

Increased current flow enhances the risk of organic carbon loss from *Zostera marina* sediments: Insights from a flume experiment

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Abstract

Hydrodynamic processes are important for carbon storage dynamics in seagrass meadows, where periods of increased hydrodynamic activity could result in erosion and the loss of buried carbon. To estimate hydrodynamic impacts on the resuspension of organic carbon (C_{org}) in seagrass-vegetated sediments, we exposed patches (0.35×0.35 cm) of *Zostera marina* (with different biomass, shoot densities, and sediment properties) to gradually increased unidirectional (current) flow velocities ranging from low (5 cm s^{-1}) to high (26 cm s^{-1}) in a hydraulic flume with a standardized water column height of 0.12 m. We found that higher flow velocities substantially increased (by more than threefold) the proportion of C_{org} in the suspended sediment resulting in a loss of up to $5.5\% \pm 1.7\%$ (mean \pm SE) C_{org} from the surface sediment. This was presumably due to increased surface erosion of larger, carbon-rich detritus particles. Resuspension of C_{org} in the seagrass plots correlated with sediment properties (i.e., bulk density, porosity, and sedimentary C_{org}) and seagrass plant structure (i.e., belowground biomass). However, shoot density had no influence on C_{org} resuspension (comparing unvegetated sediments with sparse, moderate, and dense seagrass bed types), which could be due to the relatively low shoot density in the experimental setup (with a maximum of $253 \text{ shoots m}^{-2}$) reflecting natural conditions of the Swedish west coast. The projected increase in the frequency and intensity of hydrodynamic forces due to climate change could thus negatively affect the function of seagrass meadows as natural carbon sinks.

Hydrodynamics play an important role in various processes of seagrass carbon sequestration. The high carbon storage efficiency seen in seagrass meadows (McLeod et al. 2011; Fourqurean et al. 2012) is partly related to their ability to create an environment with low hydrodynamic forces and a high sedimentation rate (Gacia and Duarte 2001) by attenuating the water velocity with the canopy (Fonseca and Fisher 1986; Fonseca and Cahalan 1992; Infantes et al. 2012). The reduction of flow velocities by seagrass canopies and associated increased particle trapping thereby contribute to the accumulation of allochthonously derived sedimentary carbon in seagrass meadows (Agawin and Duarte 2002; Hendriks et al. 2008; Kennedy et al. 2010). In concordance, seagrass meadows in

sheltered areas with less wave action have a higher sedimentary carbon content than do exposed bays (Samper-Villarreal et al. 2016), as environments with low hydrodynamic exposure usually promote the accumulation of sediment containing fine-grain-sized particles (i.e., high in silt and clay contents; Mazarrasa et al. 2017) and low bulk density (Winterwerp and van Kesteren 2004), which are factors linked to high seagrass carbon storage (Dahl et al. 2016; Röhr et al. 2016; Gullström et al. 2018).

A sudden increase in hydrodynamic activity, such as during a storm event, can cause mechanical damage to the seagrass through uprooting (Marbà and Duarte 1994; Infantes et al. 2011) as well as erosion, increased turbidity, and sediment resuspension (Preen et al. 1995; Fourqurean and Rutten 2004), with negative consequences for carbon sequestration and storage. Although storms increase the hydrodynamic forces (i.e., waves and turbulent- and current flow) only temporarily (Granata et al. 2001), the effect on the water irradiance can be long-lasting, affecting the growth and survival of the seagrass plants (Cabello-Pasini et al. 2002). It has been suggested that the frequency and intensity of storms in the

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extratropics have increased over the last century (Vose et al. 2014), while there is less evidence of any trends in the tropical regions (Webster et al. 2005). However, storms will probably be even more common in a changed future climate (Collins et al. 2013). Storm surges exert significant geophysical pressure along most of the world's coastal areas, and in a future warmer climate these are expected to become more severe due to sea-level rise and increasing storminess (Von Storch 2013). On a coastal embayment scale, storm impacts on seagrass meadows (and other nearshore habitats) vary with water depth, duration of wind event, and degree of exposure (e.g., Fagherazzi and Wiberg 2009; Mariotti et al. 2010), and therefore the geographical location of a meadow is likely to be important for its resilience to storm events (Infantes et al. 2009).

The effects of hydrodynamic forces on sediment erosion and resuspension are influenced by a range of physical and biogeochemical properties, which in combination determine sediment resistance (Winterwerp and van Kesteren 2004; Gerbersdorf et al. 2005; Grabowski et al. 2011). In seagrass beds, both the meadow structure and sediment properties of the habitat are important for sediment stabilization (Ganthy et al. 2015). Seagrasses protect the sediment by reducing the water velocity with their shoots, creating drag, and reducing momentum inside the canopy (Fonseca and Fisher 1986), and through binding the sediment with their roots and rhizomes (Ganthy et al. 2011; Christianen et al. 2013). In sparse meadows with low shoot density, however, protection against hydrodynamic processes might be lacking (Adhitya et al. 2014) or the effect could be the opposite, with increased turbulence around individual shoots (Lawson et al. 2012). Hence, the shoot density of seagrass meadows strongly influences the retention of sediment particles (Chen et al. 2007) and of associated sedimentary carbon (Asmus and Asmus 2000). Sediment bed types vary in susceptibility to hydrodynamic forces depending on their intrinsic properties (Grabowski et al. 2011). For example, sediment with low bulk density and high water content will likely have a low erosion threshold (Jacobs et al. 2011) because of fewer bonds between particles (Winterwerp and van Kesteren 2004). Therefore, in low-density muddy sediments (with high clay and silt contents), vegetation may provide less protection from erosion due to the instability of fine-grain-sized sediment (Widdows et al. 2008). This might, however, be counteracted by higher organic matter and clay contents in muddy sediments, which increase the interparticle binding (through adhesion and cohesion) and stabilize the sediment (Walker and Bob 2001).

Zostera marina is a widely abundant seagrass species in the northern temperate hemisphere and has a high capacity for storing sedimentary carbon; its presence gives the Swedish Skagerrak coast considerably higher carbon storage potential compared with other *Z. marina* areas in Europe (Dahl et al. 2016). On the Swedish west coast, *Z. marina* is found on soft bottoms all along the coastline, growing in highly variable hydrodynamic environments ranging from sheltered bays

to exposed areas (Baden and Boström 2001). Due to this wide range of suitable environments, seagrass meadows found in this region also display large natural variation in meadow density, sediment properties, and sedimentary *C_{org}* content (Gullström et al. 2012; Boström et al. 2014). The shoot density is generally lower on the Swedish west coast (normally not exceeding 300 shoots m^{-2} ; Gullström et al. 2012; Boström et al. 2014; Staveley et al. 2017) than in other *Z. marina* areas and due to the sparse canopies the meadows might be more vulnerable to increased current velocities (van Katwijk et al. 2010). Hydrodynamics (currents and waves) are well-known factors regulating sedimentation processes in aquatic environments (Winterwerp and van Kesteren 2004), but experimental studies on the direct influence of fluid dynamics on seagrass carbon storage are clearly lacking. To better understand the impacts of changing hydrodynamic conditions on *C_{org}* resuspension in seagrass meadows, we compared concentrations of particulate *C_{org}* in suspension for different sediment types (in a mud-sand mixture) and *Z. marina* biomasses to gradually increasing unidirectional flow velocities (5–26 $cm\ s^{-1}$). The major aims were to (1) assess the effects of current flow velocities on suspended *C_{org}* concentration in relation to sediment properties and seagrass biomass (from unvegetated to high-shoot-density sediments), (2) identify flow velocity thresholds for suspended *C_{org}* concentrations in sediment bed types with different sediment properties and seagrass biomass, and (3) compare the relationship between suspended sediment concentration (SSC) and suspended *C_{org}* concentration at different flow velocities. We hypothesized that (1) seagrass-vegetated sediment with a high proportion of fine grain sizes, low bulk density, and sparse shoot density would have a higher suspended *C_{org}* concentration, and that (2) these sediment bed types would also have lower suspended *C_{org}* concentration thresholds than would sediment plots with coarse sand, high bulk density, and high seagrass density. We further hypothesized that (3) the proportion of suspended *C_{org}* concentration in SSC would be higher at lower flow velocities, due to the low weight of fine-grain-sized particles and associated organic matter.

Methods

Sediment sampling

Sediment samples were collected intact to keep the sediment properties, aboveground biomass, and belowground biomass undisturbed. Four areas were sampled (i.e., Bökevik, Kristineberg, Smalsund, and Hågarmskären) in the Gullmar Fjord on the Swedish Skagerrak coast (58°16'N, 11°28'E). The sampling areas were selected based on their natural variation in meadow density (sparse- ($n = 7$), moderate- ($n = 7$) and dense ($n = 4$) *Z. marina* meadows) and sediment properties (the sediment comprises a sand-mud mixture ranging from fine-grained carbon-rich sediment to coarser sand with less sedimentary carbon; Table 1). In addition, unvegetated sediment was sampled in the vicinity of the seagrass meadows

Table 1. Summary table for the sampling sites, seagrass characteristics, and sediment composition. *C_{org}* = sedimentary organic carbon, Ag and Bg = above- and belowground seagrass biomass, DW = dry weight, Mud = grain size < 0.063 mm, Unveg. = unvegetated sediment plots.

Sites	Water depth (m)	Shoot density (m ⁻²)	Ag (g DW m ⁻²)	Bg (g DW m ⁻²)	Mud (%)	<i>C_{org}</i> (%)	Bulk density (g DW cm ⁻³)	Porosity (%)
Bökevik	2.5	24 (s)	11.4	13.9	38.1	1.7	0.5	53.0
	2.5	65 (m)	28.6	58.8	31.3	0.8	0.7	36.3
	3	41 (s)	19.6	40.0	28.4	1.3	0.8	42.8
	3	253 (d)	54.7	98.0	23.1	0.4	0.6	30.5
	3	155 (d)	28.6	109.4	33.7	1.1	0.7	42.4
	3	8 (s)	14.7	6.5	47.2	1.4	0.9	49.2
	3	65 (m)	12.2	35.9	54.5	1.5	0.7	48.4
	3.2	16 (s)	23.7	37.6	55.9	2.7	0.5	59.6
	4	131 (m)	74.3	95.5	53.5	5.2	0.2	76.3
	4.8	Unveg.	-	-	65.0	3.0	0.3	62.6
Kristineberg	0.8	171 (d)	6.5	22.9	8.9	0.3	1.5	23.4
	1.1	163 (d)	28.6	35.9	11.7	0.3	1.2	28.3
	4	24 (s)	15.5	37.6	53.2	1.5	0.7	47.1
	5	65 (m)	18.0	122.4	34.3	1.4	0.7	42.6
	6.3	Unveg.	-	-	48.4	2.4	0.4	60.9
	11	Unveg.	-	-	71.6	4.0	0.3	70.8
Smalsund	11	Unveg.	-	-	72.0	3.0	0.3	68.8
	2.6	33 (s)	4.1	58.0	50.9	4.0	0.3	71.4
Hågarnsskären	4	49 (s)	22.0	65.3	49.9	3.9	0.3	66.0
	4	65 (m)	13.9	50.6	51.6	2.9	0.5	58.5
	4.5	65 (m)	10.6	34.3	7.9	0.3	1.2	25.0
	4.5	82 (m)	8.2	26.1	5.8	0.4	0.9	29.3
	6.5	Unveg.	-	-	35.2	-	1.0	42.2

*The values in parentheses are the ranges of shoot densities (m⁻²) classified as sparse (s), moderate (m), and dense (d) meadows.

(*n* = 5). In the Gullmar Fjord, *Z. marina* grows in various substrates, in sites ranging from shallow (~ 1 m depth) exposed areas of sandy sediment to sheltered areas of soft muddy sediment, with different wave and wind exposure levels (Eriander et al. 2016; Infantes et al. 2016). Sediment samples were collected using a 35 × 35 cm box-corer (*n* = 23, Table 1) to a sediment depth of 4–16 cm depending on the compactness of the sediment, and then gently moved to custom-made trays placed underneath the box-corer. The trays with sediment were then placed in boxes to protect the sediment from tilting. The sediment trays were placed in shallow 1500 L flow-through tanks installed outdoors at the Sven Lovén Centre for Marine Infrastructure, Kristineberg Station, until used in the hydrodynamic experiments.

Sediment and biomass properties

Sediment properties determined for each sample, for example, dry weight bulk density (g DW cm⁻³), porosity (% water content), and organic carbon (% *C_{org}*), were analyzed in the topmost cm for all sediment samples (*n* = 1). The sediment was collected before the flume test using a cut-off syringe of 1.5 cm in diameter. A homogenized sample, encompassing

the entire sediment depth, was also collected for grain size analysis by pushing a cut-off syringe into the sediment. The grain size was determined using a Mastersizer 3000 particle size analyzer (Malvern Instruments) and the different grain size fractions were calculated as percent mL⁻¹. The sediment was weighed before and after drying for ~ 48 h at 60°C. The bulk density of the sediment was determined by dividing the dry weight by the volume, and porosity was defined as the difference between the wet weight and dry weight multiplied by 100 (to obtain a percentage value). The *C_{org}* content of the sediment was analyzed using a CN elemental analyzer (Flash 2000; Thermo Fischer Scientific). Before analysis, the sediment was ground into a fine powder using a mortar, treated with 1 M HCl to remove inorganic carbon, and then dried for 24 h at 60°C. After each flume test, the seagrass was collected from the sediment sample to determine the shoot density, and shoot and root-rhizome biomass. The biomass was separated into above- and belowground parts, weighed, and then dried at 60°C for about 48 h until the weight had stabilized. Since an increase in sediment pH can affect the erodability by thickening the diffusive double layer (through the decrease in H⁺; Winterwerp and van Kesteren 2004), pore-water pH was

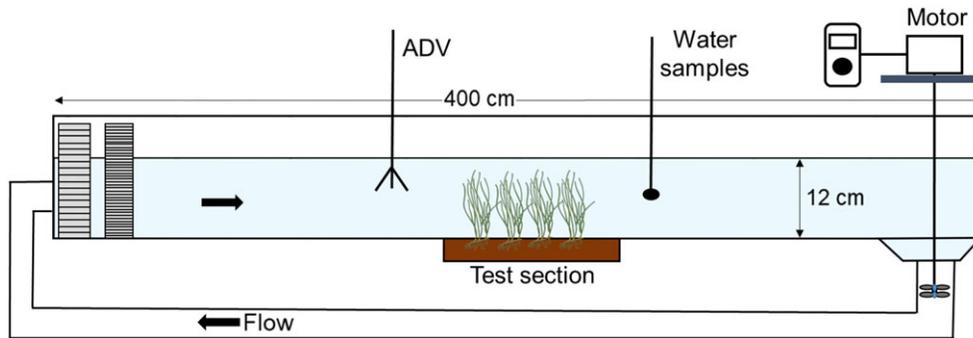


Fig. 1. Schematic of the hydraulic flume; not drawn to scale.

measured before and after each experiment. Approximately 50 mL of pore water was collected from the sediment using a syringe and pH was measured using a multimeter (WTW Multi 3430 with a FDO 925 probe; WTW/Xylem). However, no large variation in pH was detected. As we sampled intact sediment the natural infauna community was part of the sediment plots. This might have increased variability on the sediment and C_{org} resuspension but was not considered to have a large influence on this experimental setup. No large-sized infaunal specimens were observed in the sediment plots, which could otherwise potentially cause a structural weakness of the sediment (Graf and Rosenberg 1997).

Hydrodynamic exposure

A hydraulic flume (4 m long, 0.5 m wide, and 0.5 m deep) located at Kristineberg Station was used to test the impacts of step-by-step increased current flow velocities on C_{org} and sediment resuspension from the different sediment samples. The flume simulated unidirectional flow velocities from 5 cm s^{-1} to 26 cm s^{-1} (Pereda-Briones et al. 2018). Similar values recorded by an oceanographic buoy (Moored buoy) near Kristineberg, located 1–3 km from the sampled meadows, indicate flow velocities of up to 27 cm s^{-1} at 3–5 m water depth and during periods with strong winds (i.e., $14.1\text{--}19.7 \text{ m s}^{-1}$). Storm conditions are, however, also associated to increased wave action and turbulence, which due to technical constraints of the hydraulic flume could not be included in this study. The sediment trays were mounted in a $35 \times 35\text{-cm}$ cavity at the bottom of the flume and adjusted so that the sediment surface was parallel to the bottom surface of the flume (Fig. 1). The flume was filled with seawater (350 L) resulting in a fixed water depth of 0.12 m. The water depth did not entirely represent natural conditions, but the water volume used in the flume was a prerequisite to generate the high velocities (up to 26 cm s^{-1}) needed to simulate the different levels of hydrodynamic stress on the seagrass canopies and sediment surfaces. During the experiment, each sediment sample was exposed to seven stepwise increases in flow velocities, i.e., 5 cm s^{-1} , 7 cm s^{-1} , 10 cm s^{-1} , 15 cm s^{-1} , 17 cm s^{-1} , 21 cm s^{-1} , and 26 cm s^{-1} in each experimental run, which is a common method used

in hydraulic flumes to estimate erosion (Amos et al. 2004; Ganthly et al. 2011, 2015; Jacobs et al. 2011). Each flow velocity was run for 6 min before increasing the current flow velocity. The measured particle resuspension is a cumulative value as a gradually increasing current flow velocity. For some of the sediment plots, the maximum flow velocity was only $23\text{--}24 \text{ cm s}^{-1}$, despite running the propeller driving the flow at maximum speed, due to the amount of debris in the flume. Flow was generated using a propeller mounted at one end of the flume and regulated by an adjustable speed drive (6K119; Dayton Parts). The flow velocity was measured at a sampling rate of 25 Hz using an acoustic Doppler velocimeter (ADV) (Vectrino; Nortek). The ADV was placed 70 cm in front of the sediment sample and 8 cm above the bottom of the flume. Bed shear stress (τ_b) was based on the calculations (Eqs. 1, 2) used by van der Heide et al. (2007) and van Rijn (1984):

$$\tau_b = \rho g \frac{U^2}{C^2} \quad (1)$$

where ρ is the density of seawater, g is the gravitational acceleration, U is the measured current flow velocity, and C is the Chézy grain roughness:

$$C = 18 \log_{10} \frac{12}{k_{sc}} \quad (2)$$

where k_{sc} is the 90% cumulative grain size distribution (D_{90}).

Suspended sediment and C_{org} concentration

To measure the total concentration of sediment particles suspended in the water, water samples from the middle of the water column ($\sim 6 \text{ cm}$ water depth) were collected at each flow velocity using a clear PVC syphoning tube that was rinsed with clean water (Baas et al. 2004). Each flow velocity was allowed to stabilize for 3 min before a 0.5-L water sample was collected and filtered on pre-weighed and pre-burned (for 2 h at 450°C) GF/F filters. The filters were dried for 48 h at 60°C and re-weighed to quantify the concentration of sediment particles (mg L^{-1}) in the water column. To obtain the C_{org}

content of the total sediment water concentration, the filters were treated with 1 M HCl and dried for 24 h at 60°C before being analyzed with a CN elemental analyzer (Flash 2000; Thermo Fischer scientific). In this study, SSC is defined as follows:

$$SSC = TS - C_{org} \quad (3)$$

where SSC is the suspended inorganic sediment concentration, TS is the total sediment water concentration, and C_{org} is the concentration of organic carbon in the water.

In order to estimate the percentage C_{org} loss from the surface sediment (of 1 cm depth), we calculated the total C_{org} resuspension by multiplying the total water volume of the hydraulic flume (i.e., 350 L) with the C_{org} water concentration (mg L^{-1}) at the different current flow velocities. The percentage C_{org} loss due to increased current flows was then derived from the initial C_{org} content from the C_{org} density ($\text{g } C_{org} \text{ plot}^{-1}$) of the sediment surface. A smaller water sample (30 mL) was collected simultaneously with the water used for quantifying the particle concentration in the water and for measuring turbidity using a turbidity meter (Hach 2100; Hach Company). To correct for the ambient sediment particles and carbon content in the seawater used in the flume (by assessing the sediment and C_{org} particle concentration), water samples from the intake (used to fill up the hydraulic flume) were collected at six occasions during the course of the experiment and filtered on GF/F filters that had been pre-weighed and pre-burned (for 2 h at 450°C). The average (\pm SD) amount of sediment was $4.15 \pm 0.99 \text{ mg L}^{-1}$ and the carbon content was $0.12 \pm 0.02 \text{ mg L}^{-1}$.

Statistical analyses

Before any statistical testing, the assumptions of normal distribution and homogeneous variance were checked using the Shapiro–Wilks normality test and Bartlett’s test, respectively. When these assumptions were not met, log transformation was used. All statistical tests were performed in R (version 2.15.3) except for the partial least squares (PLS) modeling, which was conducted in SIMCA (Umetrics; Wold et al. 2001). The PLS models were used to assess the influence of various predictor variables on C_{org} resuspension (using the k -value of the individual slopes as the response variable) in seagrass-vegetated and unvegetated sediments. PLS regression analysis is applicable when dealing with a large number of predictor variables and multicollinearity (as seen in the dataset used). Linear regressions were used to assess the relationships of C_{org} water concentration, turbidity, and SSC. The relationship of C_{org} water concentration and % C_{org} loss from the sediment surface to flow velocity in seagrass-vegetated and unvegetated sediment as well as the relationship between bed shear stress and low- and high-bulk-density seagrass-vegetated sediment were assessed using linear mixed-effect models with the individual runs as a random factor (package lme4 in R). We

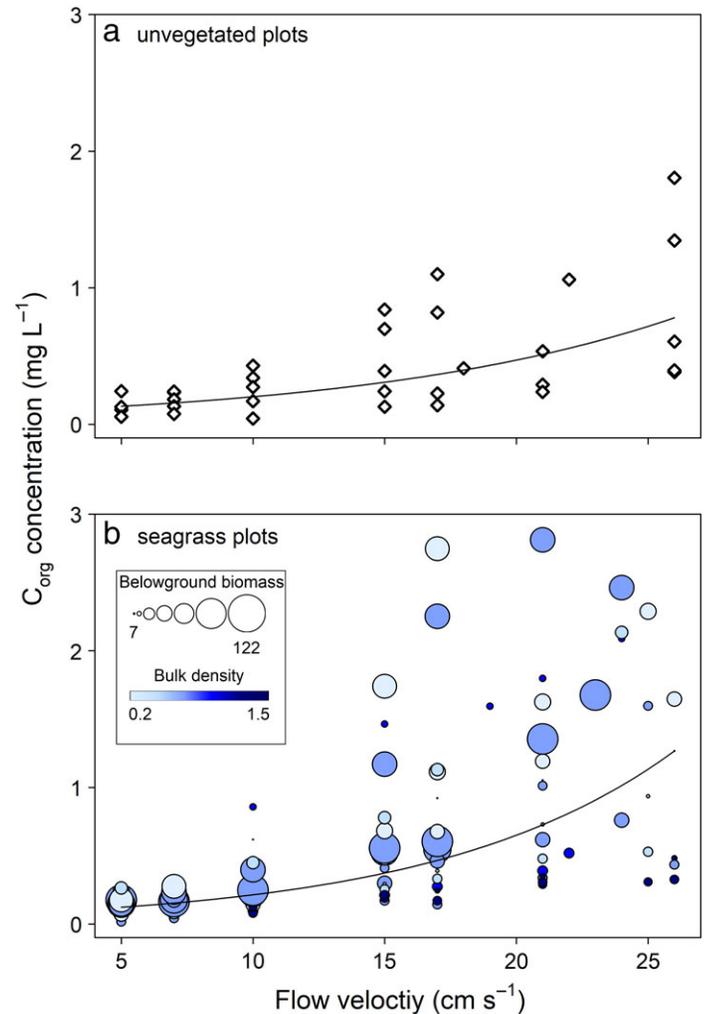


Fig. 2. Suspended C_{org} concentration in relation to flow velocity for (a) unvegetated (\diamond), and (b) seagrass-vegetated sediment. The color gradient indicates the range of sediment bulk densities (g DW cm^{-3}), while the bubble size indicates the amount of belowground biomass (g DW m^{-2}).

further explored the effect of seagrass shoot density in relation to unvegetated sediment on suspended C_{org} concentration by grouping the sediment bed types according to levels of shoot density m^{-2} as follows: unvegetated sediment (0), sparse (8–49), moderate (65–82), and dense seagrass (155–253). This division into groups was based on the distribution range of shoot densities obtained from previous in situ measurements of numerous *Z. marina* meadows ($n > 50$) on the Swedish west coast (range: 8–268 shoots m^{-2} , mean \pm SD: 84 ± 50 shoots m^{-2} , Gullström et al. 2012; range: 37–283 shoots m^{-2} , mean \pm SD: 163 ± 63 shoots m^{-2} , Staveley et al. 2017). The influence of shoot density was tested using a one-way ANOVA design.

Results

There was a positive relationship between flow velocity and suspended C_{org} concentration for both seagrass-vegetated

Table 2. Summary of partial least squares (PLS) regression analyses for seagrass-vegetated and unvegetated sediment plots with suspended C_{org} concentration as the response variable (using the k -value of the slopes). The model for unvegetated sediment plots was not significant ($Q2 < 0.05$), so no model was made. Values in bold indicate predictor variables with VIP values > 1 and thus significantly contributing to the model. The predictor variables are ranked by level of importance, as indicated by the values in parentheses (1–6), where 1 is the most important predictor variable in the model. Coeff. +/- is the model coefficient and indicates the relationship, i.e., positive (+) or negative (–), between a predictor variable and C_{org} resuspension. AgDW and BgDW = above- and belowground biomass ($\text{g dry weight m}^{-2}$), ShootDens = shoot density (m^{-2}), GrainSize = mud content (%), SedC = sedimentary C_{org} (%), SedDens = sediment bulk density (g DW cm^{-3}), and SedPor = sediment porosity (%).

Model	Q2 statistics	Model variables	Predictor variables						
			AgDW	BgDW	ShootDens	GrainSize	SedC	SedDens	SedPor
Unveg.	-0.21	No model	N/A	N/A	N/A	N/A	N/A	N/A	N/A
Seagrass	0.27	VIP ranking	0.54 (6)	1.01 (4)	0.20 (7)	0.89 (5)	1.13 (3)	1.50 (1)	1.14 (2)
		Coeff. +/-	+	+	+	+	+	-	+

(linear mixed-effect model, $R^2 = 0.88$, $p < 0.001$) and unvegetated sediment (linear mixed-effect model, $R^2 = 0.93$, $p < 0.001$; Fig. 2). The PLS model for seagrass-vegetated sediment showed that sediment bulk density was the most important predictor of suspended C_{org} concentration in seagrass-vegetated sediment plots, followed by sediment porosity, sedimentary C_{org} , and belowground biomass (Table 2). The seagrass model had a cross-validated variance ($Q2$ statistic) greater than 0.05 (Table 2) and a cumulative explanation for all predictor variables combined ($R^2 y$ cum) of 45%. The PLS model for the unvegetated sediment plots was not significant ($Q2 < 0.05$).

Two groups with different bulk densities were distinguished among the seagrass-vegetated sediment plots, where plots with sediment bulk densities above 1 g DW cm^{-3} had lower suspended C_{org} concentrations than did sediment plots with bulk densities below 1 g DW cm^{-3} (Fig. 3a). The suspended C_{org} concentration increased with bed shear stress in both high- and low-bulk-density seagrass-vegetated sediment (high bulk density: linear mixed-effect model, $R^2 = 0.82$, $p < 0.001$; low bulk density: linear mixed-effect model, $R^2 = 0.82$, $p < 0.001$), and in high-bulk-density sediment, the mean (\pm SE) C_{org} resuspension at the highest flow (26 cm s^{-1}) was clearly lower (0.37 ± 0.06) than in the low-bulk-density sediment (1.5 ± 0.07), although this could not be statistically tested (due to an imbalanced dataset; Fig. 3a). Bed shear stress increased on average (\pm SE) in unvegetated sediment plots from $0.003 \pm 0.0001 \text{ N m}^{-2}$ at 5 cm s^{-1} to $0.086 \pm 0.002 \text{ N m}^{-2}$ at 26 cm s^{-1} and in seagrass-vegetated sediment plots from $0.003 \pm 0.00004 \text{ N m}^{-2}$ at 5 cm s^{-1} to $0.092 \pm 0.001 \text{ N m}^{-2}$ at 26 cm s^{-1} . There was no difference in suspended C_{org} concentration between unvegetated sediment and any level of seagrass shoot density (One-way ANOVA, $df = 3$, $F = 1.18$, $p = 0.32$; Fig. 3b).

The mean (\pm SE) suspended C_{org} concentration in seagrass-vegetated sediment plots was $0.13 \pm 0.02 \text{ mg L}^{-1}$ at low flow velocity (5 cm s^{-1}) and $1.26 \pm 0.2 \text{ mg L}^{-1}$ at high flow velocity

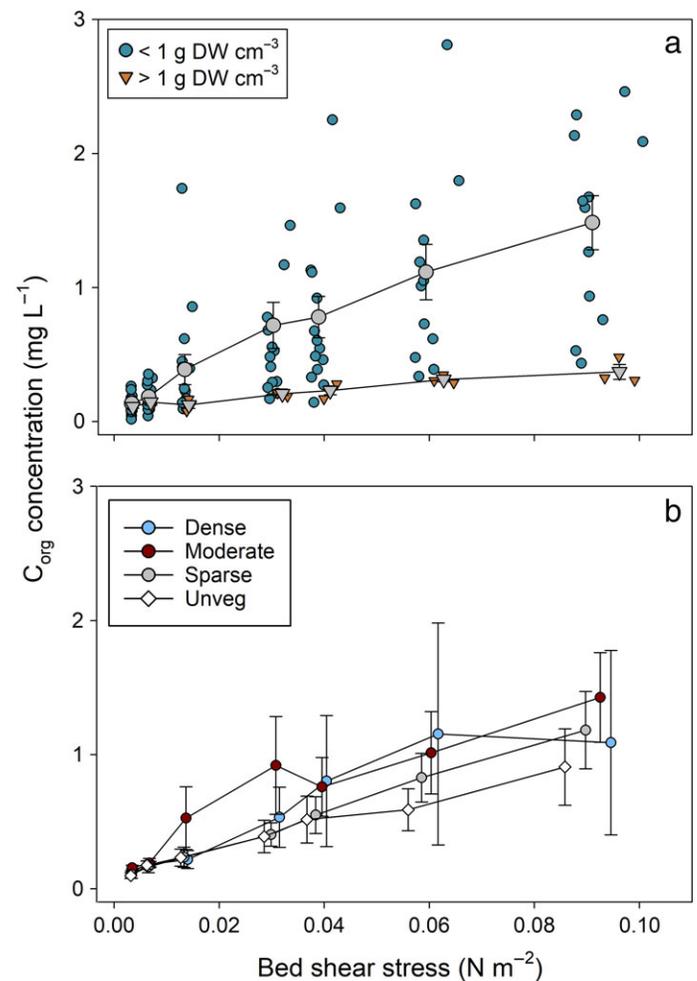


Fig. 3. Suspended C_{org} concentration in relation to bed shear stress as a function of (a) bulk density, and (b) shoot density (unvegetated as well as sparsely, moderately, and densely vegetated). Seagrass-vegetated sediment plots were divided according to bulk densities below ($n = 15$) and above ($n = 3$) 1 g DW cm^{-3} . Values represent mean \pm standard error. No statistical comparisons were made between the two bulk density groups due to the imbalance in the dataset.

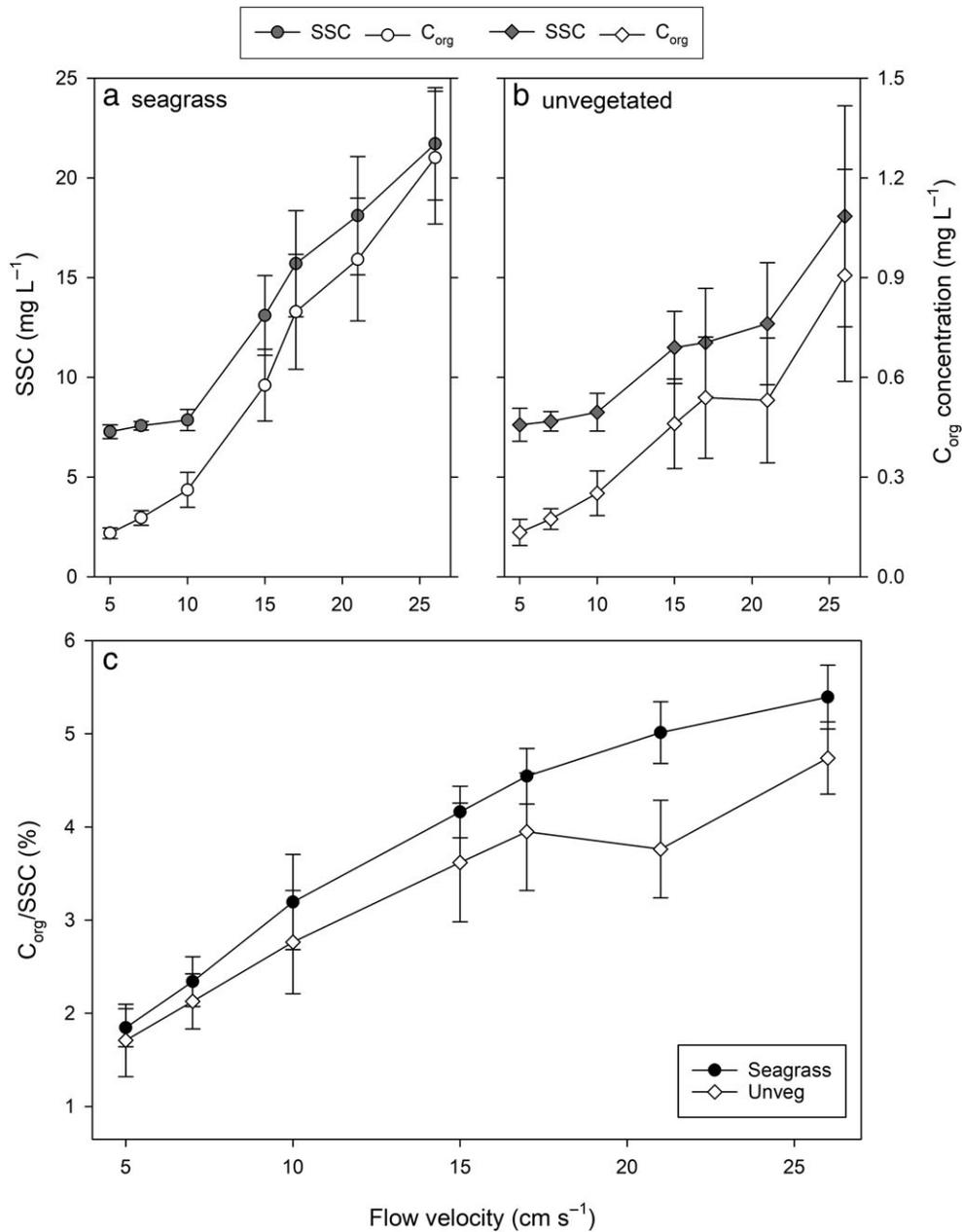


Fig. 4. SSC and suspended C_{org} concentration (mean \pm SE) at different flow velocities for (a) seagrass-vegetated sediment plots, (b) unvegetated sediment plots, and (c) proportion of C_{org} in SSC (mean \pm SE) for seagrass-vegetated and unvegetated sediment plots.

(26 cm s⁻¹), and SSC increased in seagrass-vegetated sediment plots from 7.27 ± 0.35 mg L⁻¹ to 21.71 ± 2.81 mg L⁻¹ at corresponding flows (Fig. 4a). For unvegetated plots, the mean (\pm SE) suspended C_{org} concentration was 0.16 ± 0.04 mg L⁻¹ at low flow velocity (5 cm s⁻¹) and 0.91 ± 0.32 mg L⁻¹ at high flow velocity (26 cm s⁻¹), and SSC was 7.62 ± 0.83 mg L⁻¹ and 18.08 ± 5.54 mg L⁻¹ at the low and high flow velocities, respectively (Fig. 4b). The ratio of suspended C_{org} concentration to SSC increased with flow velocity for seagrass-vegetated sediments (linear mixed-effect model, $R^2 = 0.76$, $p < 0.001$)

with a mean (\pm SE) proportion of C_{org} : SSC of $1.8\% \pm 0.19\%$ C_{org} at low flow velocity (5 cm s⁻¹) vs. $5.8\% \pm 0.30\%$ at high flow velocity (26 cm s⁻¹). This relationship was also seen in unvegetated sediment plots (linear mixed-effect model, $R^2 = 0.87$, $p < 0.001$; Fig. 4c), with an increase from $1.7\% \pm 0.39\%$ C_{org} to $4.7\% \pm 0.39\%$ C_{org} (at low and high flow velocities, respectively). The loss of C_{org} from the top cm of surface sediment significantly increased (linear mixed-effect model, $R^2 = 0.91$, $p < 0.001$) in seagrass-vegetated sediment plots from $0.55\% \pm 0.1\%$ at 5 cm s⁻¹ (mean \pm SE) to

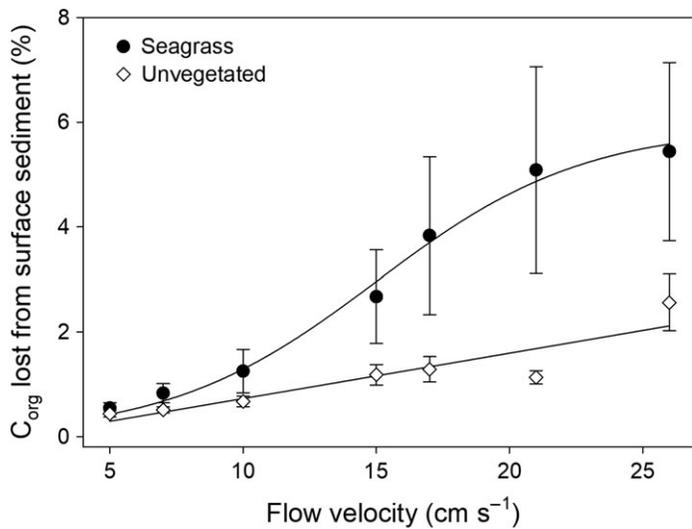


Fig. 5. The percent C_{org} lost (mean \pm SE), from surface sediment (top 1 cm) at different flow velocities for seagrass-vegetated and unvegetated sediment plots.

5.44% \pm 1.7% at 26 cm s⁻¹, while in the unvegetated sediment plots the C_{org} erosion significantly increased (linear mixed-effect model, $R^2 = 0.93$, $p < 0.001$) from 0.43% \pm 0.06% at 5 cm s⁻¹ to 2.56% \pm 0.54% at 26 cm s⁻¹ (Fig. 5). The suspended C_{org} concentration was positively correlated with SSC (linear regression, $R^2 = 0.94$, $p < 0.001$) and turbidity (linear regression, $R^2 = 0.96$, $p < 0.001$; Supporting Information Fig. S1), respectively.

Discussion

A future increase in storm frequency and intensity combined with changing sea levels under global warming will likely increase storm surges in coastal areas (e.g., Von Storch 2013). The associated increased hydrodynamic forces (i.e., waves, turbulence, and current flow) could lead to enhanced erosion of seagrass-vegetated sediment, in turn leading to the release of stored carbon and the loss of the seagrass meadows' ability to sequester carbon. In the present hydrodynamic laboratory experiment, in which we exposed several types of *Z. marina*-vegetated sediment patches with different sediment properties and shoot densities (8–253 shoots m⁻²) to one hydrodynamic-related factor associated to storm conditions, i.e., a gradually increasing current flow, we found that the proportion of C_{org} in suspended sediment increased with flow velocity. During periods of such elevated unidirectional flow, a large part of the resuspended particles will therefore likely be of organic origin, which may result in C_{org} erosion (of up to 5.5% according to this experiment) from the sediment surface. Higher C_{org} resuspension was associated with both sediment properties (i.e., low sediment bulk density, high porosity, and sedimentary C_{org}) and seagrass plant structure (i.e., high belowground biomass), which are also

important factors for carbon storage efficiency (Mateo et al. 1997; Dahl et al. 2016; Gullström et al. 2018). Meadows with high carbon storage potential could therefore experience higher resuspension of C_{org} when exposed to higher current flows, potentially reducing the accumulation of carbon for long-term storage. The combined effect of wave action and current flows on sediment surface erosion is nonlinear and depends on the direction of the currents and waves as well as the wave height and water depth (van Rijn 1993; Bradley and Houser 2009). Waves and currents in combination may therefore potentially have a greater impact on the bottom shear stress than any single process (Jing and Ridd 1996) and might efficiently induce sediment erosion, where waves cause suspension of particles that will be transported away by the unidirectional current flow (Greenwood and Sherman 1984).

Seagrasses are known to reduce near-bed flow velocities in meadows, thereby preventing particle resuspension (Hansen and Reidenbach 2012), and many hydrodynamic studies have demonstrated a negative relationship between shoot density or biomass and particle resuspension (e.g., Asmus and Asmus 2000; Gruber and Kemp 2010; Hansen and Reidenbach 2012). Despite a decrease in near-bottom flow velocity with increased seagrass shoot density, high resuspension in dense seagrass areas could still occur because particles settle on the leaves instead of the sediment, making them more easily resuspended (Ganthly et al. 2015), or because the reduced hydrodynamic force within the meadow creates a skimming flow above the canopy (Fonseca et al. 1982), which could locally penetrate the canopy and increase vertical turbulent mixing (Nepf and Vivoni 2000). On the Swedish Skagerrak coast, the density of *Z. marina* is generally lower than in many other areas (Boström et al. 2003, 2014; Gullström et al. 2012), so the shoot density used in this experiment (with a maximum of 253 shoots m⁻²) was lower than is commonly investigated in hydrodynamic studies (e.g., Gambi et al. 1990; Peterson et al. 2004; Peralta et al. 2008; Paul and Gillis 2015). In studies using low-density meadows, the seagrass seems to have less effect on hydrodynamic processes: for instance, Adhitya et al. (2014) showed that low-shoot-density *Posidonia oceanica* patches (400 shoots m⁻²) provided no protection against a horizontal flow, and Worcester (1995) observed no difference in turbulent mixing between *Z. marina* beds with densities of 100–200 shoots m⁻² and adjacent bare sand habitat. In low-density meadows, there could even be enhanced turbulence around individual plants and increased resuspension through sediment scouring (Nepf and Koch 1999; Lawson et al. 2012). It is therefore likely that the overall low shoot densities examined in this study were too low to effectively retain C_{org} and other sediment particles. In addition, we found that a higher belowground biomass positively influenced C_{org} resuspension, which is in contrast to the understanding of sediment stabilization from belowground biomass (Christianen et al. 2013). Therefore, it appears that in low-density meadows, a high C_{org} resuspension may be driven by sediment properties

(as indicated by the PLS model) or other factors, such as benthic microbial biofilms, which are known to have a stabilizing effect on the sediment (Lundkvist et al. 2007).

Low-bulk-density sediment weakens the stabilizing effect of the plant biomass (Widdows et al. 2008) and could, regardless of the level of biomass, explain high resuspension in low-density sediment. Bulk density is well known to influence erosion rates and thresholds (Jepsen et al. 1997; Bale et al. 2006, 2007), and low-bulk-density sediment can lead to a substantial increase in erosion (Lick and McNeil 2001) and sediment resuspension (Widdows et al. 2008). In our study, the response to increased flow velocity in low-bulk-density bed types seemed to be enhanced at a current flow of 15 cm s^{-1} , potentially reaching a critical velocity level for the stability of the sediment, however, this was not statistically proven. We also observed a difference between bulk densities above and below 1 g DW cm^{-3} (with correspondingly low and high porosities), sediments with densities below 1 g DW cm^{-3} on average having 4 times higher suspended C_{org} concentration at the highest flow velocity with similar bed shear stress. The fact that the high-bulk-density sediments formed the bed types mainly comprising sand particles with less mud (particle size less than 0.063 mm) likely explains this differentiation, as coarser sediment generally has a higher erosional threshold and is largely transported as bed load instead of being suspended in the water column (van Rijn 1993). In comparison, the low-bulk-density sediments contained a high proportion of mud (sometimes exceeding 50%), and in muddy sediment, the water content (porosity) influences the erodability to a higher degree. A high water content decreases the packing density of the sediment by increasing the distance between sediment particles, which in turn changes the state of the sediment from solid to fluid phase (Van Ledden et al. 2004; Jacobs et al. 2011). Just as bulk density and water content affect the stability of sediment (Grabowski et al. 2011), organic matter content can decrease the erodability by increasing the adhesiveness and critical shear stress (Walker and Bob 2001). In this experiment, however, a higher C_{org} content in the sediment corresponded to an increased suspended C_{org} concentration, possibly because the sediment surface in these types of seagrass meadows usually contains large amounts of recently deposited low-density organic detritus. It is therefore likely that a higher sedimentary C_{org} content will lead to an increased suspended C_{org} concentration.

Increased flow velocity had a more pronounced effect on suspended C_{org} concentration than on SSC, with the suspended C_{org} concentration increasing almost 10 times from low to high flow velocities compared with SSC, which only increased 3 times. The relationship between suspended C_{org} concentration and SSC was expected to be the opposite, as higher flow velocity would increase the resuspension of larger particles including fewer organic matter aggregates. The discrepancy between suspended C_{org} concentration and particle size might be due to the flocculation of low-density, carbon-

rich micro-aggregates with weights similar to those of silt and fine sand particles (Doetterl et al. 2016) or because the higher flow velocity resuspended larger seagrass litter and detritus particles accumulated on the sediment surface, which may also explain the increased C_{org} erosion from surface sediments. This shows that C_{org} continues to be resuspended at higher flow velocity and that part of the organic matter in the sediment surface layer, which otherwise could have contributed to the sedimentary carbon stock, might be removed during periods of increased unidirectional flow. The pattern of the resuspension of larger particles during a high-energy event has been observed in situ, when measuring the suspension of particles following a storm (with a mean current velocity of 17 cm s^{-1}); areas with a seagrass shoot density of about 200 m^{-2} did have an increase in large-particle resuspension, whereas areas with lower or higher shoot densities did not (Granata et al. 2001).

Hydrodynamic exposure could partially explain the variability in seagrass carbon storage seen globally (Samper-Villarreal et al. 2016; Mazarrasa et al. 2017; Oreska et al. 2017), as exposure to wind and currents largely governs the process of sedimentation (Winterwerp and van Kesteren 2004). To what degree currents affect the sedimentary carbon stocks in seagrass meadows is not known, although such data are critical for understanding the carbon sequestration and storage efficiency in coastal environments. Although this hydrodynamic experiment was done on small-sized seagrass patches and with a limited water column height, our study clearly adds new knowledge regarding how unidirectional (current) flow velocities impacts C_{org} erosion in regions characterized by low-density seagrass meadows in that we show that periods of increased current flows can result in a large loss of surface sedimentary organic carbon (ranging from 1% to 28% during one event of increased current velocity). The reduction of hydrodynamic forces and associated efficient sediment trapping comprise essential ecosystem services provided by seagrass meadows (Infantes et al. 2012; Potouroglou et al. 2017). As seagrass habitats decline worldwide (Waycott et al. 2009) and storms are predicted to increase in frequency and intensity (Vose et al. 2014), hydrodynamic forcing in coastal seas may promote erosion and sedimentary organic carbon loss. The seagrass cover on the Swedish west coast has decreased by about 60% since the 1980s (Baden et al. 2003; Nyqvist et al. 2009) as an effect of eutrophication (Baden et al. 2012), likely indirectly strengthened by overfishing (Moksnes et al. 2008; Baden et al. 2012), resulting in the fragmentation of *Z. marina* meadows (Nyqvist et al. 2009). Seagrass loss or reduced shoot density can lead to sediment instability and altered hydrodynamic properties (van der Heide et al. 2007), resulting in the erosion of buried carbon (Macreadie et al. 2015; Marbà et al. 2015) with the risk of CO_2 being released back into the atmosphere (Lovelock et al. 2017). Low shoot densities cannot sufficiently protect the sediment and C_{org} from resuspending when exposed to

increased hydrodynamic forces, as indicated by this experiment. Seagrass patch size is known to affect carbon storage (Gullström et al. 2018; Ricart et al. 2017), and the erosion of carbon will probably be higher in a fragmented seagrass landscape with smaller meadows due to the higher impact of hydrodynamic activity in the edge zones of the meadows (Adams et al. 2016; Oreska et al. 2017). It is assumed that storms will be more frequent and intense in the future (Collins et al. 2013; Von Storch 2013), and as fragmented seagrass landscapes are vulnerable to high hydrodynamic activity, this could further increase the fragmentation process by enhancing erosion, uprooting seagrass plants, and increasing turbidity. Considering climate change projections and the ongoing loss and fragmentation of seagrass habitats, our findings highlight the negative effects on the function of seagrass meadows as natural carbon sinks when the strength of hydrodynamic forces increases.

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Conflict of Interest

None declared.

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