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Sandification vs. muddification of tidal flats by benthic organisms: A flume study

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ABSTRACT

Bioturbating benthic organisms have typically been characterised by how they modify the vertical sediment erosion thresholds. By means of several annular flume experiments, we aimed to understand how benthic organisms may affect grain-size sediment properties over time, and how this depends on the sediment type and the sediment loading of the water column. We compared the effect of two bioturbating macroinvertebrate species: a local dominant species, the cockle *Cerastoderma edule* and a spreading non-indigeneous species, the clam *Ruditapes philippinarum*. Our results indicate that the effect of benthic organisms on sediment dynamics is strongly dependent on both the prevailing environmental conditions and the benthic species present. If sediment is sandy, the benthos can gradually enhance the silt content of the sediment by mixing in part of the daily tidal sediment deposition. In contrast, if sediment is muddy, benthos can gradually decrease the silt content of the sediment by specifically suspending the fine fraction. Moreover, we observed that the native cockles had a stronger impact than invasive clams. Therefore, bioturbating benthos can have an important effect in determining the local sediment properties, with the outcome depending both on the species in question and the environmental conditions the bioturbator lives in. Our findings show that sediment bioturbation may have strong implications for tidal flat stability undergoing major changes from natural or anthropogenic sources.

1. Introduction

In addition to the major influence that physical processes like waves and currents have on shaping tidal flats (Le Hir et al., 2000), benthic organisms can be highly important (Le Hir et al., 2007; Wood and Widdows, 2002). By their presence and/or activity, benthic organisms can modify the abiotic environment (Jones et al., 1994; Meadows et al., 2012; Volkenborn et al., 2009). Indeed, for tidal flats, there are many examples of studies reporting the influence of marine benthic organisms, such as seagrasses (Bos et al., 2007; van Katwijk et al., 2010), salt marsh species (Mudd et al., 2010; Yang et al., 2008), microphytobenthos (Murphy and Tolhurst, 2009; Orvain et al., 2007), polychaetes like *Arenicola marina* (Volkenborn et al., 2009), bivalves (Widdows and Brinsley, 2002; Willows et al., 1998) and tube worms (Alves et al., 2017; Borsje et al., 2014; Van Hoey et al., 2008) in modifying tidal flat characteristics. By doing so they may, in turn, influence their spatial distribution.

The spatial distribution of benthic organisms on tidal systems is typically determined by a number of dominant environmental conditions such as inundation/emergence period along the elevation gradient (Balke et al., 2016; Cozzoli et al., 2014), sediment properties along the hydrodynamic energy gradient (Li et al., 2017) and temperature fluctuations driven by the seasons (Laugier et al., 1999). For instance, benthic organisms such as cockles are preferably found in environments characterised by a median grain size of 100–250 µm (Cozzoli et al., 2013), the polychaetes *Arenicola marina* are found in sandy to muddy sediments with 2–12% silt (Philippart, 1994). Hence, it is primarily local physical settings that will determine where organisms settle and

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thus how these organisms might modify the abiotic environment. Yet, since benthic organisms may act as ecosystem engineers (*sensu* (Jones et al., 1994)), they can alter an important niche axis such as grain size by stabilising the sediment through attenuating the effect of waves and currents near the bed level (Bouma et al., 2005; Borsje et al., 2014; Friedrichs et al., 2000; Hendriks et al., 2008; McIvor et al., 2012), stabilising the sediment by increasing the critical erosion threshold via the presence of roots and rhizomes (Christianen et al., 2013; Lo et al., 2017) preventing sediment erosion through the development of protective biofilms (Andersen et al., 2010; Montserrat et al., 2008), increasing the mud content of surface sediments via biodeposition (Andersen et al., 2010; Fernandes et al., 2007; Rueda et al., 2005) or destabilising the sediment by lowering the critical erosion threshold of muddy cohesive sediments or sand-mud mixtures via bioturbation (Ciutat et al., 2006; Cozzoli et al., 2018; Donadi et al., 2014; Li et al., 2017; Orvain et al., 2006; Rakotomalala et al., 2015; Widdows et al., 2000; Willows et al., 1998). Due to this range of underlying mechanisms, the influence that benthic organisms may impose on shaping tidal areas typically depends on a range of biological traits such as their density (e.g., Eckman, 1983; Friedrichs et al., 2000), their morphology (e.g. Bouma et al., 2005), their metabolic rate (Cozzoli et al., 2018, 2019) and physiological functioning (e.g., Mermillod-Blondin and Rosenberg, 2006; Volkenborn and Reise, 2006). This habitat modification also depend on the time scale at which the organism is present (e.g., Borsje et al., 2014; Meadows et al., 2012), on environmental conditions (Fernandes et al., 2007; Ubertini et al., 2012) and on the phase in a tidal flat physical dynamics, e.g. accretion vs. erosion phase (Balke et al., 2012; Le Hir et al., 2000), at which it is active. This kind of conditionality in habitat makes it difficult to predict the long-term effects that benthic organisms can have in various environmental settings modification (Balke et al., 2012; Salvador de Paiva et al., 2018).

Whereas field observations are well suited to describe the long-term effect of benthic organisms (e.g. (Andersen et al., 2010; Orvain et al., 2007; Ubertini et al., 2012)), they often make it difficult to identify the underlying mechanisms. Flume studies allow testing on mechanisms of habitat modification by controlling external parameters and environmental conditions. However, as a trade-off, they typically focus on short-term effect (e.g. (Ciutat et al., 2007; Cozzoli et al., 2018; Orvain et al., 2006; Widdows et al., 2000; Willows et al., 1998)). In this study, we aim to *(i)* overcome the involved logistical challenges and perform a somewhat longer flume study to gain a basic mechanistic understanding of how benthic organisms may affect the long-term development of grain-size distributions on tidal flats under contrasting environmental settings and *(ii)* assess the species-specific sensitivity of such effects by comparing a native and non-indigenous species with similar size and feeding modes (Molnar et al., 2008). We hypothesise that benthic organisms affect benthic sediment composition by enhancing selective erosion and deposition processes. We study these questions using multiple-day annular flume runs where we simulated different environmental conditions: mudflat accretion (i.e. high availability of suspended sediments in the water column for deposition) and erosion (no suspended sediments available in the water column for deposition); with contrasting sediment and biotic settings. Suspended Sediment Concentrations (SSC) and grain-size distributions were measured as response variables.

2. Material and methods

2.1. Experimental design

In order to better understand how the long-term effect of benthic organisms on sediment properties and resuspension may depend on their environmental conditions, sets of flume experimental runs were initiated. We measured the effect of two model benthic organisms on sediment resuspension over 90 min-long tests that were repeated for 4 consecutive days. Four treatments were designed to mimic different environmental conditions that these benthic organisms may experience: 2 contrasting sediment types (sandy vs. muddy) and 2 contrasting water turbidity conditions (erosion condition = low SSC = clear water vs. accretion/deposition condition = high SSC = turbid water). These ‘condition treatments’ were tested with and without benthic organisms in a full factorial setup: sandy sediment in a situation of erosion [S-clear]; sandy sediment in a situation of accretion/deposition [S-turbid]; muddy sediment in a situation of erosion [M-clear]; and muddy sediment in a situation of deposition/accretion [M-turbid] (Fig. 1).

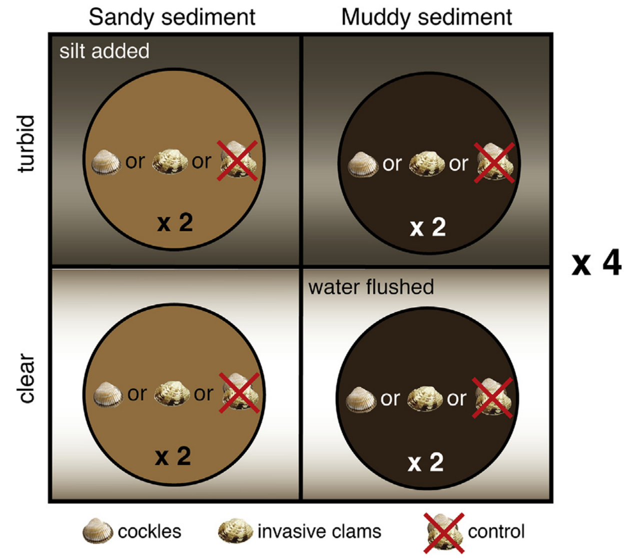

Fig. 1. Experimental setup of the flume study. Four environmental conditions were created with two sediment types (sand = S vs. mud = M) and two water column turbidity conditions (clear = erosion vs. turbid = accretion). Normal conditions were used for the S-clear and M-turbid conditions based on the expected low vs. high increase in SSC when current velocities increase in the flumes. The S-turbid treatment was created by adding silt into the water column after each daily 90 min tests. The M-clear treatment was created by flushing the water contained in the flumes after each daily 90 min tests. Each run consisted of 8 flumes with four environmental conditions (n = 2) with cockles or invasive clams or no benthic organisms present (i.e. control). Each run was replicated 4 times.

2.2. Model benthic organisms

The common cockle *Cerastoderma edule* [Linnaeus, 1758] (from now on referred to as ‘cockle’) is a widespread and dominant suspension-feeding bivalve that lives and burrows in the top few centimetres of marine sediments along the European Atlantic coastline. During the last decades, the typical cockle habitat in Europe has been invaded by the non-indigenous Manila clam *Ruditapes philippinarum* [Adams and Reeve, 1850] (from now on referred to as ‘invasive clam’), which was accidentally introduced with the pacific oyster (*Magallana gigas*) from SE-Asia to NW-Europe in the 20th century (Molnar et al., 2008). According to some experimental evidences, both organisms can contribute to changes in sediment stability by their vertical and horizontal activity (movement and feeding behaviour) and by excreting fecal pellets into the water column (Cozzoli et al., 2018; Donadi et al., 2014; Montserrat et al., 2008). Earlier studies have shown that the increasing presence of cockles can increase sediment erodibility, and significantly lower sediment erosion thresholds, making it an ideal model species to study bioturbating effects and sediment stability (Widdows et al., 1998). Little knowledge is available on the effect of the invasive clam on sediment erodibility and sediment stability. Since it shares the same habitat as cockles and has a similar feeding mode and behaviour as cockles, it is increasingly becoming competitive with the cockles (Humphreys et al., 2015) and forms a good model species to use in our study.

2.3. Experimental setup

Annular flumes (surface area of 0.157 m^2) were developed following the design described by Widdows et al. (1998). They are used to generate currents and bottom stresses similar to those experienced in field conditions. A rotation disk placed on top of the flume and empowered by a microprocessor-controlled engine generates currents. It can produce currents at different velocities depending on the rpm (revolutions per minute) setting of the disk, which can be converted to current velocities (m s^{-1}). Suspended sediment concentrations (SSC) were measured with an optical backscatter (OBS), measuring turbidity levels in the water column in NTU. Water samples were taken during the experimental runs to calibrate the turbidity levels obtained from the OBS and convert the NTU values into SSC in g.L^{-1}. A more detailed description and technical drawings of the flumes can be found in (Cozzoli et al., 2018).

Flume preparation: The flumes were prepared in a similar way as in Li et al. (2017). Prior to each experimental run (i.e. 4 days long), a 7 cm gravel bed was placed at the bottom of each flume, with a 10 cm sieved sediment layer above it, separated by a plankton net. The gravel bed under the sediment layer was used to drain the water contained in the sediment layer when filling the flume and to consolidate the sediment. The wet sieved sediment was placed into the flumes, mixing it by hand or a stainless steel plate to create a smooth and homogeneous mass. The sediment layer was left for consolidation for 4 days by opening the drainage hole under the gravel bed to allow the excess water to escape. After sediment consolidation, 31.4 L of seawater was gently pumped into the flumes, while keeping a ‘bubble wrap’ layer on top of the sediment to prevent sediment disturbances. After this step, another 3 days were necessary to enable further sediment consolidation. Prior to each experimental run, the top sediment layer was carefully removed by hand, and the flume walls cleaned to avoid the potential development of microphytobenthos inside the flumes, that may influence sediment properties and erosion (Murphy and Tolhurst, 2009).

Sediment preparation: Two sediment types, i.e. sandy and muddy, were used for the flume runs and prepared beforehand. To prepare the two sediment types, natural sediment containing 75% of silt (% of particles with a size of 3.9–62.5 μm according to the Udden-Wentworth scale) was collected from Kapellebank in the Westerschelde estuary (N 51.459639, E 3.968422). This natural sediment was firstly cleaned and sieved through 0.5 mm mesh size to remove any living organisms and shells and to homogenize the sediment. The sieved sediment was then mixed with pure sand (washed and nutrient-free sand) to obtain the two sediment types. Sediment composition and grain size was checked prior to the flumes runs (see section 2.4 on sediment samples and analysis). The two sediment types obtained were thus composed of: 0% silt for the sandy sediment; and 8% silt for the muddy sediment.

Benthic organisms' addition: The benthic organisms were collected 48 h before each experimental run in the Eastern Scheldt estuary, Netherlands (cockles: 51°27′57.05N, 4°13′9.62E; invasive clams: 51°39′21.41N, 3°47′59.47E) and left for acclimation in tanks filled with aerated seawater. After acclimation, only the active and healthy benthic organisms were selected and placed in the annular flumes. The collected cockles measured 26–28.5 mm, whereas the invasive clams measured 27.5–31.5 mm. Experiments were performed in condition of biomass equivalence to allow comparison between both species, and based on local density estimates of cockle presence (around 100 ind.m^{-2} (Beukema and Dekker, 2015; Ysebaert and Herman, 2002);). As the area of one flume is 0.2 m^2, we placed 18 individuals per flume for the cockles (i.e. 90 ind.m^{-2}) and 15 individuals for the invasive clams (i.e. 75 ind.m^{-2}).

Experimental runs: Each experimental run consisted of a 90 min test per day repeated for 4 days. For each 90 min test, current velocities in the flumes were increased in increments of 0.05 m s^{-1} every 5 min until a maximum speed of 0.2 m s^{-1} (corresponding to local hydrodynamic conditions, see (Cozzoli et al., 2019; Li et al., 2017)). The aim of our study being to investigate the change in sediment composition and properties in presence/absence of benthic organisms, only the last velocity was used for data analysis and was maintained until the end of the 90 min test (i.e. when SSC values were stable). After each 90 min test, the rotation disk was gradually stopped and the flumes left at rest until the next day, leaving the benthic organisms inside. The 90 min tests were repeated for all flumes over 4 days to assess longer-term effects. The current velocity profile we simulated was chosen to provide a more realistic image of the natural situation (see Cozzoli et al. (2019) and to ensure a gradual increase of turbidity in the flumes. Average turbidity values were calculated with an interval time of 30 s, resulting in 180 data points per 90 min test.

A total of 8 flumes were used simultaneously during each 90 min test (Fig. 1). Four flumes were filled with a muddy sediment and four others with a sandy sediment.

For the muddy sediment, two flumes were used for the [M-turbid] treatment. This implies that the water got turbid as a result of the flume treatment, as no additional silt was added to the flume water. That is, we used the flume-induced increase in SSC when current velocities increase in the flumes to simulate a situation of deposition/accretion following a situation of erosion. In contrast, in the two other flumes for the [M-clear] treatment, the water above the sediment was flushed right after the 90 min test, and filled with 31.4 L of clean filtered seawater at the end of the day to simulate a situation of erosion or the effect of tidal flushing. As a result, all suspended matter that was present in the water was washed away daily.

For the sandy sediment, two flumes were used for the [S-turbid] treatment. In these flumes, 3.1 g of silt was added (i.e. 0.1 g.L^{-1}) to increase water turbidity as would be caused by human activity such as dredging for instance, creating a situation of accretion/deposition. The added silt was freeze-dried prior to the experiment to remove any living organisms. For the [S-clear] treatment simulating a situation of erosion, no silt was added. Thus SSC remained low in all sequential runs, as there can only be a minimal increase in SSC due to current velocities being too slow to suspend a large amount of sandy sediment.

For all experimental runs, flumes were filled with either cockles, or invasive clams or no benthic organisms (control). Each combination of condition treatments x benthic organisms was replicated 4 times (Fig. 1).

2.4. Sediment samples and analysis

Sediment samples were collected before (i.e. before being added to the flumes, when the sediment was prepared) and after the 4 days experimental runs in the top 5 cm of the bottom sediment surface in the flumes. Sediment was sampled by using 5 cm deep and 2.9 cm diameter cores (n = 5 per flume), and then sliced every cm for sediment grain size analysis. The sediment samples were only taken in the flumes with cockles and controls; no samples were taken for the invasive clam. The median grain size (D50), and percent silt content of the freeze-dried sediment samples were measured using a Mastersizer 2000 (Malvern Instruments Ltd., Malvern, UK).

2.5. Statistical analysis

Suspended sediment concentration (SSC, g.L^{-1}) data were obtained after calibration of the OBS. As our study aimed at investigating the final effect of benthic organisms on sediment properties and composition, the measured SSC values from Day 4 (last day of the flume runs) were averaged from 40 min after the start of the flume run when current velocity reached 0.2 m s^{-1} and until 80 min, i.e. 10 min before the end of the experiment. The mechanisms related to the final SSC values (i.e. erosion profiles, changes in averaged final SSC per day) are presented as supplementary material. To test for the influence of benthic organisms (i.e. cockles vs. invasive clams vs. control) on changes in SSC at the end of each 4 days experiment runs, a mixed effect model was used. The model accounted for the effect of benthic organism as a fixed factor, and two random factors to include the potential effect of the flume setup and experimental design on the tested results. The first random factor considered was: 'Experiment type', as we ran a total of 8 series of flumes run in which there were 8 annular flumes running simultaneously including, in the 4 first series, the experiment: cockles (n = 4) vs. controls (n = 4); and, in the 4 last series, the experiment: clams (n = 4) vs. controls (n = 4). Each experiment type was replicated 4 times (hence the total of: 2 experiment types x 4 replicates = 8 series of flume runs), this is why a second random factor: 'Replica' nested within 'Experiment type' (hereafter referred to as: 'Replica:Experiment') was also added to the model. The mixed effect model was done using the lmer function from the 'lmerTest' R-package. Posthoc Tukey tests were performed on the tested results using the 'emmeans' R-package. This type of model also allows to account for the temporal pseudoreplication of the experiment ((Millar and Anderson, 2004). The influence of benthic organisms, depth sampled (as fixed factors) and their interaction was tested with a mixed effect model on final sediment properties (D50, percent silt) for each condition treatment (the 5 cores per flume were pulled per depth sampled) using the lme function with the 'lme4' R-package. Normality of the data was checked on the different models by using QQplots of the residuals with the 'qqnorm' function. All statistical analyses were realised using R version 3.5.1 (R core Team, 2018). Data are presented as means ± SE.

3. Results

3.1. Bioturbating effect of benthic organisms depending on environmental conditions

Under normal sandy sediment conditions, i.e. flumes in which we did not modify the SSC by adding silt to the water ([S-clear] treatment), the presence of benthic organisms after 4 days led to a decrease of the water column SSC (Fig. 2; Table 1). The decrease was particularly strong for the invasive clams, for which SSC was about half that of the controls (Fig. 2).

In contrast, higher SSC was observed for the [M-turbid] flumes, in presence of both benthic organisms as compared to the control flumes (Fig. 2, Table 1). Cockles generally led to higher resuspension than the invasive clams (Fig. 2). That is, we observed an increase in SSC of almost 4-fold in the presence of cockles and of about 2-fold in the presence of invasive clams compared to controls in the [M-turbid] flumes (Fig. 2d).

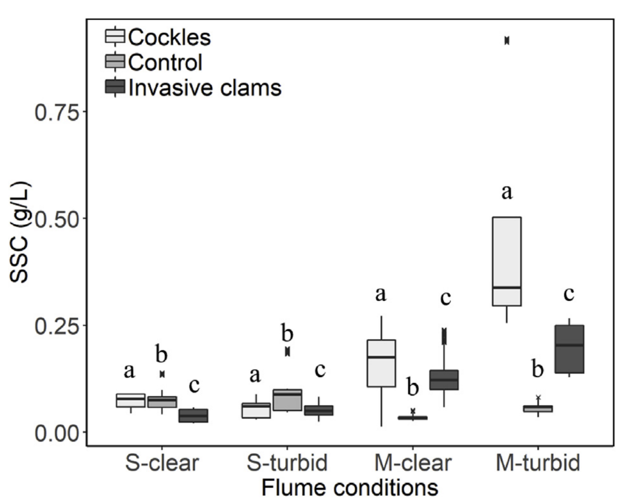

Fig. 2. Boxplots of the suspended sediment concentration (SSC) in g. L^{-1} at Day 4 for the different benthic organisms tested, i.e. control = no benthic organisms, cockles, invasive clams and for the different flume conditions (X-axis). Small letters (a,b,c) represents different statistical groups from the posthoc Tukey tests per flume condition.

Table 1
Results from the mixed effect model on the SSC values measured at current velocity = 0.02 m s^{-1} at day 4 and averaged over the last 30 min of the 90 min tests for each flume condition. The model accounts for: 'Benthic org.' (org. = organism) as a fixed factor and 'Replica:Experiment' and 'Experiment' are random factors. 'Replica:Experiment' represents the nested effect of Replica within the factor Experiment. The p-values for the fixed factor are based on a F-test, the p-values for the two random effects are based on a Chi-square test.

Condition treatment	Factor	df	F	p-value
S-clear	Benthic org.	2	842.15	< 0.001*
	Replica:Experiment	1		< 0.001*
	Experiment	1		0.9997
S-turbid	Benthic org.	2	394.55	< 0.001*
	Replica:Experiment	1		< 0.001*
	Experiment	1		1
M-clear	Benthic org.	2	879.77	< 0.001*
	Replica:Experiment	1		< 0.001*
	Experiment	1		1
M-turbid	Benthic org.	2	1297.8	< 0.001*
	Replica:Experiment	1		
	Experiment	1		1

A decrease in SSC was observed when silt was repeatedly added into the water column for both benthic organisms present in sandy sediments (situation of accretion, i.e. treatment [S-turbid]) (Fig. 2, Table 1). In contrast, the presence of benthic organisms increased SSC compared to controls when the water was repeatedly flushed in the flumes with muddy sediment (i.e. situation of erosion, treatment [M-clear]). This indicates a strong bioturbation effect of both invasive clams and cockles in the sediment, removing fines from the sediment, thereby causing less fines to be available during the next flume run (Fig. 2). The effect of cockles was higher than the effect of invasive clams on resuspending SSC in the [M-clear] flumes (Fig. 2).

3.2. Net effect of cockle presence on sediment properties

The presence of cockles in the sandy sediment after day 4, when silt was added daily (i.e. [S-turbid]), led to an increase in sediment silt content in the top centimetres of sediment and a significant decrease in sediment D50 (comparing control vs. cockle flumes: Table 2 and 3). The effect on silt content was however not significant due to the large variation between replicates (high standard error, Table 2 and 3). No significant differences due to the presence of cockles were found on grain size in the [S-clear] flumes (Table 3). When compared to control flumes, the presence of cockles led to an increase in sediment silt content in the [M-clear] flumes (Table 2 and 3) and a significant decrease in sediment median grain size (D50; Table 2 and 3). A decrease in sediment silt content was also found due to the presence of cockles in the [M-turbid] flumes after 4 days (Table 2); be it only marginally significant (Table 3). Sediment D50 did not significantly change in the [M-turbid] flumes when cockles were present (Table 2 and 3).

4. Discussion

In our study we confirmed that, by resuspending fine particles into the water column due to their movement and feeding activity, benthic organisms increase suspended sediment concentration in the overlying water (Ciutat et al., 2006; Fernandes et al., 2007; Mermillod-Blondin et al., 2005; Rakotomalala et al., 2015; Ubertini et al., 2012). This may potentially lead to a decrease in sediment silt content and thus a 'sandification' of the sediment (Fig. 3). In addition, our flume study also demonstrated that, in sandy sediments, benthic organisms could actively contribute to sediment modification by reducing sediment

Table 2
Averaged and depth-specific grain size values (Silt content and D50) at the end of the 4 days experimental runs for the different condition treatments in controls and in flumes where cockles were added.

	Control							Cockles						
	average	0–0.5 cm	0.5–1 cm	1–1.5 cm	1.5–2 cm	2–2.5 cm	2.5–3 cm	**average**	0–0.5 cm	0.5–1 cm	1–1.5 cm	1.5–2 cm	2–2.5 cm	2.5–3 cm
Silt (%)														
S-clear	**0.05 ± 0.05**	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.3 ± 0.2	0.0 ± 0.0	**0.0 ± 0.0**	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0
S-turbid	**0.0 ± 0.0**	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	**0.2 ± 0.1**	0.7 ± 0.5	0.2 ± 0.1	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0
M-clear	**10.9 ± 0.4**	10.5 ± 0.8	10.6 ± 0.8	11.1 ± 0.9	10.6 ± 0.9	11.3 ± 1.2	11.6 ± 1.0	**12.6 ± 0.6**	11.7 ± 2.0	12.5 ± 1.4	12.0 ± 1.0	12.4 ± 1.5	13.8 ± 1.9	13.0 ± 1.7
M-turbid	**11.4 ± 0.4**	11.4 ± 0.7	11.1 ± 0.9	11.8 ± 1.1	10.9 ± 0.7	10.9 ± 1.0	11.9 ± 1.1	**10.3 ± 0.5**	10.2 ± 1.9	9.3 ± 1.5	9.1 ± 1.4	11.3 ± 1.4	11.2 ± 1.2	10.8 ± 0.7
D50 (mum)														
S-clear	**311.9 ± 2.6**	314.8 ± 7.0	315.2 ± 6.1	309.8 ± 7.5	309.4 ± 7.1	307.0 ± 5.7	316.2 ± 8.6	**312.1 ± 1.4**	310.2 ± 6.7	311.0 ± 4.2	312.2 ± 2.1	313.3 ± 1.9	313.0 ± 1.7	312.6 ± 1.7
S-turbid	**311.9 ± 1.3**	309.5 ± 4.3	312.2 ± 3.5	309.0 ± 3.0	313.4 ± 2.6	314.2 ± 2.9	313.2 ± 2.4	**307.0 ± 1.4**	299.0 ± 4.5	307.6 ± 2.8	308.3 ± 3.5	310.1 ± 2.6	309.1 ± 3.3	307.7 ± 2.6
M-clear	**301.3 ± 1.0**	301.2 ± 2.2	300.7 ± 2.4	300.7 ± 2.8	302.5 ± 2.2	302.4 ± 2.6	300.2 ± 3.1	**295.0 ± 1.9**	295.9 ± 5.4	298.4 ± 4.0	296.3 ± 3.2	296.4 ± 5.0	290.7 ± 5.8	292.3 ± 5.9
M-turbid	**297.9 ± 1.3**	299.7 ± 3.5	299.1 ± 3.9	297.3 ± 3.3	297.6 ± 2.5	299.6 ± 2.4	293.6 ± 4.0	**299.7 ± 1.8**	297.7 ± 5.0	304.2 ± 4.0	303.5 ± 3.8	297.7 ± 5.4	297.3 ± 5.3	297.9 ± 3.0

Table 3
Results from the mixed effect model on the sediment D50 (mum) and silt content (silt in %) testing the effect of depth sampled and benthic organism (control vs. cockles) and their interaction for the different condition treatments. Highly significant p-values ($p < 0.05$) are followed by two stars (**); marginally significant p-values ($p < 0.1$) are followed by one star (*).

Condition treatment	Factor	Silt			D50		
		df	F	p-value	df	F	p-value
S-clear	Depth		1000	0.5	5	0.434	0.81
	Benthic org.		0.973	0.369	1	0,000	0.995
	Depth * Benthic org		2.172	0.069	5	0.442	0.817
S-turbid	Depth		1000	0.5	5	2.987	0.128
	Benthic org.		1.552	0.268	1	14.086	0.013**
	Depth * Benthic org.		1.516	0.194	5	0.495	0.779
M-clear	Depth		4000	0.07*	5	0.754	0.618
	Benthic org.		50.437	0.001**	1	22.277	0.005**
	Depth * Benthic org.	5	0.08	0.995	5	0.335	0.89
M-turbid	Depth	5	0.571	0.723	5	1.204	0.422
	Benthic org.	1	4.465	0.08*	1	1.441	0.284
	Depth * Benthic org.	5	0.492	0.781	5	0.44	0.819

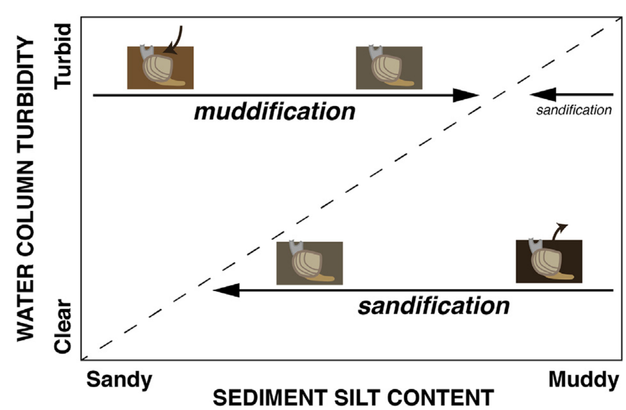

Fig. 3. Conceptual diagram on the effect of benthic organisms on sediment properties depending on their environmental conditions (i.e. water column turbidity and sediment silt content). If sediment is sandy, benthic organisms can gradually enhance the silt content of the sediment by mixing in part of the daily tidal sediment deposition, particularly in turbid = accretion conditions. This leads to the muddification of the sediment. If sediment is muddy, benthos can gradually decrease the silt content of the sediment by specifically resuspending the fine fraction, leading to a sandification of the sediment. In our experiment, we observed this sandification in both clear = erosion and turbid = accretion conditions.

resuspension and by trapping silt particles into the sediment thereby reducing the sediment median grain size. By doing so, they lead to the 'muddification' of sediment (Fig. 3). The outcome of the habitat modification effect by bioturbating animals is thus conditional, depending on grain size and SSC.

4.1. Sediment modification by benthic organisms

The influence of benthic organisms in modifying sediment properties has been observed in field studies on seagrasses (van Katwijk et al., 2010), as well as on the polychaetes *Arenicola marina* (Volkenborn et al., 2009, 2007), microphytobenthos (Montserrat et al., 2008; Murphy and Tolhurst, 2009), the tube worm *Lanice conchilega* (Alves et al., 2017; Van Hoey et al., 2008) and the cockle *Cerastoderma edule* (Andersen et al., 2010; Van Colen et al., 2013). Those studies showed that the extent at which benthic organisms may modify the sediment properties depends on their morphological and mechanical structures, but also on their body size and density (Queirós et al., 2015; Solan et al., 2004). For instance, the presence of seagrasses or tube worms in high densities can lead to the muddification of the sediment (Van Hoey et al., 2008; van Katwijk et al., 2010). In contrast, the presence of seagrasses in low densities, the absence of microphytobenthos and the presence of the polychaete *Arenicola marina* lead to a sandification of the sediment (Murphy and Tolhurst, 2009; van Katwijk et al., 2010; Volkenborn et al., 2007). In our study, we measured that suspended particles resuspension was higher in the presence of cockles as compared to invasive clams; particularly in muddy sediments, hence leading to a potential sandification of the sediment. Although our rather short-term study (which is however relatively long-term for annular flume approaches) did not allow the detection of significant changes in sediment composition directly, sandification was clear from the increase in SSC for the muddy sediment treatment in clear water conditions. The species difference may suggest that at similar densities, the cockles were more active, if not more efficient, in resuspending particles. This could also be related to the size of the selected organisms (i.e., cockles were smaller than invasive clams in our experiment), as smaller organisms have a higher activity rate per unit of mass than larger ones (Cozzoli et al., 2018). Nevertheless, the contribution of benthic organisms to sediment processes may also be species-specific due to differences in e.g. behaviour. This might have an impact on the overall ecosystem functioning in the long-term if, for instance, the invasive clams outcompeted the local cockles.

4.2. Muddification vs. sandification by benthic organisms: under which conditions?

The mechanism of sediment modification by benthic organisms is not only due to their presence and/or their biological properties. It is also linked to the feedback mechanisms that benthic organisms can create with their environment (Herman et al., 2001; Maxwell et al., 2016). With our study, we showed that changes in environmental conditions, i.e. sediment type and turbidity levels (SSC), might also be an important driver of how benthic organisms impact on sediment erosion and properties (Fig. 3). Environmental conditions such as sediment properties or turbidity levels play a significant role in determining the presence/absence of benthic organisms (Cozzoli et al., 2013; Willems et al., 2008). But, in our study, we showed that benthic organisms were able to trap the silty particles available in the water column to make a sandy sediment (containing 0% silt) muddier (i.e. muddification = increase in sediment silt content and decrease in SSC over time; Fig. 3). A ‘muddification’ of the top sediment layers may also be related to the occurrence of advective pore water flows, incorporating fines into sandy substrates due to sediment permeability and the formation of sand ripples when current speed increases (Huettel et al., 1996; Huettel and Rusch, 2000). The process was not directly investigated in our study. It was likely not very important in this relatively fine sediment (D50 = 300 μm), but if important it should also have occurred in our experimental controls (i.e. flumes with no organism present), although benthic organisms could have intensified the process by enhancing sediment relief. Both benthic organisms were also able, when silt content was too high (i.e. muddy sediment in situation of deposition) to further increase SSC, potentially leading to a sandification of the sediment (i.e. decrease in SSC over time and decrease in the amount of small and silty particles in the bottom sediment; Fig. 3). Therefore, the combination of both changes in environmental conditions and the presence of benthic organisms, acting as ecosystem engineers (*sensu* Jones et al., 1994) may lead to a feedback mechanism between the organism and its environment that creates optimal conditions for its own development (cf. Bouma et al., 2005). The effect (muddification vs. sandification) of those feedback mechanisms or biophysical interactions hence depends on the environmental conditions (in this study: sediment type and condition/turbidity levels) the benthic organism lives in. It may also depend on the presence of other organisms that develop in the same environment, such as microphytobenthos (not considered in our study), which presence is stimulated by cockles' bioturbation (Andersen et al., 2010; Rakotomalala et al., 2015). These feedback mechanisms may have a particular relevance in determining the establishment of new equilibrium conditions in coastal systems subjected to local perturbations *e.g.* coastal infrastructure construction (Cozzoli et al., 2017).

5. Conclusions and implications for the stability of tidal flats

Increasing evidence corroborates that biophysical interactions play a role in the sediment dynamics of tidal flats, especially on relatively short time scales. Organisms influence their environment, and by doing so, they also affect sedimentation and erosion processes on tidal flats. With this study, we showed that the impact organisms have on sediment dynamics are context dependent, depending both on the species under consideration, as well as local prevailing environmental conditions, especially sediment properties. If sediment is sandy, benthic organisms can gradually enhance the silt content of the sediment by mixing in part of the daily tidal sediment deposition. In contrast, if sediment is muddy, benthic organisms can gradually decrease the silt content of the sediment by specifically resuspending the fine fraction. We also observed that the magnitude of this effect was species-specific, raising the need to carefully consider the impact of invasive species as they might influence some important processes. Taking into account these biophysical interactions will contribute to a better prediction of the ecological functioning and long-term evolution of tidal flats undergoing major changes due to natural changes (i.e. due to increasing storm frequency) or human activities (i.e. land reclamation, sand nourishments).

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecss.2019.106355.

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