that are characterized by different environment characteristics: sheltered inner Puck Bay (Inner), exposed outer Puck Bay (Outer), and exposed shallow nearshore area (close to the Gdynia-Sopot agglomeration) in the main basin of the gulf (GS) (Figure 1).

The trajectory of eelgrass meadows extent in the study area has shown dramatic changes over the past 60 years. Before 1950, most of the seafloor of the Inner Puck Bay was covered by the meadows reaching thousands of hectares. Caused most probably by eutrophication and replacement by filamentous algae, a significant decrease in the area of *Zoster marina* occurrence has been observed in 1987—where eelgrass area amounted only to 16.0 ha [*Kruk-Dowigałło*, 1991]. A recent inventory of the seabed habitats in the Polish Exclusive Economic Zone documented that areas covered by *Z. marina* meadows are rapidly growing in size, with 320 ha of the seabed covered by eelgrass vegetation in 2009 for the inner Puck Bay [*Węsławski et al.*, 2013]. At the moment, the actual eelgrass-covered area may be even higher, as new locations of seagrass occurrence in the Gulf of Gdańsk have been observed during sampling campaigns in 2012–2014 (E. Jankowska, personal observations, 2012–2014).

2.2. Sampling

Sampling took place in the summer (the season of maximum seagrass vegetation development in the Gulf of Gdańsk [*Jankowska et al.*, 2014]) in July 2012 and 2013 at three locations—Inner, Outer, and GS. At each location, the water temperature and salinity were measured (using a Mettler-Toledo salinometer). Suspended POM (Particulate Organic Matter as a proxy of phytoplankton), benthic macrophytes, and epiphytes were sampled as possible sources of organic matter. Six liters of water for POM and seagrass leaves together with epiphytes, and other macroalgae species were collected at each locality for isotopic analysis. Samples were collected at 96 stations: 24 stations at the GS location (at 3.0 m depth), 36 stations at Inner (from 1.5 m to 2.0 m depth), and 36 stations at Outer (1.5 m depth). At each location, half the stations were located on vegetated bottoms and the other half on bare sands. Vegetated stations were placed in the center of meadow, and bare sand stations were placed at least 50 m away from the nearest meadow's edge. A set of samples was collected by a SCUBA diver and included the following: a sample of macrophytes (collected with use of 15 cm diameter cores) for vegetation cover characteristics and sediment samples (collected with use of 2 cm diameter core) for the photopigments concentration (upper 2 cm), POC (%), TN (%), carbon, and nitrogen stable isotope ratios assessment (upper 2 cm) and grain size analysis (upper 10 cm). Moreover, at four stations in each location (two randomly selected stations at each bottom type: vegetated and unvegetated), 10 cm long cores were collected to explore the vertical variability in the sediment characteristics. Four 72 cm long sediment cores (5 cm diameter) were collected for Pb^{210} dating and organic matter description (POC, TN, $\delta^{13}C$, and $\delta^{15}N$) at the Inner location. The cores were sliced into 2 cm layers. The samples from the four long cores were combined to provide satisfactory (0.2 g) amounts of pelite fractions (>0.063 mm), which were needed for effective ^{210}Pb dating. The sediment compaction during the sampling amounts to 63.8 cm (12%); therefore, 60 cm of the core was further analyzed.

The sediment samples were preserved at −20°C, except for the samples for the photopigments analyses, which were stored at −80°C; the macrophytes collected for the abundance and biomass analysis were fixed and preserved in 4% formaldehyde.

2.3. Laboratory Analysis

Samples of each potential organic matter source were prepared immediately after sampling: 1 L of water per replicate was filtered through 47 mm GF/F Whatman filters, macrophytes were identified, epiphytes were scraped from the seagrass leaves and then frozen at −20°C.

The macrophytes collected in the cores were identified to the lowest possible taxonomic level. Algae and plants were dried at 60°C for 48 h and weighed. Seagrass shoots were counted, the leaf length was measured, and the dry mass of the aboveground and belowground parts was determined. The term "shoot" was used for seagrass clusters of leaves supported by a single basal meristem [*Olesen and Sand-Jensen*, 1993].

To determine the grain size distribution, the sediment samples were dried (48 h, 60°C) and sieved through 13 sieves at 0.5 phi size intervals from 0.063 to 2 mm [*Folk and Ward*, 1957]. To measure the chlorophyll *a* (Chl *a*) and pheopigment (Pheo) concentrations in the sediment samples, a fluorometric method was used. Freeze-dried sediments were used for pigments extraction in 90% acetone for 24 h at 4°C [*Evans et al.*, 1987]. Measurements were performed via PerkinElmer LS 55 Fluorescence Spectrometer, marking emissions at 671 nm and excitations at 431 nm, before and after sample acidification with 1 M HCl. As chlorophyll *a* and pheopigment concentrations may be used to describe organic matter characteristics (fresh versus degraded), their concentrations in the sediment were calculated according to the method described by *Evans and O'Reilly* [1982] and expressed as microgram per gram ($\mu g\ g^{-1}$) of dry sediment. Analyses for the POC (%), TN (%), and carbon and nitrogen stable isotope ratios were performed via continuous flow-elemental analysis-isotope ratio mass spectrometry (CF-EA-IRMS) at the University of Liège using a Vario Micro Cube elemental analyzer (Elementar Analysensysteme GmbH, Hanau, Germany) coupled to an Isoprime 100 mass spectrometer (Isoprime, Cheadle, United Kingdom). The freeze-dried, ground sediment samples, filters, macrophyte, and epiphyte samples were packed into tin capsules and weighed to the nearest 10 μg. Prior to the measurements, part of all the sediment samples were acidified with direct addition of HCl to remove carbonates [*Hedges and Stern*, 1984] and then dried again at 60°C for 24 h. The measurements were done on both acidified (HCl) and nonacidified samples to exclude potential impact of inorganic carbon on carbon isotope ratios and potential impact of acidification on nitrogen isotope ratios. Isotopic ratios were expressed using the widespread δ notation [*Coplen*, 2011]. Sucrose (IAEA-C6, $\delta^{13}C = -10.8 \pm 0.5‰$, mean ± SD) and ammonium sulfate (IAEA-N2, $\delta^{15}N = 20.3 \pm 0.2‰$, mean ± SD) were used as certified reference materials (CRM). Both CRMs are calibrated against international isotopic references, i.e., the Vienna Pee Dee Belemnite (VPBD) for carbon and Atmospheric Air for nitrogen. The standard deviations of the multibatch replicate measurements of the lab standards (amphipod crustaceans) interspersed among the samples were 0.1‰ for $\delta^{13}C$ and 0.2‰ for $\delta^{15}N$. Glycine (Merck, Darmstadt, Germany) was used as a standard for the elemental content measurements. The analytical precision was 2% of the relative content of the samples (i.e., 0.04% for a sample containing 2% of a given element). The photopigment concentrations were assessed by the spectrophotometric method (extinction at 665 nm and 750 nm) after extraction in 90% acetone for 24 h [*Dalsgaard et al.*, 2000]. These sediment characteristics analyses were performed in 96 samples of surface sediments (upper 2 cm), 120 samples from 10 cm long sediment cores, and 36 samples from (combined) four 60 cm long cores.

The ^{210}Pb dating method introduced by *Goldberg* [1963] was applied. The sediment samples for ^{210}Pb dating (60 cm long cores) were freeze dried and grounded in the laboratory. The sediment moisture and porosity were calculated. Because most of the sediment consisted of sandy fraction, the sediments were sieved through a 0.063 mm sieve so only fine, pelite fraction material was dedicated to ^{210}Pb activity concentration analyses. The ^{210}Pb activity concentration was measured indirectly by alpha spectrometry counting its daughter nuclide, ^{210}Po. Radiochemical separation of ^{210}Po was performed by the method presented in *Zaborska et al.* [2007]. The sediment samples were briefly spiked with ^{209}Po (chemical yield tracer) and digested. Polonium isotopes were spontaneously deposited onto silver discs. The discs were analyzed for ^{210}Po and ^{209}Po activity concentrations in a multichannel analyzer (Canberra) equipped with Si/Li detectors. The samples were counted over 1 day. The activity concentration of ^{210}Po in the sample was determined based on chemical recovery by comparing the measured and spiked activity concentrations of ^{209}Po. Blanks and standards were measured to verify the efficiency of the separation procedure and detection. Standard reference materials (e.g., IAEA-326) were measured to verify the measurements. One blank sample (without sediment) was measured for every seven sediment samples. The analytical procedure background was negligible. Additionally, the rest of the pelite fraction was used for POC, TN, δ^{13}C, and δ^{15}N analysis (as described above).

2.4. Data Analysis

The differences in the macrophyte vegetation characteristics (seagrass shoot density (shoot m^{-2}), aboveground seagrass biomass, total seagrass biomass, and total macrophyte (seagrass + other macrophytes) biomass (g dry mass m^{-2})) among the sampling locations (Loc) were tested using a one-way univariate PERMANOVA model (with one fixed factor: Loc) based on a similarity matrix created from the Euclidean distances among the samples (untransformed data) [*Anderson et al.*, 2008].

The grain size statistics were calculated using the Folk-Word method with the Gradistat software [*Blott and Pye*, 2001]. The sediments were classified according to *Friedman and Sanders* [1978. Sediment porosity and density were calculated. The concentrations of both chlorophyll *a* (Chl *a*) and pheopigments (Pheo) were summed to a total and referred to as the chloroplast pigment equivalent (CPE). Chlorophyll *a* was expressed both in μg g^{-1} and percent of chlorophyll in the CPE. The chlorophyll *a* to POC (%) ratio was calculated. The differences in the sediment characteristics (Chl *a*, Pheo, Chl *a*, CPE concentrations, Chl *a*/POC, POC, carbon to nitrogen ratio (POC/TN), δ^{13}C, δ^{15}N, mean grain size, and fine sand content) between the bottom types (Bottom-vegetated bottom versus bare sands) and among locations (Loc) were tested using a two-way univariate PERMANOVA model (with two fixed factors: Bottom and Loc) based on a similarity matrix created with the Euclidean distances among the samples (untransformed data). When significant effects were found with the main test, post hoc pairwise tests were conducted. Carbon enhancement at vegetated bottom for three locations was expressed as the ratio of POC recorded at vegetated to unvegetated bottom. Spearman correlation tests were performed to check whether the organic matter and sediment descriptors (Chl *a*, Pheo, Chl *a*, CPE concentrations, Chl *a*/POC, POC, carbon to nitrogen ratio (POC/TN), δ^{13}C, δ^{15}N, mean grain size, and fine sand content) were correlated to the characteristics of the seagrass meadows (seagrass shoot density, aboveground seagrass biomass, total seagrass biomass, and total macrophyte biomass).

SIAR mixing models (Stable Isotopes Analysis in R package) were used to numerically estimate the contributions of sources to the sediment organic matter pools. Two stable isotope ratios were used—δ^{13}C and δ^{15}N. The SIAR mixing model is based on Bayesian methods, which are capable of dealing with uncertainty and variability in input data, even in underdetermined systems [*Parnell et al.*, 2010]. Several potential sources were sampled and analyzed—POM (particulate organic matter), *Zostera marina* [*Linneus*, 1753] leaves and roots, *Ruppia maritima* [*J. V. Lamouroux*, 1753], *Potamogeton* spp. (*P. perfoliatus* [*Linneus*, 1753]) and *pectinatus* [*Börner*, 1912], *Zostera marina* detritus (regarded as degraded, black parts of seagrass material), macrophytes with filamentous structure (*Pylaiella littoralis* [*Kjellman*, 1872], *Cladophora* [*Kützing*, 1843]), and *Polysiphonia*

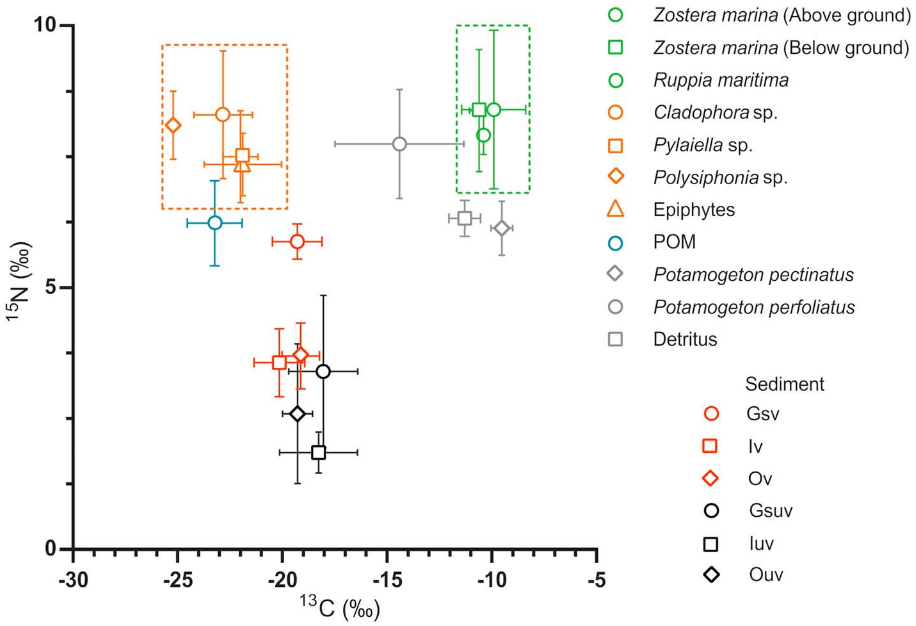

Figure 2. Mean values (± SD) of δ^{13}C (‰) and δ^{15}N (‰) in the bulk sediment samples for three stations (vegetated indicated by red dots, unvegetated black dots) and potential organic matter sources. Dashed rectangles indicate grouped sources (orange, Epiphytes; green, Zostera as vascular plants).

[*Greville*, 1823] and epiphytes (mainly diatoms overgrowing seagrass leaves). The isotopic compositions of all the potential organic matter sources and sediment at the three study locations were presented on a biplot graph with the mean values and standard deviations of the isotopes measurements (Figure 2).

The differences in the isotopic signals (δ^{13}C, δ^{15}N) of the potential sources were tested by two-way univariate PERMANOVA (with two fixed factors: Loc and Source) based on a similarity matrix created with the Euclidean distances among the samples (untransformed data). The isotope signatures in the Z. *marina* leaves and roots did not differ from those of *R. maritima*. There were significant differences (considering both isotopes) between the POM and epiphytes and between those two sources and the Z. *marina* leaves and roots and *R. maritima* ($P < 0.05$). In addition, the *Potamogeton* spp. and *Z. marina* detritus differed significantly from the other sources ($P < 0.05$). Based on these results and data on the dominant components in the macrophyte biomass in the study area [*Jankowska et al*., 2014, this study], three sources were chosen for the mixing model —Zostera (*Zostera marina* living leaves and roots and *Ruppia maritima* grouped together), POM and epiphytes (epiphytes—scratched diatoms and filamentous algae—*Pylaiella littoralis*, *Cladophora*, and *Polysiphonia*, grouped together as their δ^{13}C and δ^{15}N values were similar). Other potential sources were neglected as their biomass and, thus, potential importance is relatively low in the study area. Isotopic fractionation factors were applied to sources following *Lehmann et al*., [2002] recommendations based on measurements of in situ survey and 3 months long experimental incubations of aquatic sediments and expressed as an organic matter diagenesis values—1.5‰ for δ^{13}C and 1.2‰ for δ^{15}N. The model solutions were presented using credibility intervals (5, 25, 75, and 95%) of probability density function distributions [*Parnell et al*., 2010].

The profiles of the total ^{210}Pb activity concentrations as the function of sediment depth (cm) were prepared. The supported Pb-210 was calculated as an arithmetic mean activity of sediment layers where no further decrease in ^{210}Pb activity was noted. The sediment accumulation rates were estimated from the profile of ^{210}Pb$_{ex}$ activity concentration versus porosity-corrected sediment depth (cm) and mass sediment depth (calculated using sediment porosity and density). The linear accumulation rate (LAR, cm yr^{-1}) and mass accumulation rate (MAR, g m^{-2} yr^{-1}) were calculated assuming an exponential decrease in ^{210}Pb$_{ex}$ with sediment depth and using Simple Constant CS:CS model [*Robbins and Edgington*, 1975]:

$$A_t = A_0 e^{-\lambda t}$$

where A_t is the ^{210}Pb activity at time t, A_0 is the activity at time 0, and λ is the radionuclide decay constant (for ^{210}Pb, $\lambda = 0.031$).

Table 1. Seagrass (Density (shoot m^{-1}), Total Macrophyte Biomass (g dwt^{-1})) and Sediment Granulometry Characteristcs (Fine Sand Contribution (%), Mean Grain Size (φ)) at Two Bottom Types and Three Study Locations

	GS				Outer				Inner			
	Veg		Unveg		Veg		Unveg		Veg		Unveg	
	Mean	Stdev	Mean	Stdev	Mean	Stdev	Mean	Stdev	Mean	Stdev	Mean	Stdev
Shoot density	84.93	29.96	-	-	46.87	18.30	-	-	53.16	23.95	-	-
Total macrophyte biomass	24.01	12.70	-	-	15.25	4.34	-	-	13.39	4.63	-	-
Fine sand	0.29	0.18	0.44	0.30	0.32	0.11	0.09	0.02	0.26	0.11	0.57	0.34
Mean grain size	2.39	0.48	1.88	0.56	1.68	0.17	1.50	0.07	2.01	0.42	2.02	0.37

When t is replaced by $t = x/v$ (x, depth of a given sediment layer; v, sedimentation rate), the above formula can be rewritten as follows:

$$A_t = A_0 e^{-\lambda\, x/v}$$

$\ln A^{210}\mathrm{Pb}_{ex}(x) = \ln A^{210}\mathrm{Pb}_{ex}(0) - (\lambda/v)x$where $A^{210}\mathrm{Pb}_{ex}(x)$ is the activity at layer x, $A^{210}\mathrm{Pb}_{ex}(0)$ is the activity at the surface (layer 0), λ is the decay constant, and v is the sediment accumulation rate.

The estimations of C_{stock} (organic carbon amount in the sediment) and C_{accu} (organic carbon accumulation rate), done on 10 cm sediment cores were expressed in g m^{-2} and g m^{-2} yr^{-1}, respectively, for three locations. Estimations of total carbon stored and accumulated within eelgrass meadows in the study area were performed using formula described in *Lavery et al.* [2013]:

C_{stock}	$\sum S \times A \times D$
S	mean organic carbon amount in the seagrass vegetated sediments (mg m^{-3})
A	estimated area of seagrass (m^2)
D	depth of sediment layer (m) (calculated for 0.10 m)
C_{accu}	$\sum S \times A \times R$
R	rate of sediment accumulation (m yr^{-1})

Calculations were performed for the most recent estimations of eelgrass area coverage for the Inner Puck Bay (48 km^2) [*Węsławski et al.*, 2013]. The calculations have been done for upper 10 cm of sediment (i.e., last 50–60 years; the profile slope indicated that the upper 10 cm layer is also mixed).. Sediment accumulation rate measured for the Inner location of 0.13 cm yr^{-1} (see below) has been applied for carbon accumulation calculations.

3. Results

3.1. Macrophyte Vegetation Biometrics

Eight macrophyte taxa were identified in the collected material: Ectocarpales (*Pylaiella littoralis*), Ceramiales (*Ceramium* sp., *Polysiphonia* sp.), and Angiospermae (*Z. marina*, *Ruppia maritima*, *Zanichella palustris*, *Chara* sp., *Potamogeton perfoliatus*, *Myriophyllum* sp.). All the taxa were present at Inner and Outer, while only *Z. marina*, *P. littoralis*, *Ceramium* sp., and *Polysiphonia* sp. were collected at GS. *Z. marina* was dominant in terms of biomass at all three study sites, comprising 99.5% of the total biomass at GS, 74.9% at Outer, and 72.7% at Inner. Seagrass shoot density, total seagrass biomass, and total macrophyte biomass were significantly higher at GS than at the Inner and Outer locations ($P < 0.01$, Table 1). The seagrass shoot density ranged from 46.9 ± 18.3 shoot m^{-2} (Outer) to 84.9 ± 29.9 (GS), while the total seagrass biomass ranged from 13.4 ± 7.0 (Inner) to 24.0 ± 12.4 (GS) g dry mass m^{-2}. The same trend was observed for the total macrophyte biomass—the highest values were found at GS (24.02 ± 12.41 g dry mass m^{-2}), and the lowest at Inner, (18.55 ± 7.41 g dry mass m^{-2}).

3.2. Organic Matter Content in Surface Sediments

The sediments in the study area were either medium or fine sand (according to the Fork and Word classification). There was no significant difference in either the mean grain size or fine sand percent between the two bottom types (pattern consistent across the three studied sites, Table 1).

Table 2. Results of Two-Way PERMANOVA Tests for Differences in Sediment Characteristics (POC, δ^{13}C, δ^{15}N, POC/TN, Chl*a*, Pheo, Chl*a*/POC, Chl*a*%, CPE, Sediment Granulometry) Between Two Bottom Types (BT) and Among Three Locations (Loc)

		POC	δ^{13}C	δ^{15}N	POC/ TN	Chl*a*	Pheo	Chl*a*%	Chl*a*/POC	CPE	Mean Grain Size	Fine Sand	Sorting
Source	df	Ps-F	Ps-F	Ps-F	Ps-F	Ps-F	Ps-F	Ps-F	Ps-F	Ps-F	Ps-F	Ps-F	Ps-F
BT	1	33.2***	1.4	23.8***	0.6	42.6***	69.9***	35.7***	0.4	58.5***	3.4	0.6	12.2**
Loc	2	6.7***	0.5	0.2	1.2	19.5***	10.6***	2.8	0.8	14.1***	6.7**	3.5*	11.0***
Btx Loc	2	0.3	0.4	0.1	0.6	2.3	1	5.3**	2.1	0.5	1.4	6.0**	0.5
Res	90												
Pairwise tests for S		GS > Inner > Outer	-	-	-	GS > Inner > Outer	GS > Inner, Outer	-	-	GS > Inner > Outer	Inner > Outer > GS	Inner > Outer, GS	GS > Inner > Outer

*$P < 0.05$ level of significance.
**$P < 0.01$ level of significance.
***$P < 0.001$ level of significance.

The POC content in the sediments varied from 0.03 ± 0.02% (recorded at the unvegetated Outer) to 0.14 ± 0.03% (recorded at the vegetated GS), while the δ^{13}C varied from −20.1 ± −1.4‰ (recorded at the vegetated Inner) to −18.0 ± −0.7‰ (recorded at the nonvegetated GS). The Chl *a* content in the sediments ranged from 4.0 ± 2.7 μg g^{-1} (recorded at the unvegetated Outer) to 10.0 ± 3.4 μg g^{-1} (recorded at the vegetated GS) to and the CPE varied from 4.8 ± 3.5 μg g^{-1} (recorded at the unvegetated Outer) to 15.3 ± 7.8 μg g^{-1} (recorded at the vegetated GS). Higher values of POC, δ^{15}N, Chl *a*, Pheo, and CPE were documented in the vegetated sediments compared to the bare sands. Only Chl *a*% was significantly higher in the unvegetated bottom (PERMANOVA $P < 0.05$, Figure 2, and Table 2).

No significant differences between the two bottom types were observed for δ^{13}C, POC/TN, or Chl *a*/POC ($P > 0.05$, Table 2). For five parameters (POC, Chl *a*, Pheo, and CPE), differences among the sites were also identified (Table 2). In most cases, the highest values were observed at GS and the lowest at Outer. The largest differences between the mean values recorded at the two bottom types were found at GS. For example, the difference in the respective mean values for Pheo was 3.8 μg g^{-1} at GS, 2.9 μg g^{-1} at Outer, and 2.0 μg g^{-1} at Inner ($P < 0.001$). In the vegetated areas, no significant correlation (at $P < 0.05$) was detected between the macrophyte vegetation and sediment characteristics (Spearman rank correlation). Significant differences between the layers in 10 cm cores were only noted for sediment characteristics related to photosynthetic pigments—Chl *a* ($P < 0.001$, Table 3), Pheo, Chl *a*% ($P < 0.05$), Chl *a*/POC and CPE ($P < 0.001$).

In the first (0–2 cm) or second (2–4 cm) upper layers of the cores, the values of these characteristics were much higher than those in the deeper layers (Figure 3 and Table S1 in the supporting information). That was observed for samples from both vegetated and nonvegetated bottoms; however, the magnitude of differences among the upper and lower layers was larger for the vegetated bottom samples. The sediment characteristics in the core samples that differed between the two bottom types were reported for POC, ($P < 0.01$), δ^{15}N ($P < 0.05$), Pheo, Chl *a*% ($P < 0.001$), Chl *a*/POC and CPE ($P < 0.01$, Table 3). Some differences in the organic matter descriptors among localities for vegetated bottom were also noted, e.g., POC (GS 0.11 ± 0.03%, Inner 0.24 ± 0.10%, and Outer 0.03 ± 0.02%), POC/TN (GS 7.0 ± 4.1, Inner 4.7 ± 1.7, and Outer 4.2 ± 2.0), Chl *a*% (GS 43.8 ± 16.7, Inner 29.5 ± 16.7, and Outer 38.5 ± 16.0) ($P < 0.05$), and δ^{13}C (GS −19.1 ± −3.7, Inner −21.1 ± −2.2, and Outer −20.2 ± −0.6) ($P < 0.001$, Table 2).

3.3. Organic Matter Sources

The SIAR mixing model (Figure 4) noted that the proportions of the three potential organic matter sources to the sediment pool were not consistent between the vegetated and unvegetated bottoms.

The strongest contrast was observed in the modeled contributions of Zostera as a potential organic matter source. The contribution of seagrass tissue in the bulk sediment organic matter pool was

Table 3. Results of Three-Way PERMANOVA Tests for Differences in Sediment Characteristics (POC, δ^{13}C, δ^{15}N, POC/PON, Chl*a*, Pheo, Chl*a*%, Chl*a*/POC, CPE) Between Two Bottom Types (BT), Among Three Locations (Loc), and Five Layers (L) for Samples Representing Vertical Cores

		POC	δ^{13}C	δ^{15}N	POC/TN	Chl*a*	Pheo	Chl*a*%	Chl*a*/POC	CPE
Source	df	Ps-F	Ps-F	Ps-F	Ps-F	Ps-F	Ps-F	Ps-F	Ps-F	Ps-F
BT	1	9.2**	3.5	7.4*	0.0	0.0	19.8***	23.0***	8.5**	8.1**
Loc	2	4.5*	5.4**	2.7	4.8*	4.8*	0.4	4.6*	9.0***	1.4
L	4	0.1	0.0	1.7	1.0	12.1***	3.3*	2.9*	5.7***	7.1***
BTxLoc	2	1.5	4.2*	0.5	1.8	1.2	1.2	0.4	1.5	1.1
BTxL	4	0.1	0.0	1.7	1.0	2.0	1.3	0.5	1.2	1.5
LocxL	8	0.1	0.0	0.5	0.7	0.5	0.1	0.7	0.5	0.1
BTxLocxL	8	0.1	0.0	1.0	0.4	0.4	0.4	0.3	0.3	0.3
Res	30									

*$P < 0.05$ level of significance.
**$P < 0.01$ level of significance.
***$P < 0.001$ level of significance.

much higher in the vegetated bottom (average, i.e., "mode of solutions", of approximately 0.4) compared to the bare sands (below 0.2) at all sites (Figure 5). The range of the credibility interval (CI_{75}) for vegetated sediments was very narrow, from 40 to 45% (average organic carbon contribution from that source amounts to 63.0 g m^{-2}), while the range for unvegetated sands was much wider, with CI_{75} from 4.5 to 21% (6.9 g m^{-2}). In addition, contribution of seagrass-derived material to sediments was higher in sediments from vegetated bottoms in all performed model runs (probability that a given situation occurs—$Pr = 0.00$ for all locations). On the other hand, epiphytes and macroalgae contributed much less to the bulk organic matter pool in vegetated sediments, with CI_{75} from 6 to 20% (19.3 g m^{-2})., compared to the unvegetated bottom, where the contribution was much higher with narrow credibility interval ranges (CI_{75} = [31%–45%], 20.5 g m^{-2}). Epiphytes and algae contribution to sediment organic matter was actually higher for unvegetated bottoms in 50 to 90% of model runs (*Pr* is equal to 0.5 for Inner, 0.3 for GS, and 0.1 for Outer).

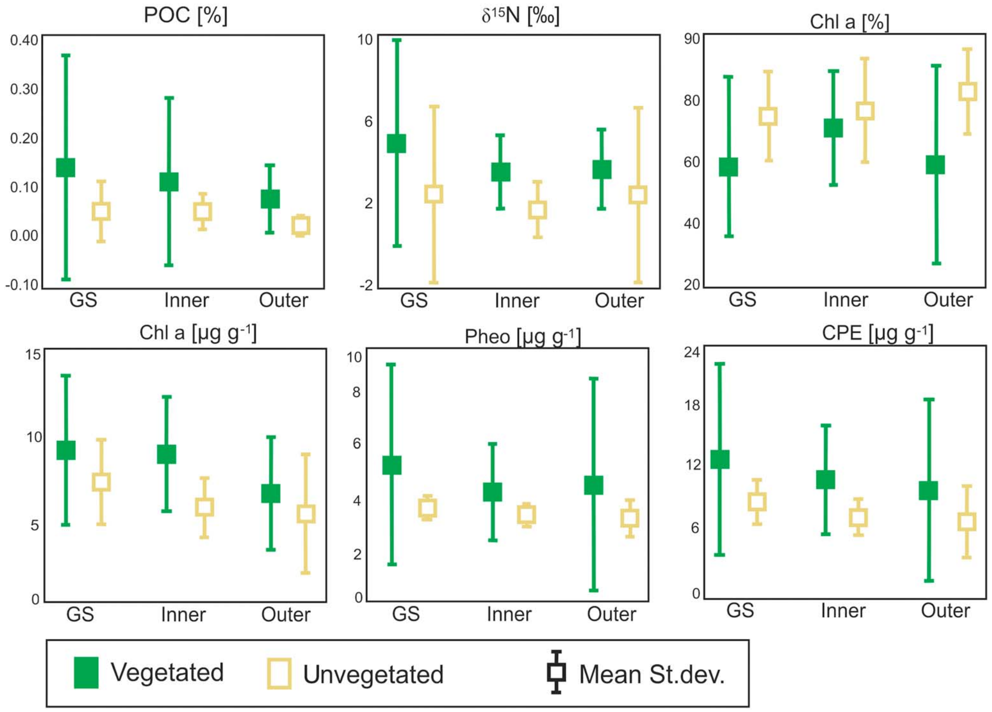

Figure 3. Organic matter (POC, particulate organic carbon, δ^{15}N), photosynthetic pigments (chl *a*, chlorophyll *a*; pheo, pheopigments; chl *a* (%) and CPE, chloroplastic pigment equivalents) and grain size (sorting) characteristics in the surface sediments (upper 2 cm) at three sites (GS, Inner, and Outer) and two bottom types (vegetated and unvegetated). The means and standard deviations are presented (for Inner and Outer of 36 replicates, for GS of 24 replicates).

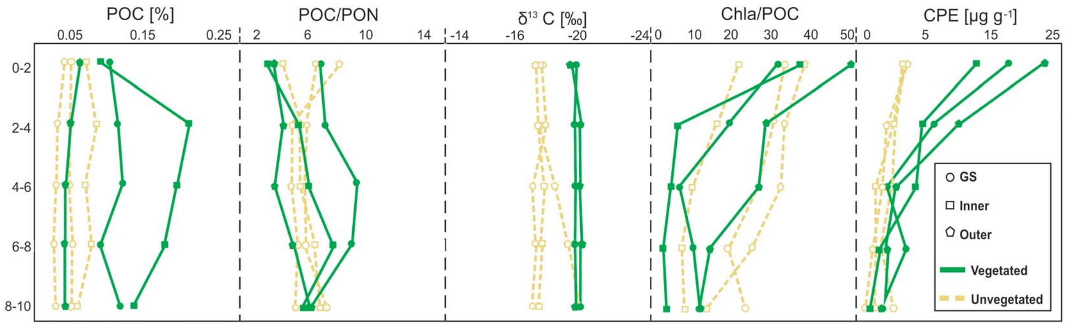

Figure 4. Vertical profiles of organic matter and photosynthetic pigment characteristics in the 10 cm sediment cores collected at the three locations and two bottom types. POC (%), particulate organic matter; POC/TN, particulate organic matter to particulate organic nitrogen ratio; δ_{13}C (‰), carbon isotope ratio; chla/POC, chlorophyll to particulate organic matter ratio; CPE (μg g_{-1}), chloroplastic pigment equivalent.

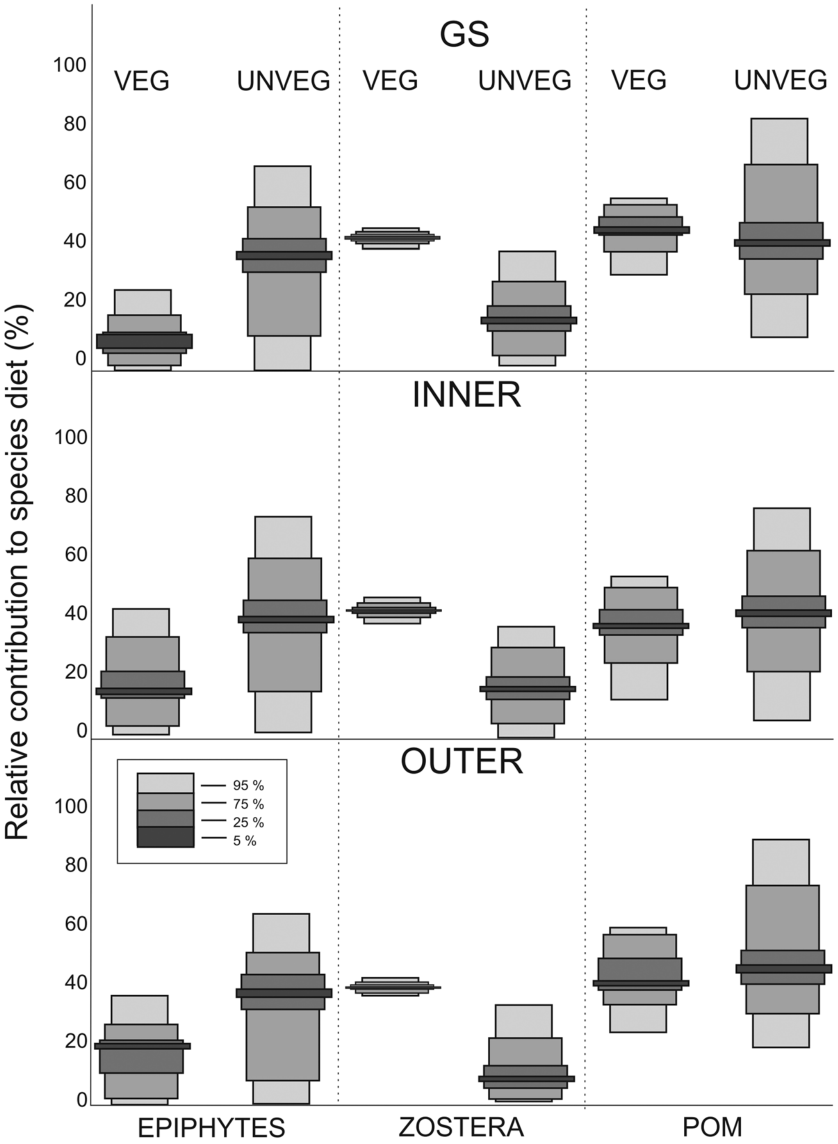

Figure 5. Boxplots of the relative contributions of the most likely organic matter sources (epiphytes, Zostera, POM) to the bulk sediment suspended organic matter pool compared to the vegetated and nonvegetated bottoms at three locations. The boxes indicated 5%, 25%, 75%, and 95% credibility intervals, as defined in the plot legend.

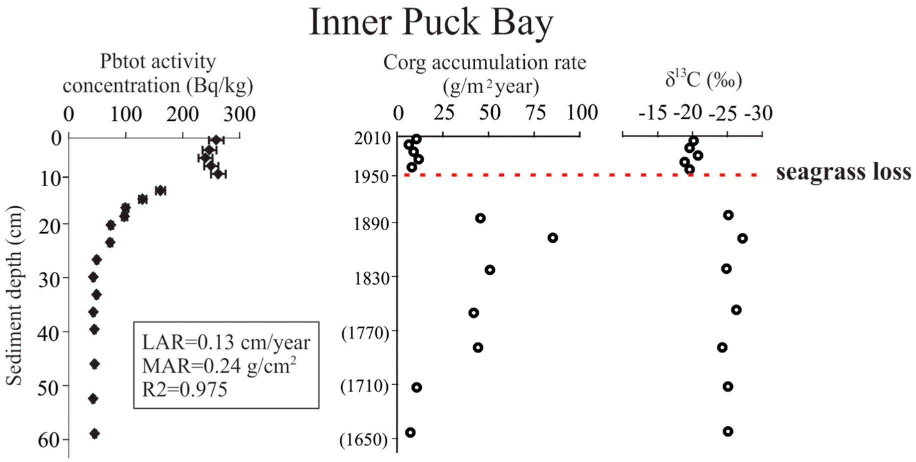

Figure 6. (left) ^{210}Pb activity concentration (Bq/kg) and water content versus porosity-corrected sediment depth (cm) plus (right) Corg and δ^{13}C in the sediment cores collected at the Inner location (corrected for sediment compaction during sampling). The red dotted line on Figure 6 (right) indicates the 10 cm depth representing mid twentieth century—the starting time of the seagrass decline in the Gulf of Gdańsk.

Additionally, the model showed that POM was an important source of organic matter in the studied area, with little difference between the two bottom types ($\mathrm{CI}_{75} = [34\%–51\%]$ ($63.0\ \mathrm{g\ m^{-2}}$) for vegetated and $\mathrm{CI}_{75} = [36\%–53\%]$ ($24.1\ \mathrm{g\ m^{-2}}$) for unvegetated bottoms). The proportion of model runs where POM contributed more to sediment organic matter in vegetated bottoms varied widely according to the site, with *Pr* ranging from 0.1 to 0.9.

3.4. Sediment Accumulation Rate

The water content in all the sediment samples from the 60 cm long cores was very low (ranging from 10% to 19%) due to the high sand fraction content in the sediments. The pelite sediment fraction (<0.063 mm) constituted approximately 0.1% of the sediment in these samples. The upper 40 cm of the core contained much more sand than the lower part of the core, probably due to constant resuspension in the upper sediment layer.

The total ^{210}Pb activity concentrations decreased from $262.6 \pm 9.1\ \mathrm{Bq\ kg^{-1}}$ to $33.1 \pm 1.0\ \mathrm{Bq\ kg^{-1}}$ in the lower part of the core (Figure 6). The ^{210}Pb-supported activity was estimated to be $39.0 \pm 2.8\ \mathrm{Bq\ kg^{-1}}$. The four top layers (0–10 cm) showed similar ^{210}Pb, indicating sediment mixing in the top sediment layers. Below 10 cm, the ^{210}Pb excess activities exhibited an exponential decrease until 22–24 cm. The ln of the ^{210}Pb excess activities versus the porosity-corrected sediment depth is shown in Figure 6. The best fit equation determination coefficient is satisfactory ($r^2 = 0.93$). The LAR was estimated to be $0.13 \pm 0.02\ \mathrm{cm\ yr^{-1}}$, while the MAR was estimated to be $0.24 \pm 0.01\ \mathrm{g\ cm^{-2}\ yr^{-1}}$.

3.5. Estimates of Carbon Stocks and Accumulation Rates

Carbon stock (Corg $\mathrm{g\ m^{-2}}$) and carbon accumulation (Caccu $\mathrm{g\ m^{-2}\ yr^{-1}}$) of the upper 10 cm varied among three locations—the highest values were presented for Inner location described as sheltered, low density ($228.0 \pm 11.57\ \mathrm{g\ m^{-2}}$, $3.85 \pm 1.15\ \mathrm{g\ m^{-2}\ yr^{-1}}$), lower for GS described as exposed, high density ($116.5 \pm 4.1\ \mathrm{g\ m^{-2}}$, $2.78 \pm 0.3\ \mathrm{g\ m^{-2}\ yr^{-1}}$), and the lowest for Outer described as exposed, low density ($50.2 \pm 2.2\ \mathrm{g\ m^{-2}}$, $0.8 \pm 0.2\ \mathrm{g\ m^{-2}\ yr^{-1}}$). The total carbon stock C_{stock} and total carbon accumulation C_{accu} calculated for the Inner location for upper 10 cm sediment amounts to 0.10 ± 0.01 Mt and $0.02 \pm 0.01\ \mathrm{Mt\ yr^{-1}}$, respectively, whereas for sediment from 10 to 60 cm 7.46 ± 0.68 Mt, $0.28 \pm 0.18\ \mathrm{Mt\ yr^{-1}}$ (for the most recent estimation of the eelgrass area, i.e., 48 $\mathrm{km^2}$, Table 4).

4. Discussion

This is the first study examining the carbon sink capacities of the underwater *Zostera marina* meadows in the Baltic Sea. Our results indicate that eelgrass meadows in the southern Baltic Sea can act as sediment blue

Table 4. C Concentration (% C Bulk), Carbon Stock (Cstock g m^{-2}), Carbon Accumulation (Caccu g m^{-2} $y-^{1}$) Calculated for Upper 10 cm at Three Studied Locations and for 10–60 cm Layer Based On Cores Collected at a Station at Inner Location (Veg-Vegetated Bottom)[a]

			Veg			Unveg		Ratio of Differences Veg/Unveg
Location (Number of Replicate Cores)	Environmental Settings	Sediment Depth (cm)	%C Bulk	C Stock (g m^{-2})	C Accu (g m^{-2} $y-^{1}$)	%C Bulk	C Stock (g m^{-2})	%C Bulk
GS (4)	exposed, high density	10	0.11 ± 0.03	166.46 ± 4.10	2.78 ± 0.28	0.03 ± 0.00	52.38 ± 1.21	3.67 ± 0.00
Outer (4)	exposed, low density	10	0.03 ± 0.02	50.17 ± 2.20	0.84 ± 0.16	0.02 ± 0.00	77.56 ± 1.70	4.8 ± 0.00
Inner (4)	sheltered, low density	10	0.24 ± 0.10	228.00 ± 11.57	3.85 ± 1.15	0.05 ± 0.00	31.51 ± 1.53	1.50 ± 0.00
Inner (4)	sheltered, low density	10–60	1.70 ± 1.10	3630.17 ± 222.39	41.00 ± 26.00			

[a] Accordingly, C concentration and C stock for unvegetated bottom and ratio of differences for C concentration between veg/unveg is presented. Accumulation rate measured only for the Inner location has been used for carbon accumulation calculations at three locations.

carbon sinks by accumulating larger amounts of organic carbon than the unvegetated sediments. The estimated C_{stock} for the top 10 cm of sediment of the present study range from 50.2 to 228.0 g m^{-2}, whereas C_{accu} ranges from 0.84 to 3.85 g m^{-2} yr^{-1}. The estimation of total stored carbon within eelgrass meadows in the Inner Puck Bay area (based on total eelgrass area of 48 km^2) amounts to 0.1 Mt with annual rate of carbon accumulation of 0.02 Mt. Despite the relatively low development of seagrass vegetation (low density and biomass values compared to other seagrass meadows [*Jankowska et al*., 2014; *Clausen et al*., 2014]), the C_{stock} and C_{accu} values documented for the southern Baltic Sea are in the range of the results reported for *Zostera*-dominated meadows worldwide. They are representative of the lower end values, similar to disturbed eelgrass meadow from east Atlantic coast (Table 5). On the other hand, both our results and values reported from other *Zostera* meadows were much smaller than those reported for *Posidonia*-dominated systems in warmer regions. The Mediterranean Sea species *Posidonia oceanic*a is considered to comprise the largest pool of stored carbon in both leaf structures and soils, and the stored organic carbon in its meadows is estimated to be between 100 and 410 kgC m^{-2} [*Mateo et al*., 2006; *Fourqurean et al*., 2012; *Serrano et al*., 2012], i.e. 3 orders of magnitude higher than those recorded in the present study. A recent study on Australian seagrass meadows dominated by various species (total area of 92569 km^2) reported a mean C_{stock} as high as 155.5 Mt for the top 25 cm of sediment and a mean annual C_{accu} rate from 0.09 to 6.16 Mt (considering different sediment accumulation rates applied for different regions) [*Lavery et al*., 2013]. That particular study proved that the carbon sink capacity of seagrass strongly depended on particular habitat and species characteristics. The largest species—*Posidonia australis*—was found to be the most efficient for carbon storage. However, the nearby terrigenous material inflows, hydrodynamic regime, and depth were indicated as even more important factors that influence the stock capacity than seagrass species [*Lavery et al*., 2013]. Our study also shows that sediment enhancement in organic carbon varies depending on

Table 5. Organic Carbon Stock (C stock g m^{-2}) and Accumulation (C accu g m^{-2} yr^{-1}) for Different Seagrass Species and Geographic Regions as Reported by Literature and the Present Study[a]

Seagrass Species	Region	Sediment Layer (cm)	C Stock (g m^{-2})	C Accu (g m^{-2} yr)	Reference
Multispecies	global	-	-	83	*Duarte et al.* [2005]
Multispecies	global	-	-	138 ± 38	*McLeod et al.* [2011]
Multispecies	global	0–100	252	-	*Fourqurean et al.* [2012]
Z.marina	Virginia, Atlantic coast	0-5	208 ± 99	-	*McGlathery et al.* [2012]
Multispecies	Australia coast	0-25	1262 ± 1483	-	*Lavery et al.* [2013]
Z.marina	Virginia, Atlantic coast	0–10	-	37 ± 3	*Greiner et al.* [2013]
Multispecies	Dongsha Island, South China Sea	0–5	443 ± 6	33	*Huang et al.* [2015]
Z.muelleri	Port Curtis, central Australia	0–10	600	-	*Ricart et al.* [2015]
P.australis	Jervis Bay, NSW Australia	0–100	750 ± 212	-	*Macreadie et al.* [2014]
P.australis	Oyster Harbour, Western Australia	0–15	2770 ± 117	26 ± 1	*Marbà et al.* [2015]
P.australis	Oyster Harbour, Western Australia	0–150	10790 ± 120	3	*Rozaimi et al.* [2016]
Z.marina	Inner Puck Bay, South Baltic Sea	0–10	228 ± 12	3.9 ± 1	present study
Z.marina	Inner Puck Bay, South Baltic Sea	10–60	3630 ± 222	41 ± 27	
Z.marina	Outer Puck Bay, South Baltic Sea	0–10	50 ± 2	0.8 ± 0	
Z.marina	GS, South Baltic Sea	0–10	166 ± 4	2.78 ± 0	

[a] Mean ± st.dev. are reported if available.

the local environmental settings and the macrophyte species composition of a meadow (see the discussion on the differences in organic carbon descriptions among the studied localities below). The existing present-day global estimates of seagrass carbon stock that are based mostly on data for warmer, *Posidonia*-dominated meadows, should be revisited to take into account this worldwide variability. Carbon stock and accumulation values estimated for the Gulf of Gdańsk meadows may serve as useful, low-density case for global seagrass carbon stock estimations.

Based on the information provided by the ^{210}Pb analysis, the upper 10 cm of sediment represents approximately the last 60 years, so the period after eelgrass decline in the second half of the twentieth century and the last years after recent natural reintroduction. The sediment layer from 10 cm down to 60 cm depth represents the estimated time before 1950 year. The higher concentrations of Corg in sediments in deeper layers (10–60 cm) indicate a much higher carbon stocks in the past and very high potential in carbon sequestration of the studied habitats (C stock 3630.17 ± 222.39 g m^{-2}. C accu 41.00 ± 26.00 g m^{-2} yr^{-1}). Sediments deeper than 10 cm represent time before 1950, i.e., period before eelgrass decline, when eelgrass meadows covered larger area (almost whole Inner Puck Bay [*Ciszewski et al*., 1992]) and presumably were better developed, with higher plant density and biomass than at present. It also corroborates the notion that present meadows are still in the recovery phase and have not attained the levels of vegetation development and carbon storage capacity from before 1950.

The comparison of organic matter descriptors in vegetated and bare sediments indicates that the *Z. marina* meadows in the Gulf of Gdańsk support a higher concentration of organic matter than the neighboring bare sands. The increased concentrations of POC and TN in the vegetated bottom are clearly noticeable at all the three studied locations. These effects are clearly visible both at the very surface of the seabed (upper 2 cm) and when deeper sediment layers are explored—the pattern of increased POC and TN in vegetated habitats is consistent across the upper 10 cm of sediments at the three sites. Various scenarios of seagrass influence on sediment organic enrichment were documented in other coastal locations worldwide [*Gacia et al*., 1999; *Peralta et al*., 2008; *Bos et al*., 2007]. No significant enhancement of organic carbon was observed in the 10 cm sediment profile in the experimental field study of sediment accretion within artificially planted seagrass units in the Wadden Sea [*Bos et al*., 2007]. On the other hand, a twofold increase in organic matter in the sediments covered by the dwarf eelgrass *Zostera noltii* from the Mauritanian coast was observed within the whole 10 cm profile compared to that in the bare bottoms [*Hankoop et al*., 2008]. The increased amounts of organic matter in seagrass vegetated sediments are explained by favorable conditions for particle trapping by meadows and were reported by several studies performed in a range of geographical locations and meadows formed by various seagrass species [*Fry et al*., 1977; *Bowden et al*., 2001; *Gacia et al*., 2002]. Ecosystem engineering effects in seagrass meadows can depend on shoot density and biomass [*Fonseca and Fisher*, 1986], for example, *Duarte et al*. [2010] proved that *Z. marina* meadows tend to be autotrophic, CO_2 sinks, after reaching threshold biomass of 92 g dwt m^{-2}. Other factors controlling engineering effects are the hydrodynamic regime of the locality and neighborhood of rivers and other sources of organic material [*van Katwijk et al*., 2010; *Lavery et al*., 2013]. Indeed, in the present study, the carbon stock and organic enrichment (Corg in vegetated to Corg in bare sediments ratio) were much higher at the sheltered location (Inner) than at the other two exposed ones (GS, Outer). The concentration of organic matter in sediments within the vegetated habitats in the Gulf of Gdańsk does not seem to be macrophyte density dependent (within the range of densities observed in the present study, i.e., from 46.9 ± 18.3 to 84.9 ± 29.9 shoots m^{-2}) as no significant correlation between any of the vegetation descriptors to any of the geochemical sediment properties was documented within the seagrass meadows. The environmental engineering effects of seagrass vegetation seem to operate efficiently even in the relatively sparse and recently grown vegetation in the regenerating meadows in the Gulf of Gdańsk, and no threshold in the seagrass density (i.e., the density of seagrass too low to produce organic enrichment effects) could be observed. In *Jankowska et al*.'s [2014] seasonal study, these effects persisted throughout the year, regardless of the dramatic seasonal variability in seagrass cover (significant effects occurred even at very low biomass and density in winter). However, when the two exposed sites (GS, Outer) were compared, the higher carbon enhancement was noted at the one with higher *Z. marina* density, indicating the significance of vegetation development in a meadow for its engineering effects.

The quantity of the organic matter (as indicated by POC concentration) and the differences in this parameter between the vegetated and unvegetated sediments at the three sites remained constant within the vertical profile of the upper 10 cm of the sediments. This agrees with sediment dating results—the upper 10 cm layer was indicated as constantly mixed. A different pattern was observed for photosynthetic pigments, especially the chlorophyll *a* concentration, which is an indicator of fresh, recently produced organic and unstable material [*Gacia et al*., 2002]. The increased concentrations of chlorophyll *a* and CPE were documented only down to 4 cm; at deeper depths, the contrasts between vegetated and unvegetated sediments were much less visible or not detected. The differences in the vertical distribution patterns of the POC and photosynthetic pigments result from the different natures of these two descriptors of organic matter. Photopigments reflect recent organic matter production and accumulation in the sediments, while the more stable particles of organic carbon and nitrogen in the sediment reflect accumulation over a longer period [*Fry et al*., 1977]; in addition, their vertical distribution can be influenced by deep sediment mixing events that occur mostly during heavy storms, which are common in spring and autumn. In the surface layers (as indicated by the analyses of 2 cm surface samples and analyses down to 4 cm in the 10 cm core samples), the concentrations of chlorophyll *a* and CPE are much higher in vegetated bottoms, which agrees with the difference pattern observed for POC. On the other hand, chlorophyll *a* comprised a much larger portion of the total organic matter pool in bare sands (as indicated by higher values of chl *a*% and chl *a*/POC). That indicates a higher proportional input from recent production and likely the better development and higher productivity of microphytobenthos in unvegetated sea bottoms.

The POC enhancement in the seagrass beds was not accompanied by a change in the mean δ^{13}C signatures (as indicated by no significant effects detected by the PERMANOVA tests). This discrepancy between the clear effect on POC and the absence of response in the mean δ^{13}C values in the vegetated sediments was noted in other studies [*Simenstad and Wissmar*, 1985; *Boeschker et al*., 2000; *Hemminga et al*., 1994; *Kennedy et al*., 2010]. The clear difference between different habitats was only noted for δ^{15}N (as for TN), with higher values recorded in the vegetated bottom. The variation in δ^{15}N values among the vegetated and unvegetated habitats remains poorly understood but is usually correlated to inorganic nitrogen incorporation by seagrass and sediments [*Lepoint et al*., 2004]. The fixation of nitrogen by sulfate reducers in seagrass bed rhizospheres has been previously detected [*Welsh*, 2000]. This microbial fixation is an additional source of organic nitrogen for seagrass bed sediments, pore waters, and living plants [*Sacks and Repeta*, 1999]. *Papadimitriou et al*. [2005] stated that δ^{15}N changes within the sediments of Western Mediterranean *Posidonia* meadows, which may be a result of the mixing of ^{15}N-enriched nitrogen from primary sources with ^{15}N-depleted nitrogen fixed in the sediments. Indeed, significantly higher bacteria abundance and biomass were detected in the Puck Bay sediments within the seagrass meadows compared to the bare bottoms in the studied area [*Jankowska et al*., 2015] and other coastal locations [*Pollard and Moriarty*, 1989; *Danovaro*, 1996]. The increased numbers of bacteria in the vegetated bottoms may also more efficiently decay organic matter, resulting in higher δ^{15}N signatures. Despite the nearby location of the Gdańsk-Sopot agglomeration, no effects of sewage disposal (i.e., sewage-derived NH_4^+, which can be the source of 15 N-enriched particulate matter, [*Cifuentes et al*., 1988]) could be detected at the GS site, which did not differ in its δ^{15}N signature from other sites.

The SIAR modeling of the stable isotope signatures of the organic matter deposited in the sediments showed that an important fraction of organic matter in the Gulf of Gdańsk is derived from seagrass tissues. This fraction was much higher in vegetated bottoms, where seagrass-derived organic matter comprised 40–45% of the organic carbon in the surface sedimentary organic matter pool. This is similar to values reported from other seagrass meadows systems—previous studies in the Mediterranean Sea and in Australian seagrass meadows documented that approximately 50% of the organic matter in the sediments originated from seagrass tissues [*Papadimitriou et al*., 2005; *Lavery et al*., 2013]. On the other hand, macroalgae-derived organic matter in the intertidal sediment of southern France was as low as 17% [*Dubois et al*., 2010]. At a global scale, it is estimated that 30 to 50% of the net community production of seagrass meadows is buried in situ within the meadows with a similar contribution from allochthonous organic carbon [*Kennedy et al*., 2010]. The rest of the seagrass material (not buried) is probably consumed and exported to surrounding areas [*Kennedy et al*., 2010]. In the present study, much less organic matter that originated from seagrass was detected on bare bottoms than in vegetated sediments, which suggests that seagrass-produced organic matter is decomposed and stored mostly within the meadows. The seagrass tissues decompose relatively slowly (because of the high C:N:P ratio and a refractory carbon structure) and are not commonly consumed by invertebrates [*Jaschinski et al*., 2008] or intensively decomposed by bacteria [*Boeschker et al*., 2000], so their remnants can be detected in the sediment even after several months [*Mateo et al*., 1997; *Duarte et al*., 2010]. It is important to note that the SIAR modeling has identified differences in the organic matter sources' compositions between vegetated and unvegetated bottoms, while simple comparisons (statistical testing for differences in mean values) of $\delta^{13}C$ suggested very similar situation in both habitats. That result points to the need of applying analysis methods that explore the full spectrum of data and take uncertainty into consideration (such as SIAR mixing models, [*Parnell et al*., 2010]).

Other sources of sediment organic matter usually considered in seagrass meadow system studies are plankton and terrestrial sources along with bacterial carbon sources, but the last one usually does not exceed 10% [*Bouillon et al*., 2006]. The isotopic POM signatures ($\delta^{13}C = -23.3 \pm 1.3‰$, $\delta^{15}N = 6.23 \pm 0.8‰$) in the present study were similar to the values reported in other studies in the southern Baltic Sea [*Maksymowska et al*., 2000]. The POM had similar, relatively high contributions in both vegetated and unvegetated sediments (34–53‰), reflecting the importance of pelagic production in the organic matter pools in both habitats. The lower input of seagrass-derived carbon in bare sands was compensated by a higher portion of material defined in the model as derived from filamentous algae and epiphytes (31–45%). The significant epiphyte contribution in the bare sands may seem intriguing because the isotopic signal of the epiphytes in this study was measured in samples of epiphytes growing on seagrass leaves and filamentous algae occurring within the meadows. However, the epiphytes in Puck Bay that grow on seagrass leaves are represented mostly by diatoms. Reports from other coastal systems indicate that the taxonomic compositions of the epiphyte and benthic diatom communities are very similar [e.g., *Kasim and Mukai*, 2006]. Thus, the high proportion of “epiphyte”-derived organic carbon in the bare sand samples may reflect the stronger input of microphytobenthos production to the total organic matter pool compared to that in vegetated systems. This would also agree with the higher proportions of chlorophyll *a* (recently produced OM) in the total bulk of the organic matter in the bare sands.

5. Conclusions

Our study shows that even relatively sparse vegetation of the small temperate eelgrass species *Zostera marina* may play a considerable role in carbon sequestration at the local scale in the southern Baltic Sea, as the C_{stock} (from 228.0 to 50.17 g m^{-2}) were in the range of those recorded for other *Zostera*-based meadows from east Atlantic or Australia's coast; however, annual C_{accu} values (from 3.85 to 0.84 g m^{-2} yr^{-1}) was much lower than ever reported elsewhere (Table 5). Moreover, the organic matter content (POC%), including its fresh components (as indicated by the chlorophyll *a* concentration), was enhanced at vegetated compared to unvegetated bottoms. Accordingly, SIAR showed that the percentage of seagrass-derived organic matter was higher in vegetated sediment, indicating that seagrass-produced matter is mostly buried within the vegetated patches. Our results, showing the differences between the present results and those reported for other *Zostera* and *Posidonia* beds, indicate that a number of regional assessments (reflecting the species, local hydrodynamic regimes, geographical variability, and sediment depth profile), such as the presented one (representing the lower end of variability range), need to be considered to update the present seagrass carbon sink estimations, as recent ones, based mostly on estimates from warmer regions and *Posidonia* beds, may be overestimated.

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