What Came First, Mud or Biostabilizers? Elucidating Interacting Effects in a Coupled Model of Mud, Saltmarsh, Microphytobenthos, and Estuarine Morphology

Muriel Z. M. Brückner1, Lisanne Braat1, Christian Schwarz1,2, and Maarten G. Kleinhans1

1Faculty of Geosciences, Utrecht University, Utrecht, The Netherlands, 2College of Earth, Ocean, and Environment, University of Delaware, Lewes, DE, USA

Abstract Mud accretion and establishment of biostabilizers, such as microphytobenthos and saltmarsh vegetation, govern the development of estuarine morphology. Mud facilitates saltmarsh survival and microphytobenthos growth, which in turn promotes sedimentation and reduces mud erosion. Consequently, an increasing extent and thickness of mud cover might lead to a stabilization of large-scale estuarine morphology. To disentangle the interactions between saltmarsh establishment, microphytobenthos colonization, and mud layer formation, we use our novel eco-morphodynamic model applied to the Western Scheldt estuary. Our model shows that presence of dynamic saltmarsh vegetation and microphytobenthos enhances predictions of mud location in the computations compared to field data. Saltmarsh establishment is partly determined by the antecedent mud content in the bed, resulting in varying emerging vegetation coverage between model experiments of a generic saltmarsh and a saltmarsh species that requires prior mud for establishment. In contrast to microphytobenthos enhancing seasonal mud accretion during their growth period, saltmarshes promote largest accretion when lower biomass and high water levels are present. Interestingly, thick long-term mud is enhanced despite the biostabilizers seasonal growth. The combination of saltmarsh and microphytobenthos leads to expanding saltmarsh cover and mud area. Generally, mud layer thickness is governed by the ratio of hydroperiod and maximum flow velocity that is mediated by the biostabilizers. On estuary scale, the presence of intertidal vegetation leads to increased mud volumes in the intertidal. Mud layers are enhanced in extent by a mud-dependent species and in thickness by a generic species. Thus, local biostabilization alters large-scale morphology controlling long-term estuarine development.

1. Introduction

Estuaries are important coastal ecosystems, providing coastal populations with a variety of ecosystem services, such as habitat provision for aquatic plants and animals, regulation of water quality, and coastal protection (Barbier et al., 2011; Gill et al., 2001). As transition zones between the river and the sea, estuaries are characterized through dynamically changing morphologies (Dalrymple & Choi, 2007). Varying sediment fractions lead to spatiotemporal differences in sediment transport magnitudes, which affect bed stability through dynamic erosion and deposition patterns (Dam et al., 2016; Van Ledden et al., 2004; Van der Wegen & Roelvink, 2012). The presence of muddy sediments, a mixture of silt and clay ($D_{50} < 63 \mu m$), reduces erodibility through cohesive properties that protect the top layer of the bed (Braat et al., 2017; van de Lageweg et al., 2018). Similarly, eco-engineering species, such as microphytobenthos and saltmarsh vegetation, can stabilize bars and shorelines (Austen et al., 1999; Fagherazzi et al., 2012; Kirwan & Megenigal, 2013). Consequently, understanding the interactions between hydrodynamics, sand and mud erosion and deposition, and biological communities becomes crucial for the sustainable management of estuaries (e.g., FitzGerald & Hughes, 2019; Wiberg et al., 2019). Here we address the lack of sufficient understanding on the large-scale interactions between biostabilizers and morphodynamics related to sand and mud over decadal time scales.

Mud affects the erosion properties of shorelines and tidal bars (De Jorge & Van Beusekom, 1995; Mitchener & Torfs, 1996). Deposition of muddy sediments strongly depends on hydrodynamics conditions, generally...
leading to muddy sites in morphologically low-dynamic areas such as the higher intertidal and areas sheltered by vegetation (Braat et al., 2017; Lokhorst et al., 2018). In the lower intertidal and subtidal parts, thin mud layers can be observed close to the surface as a result of seasonal variations in water levels or spring-neap variations, which are often stabilized by microphytobenthos during spring and summer and can be grazed by macrobenthic species or shore birds (Daggers et al., 2018; Herman et al., 2001; Mathot et al., 2018; van de Lageweg et al., 2018; Van der Wal et al., 2008; Widdows & Brinsley, 2002). However, interannual preservation of deposited mud in the deeper layers of the bed is often prevented by large floods that erode the sediment in winter (Herman et al., 2001). While mud can have positive effects on bank accretion and stability, impacts on water quality, pollution, and enhanced siltation rates can also negatively affect human activities and ecology (Van Ledden et al., 2004; Wang et al., 2015). We require a better understanding of the mechanisms driving formation and preservation of mud layers and their consequences on estuarine planform and morphology.

Eco-engineering effects by saltmarsh vegetation can cause rapid adaptations of the morphology of coastal and estuarine systems (Corenblit et al., 2015; Holling, 1973; Jones et al., 1994; Kleinhans et al., 2018; Lokhorst et al., 2018; Silinski et al., 2016; Wang & Temmerman, 2013). Saltmarshes grow in the intertidal area between mean high water (MHW) and mean low water (MLW) where they increase roughness and drag on the flow. Through their roots, stems, and leaves, they reduce local flow velocities and enhance inundation period (Brückner et al., 2019), promoting accretion of suspended sediments and enhanced local bed elevation (Leonard & Luther, 1995). In estuaries with high sediment availability, accretion rates in saltmarshes are governed by allochthonous sediment supply that is controlled by hydroperiod (Fagherazzi et al., 2012; FitzGerald & Hughes, 2019; Temmerman et al., 2004). While hydroperiod is an indicator of the lateral suspended sediment gradient from low marsh to high marsh, it also correlates with saltmarsh mortality, as high hydroperiod generally coincides with increased flow velocities causing plant uprooting and reduced oxygen supply (Balke et al., 2016; D’Alpaos et al., 2006; Friedrichs & Perry, 2001; Hughes et al., 2012; Mendelssohn & Morris, 2002; Morris & Haskin, 1990; Morris et al., 2002; Reed, 1990). As the plants eco-engineering effect depends on its physical attributes, such as plant properties (stem height, flexibility, and diameter) and abundance (density), the spatiotemporal changes of saltmarshes linked to mortality and season (phenology) are one main driver of seasonal mud collection (Silinski et al., 2016; Van der Wal et al., 2011). As a result, the dynamics in vegetation growth and mortality define the variability in saltmarsh and mudflat extent and result in refinement of marsh sediments (Schuerch et al., 2014). Even though the mechanism of mud accumulation by already established vegetation is well known, we lack knowledge whether mud layers facilitate vegetation establishment or vice versa. In systems with limited mud supply the drivers for the formation of mud layers and establishment of saltmarsh vegetation remain entangled. We require a close look at those drivers to understand where mud layer formation or saltmarsh growth precedes the other.

Similarly, microphytobenthos that consists of diverse assemblages of photosynthetic diatoms, cyanobacteria, flagellates, and green algae that grow in the upper layer of illuminated sediments (Steele et al., 2001), further referred to as MPB, contribute to seasonal stabilization of the lower mudflats. The growth of MPB has been linked to bed elevation, emersion time, or water content of the sediments (Friedrichs & Perry, 2001; Hughes et al., 2012; Mendelssohn & Morris, 2002; Morris & Haskin, 1990; Morris et al., 2002; Reed, 1990). The biomass of MPB is usually concentrated at the sediment surface, which alters the erosion properties of the sediment in the top layer and thus affects local morphology (De Brouwer & Stal, 2001). This reduction in erodibility can lead to reduced sediment resuspension and transport in the water column (de Jonge, 2000; Staats et al., 2001). A stabilization of 100–500% compared to non-colonized sediment has been reported by many authors (Le Hir et al., 2007; Zhu et al., 2019), suggesting that the effect of EPS is more important than sediment cohesion (Malarkey et al., 2015). On intertidal flats, consideration of the stabilization by MPB is especially important when predicting morphological change (Zhu et al., 2019). However, we still lack understanding of the long-term effects of MPB and how they contribute to anticipated changes in mud availability and bed accretion, including large-scale morphological adaptation of estuaries.

Numerical modeling is a convenient tool to untangle complex interactions between several constituents and subsequently explain emerging patterns that we have yet to fully understand (Fagherazzi et al., 2012; Wiberg
et al., 2019). Even though recent morphological models are increasingly rich in processes, only few studies on estuaries or deltas have included sediment mixtures (Braat et al., 2017; Edmonds & Slingerland, 2010; Waeles et al., 2007) and many neglect detailed representations of biostabilizers (Kleinhans et al., 2018; Le Hir et al., 2007). However, to be able to disentangle and quantify the drivers that contribute to the formation of mudflats, mud preservation, and saltmarsh development, a dynamic, meaning temporally and spatially varying, representation of biostabilizers needs to be combined with an extensive hydro-morphodynamic model that includes sand and mud. This allows an assessment of the role of biostabilization on redistribution of fine sediments and whether biostabilizers improve predictions of mud layer formation. We hypothesize that the inclusion of dynamic vegetation abundances and MPB growth will improve the predictions of mud deposition and, hence, the large-scale morphological development of estuaries.

In this paper, a dynamic eco-morphodynamic model is formulated to represent temporal and spatially varying saltmarsh vegetation through colonization, growth, and mortality rules as described in literature. Moreover, the model includes a module that parameterizes seasonal MPB growth to investigate its effect on sediment accretion. Additionally, the model computes sand and mud transport allowing to investigate the feedback between two types of biostabilizers, sediment transport of two grain sizes, and morphology that until now have not been combined in previous numerical models. To disentangle the main parameters that promote mud layer formation affected by the presence of biostabilizers, we studied the interactions between dynamics of a generic saltmarsh species, a mud-dependent saltmarsh species, and MPB on mud accretion patterns in the Western Scheldt estuary. First, we investigate the eco-morphological causality dilemma, whether ecology facilitates mud settlement or vice versa. This was studied on a tidal bar of a dynamic estuary, where we compared mud and vegetation patterns between two numerical experiments: generic saltmarsh establishment and saltmarsh establishment that requires mud in the bed. Second, we determine the effect of biostabilizers on seasonal and interannual mud preservation to quantify biostabilization effects on long-term morphology. Finally, we analyzed the large-scale mud redistribution promoted by generic saltmarsh vegetation and a mud-dependent species to enhance the understanding of the role of biostabilization in estuarine morphological change and to investigate if the trends observed on the tidal bar hold for the estuary scale.

2. Methods

Our ecological model parameterized spatiotemporal growth of two important biostabilizers, saltmarsh and microphytobenthos (MPB), in combination with mud in the sediment bed. To study the succession of mud settling and vegetation establishment, we further distinguish between a generic saltmarsh species...
governed by hydroperiod and a mud-dependent species governed by hydroperiod and mud content. The ecological computations are coupled biweekly to a calibrated 2-D hydro-morphodynamic model with sand and mud in Delft3D. We use this eco-morphodynamic model to investigate the mud, vegetation, and MPB patterns in the Western Scheldt: While the Western Scheldt estuary serves as a case study to predict large-scale effects of biostabilization on mud redistribution in dynamic estuaries, the tidal bar of Walsoorden allows for a detailed analysis of the feedback between abiotic and biotic stabilization and associated mud and species abundance on bar scale. At the same time, large data availability on both the tidal bar and the entire estuary allow for validation of our model results and verify our findings derive generalizations for similar systems beyond the Western Scheldt estuary. Below, we first present the site and general model setup before the coupling between the ecological and hydro-morphodynamic models are outlined.

2.1. Site Description

The Western Scheldt estuary is located in the southwest of the Netherlands (51°7′ N, 54°0′ E) and represents the seaward part (60 km) of the Scheldt estuary (see Figure 1). The well-studied and monitored estuary (e.g., Bolle et al., 2010; Wang et al., 1999; Winterwerp et al., 2000) is a mesotidal to macrotidal environment with a tidal prism of $2 \times 10^6$ m$^3$ (Wang et al., 1999) and a relatively small yearly averaged discharge of 120 m$^3$/s (De Vriend et al., 2011). The estuary provides access to several harbors with the port of Antwerp being the largest.

The Western Scheldt estuary is characterized by a convergent geometry and contains several vegetated and unvegetated bars that are located between the ebb and flood channels. The dominant species are the pioneer species *Spartina anglica* and *Salicornia ssp.* and at later succession stages *Aster tripolium* (De Vriend et al., 2011). While the mostly sandy estuary contains less than 10% mud, mud contents over 25% can be found on the intertidal bars and on the shorelines (Braat et al., 2019; van de Lageweg et al., 2018). The extent and thickness of existing mud layers have increased in recent years, which was linked to the shift of both subtidal to intertidal and bare to vegetated areas (Wang et al., 2015). During the last decades, heavy dredging and dumping activities have been carried out to provide sufficiently deep channels to access the port of Antwerp (Leys et al., 2006; Plancke et al., 2017). To understand ecological functioning, many studies investigated human-induced effects on biodiversity and development of tidal shoals (e.g., Ides et al., 2007; Van der Wal & Herman, 2012; Van der Wal et al., 2008, 2011). The entire Western Scheldt was mapped for specific years as ecotope maps by the Dutch Water Authorities (RWS) that give information on the vegetation cover, different morphological classes, and sediment types in a 3- to 4-year interval (available on the
website of RWS). These maps were reduced to vegetated, muddy, and bare cells (see Figure 2b as an example) and used to validate the model results by comparing vegetation coverage and location of muddy sediments for several years.

The tidal shoal of Walsroode (blue rectangle in Figure 1) formed during the second half of the last century and developed a saltmarsh vegetation cover from the 1990s onward. The shoal showed dynamic morphological changes throughout the last 20 years, mostly expanding probably because of natural and human-induced accumulation of sediments and a resulting growth in vegetation cover (Brückner et al., 2019; Cleveringa, 2014; De Vet et al., 2017). At the same time, the intertidal area increased and shoal-margin slopes steepened, creating habitat that is less regularly flooded and prone to biodiversity change. Additionally, along with a larger species richness, increased mud content, MPB growth, and sediment refinement were observed (Daggers et al., 2018; Van der Wal et al., 2008, 2011). A recent field study showed that large parts of the saltmarsh contain muddy sediment in the top layer (Braat et al., 2019), indicating a potential sediment sink within the vegetated area. The presence of several biostabilizers and recent accumulation of fines on the shoal make this area an interesting case study to investigate their interactions and draw conclusions about drivers of mud accumulation.

Figure 3. (a) Concept of the eco-morphodynamic model with its three divisions: hydro-morphodynamic model in Delft3D, dynamic vegetation model, and MPB model. The arrows show the interactions between the three divisions. Blue arrows indicate the interactions between hydrodynamics and vegetation establishment and growth, while red arrows show interactions causing mortality. (b) Qualitative seasonal growth curve of the height ($H_v$), diameter ($D$) and root length ($L_r$) of the vegetation throughout each year with $t_1$ establishment size, $t_2$ maximum size, and $t_3$ winter size. For the plant diameter and root length the winter size equals the maximum size (dotted line). All values used in the model can be found in Table A1.
### 2.2. Model Description

Our eco-morphodynamic model consists of three modules, a 2-D depth-averaged hydro-morphodynamic model (HM) in Delft3D, and two ecological models simulating the two types of biostabilizers (see Figure 3): a dynamic vegetation model and a dynamic microphytobenthos model, both parameterized in Matlab (version 2016a). A third important biostabilizer, the eelgrass, has been excluded from the study since its distribution in the Western Scheldt estuary is limited and more abundant in the muddy Eastern Scheldt (Suykerbuyk, 2019). Both ecological models consist of separate modules individually coupled biweekly with the Delft3D model to update the ecological parameters and further incorporate their effects on flow in the Delft3D model. Delft3D solves the shallow-water equations (Lesser et al., 2004), sediment transport of sand with the Van Rijn transport predictor (Van Rijn et al., 2004), mud transport with the Partheniades-Krone formulation (Partheniades, 1965), and morphological development by diffusion after an active layer concept.

#### 2.2.1. The Setup of the Eco-morphodynamic Model

The hydro-morphodynamic model is based on a two-dimensional model of the Western Scheldt (the Dutch-Flemish model [Nevla model]) calibrated for hydrodynamics (Maximova et al., 2009a, 2009b; Vroom et al., 2015) and optimized for morphology (Grasmeijer et al., 2013; Schrijvershof & Vroom, 2016; van Dijk et al., 2019) and includes an additional fine mud fraction (Braat et al., 2019). Waves and stratification linked to salinity are neglected as the estuary is generally well mixed (Meire et al., 2005; Savenije, 2006) and the energy by tidal currents dominates sediment transport in the landward part of the estuary (Hu et al., 2018). Furthermore, compaction is not included in the Delft3D model as we look at qualitative analyses of accretion induced by the presence of biostabilizers as compared to abiotic mud settling. For our analysis we looked at two grid scales (Figure 1). First, we used a decomposed domain of the tidal shoal of Walsoorden to investigate mud accumulation, microphytobenthos growth, and saltmarsh colonization on a fine grid size of approximately 30 m (as described in Braat et al., 2019, and van Dijk et al., 2019) (Table 3, Run1). Second, we study the MPB, saltmarsh, and mud patterns that emerge from their interaction on a coarser grid (100-m grid sizes) along the entire Western Scheldt model domain (Table 3, Run2). The large domain represents the part between the mouth and the Dutch-Belgian border (see colored shades in Figure 1).

The hydrodynamic boundaries consist of a time series of four representative spring-neap cycles in 2013 based on water-level measurements, meaning that the model considers most tidal constituents, storm surges, and discharge and result in sediment input variations as sediment transport is computed using equilibrium sand transport (van Dijk et al., 2019) and a constant mud input at the river boundary of 0.02 kg/m³ (Braat et al., 2019). To fit the tidal signal into an integer number (Duran-Matute & Gerkema, 2015), the tidal cycle of the dominant M2-tide was reduced to 720 min (as in Brückner et al., 2019). This step was necessary to allow for a constant forcing period of one tidal cycle when upscaling the model for the morphological and ecological computations as described below. To accelerate morphological development, the model included a morphological acceleration factor of 24 that enhanced the computations of erosion and deposition by multiplication. Morphological and ecological time were set equal, which led to one tidal signal (12 hr) representing 12 days of morphological and ecological development. To fit the spring-neap cycle (14 tidal signals) into one morphological, or ecological, year, we applied 28 couplings, leading to 28 ecological time steps (ETSs) with each being one tidal signal of 720 min. This led to a total simulation time of 20,160 min per ecological year. In total, we simulated 12 ecological years for the small domain and 8 years for the large domain. All model parameters are defined in Table 1.

#### 2.2.2. Dynamic Vegetation Model

To account for vegetation effects in the hydro-morphodynamic model, we used the trachytope approach with the Baptist formula (Baptist et al., 2007) that allows for several vegetation fractions of different vegetation types and life stages in one numerical cell. The Baptist formula calculates a net roughness $C_{w} (\sqrt{m/s})$ from a combination of the bed roughness $C_{b} (\sqrt{m/s})$ and detailed vegetation parameters, such as

---

**Table 1**

| Parameter                          | Value    | Unit         |
|-----------------------------------|----------|--------------|
| Simulation time ecological year   | 20,160   | min          |
| Numerical time step               | 0.1      | min          |
| No. ecological time steps         | 28       | 1/ecological year |
| $D_{50}$ sand                      | $\text{m}^{-4}$ | m          |
| Dry bed density                   | 1,600    | kg/m³        |
| Mud                               | $5\text{m}^{-2}$ | m          |
| Erosion parameter                 | $1\text{g/m}^{3}/s$ | kg/m³/s |
| Dry bed density                   | 1,000    | kg/m³        |
| Boundary concentration            | 40       | mg/L         |
| Active layer thickness            | $5\text{m}^{-2}$ | m          |
| Max. storage layer thickness      | $5\text{m}^{-2}$ | m          |
| Morphological acceleration factor | 24       |             |

*Note: More details can be found in van Dijk et al. (2019) and Braat et al. (2019).*
vegetation height $h_v$ (m), vegetation density $n$ (m/m$^2$), and a bulk drag $C_D$ (-). Depending on the relative local water depth $h$ (m), $C$ is computed as

$$C = \left\{ \begin{array}{ll} C_3 + \frac{\sqrt{h_v}}{\kappa} \left( \frac{h}{h_v} \right) \left( 1 + \frac{C_b h_v C_d^2}{2g} \right), & \text{if } h \geq h_v \\ C_4, & \text{if } h < h_v \end{array} \right. \quad (1a)$$

with $g$ is gravity (m/s$^2$), $\kappa = 0.41$ (-) von-Kármán constant, and $C_b = 25$ (m/s), which is derived from the Manning of the vegetated bars of 0.028 and a water depth of 0.1 m. To compensate for higher local sediment transport induced by increased $C$, an additional flow resistance $-\lambda/2*u^2$ is included in the flow solver, where $\lambda$ is defined as

$$\lambda = \left\{ \begin{array}{ll} C_D n \frac{h_v}{C_d}, & \text{if } h \geq h_v \\ C_D n, & \text{if } h < h_v \end{array} \right. \quad (2a)$$

Finally, for each vegetation fraction present in each cell, both $\lambda$ and $C$ are weighted according to their relative coverage $f_i$

$$C_{\text{total}} = \sum f_i C_i \quad (3)$$

and

$$\lambda_{\text{total}} = \sum f_i \lambda_i \quad (4)$$

To investigate the effect of saltmarshes on mud accumulation and bed accretion, we tested both a generic saltmarsh species as in Brückner et al. (2019) and a mud-dependent species that only colonizes cells with a mud fraction in the top layer larger than 40% that is similar to the critical mud fraction for cohesion (Van Ledden et al., 2004). At each coupling time step, the results of the Delft3D model are fed into the dynamic vegetation model to calculate the new vegetation parameters. Below, we briefly describe the vegetation rules that determine species establishment, growth, and mortality. For more detail on the dynamic vegetation model, please see Brückner et al. (2019).

The dynamic vegetation model includes colonization, growth, aging, and mortality rules based on literature (Brückner et al., 2019). Colonization is defined at the beginning of each year while vegetation growth is defined by a seasonal increase in biomass, based on height and stem diameter, throughout the ecological year. Aging is accounted for by parameterization of a second life stage for plants that survive their first year, consequently reaching larger maximum plant sizes and higher resilience to stresses. Mortality induced by hydro-morphodynamic stresses reduces the vegetation fraction in a cell and makes room for new seedling establishment.

Establishment occurs at the beginning of each ecological year. For the generic species, cells that are located in the intertidal area (flooded and subsequently dried during one ETS) are filled with an initial fraction of 0.4. The mud-dependent species additionally requires a 40% mud fraction in the top bed layer, which is characteristic of Spartina (Huckle et al., 2000). After initial settling in $t_1$, vegetation grows linearly until the ecological summer ($t_2$), remains constant until autumn ($t_3$), and above-ground biomass decays at the beginning of winter ($t_3$) (see Figure 3b). After surviving their first year, the vegetation enters a new life stage with larger sizes and higher resilience and regrows. At the same time, new seedlings can establish as long as the maximum fraction of 1 in the cells is not exceeded. The parameters for the vegetation growth can be found in Table A1. Vegetation cover can decline through mortality that is calculated every coupling interval. Mortality rules include dying due to inundation period, uprooting by velocity, erosion of roots, and burial of

$$10.1029/2019WR026945$$
above-ground biomass. Hereby, inundation period and velocity cause
gradual, linear mortality depending on pressure strength while burial and
scour immediately remove the entire fraction if a threshold value is
exceeded. The mortality parameters are summarized in Table A2.

The dynamic vegetation model is mortality driven, which means that spe-
cies can settle with an initial fraction, which represents patch density
rather than individual plant density and makes rhizomal growth of, for
example, *S. anglica* irrelevant. In suitable cells, every year new fractions
are added to the cell, which account for lateral expansion or seedling
establishment, leading to the saltmarsh growth that is observed in reality (Brückner et al., 2019).

Mortality is a percentage of the initial fraction, which allows for constant die-off rates independent of the
plant fraction present. This strategy allows us to model several ecological concepts of saltmarsh vegetation,
both rhizomal expansion and single seedling establishment, which leads to dense vegetation higher up the
marsh and single species surviving more difficult abiotic conditions at lower elevations (Brückner et al.,
2019).

### 2.2.3. The Microphytobenthos Model

The effect of MPB growth on mud stabilization was investigated for both domains. Linked to the secretion of
EPSs, MPB stabilize the sediment and reduce local erosion (van de Koppel et al., 2001). We account for this
effect by an alteration of the resuspension properties of the mud fraction in cells where MPB grow. Hereby,
we assume that MPB live on top of the sediments altering the critical bed shear stress for erosion $\tau_{cr,e}$ of the
mud while the erosion parameter $M$ (kg/m²/s) remains unchanged. This directly affects the erosion flux $E_m$
of the mud between the bed and the water column (kg/m²/s) in the Partheniades-Krone formulations
(Partheniades, 1965) as

$$E_m = MS(\tau_{cw}, \tau_{cr,e})$$  \hspace{1cm} (5)

with $\tau_{cw}$ maximum shear stress at the bed (N/m²) and $S$ erosional step function. This equation is used for
the computations of mud erosion and deposition while the Van Rijn et al. (2004) transport predictor computes sand transport.

Since MPB in the Western Scheldt grows seasonally under warm temperatures and sufficient sunlight
(Herman et al., 2001), we defined a growth period of 10 ecological time steps. In contrast to the dynamic vege-
tation model, newly establishing MPB was calculated each coupling interval with the Delft3D model (every
ETS) as a function of inundation period $i$ and mud fraction $f_{mud}$ in the top layer and was added to the already
established MPB cover $MPB_{pre}$ leading to increasing MPB cover $MPB_{est}$ throughout the growth period

$$MPB_{est} = f(i, f_{mud}) + MPB_{pre}$$  \hspace{1cm} (6)

indirectly selecting sheltered areas with limited erosional and depositional processes (Herman et al., 2001). The colonization thresholds can be found in Table 2.

In cells where MPB was present, the critical shear stress of the mud fraction was increased by a factor of 4
from 0.2 to 0.8 N/m² as reported in Le Hir et al. (2007) that provide a literature review of the effects of bios-
tabilizers on erodibility. Consequently, the microphytobenthos model was driven by colonization, which
accounted for a gradual spread of the MPB in summer when water levels are reduced. As a result, no
cell-specific growth or mortality through hydro-morphodynamic pressures or grazing were considered (Le
Hir et al., 2007). At the end of the growth season, MPB was entirely removed and the critical bed shear
was set to its abiotic value in all cells.

### 3. Results

To quantify interactions between mud layers, saltmarsh growth, and microphytobenthic stabilization, our
eco-morphodynamic model is based on a calibrated and optimized two-dimensional hydro-morphodynamic
model combined with a dynamic and interactive representation of vegetation and microphytobenthos
(MPB). We ran the model on a medium-scale grid of the tidal bar of Walsoorden to investigate the interact-
ions between the two biostabilizers and seasonal mud layer formation and preservation. A large-scale grid

### Table 2

| Microphytobenthos   | Min. threshold | Max. threshold |
|---------------------|----------------|----------------|
| Inundation period$^a$ | 0.35           | 0.5            |
| Mud fraction$^b$    | 0.3            |                |

$^a$Daggers et al. (2018) and van de Koppel et al. (2001). $^b$Widdows and Brinsley (2002).
of the Western Scheldt estuary allowed to investigate the large-scale effect of biostabilization on redistribution of mud and consequences for mud layer thickness (see Figure 1). Using the medium-scale grid, we first validate and quantify the spatial representations by our model compared to the ecological development over several years in the ecotope maps (2004, 2008, and 2012) to investigate decadal saltmarsh establishment and MPB growth on bar scale. To gain insights into the feedbacks between mud and saltmarsh vegetation growth, we compare vegetation pattern for the generic and the mud-dependent species as well as to a run with only sand. Second, we disentangle the effect of several biostabilizers on mud layer formation by comparing a mud pattern resulting from generic or mud-dependent saltmarsh colonization and presence of MPB (see Table 3, Run1-scenarios). Here we distinguish in (a) seasonal mud layers with a thickness of smaller than 10 cm (Herman et al., 2001) that are washed away between years and have ecological but insignificant morphological effects and (b) mud preservation defined as layers reaching 10 cm or larger thicknesses that are preserved in the lower layers of the bed and become part of the morphology.

Finally, we look at the mud distribution along the Western Scheldt estuary to predict large-scale morphological change and subsequently investigate the influence of the generic saltmarsh and a mud-dependent saltmarsh to quantify their effects on the large-scale morphological development of estuaries (Table 3, Run2-scenarios). We compare trends of seasonal mud and preserved mud layers to make generalization on large-scale pattern of mud and biostabilizers and their interactive effects.

### 3.1. Mud Settling and Biostabilizers

To investigate the interaction between the spatial distribution of saltmarsh vegetation and mud, we compared the results of the vegetation pattern of all scenarios of Run1 in Figure 4. A comparison between the generic saltmarsh species cover on only sand (Figure 4b) with a scenario with mud (Figure 4c) did not show a significant difference in cover location, implying that the mud accumulation did not affect generic saltmarsh growth significantly. In comparison with the ecotope maps that show an increase in vegetation cover through time, the generic saltmarsh species (Figure 4c) overpredicted total cover toward the north-west of the bar by predicting nearly constant growth through time. On the other hand, the mud-dependent species underpredicted coverage as mapped in the southwest of the bar but showed better correspondence in saltmarsh pattern over time (Figure 4d). Figure 4e represents the mean growth period that MPB was present during the growth period showing main growth on the lower mudflats especially at the southwestern tip of the bar as has already been reported by previous studies (Daggers et al., 2018; Van der Wal et al., 2008). A combination of the generic saltmarsh and MPB (Figure 4f) led to increased MPB coverage at the edges of the bar. Figure 4 illustrates that vegetation and microphytobenthos growth locations on Walsooorden can locally be affected by the presence of mud.

### Table 3

**Model Scenarios Based on Initial Bathymetries, Years of Simulation Time, Grid Cell Sizes, and the Years of the Ecotope Maps that the Model Results Were Compared to**

| Model scenario       | Ecol. sim. time | Ecotope maps | Grid cell size | Biostabilizer               |
|----------------------|-----------------|--------------|----------------|-----------------------------|
| Run1_GVegSand        | 12              | 2004, 2008, 2012 | ~16 m × 27 m  | Generic SM                  |
| Run1_GVeg            | 12              | 2004, 2008, 2012 | ~16 m × 27 m  | Generic SM                  |
| Run1_MVeg            | 12              | 2004, 2008, 2012 | ~16 m × 27 m  | Mud-dependent SM            |
| Run1_MPB             | 12              | 2004, 2008, 2012 | ~16 m × 27 m  | MPB                         |
| Run1_GVegMPB         | 12              | 2004, 2008, 2012 | ~16 m × 27 m  | Generic SM + MPB            |
| Run1_Ref             | 12              | 2004, 2008, 2012 | ~16 m × 27 m  | -                           |
| Run2_GVeg            | 8               | 2008         | ~50 m × 180 m  | Generic SM                  |
| Run2_MVeg            | 8               | 2008         | ~50 m × 180 m  | Mud-dependent SM            |
| Run2_Ref             | 8               | 2008         | ~50 m × 180 m  | -                           |

**Note:** We investigated the eco-morphodynamic model over 12 years of morphological development (2000, 2004, 2008, and 2012) for the generic saltmarsh (SM) with only sand (Run1_GVegSand) as well as sand and mud (Run1_GVeg), mud-dependent saltmarsh (Run1_MVeg), microphytobenthos (Run1_MPB), the combination of generic saltmarsh and MPB (Run1_GVegMPB), and reference scenarios without biostabilizers (Run1_Ref). Model runs for a coarser grid spanning the entire estuary (Run2-scenarios) were conducted to investigate large-scale effects of generic and mud-dependent saltmarsh vegetation (SM) on mud accretion.
The generic and mud-dependent vegetation types both led to different vegetation and mud patterns on the bar. The generic species (Figure 5c) largely covered the bar in year 4 and only spread partly during the remaining simulation time, while the mud-dependent species gradually expanded in cover with time (Figure 5d). The mud cover increased with increasing vegetation cover in the vegetated cells for both vegetation types, leading to mud fractions larger than 0.5 in the top layer, while adjacent to the saltmarsh mud in the bed only appeared in lower fractions of around 0.25. This increase in mud on the bar led to a gradual spread of the mud-dependent species, which enhanced settling within young patches and initiated a positive feedback between mud layers and saltmarsh growth (Figure 4d). Thus, saltmarsh growth resulted in high mud contents covering large parts of the bar for the vegetated scenarios. In contrast, the reference scenario without vegetation (Figure 5b) showed similar mud fractions at the southern tip as the vegetation scenarios while the center and western parts of the shoal were covered with lower mud fractions in the top layer. As a result, under hydrodynamically calm conditions mud can settle without saltmarsh vegetation, whereas vegetation promotes mud layer formation at exposed areas where it acts as a local sediment sink.

In contrast to the saltmarsh scenarios, the scenario with MPB (Figure 5d) showed similar mud locations as the reference scenario while a scenario with both the generic saltmarsh and MPB (Figure 5f) resembled the results of Run1_GVeg. As the MPB required sufficient mud in the top layer, it was mainly found at southwestern tip of the bar where prior mud settling occurred (Figure 4e) and showed limited effects on mud area extent. Interestingly, the locations where MPB were present do not necessarily co-occur with the highest mud fraction in the top layer, suggesting that there is a more complex feedback between biostabilization by MPB and mud.

The performance of the mud model, as evaluated by the ecotope maps, was significantly improved by the presence of vegetation (Figure 5 bar plot). The generic vegetation scenario improved the predictions for cells that contained a substantial amount of mud compared with the reference scenario by over 50%. Similarly, the mud-dependent species increasingly enhanced predictions over time while MPB resulted in limited improvements. As we started from a bed without mud, the generic vegetation enhanced predictions

Figure 4. Saltmarsh and MPB growth for simulation years 4, 8, and 12 compared to the ecotopes (2004, 2008, and 2012) for all scenarios. Colors in ecotope maps: dark green is dense vegetation cover (>50%), light green is sparse vegetation cover (<50%), and gray is sand (a). Our results show good correspondence in location of dense vegetation coverage (b and c) with the mud-dependent vegetation expanding in cover with time (d). Relative MPB presence in growth period increases with time toward the southern tip of the bar (e). Combined generic saltmarsh and MPB growth leads to enhanced growth periods of MPB (f). Blue shades represent bed elevations with contour lines in 4-m intervals.
especially in the first years of the simulation and became less important with accumulation of the mud in the bed whereas the mud-dependent species enhanced predictions with increasing cover and time. Best predictions were obtained when both saltmarsh vegetation and MPB were present. In general, this shows that predictions of surface mud are improved when vegetation establishment and growth are included.

We investigated the effects of biostabilization on seasonal mud accretion by comparing mean mud accretion for all scenarios that include mud over one ecological year (Figure 6). For MPB, mud accretion was greatest during its growth period and low water levels and reduced with increasing water levels toward the end of the year. For the scenarios including saltmarsh vegetation, mud accretion was greatest induced by a combination of low plant sizes and high water levels at the beginning and end of the year, possibly due to enhanced inundation periods on the bar. On the other hand, the combination of low water levels and high biomass during growth season prevented flooding of the marsh during summer, leading to lower accretion rates than the reference scenarios. As a result, seasonal variations in vegetation size had negative impacts on mud accumulation during growth season while low vegetation biomass and high water levels in winter led to largest accretion through both enhanced trapping and protection of the existing surface mud. The combination of both the generic saltmarsh and MPB led to enhanced accretion along the entire ecological year.

Interestingly, in this scenario accretion during the growth period of MPB was lower than when only MPB was present but promoted larger sedimentation rates toward the end of the year.

3.2. Mud Preservation and the Role of Biostabilization

To better understand the influence of biostabilizers on mud preservation in the bed, we compared mud thickness among five scenarios (Figure 7). The thickness of mud layers was enhanced by the presence of saltmarsh
Figure 6. Seasonal trapping efficiency for intertidal area (above MLW = −2.5 NAP) averaged over the last 4 years of simulation time is compared to the relative high water level at the boundaries over one ecological year (one hydrological spring-neap cycle), showing mud accumulation for all scenarios. Arrows indicate qualitative plant sizes for the saltmarsh growth cycle (SM) and start and end of the growth period of MPB within the ecological year. In contrast to the reference scenario, the accretion under biostabilization is governed by a combination of the variations in water level and seasonal growth: While MPB clearly enhances trapping during its growth period vegetation promotes largest variations in water level and seasonal growth. While MPB clearly enhances trapping at the beginning and end of the year with reduced accretion during its growth season. The combination GVegMPB enhances accretion throughout the entire ecological year.

vegetation compared to the reference scenario with only mud. Mud preservation was strongest at the southern tip and also the only part of the bar where mud settled without vegetation cover (Figure 7-1). Especially in the center and western parts of the bar, mud could only settle within vegetation patches and thickness increased over the period that vegetation was present (cf. Figures 7-2 and 7-3). This indicates that shielding makes the saltmarsh the driver of mud accretion on top of the shoal of Walsoorden that allows for preservation in the lower layers of the bed.

Cross-sectional analysis revealed higher absolute accretion thickness by the three biostabilizing species (Figures 7-2, 7-3, 7-4, and 7-5). The transects (displayed in Figure 7-1) are representative for several bed elevation gradients and vegetation densities, showing that relative mud accretion was enhanced at higher elevations and in vegetated cells. This in turn led to an increase in bed elevation and preserved a large part of the available fine sediment in the first few top decimeters of the bar. However, the accretion was not directly dependent on the vegetation density of the computational cell, showing accumulation in but also next to the densely colonized cells. The mud-dependent species showed the same mud accretion pattern. Mud layer thickness was observed at intermediate elevations for transect 1 in all scenarios (coordinate 64.5–65 km), showing that mud preservation not necessarily correlated with bed elevation. MPB presence showed similar trends as the saltmarsh vegetation, where accretion occurred at high elevations and in cells adjacent to colonized cells (Figure 7-4a–h). Mud thickness and vegetation fractions increased when both vegetation and MPB were combined (Figure 7-5q–t), suggesting a positive feedback that enhanced saltmarsh abundance when MPB were present (Figure A1). Consequently, and in contrast with the results from Figure 5 that shows top layer mud fractions were enhanced within colonized cells, mud preservation in the lower layers of the bed was governed by local effects at bar scale that emerged from a combination of local bed elevations and biostabilization.

### 3.3. Vegetation Effects Along the Estuarine Gradient

Similar to the processes on the tidal bar of Walsoorden, we observed enhanced mud accretion by vegetation presence along the entire Western Scheldt estuary. Vegetation occurred at the high elevations on the shoals and at the shores (Figures 8a1 and 8a2). Hereby, vegetation densities were largest toward the highest parts of the estuary. Mud (Figures 8b1 and 8b2) accreted mainly on the higher mudflats at the edges of the estuary while only limited deposition was observed in the channels and on the bars. Smaller mud fractions occurred in hydrodynamically active areas while large mud fractions were exclusively observed in colonized areas. The presence of saltmarsh vegetation promoted mud settling on the bars and along the sides of the estuary. The mud difference maps (Figures 8c1 and 8c2) show that vegetation increased mud settling (Hoge Platen, Walsoorden, Saeftinghe). However, at the highest areas along the estuary fringes accretion rates were lower than in the reference scenario as the vegetation slowed down the flow, causing settling closer to the channels with limited fine sediment transport toward the shores. The presence of the mud-dependent species led to reduced fractions but larger extent of mud in the top layer.

A more detailed analysis of the trends observed in Figure 8 reveals that the total mud area for thin layers reduced toward higher elevations while extent of thick mud layers increased (Figure 9). Once vegetation was introduced, the mud layer extent increased for both thick and thin layers with distinct peaks at higher intertidal elevations (GVeg and MVeg). Hereby, thick layers were found at higher elevations than the thin layers. However, the settling of mud within the vegetation led to reduced mud availability at the highest elevations, reducing mud extent at high bed elevations where the largest vegetation cover occurred.

Interestingly, the generic saltmarsh enhanced thick mud layers close to the vegetation edge compared to a mud-dependent species linked with enhanced sedimentation within the sparse vegetation at the marsh.
edge. On the other hand, the mud-dependent species was able to increase thin mud layer extent along large parts of the intertidal domain leading to the establishment of new mud layers away from the marsh. This can be linked with the gradually expanding saltmarsh already observed in Figure 4 allowing for more gradual sedimentation with expanding plant cover. As a result of the modification of the mud pattern by vegetation, the area of the thin and thick mud layers in the estuary was increased by 15–25% and 55% of the reference run, respectively (Figures 9a and 9b).

3.4. Discussion

Spatiotemporal variations in mud deposition, saltmarsh, and microphytobenthos (MPB) growth govern the morphology of tidal systems by stabilization of shorelines and tidal bars that define multi-channel systems in estuaries (Allen, 2000; Braat et al., 2017; Le Hir et al., 2007; Temmerman et al., 2003). To be able to understand the feedback between biostabilization, mud layer formation, and morphology, a detailed eco-morphodynamic model is required that accounts for eco-engineering effects on dense temporal and spatial scales (Brückner et al., 2019). Models that simplify saltmarsh growth and sediment settling as monotonously increasing are only applicable in systems with unlimited suspended sediment supply and where saltmarshes matured to a cohesive cover that leads to sheet flow above the canopy with constant sedimentation rates (Fagherazzi et al., 2012). For the first time, this model enables us to study the feedbacks between differences in mud layer formation and biostabilization to draw conclusions on the effects on morphology in a dynamic, large-scale estuarine system.

The models including the generic saltmarsh and both the generic saltmarsh and MPB improve predictions of mud locations by more than 50% compared to the reference run without biostabilization, as evaluated by the ecotope maps. The performance reduces with simulation time as the reference scenario accumulates mud with simulation time. On the other hand, a mud-dependent species leads to improved model predictions over time as mud and vegetation spread gradually, which increases performance in the later years. Overall, this shows that including saltmarsh vegetation into hydro-morphological computations enhances mud predictions depending on the initial state of the model and the choice of the vegetation. However, MPB does not enhance predictions of mud layer formation.

Our model computes sediment transport and morphodynamics by state of the art relations and includes literature-based seasonal saltmarsh and microphytobenthos (MPB) dynamics that predicts patterns comparable to field data (Figures 4 and 5). The simulation results of Run1_MPB show similar locations of MPB growth as previously reported in literature at the lower mudflats of the tidal bar (Daggers et al., 2018; Van der Wal et al., 2008; Widdows & Brinsley, 2002). Our model predicted enhanced mud layers on the tidal shoal of Walsoorden in the presence of vegetation and MPB despite their seasonality (Figure 7). By comparing a generic saltmarsh growing independently of mud thickness with a mud-dependent species expanding gradually with increasing mud cover, our results suggest that antecedent presence of mud can control saltmarsh cover. As a result, on a bar scale local hydro-morphodynamic conditions control if mud settling precedes vegetation establishment or vice versa. Large-scale morphology is altered by the presence of biostabilizers through their capability to facilitate mud layer formation and thus limiting mud availability on adjacent mudflats and in marshes.

3.4.1. Interactions Between Biotic and Abiotic Stabilization

Saltmarsh growth and expansion depend on several environmental factors, including hydrodynamic stresses and sediment type. Our results show that bed level accretion is not necessarily the main mechanism facilitating plant survival of the generic saltmarsh type even though sediment supply is known to be one important factor for saltmarsh resilience (FitzGerald & Hughes, 2019). Our generic saltmarsh species covers a similar area on the bar from the beginning of the simulation and barely expands with increasing bed elevation (Figure 4c). This is especially pronounced compared to the scenario with sand only, where very low sedimentation on the shallow parts of the bar leads to a similar extent in generic saltmarsh species pattern (Figure 4b). Instead, flow reduction through plant growth appears to be controlling marsh extent of the generic saltmarsh species, similarly as in Brückner et al. (2019). Mud layers, however, form at different parts of the shoal and drastically increase in extent post vegetation establishment (Figures 5c and 5d). As a result, the accretion of the mud observed in the ecotope maps requires prior saltmarsh growth for large parts of the bar, suggesting that preservation of mud on the shoal of Walsoorden is strongly driven by the presence of vegetation. We think that this mechanism can be characteristic for dynamic morphological features, such as tidal
bars that experience high flow velocities that prevent large mud fractions on bare flats: While mud can accrete on sheltered, unvegetated parts on the bar, vegetation helps accrete mud in otherwise too dynamic locations (Figures 5 and 7). This process is based on higher resilience of saltmarshes to hydrodynamics than inherent to mud, which leads to an alteration of the hydrodynamic forcing as soon as vegetation is present and facilitates mud layer formation. As a result, limited saltmarsh growth by hydrodynamic stresses at exposed sites is potentially limiting mud flat formation and expansion.

We find varying behavior of vegetation species that require different sedimentary conditions for their establishment. The generic saltmarsh, governed by hydrodynamic stresses only, can colonize large parts of the bar while a mud-dependent species gradually increases with enhanced mud settling as mud is not present in the initial bathymetry (Figure 4). While the former alters hydrodynamics and sedimentation instantaneously and causes strong mud accretion along the vegetated surface, the latter facilitates gradual increase in surface mud content by concurrent saltmarsh expansion. On a decadal time scale, the mud-dependent species is not capable of covering the same extent as the generic species but nevertheless shows closer resemblance to observed saltmarsh development. This suggests that mud-dependent saltmarsh establishment might be an important factor constraining saltmarsh development observed in nature.

Van Hulzen et al. (2007) showed that <em>Spartina</em> prefers muddy sediment due to enhanced nutrient availability and soil drainage. Moreover, seed retention in the bed was linked to both a lack of mud erosion (Zhu et al., 2014) or mud deposition (Xiao et al., 2009). Consequently, the suggestion from literature
that antecedent mud presence can facilitate saltmarsh growth together with our model results points to the presence of a geomorphological window of opportunity similar to Balke et al. (2014). If saltmarsh formation is strongly governed by mud presence during recruitment in early spring, then the presence or absence of winter storms, removing or conserving the top mud layer, exerts a major control on saltmarsh development. Thus, initial saltmarsh colonization might not only depend on the hydrodynamic conditions during seed dispersal but similarly on the preceding hydrodynamics allowing for mud settling prior to seedling germination. The existence of a geomorphologic window of opportunity is thus based on the occurrence of seasonal disturbances such as winter storms and might help elucidate observed differences in interannual saltmarsh growth in dynamic coastal environments. However, we expect that as soon as saltmarsh establishment takes place vegetation potentially relies less on mud for survival due to its eco-engineering capabilities (Brückner et al., 2019) but still constitutes an important habitat for mud to settle. We show that the feedback loop between mud sedimentation and species growth leads to different emerging species abundances that are controlled by the preceding geomorphic setting and lead to species-specific mud layer formation.

In contrast to the enhanced settling by the saltmarsh vegetation, MPB leads to similar muddy locations as the reference scenario but stabilizes the deposited mud (Figures 5 and 7) on the shoal of Walsoorden. Stabilization of fine sediments by MPB has been observed by field studies on intertidal flats in the Western Scheldt (Herman et al., 2001; van de Koppel et al., 2001), the Humber estuary (Widdows &

Figure 8. (1) Run2_GVeg and (2) Run2_MVeg at the end of eight morphodynamic years for vegetation fraction on bathymetry (a) and mud fraction in top layer (>5%) (b). The mud fraction difference to the Run2_Ref-scenario (c) with red larger and blue reduced mud fractions shows larger deposition within vegetation and reduced deposition at higher bed elevations on the bars and toward the sides of the estuary. Flow velocities along estuary (d) show flow deviation into the channels by the vegetation. Black lines define the mean low water line.
Brinsley, 2002), and the Wadden Sea (Riethmüller et al., 2000). However, on intertidal flats the destruction of the biofilm by grazing through macrofauna and shore birds is an important control on the stability of the mudflat that we do not account for (Herman et al., 2001; Mathot et al., 2018; Van der Wal et al., 2008; Widdows & Brinsley, 2002). Similarly, we simplify erodibility reduction by MPB by assuming a constant biomass that possibly overpredicts local biostabilization. The balance between biostabilization through MPB and grazing by *Macoma balthica* largely depends on yearly variations in temperature, where warm winters can lead to decreased grazer densities (e.g., *M. balthica*) and large microphytobenthic cover (Widdows & Brinsley, 2002). In the face of global warming increasing biofilms will affect fine sediment dynamics by local stabilization and accretion. We found that MPB occurs only 20% of the total simulation time (not shown) but surprisingly can lead to higher mud fractions in the bed layers over several years. Consequently, the seasonal effect of MPB can have a long-term effect on mud retention. Resulting emerging patterns contribute to locally enhanced bed elevation, sediment refinement, and increasing stability of the intertidal area that persist throughout several years.

Our results show that mud layer formation is largely governed by local interactions between biotic and abiotic processes. The elevational gradient of stabilization along the mudflat-saltmarsh interface leads to increasing local mud layer thickness and as a result controls the development of the cross shoal profile. New vegetation establishment on tidal bars enhances sedimentation and acts as a local sediment sink that can facilitate saltmarsh establishment. However, maturity of the marsh leads to organic accretion rates enhancing bed elevations while autocompaction (not modeled here) reduces mud thickness that add further challenges to the predictions of mud sedimentation and bed level changes in estuarine systems (Allen, 2000).

**Figure 9.** Total mud area along bed elevation (0.1-m steps) of thin and thick mud layers of the intertidal area (lines) shows largest thin mud area at lowest elevations that reduce toward the higher intertidal while thick mud layers peak at intermediate and high elevations in the reference run. When vegetation is present, the total mud area for both thick and thin layers increases toward the higher intertidal. The values are smoothed by a moving average of 5 points. The qualitative mean vegetated area (surface area) shows largest vegetation cover at the highest elevations. The bar plots show enhanced mean mud area compared to a reference run (a) and total vegetated area (b) confirming that GVeg has a larger extent than MVeg.
However, we do not expect these simplifications to change the main trends observed in our results, where biostabilizers facilitate mudflat formation and expansion and on a secondary level control the extent of marshes and MPB. Vegetation establishment in areas with high flow velocities is crucial to allow for mudflat formation, whereas mud was not a prerequisite for saltmarsh growth, but potentially an important factor limiting their extent.

### 3.4.2. Conditions for Interannual Mud Preservation

Deposition of fine sediments in intertidal areas is controlled by the hydrodynamics, such as flow velocity and inundation period, as well as sediment supply. Generally, the total trapping within the vegetation is highest for a combination of high water levels and low biomass, leading to largest accretion at the beginning and end of the growth season. Increasing water levels and reduced plant sizes during winter allow for longer inundation times that lead to larger sediment accretion. On the other hand, mud accretion under MPB presence mainly occurs during their growth period stabilizing present mud layers (Figure 6). Understanding the conditions under which seasonal mud layers form and get preserved in the stratigraphy is crucial for ecological functioning, the prediction of bar stability, and marsh resilience in threatened environments through sea level rise or human impact (FitzGerald & Hughes, 2019). To be able to determine which parameters control mud layers under two types of biostabilizers, we analyze the relationship between mud thickness, mean inundation period, 90-percentile maximum flow velocities, and bed elevation over the last 4 years of simulation time on the shoal of Walsoorden (Figure 10). We define two mud thicknesses: thin or seasonal and thick or multi-annual mud (Herman et al., 2001).

The reference scenario (triangles), the generic vegetation species scenario (circles), and the microphytobenthos scenario (crosses) are linked to bed elevation (color shades), while the regression line represents the averaged ratio between inundation period and velocity.

On the shoal of Walsoorden, the hydrodynamic forcing is reduced through the presence of vegetation, which shields the mud layers from erosion and enhances bed accretion up to several decimeters thickness (Figures 6 and 10). As a result, seasonal mud that is otherwise removed during winter can be preserved in the stratigraphy as has been reported by other authors (Le Hir et al., 2007). As the top 1–2 cm of the sediment are the biologically active part of the mudflat that acts as an interface between the benthic and aquatic as well as the atmospheric and anaerobic system (Chen et al., 2016), the understanding of seasonal mud layer formation is crucial to guarantee ecological functioning of estuaries. We found that thin layers (red data points) can establish under dynamic conditions characterized by high velocities and long hydroperiods (Figure 10). Contrastingly, thick layers (blue data points) form at low flow velocities and short inundation periods. This indicates that seasonal mud settling can occur under a wide range of hydrodynamic combinations while thick layers require calm conditions. The MPB scenario preserves mud at lower bed elevations than the reference run, while vegetation promotes settling at higher elevations on the bar (see also Figures 4 and 7). The latter induces small flow velocities and slightly shorter inundation periods that are caused by the vegetation roughness. Contrastingly, MPB allows formation of thin layers at locations with higher flow velocities and inundation period than the reference scenario through reduced erodibility of the mud. In contrast to previously reported results (e.g., Le Hir et al., 2007), the formation and stability of thick mud layers is strongly enhanced by biostabilization that controls mud preservation beyond its direct seasonal impact.

The slope of the regression line is an indicator for the ratio of hydroperiod and flow velocity required for mud layer formation (Figure 10b). While the reference scenario has a ratio based on the physical and empirical relations in the model, biostabilization-induced effects alter the inundation period-velocity ratio in two ways: MPB has largest effects on the formation of thin layers that are facilitated under higher relative velocities while vegetation strongly reduces velocities with relatively high inundation periods causing the ratio to increase. Ultimately, these mechanisms determine mud thickness along bed elevation (numbers in brackets) with thick layers generally occurring at higher bed elevations. The graph confirms that mean bed elevation for the two mud thickness classes increase under vegetation but surprisingly reduce under the presence of MPB. Thus, biostabilization plays a fundamental role in facilitating mud layer thickness along the elevational gradient that emerges from the alteration of the hydrodynamic drivers.

Understanding the importance of biostabilizers and their interaction with their environment for predictions of mud preservation is crucial for dynamic estuarine systems. Even though both biostabilizers have a similar effect on mud preservation, the causes differ: Vegetation promotes accretion by a reduction of...
the flow velocity while MPB reduces erosion by reducing erodibility of the sediment, which in turn allows mud accretion at higher velocities. While the former promotes mud layers in sheltered parts of the bar, the latter facilitates mud settling mainly on unvegetated mudflats where the flow is more dynamic. These two contrasting processes lead to new emerging biota and mud patterns that in turn control the establishment of the type of biostabilizer. The contrasting preservation of fine sediments affects the stability of bars and shorelines and the ecology on intertidal mudflats (Braat et al., 2017; van de Lageweg et al., 2018).

### 3.4.3. Large-Scale Redistribution of Sediments

Our results confirm that mud distribution in the Western Scheldt as reported by previous authors mainly settles at sheltered sites and increases toward the flanks of the estuary (Figure 8) (Braat et al., 2017; van de Lageweg et al., 2018). Similarly, we predict higher mud percentages (>50%) at the higher elevations along the estuary and the tidal bars creating a more cohesive and ecologically diverse habitat (Braat et al., 2017; Herman et al., 2001; Meire et al., 2005). As was shown for the tidal shoal of Walsoorden, mud is captured by the establishing saltmarsh at intertidal elevations that otherwise are too dynamic to preserve mud (Figure 5). Interestingly, sparse local vegetation cover enhances the total mud area implying that mud accretion is largely facilitated by the vegetation. Consequently, higher up the marsh sediment transport is limited, which reduces mud percentages toward the flanks of the estuary compared to the reference run (Figure 9). As a result, thick mud layers move from intermediate elevations in the reference scenario toward the higher intertidal under vegetation presence, having wide-ranging effects on the morphological development of estuaries. Similar patterns have been observed in well-established marshes where levee formation leads to reduced transport into the marsh, which can threaten the survival of vegetation at higher elevations (Temmerman et al., 2003). At the same time, thin layers can form under vegetation along the entire intertidal domain. This effect is especially pronounced under a gradually expanding saltmarsh that requires increasing mud in the bed for establishment. Consequently, local marsh species can lead to different mud

**Figure 10.** Corresponding maximum 90-percentile velocity and hydroperiod of cells containing mud along the last two morphological years of the simulation time on the shoal of Walsoorden. Colors indicate mud layer thickness class (thin: red and thick: blue) and shades bed elevations. Thin layers (red) form at lower bed elevations and similar inundation-velocity ratios for all scenarios, while thick layers (blue) occur higher on the bar and are promoted by contrasting stabilization mechanisms: Vegetation reduces velocity while MPB facilitates mud layer formation at higher velocities and inundation period. Vegetation promotes thick layer formation on the highest elevations of the bar. The bar plot displays the slope of the linear fit in the scatter plot for both thickness classes and all scenarios. Numbers are slope value and corresponding mean elevation in brackets. Vegetation promotes mud at higher whereas MPB controls mud at lower elevations than the reference.
patterns along the intertidal domain and determine the area covered with mud. As a result, we show that in dynamic estuaries with limited sediment supply large-scale mud pattern and bed accretion are affected by local vegetation.

As a result, changes in fine sediment availability by dredging and dumping activities, construction of dams or storm surge barriers, or nature preservation projects can have wide-ranging effects on settling locations and accretion rates. Waves that have been excluded due to tide domination in the Western Scheldt might lead to enhanced mud transport toward the upstream part of the estuary and reduces mud accumulation on “Hoge Platen.” Consequently, vegetation cover might be reduced in the more offshore parts of the estuary and lead to larger mud accretion upstream. As a result, the observed redistribution of sediments along the elevational gradient will have large effects on the survival of marsh species that possibly get destroyed under low sediment supply and wave action (FitzGerald & Hughes, 2019). Human-induced local changes in sediment availability can therefore have large effects on the survival of marshes and mud layer formation at the larger scale. The amount of vegetation in intertidal areas significantly affects sediment budgets, redistribution of fines, turbidity and siltation, multi-channel formation, and ecology.

The large-scale redistribution of sediments differs with inclusion of vegetation that creates sediment scarcity adjacent to and within the marsh. We show that local variations in saltmarsh coverage can lead to a redistribution of fine sediment that holds for similar systems with moderate mud transport rates. The establishment of the vegetation causes sediment scarcity adjacent to the marsh due to enhanced mud settling within the vegetation patch. Consequently, the enhanced local mud settling promotes mud pattern that does not necessarily coincide with the highest bed elevations or vegetation cover (Figure 7) but is governed by the hydrodynamics (Figure 10). We show that mud layer formation is governed by the interactions between hydro-morphodynamics and dynamic biostabilization that lead to enhanced local mud cover, which persists over decadal time scales. As a result, the interaction between saltmarsh species, flow, and sediment availability controls local mud thickness (Figures 4 and 8) and marsh expansion, which in turn affects large-scale mud and saltmarsh pattern.

4. Conclusions

Our novel eco-morphodynamic model shows that saltmarsh growth considerably improves predicted mud deposition. We show that detailed seasonal representations of saltmarsh vegetation, microphytobenthos (MPB), and empirical sediment transport relations determine mud layer location in dynamic estuarine systems. Local mud settling is controlled by saltmarsh species and marsh extent, while generic saltmarsh establishment occurs independently of mud accretion, and mud accretion can also occur without prior vegetation establishment. Contrarily, a mud-dependent species shows different expansion and mud accumulation pattern, demonstrating that species type determines mud accretion and that saltmarsh abundance can be controlled by mud.

Seasonal and interannual mud layers control saltmarsh establishment and marsh extent as vegetation growth partly depends on a geomorphological window of opportunity that provides sufficient mud cover for plant establishment. Vice versa, mud layers form under different flow conditions mediated by biostabilization. While thin, seasonal layers form under dynamic conditions determined by high flow velocities and hydroperiods, thick, multi-annual mud layers occur in calmer areas. Biostabilizers affect this ratio between hydroperiod and velocity that determines mud layer formation. Vegetation reduces flow velocity more efficiently than it enhances hydroperiod, which leads to higher slopes for the mean ratio of hydroperiod and velocity for both thin and thick mud layers. MPB, on the other hand, promotes thin mud layer formation under higher velocities than the reference run. Interestingly, despite the seasonality of the biostabilizers, mud is preserved interannually and can lead to long-term changes in morphology. For large-scale morphologies, increasing local mud deposition induced by vegetation leads to reduced large-scale sediment availability: The presence of saltmarsh strongly increases accretion rates at the marsh edge, which leads to sediment scarcity adjacent to the marsh and determines accretion rate in the high marsh. This feedback depends on species type as a generic species promotes thick mud layers at lower elevations in the marsh and a mud-dependent species facilitates new thin mud layer formation in and adjacent to the marsh. Consequently, mediated sedimentation through biostabilization has large-scale implications for sediment availability and hence large-scale morphology.
Our results show that local biostabilization can have large-scale effects on morphology by altering the location and thickness of local mud layers, which results in higher local sedimentation and reduced sediment availability in uncolonized parts of the estuary. For highly managed systems, such as the Western Scheldt, knowledge of sediment budgets and fine sediment accretion is essential for understanding and managing ecological functioning of the estuary. Our findings are applicable to dynamic sandy systems that undergo continuous morphological change through vegetation establishment, benthic activity, changes in sediment availability, or human-induced engineering works.

Appendix A: Vegetation Parameters

Here the parameters used for the dynamic vegetation model are summarized with according references. Two life stages were parameterized to account for aging of the plants after 1 year from seedlings to mature vegetation. As a result, plant size, density, and resilience against mortality change between life stages. For both saltmarsh species all parameters are the same.

### Table A1
Physical Parameters of the Generic Saltmarsh Vegetation Type Based on a Combination Between Spartina anglica and Salicornia ssp.

| Generic and mud-dependent species | Unit | t<sub>1</sub> | t<sub>2</sub> | t<sub>3</sub> |
|----------------------------------|------|-------------|-------------|-------------|
| **Seedling stage (1 year)** | | | | |
| Plant height<sup>a,b</sup> (m) | 0.1 | 0.6 | 0.3 |
| Stem diameter<sup>c</sup> (m) | 0.005 | 0.01 | 0.01 |
| Root length<sup>d</sup> (m) | 0.05 | 0.2 | 0.2 |
| Plant density<sup>e</sup> (stems/m<sup>2</sup>) | 500 | 500 | 500 |
| Bulk drag C<sub>D</sub> ( ) | 1.0 | 1.0 | 1.0 |
| Bed roughness C<sub>b</sub> (√m/s) | 25 | 25 | 25 |
| **Mature vegetation (19 years)** | | | | |
| Plant height<sup>a,c,e</sup> (m) | 0.5 | 1.0 | 0.5 |
| Stem diameter<sup>e</sup> (m) | 0.01 | 0.01 | 0.01 |
| Root length<sup>a</sup> (m) | 1.0 | 1.0 | 1.0 |
| Plant density<sup>e</sup> (stems/m<sup>2</sup>) | 600 | 600 | 600 |
| Bulk drag C<sub>D</sub> ( ) | 1.1 | 1.1 | 1.1 |
| Bed roughness C<sub>b</sub> (√m/s) | 25 | 25 | 25 |

*Note.* t<sub>1</sub>, t<sub>2</sub>, and t<sub>3</sub> are onset of growth season, onset of maximum biomass in summer, and onset of reduced biomass in winter. The seedling stage changes into mature vegetation after year 1 with a maximum total age of the plant of 20 years. |<sup>a</sup>Davy et al. (2001). |<sup>b</sup>Poppema et al. (2017). |<sup>c</sup>Nehring and Hesse (2008). |<sup>d</sup>Cooper (1982). |<sup>e</sup>Bouma et al. (2013). |

### Table A2
Mortality Parameters of Our Generic and Mud-Dependent Saltmarsh Vegetation Species

| Saltmarsh species | Min. threshold | Max. threshold |
|-------------------|---------------|---------------|
| **Seedling stage (1 year)** | | |
| Inundation period<sup>a</sup> | 0.3 | 0.45 |
| Uprooting<sup>b</sup> | 0.25 m/s | 0.4 m/s |
| **Mature vegetation (19 years)** | | |
| Inundation period<sup>a</sup> | 0.3 | 0.45 |
| Uprooting<sup>b</sup> | 0.4 m/s | 0.56 m/s |

*Note.* The values are based on a combination between Spartina anglica and Salicornia ssp. The seedling stage changes into mature vegetation after year 1 with a maximum total age of the plant of 20 years. |<sup>a</sup>Van Belzen et al. (2017). |<sup>b</sup>Bouma et al. (2013). |
Figure A1. Mean mud thickness along bed elevation (0.1-m steps) on the tidal shoal of Walsoorden (lines) compared to mean biostabilizer fraction at the end of the simulation (shaded areas). For MPB, the last time step in the growth season was analyzed. Mean mud thickness increases toward higher bed elevations and reduces at the highest elevations. Saltmarsh vegetation promotes mud accretion at the higher elevations while MPB enhances mud thickness at intermediate elevations. The combined run with both the generic saltmarsh and MPB leads to an overall increasing mud thickness through positive feedbacks that facilitate vegetation growth. The shaded areas represent the mean fraction at each bed elevation class, separated into vegetation and MPB. The bar plot shows the total increase in mean mud thickness (D) on the bar as a ratio compared to the reference run, which is related to increasing biota cover. Biota fraction of GVegMPB combines MPB (red) and GVeg (yellow) as staggered bar.

Data Availability Statement

The ecotope maps were created by the Dutch Water Authorities (Rijkswaterstaat) and can be found on their website (https://www.rijkswaterstaat.nl). The Nederlands-Vlaams-Model was created and calibrated by Deltares. Delft3D is an open source code available online (at https://oss.deltares.nl). The dynamic model code is provided under https://doi.org/10.5281/zenodo.3862032.

Acknowledgments

We thank the reviewers for careful reading and contribution to the quality of this work. This research was funded by the ERC Consolidator project 647570 and Utrecht University.

References

Allen, J. R. L. (2000). Morphodynamics of Holocene salt marshes: A review sketch from the Atlantic and Southern North Sea coasts of Europe. Quaternary Science Reviews, 19(12), 1155–1231. https://doi.org/10.1016/S0277-3791(99)00034-7

Austen, I., Andersen, T. J., & Edelvang, K. (1999). The influence of benthic diatoms and invertebrates on the erodibility of an intertidal mudflat, the Danish Wadden Sea. Estuarine, Coastal and Shelf Science, 49(1), 99–111.

Balke, T., Herman, P. M. J., & Bouma, T. J. (2014). Critical transitions in disturbance-driven ecosystems: Identifying Windows of Opportunity for recovery. Journal of Ecology, 102(3), 700–708.

Balke, T., Stock, M., Jensen, K., Bouma, T. J., & Kleyer, M. (2016). A global analysis of the seaward salt marsh extent: The importance of tidal range. Water Resources Research, 52, 3775–3786. https://doi.org/10.1002/2015WR018318

Baptist, M. J., Babovic, V., Rodríguez Uthurburu, J., Keijzer, M., Uittenbogaard, R. E., Mynett, A., & Verwey, A. (2007). On inducing equations for vegetation resistance. Journal of Hydraulic Research, 45(4), 435–450. https://doi.org/10.1080/00221686.2007.11994822

Barbier, E. B., Hacker, S. D., Kennedy, C., Koch, E. W., Stier, A. C., & Silliman, B. R. (2011). The value of estuarine and coastal ecosystem services. Ecological Monographs, 81(2), 169–193.

Bolle, A., Wang, Z. B., Amos, C., & De Ronde, J. (2010). The influence of changes in tidal asymmetry on residual sediment transport in the Western Scheldt. Continental Shelf Research, 30(8), 871–882.

Bouma, T. J., Temmerman, S., van Duren, L. A., Martini, E., Vandenbruwaene, W., Callaghan, D. P., et al. (2013). Organism traits determine the strength of scale-dependent bio-geomorphic feedbacks: A flume study on three intertidal plant species. Geomorphology, 180, 57–65. https://doi.org/10.1016/j.geomorph.2012.09.005

Braat, L., Kessel, T., Leuven, J. R. F. W., & Kleinhans, M. G. (2017). Effects of mud supply on large-scale estuary morphology and development over centuries to millennia. Earth Surface Dynamics, 5(4), 617–652.

Braat, L., van Dijk, W. M., Pierik, H. J., van de Lageweg, W., Brückner, M., Wagner-Crémers, F., & Kleinhans, M. G. (2019). Tidal bar accretion by mudflat sedimentation. EarthArXiv https://doi.org/10.31223/osf.io/gq9pt

Brückner, M. Z. M., Schwarz, C., van Dijk, W. M., van Oorschot, M., Douma, H., & Kleinhans, M. G. (2019). Salt marsh establishment and ecoengineering effects in dynamic estuaries determined by species growth and mortality. Journal of Geophysical Research: Earth Surface, 124, 2962–2986. https://doi.org/10.1002/2019JF005092
Chen, S., Torres, R., & Graf, M. A. (2016). The role of salt marsh structure in the distribution of surface sedimentary organic matter. Estuaries and coasts, 39(3), 108–122.

Cleveringa, J. (2014). Etv - veiligheid en toegankelijkheid: Ecotopen in de westerschelde (in Dutch) (Tech. Rep.): International Marine & Dredging Consultants, Deltares, Swaë & Hydraulics BV and ARCADIS.

Cooper, A. (1982). The effects of salinity and waterlogging on the growth and cation uptake of salt marsh plants. New Phytologist, 90(2), 263–275.

Corenblit, D., Baas, A., Balke, T., Bouna, T., Fromard, F., Garofano-Gómez, V., et al. (2015). Engineer pioneer plants respond to and affect geomorphic constraints similarly along water-terrestrial interfaces world-wide. Global Ecology and Biogeography, 24(12), 1363–1376. https://doi.org/10.1111/gge.12373

D’Alpaos, A., Lanzoni, S., Mudd, S. M., & Fagherazzi, S. (2006). Modeling the influence of hydroperiod and vegetation on the cross-sectional formation of tidal channels. Estuarine, Coastal and Shelf Science, 69(4–3), 311–324.

Daggers, T. D., Kromkamp, J. C., Herman, P. M. J., & Van Der Wal, D. (2018). A model to assess microphytobenthic primary production in tidal systems using satellite remote sensing. Remote Sensing of Environment, 211, 129–145.

Dalrymple, R. W., & Choi, K. (2007). Morphologic and facies trends through the fluvial-marine transition in tide-dominated depositional systems: A schematic framework for environmental and sequence-stratigraphic interpretation. Earth-Science Reviews, 83(3–4), 135–174.

Dam, G., Van der Wegen, M., Labeur, R. J., & Roelvink, D. (2016). Modeling centuries of estuarine morphodynamics in the Western Scheldt estuary. Geophysical Research Letters, 43, 3839–3847. https://doi.org/10.1002/2015GL066725

Davy, A. J., Bishop, G. F., & Costa, C. S. B. (2001). Salicornia pusilla J. woods, S. ramosissima J. woods, S. europaea L., S. obscura PW ball & tutin, S. nitens PW ball & tutin, S. fragilis PW ball & tutin and S. dolichochastaxa moss. Journal of Ecology, 89(4), 681–707.

De Brouwer, J. F. C., & Stal, L. J. (2001). Short-term and long-term effects of macrophytes on sediment characteristics. Estuarine, Coastal and Shelf Science, 52(1), 1–12.

De Jonge, V. N. (2000). Importance of temporal and spatial scales in applying biological and physical process knowledge in coastal management, an example for the Ems estuary. Continental Shelf Research, 20(12–13), 1655–1686.

De Jorge, V. N., & Van Beusekom, J. E. E. (1995). Wind- and tide-induced resuspension of sediment and microphytobenthos from tidal flats in the Ems estuary. Limnology and Oceanography, 40(4), 776–778.

De Vet, P. L. M., van Prooijen, B. C., & Wang, Z. B. (2017). The differences in morphological development between the intertidal flats of the Eastern and Western Scheldt. Geomorphology, 281, 31–42.

De Vriend, H. J., Wang, Z. B., Ysebaert, T., Herman, P. M. J., & Ding, P. (2011). Eco-morphological problems in the Yangtze Estuary and the Western Scheldt. Wetlands, 31(6), 1033–1042.

Duran-Statute, M., & Gerkena, T. (2015). Calculating residual flows through a multiple-inlet system: The conundrum of the periodical tidal. Ocean Dynamics, 65(11), 1463–1473.

Edmonds, D. A., & Slingerland, R. L. (2010). Significant effect of sediment cohesion on delta morphology. Nature Geoscience, 3(2), 105.

Fagherazzi, S., Kirwan, M. L., Mudd, S. M., Guntenaspergen, G. R., Temmerman, S., D’Alpaos, A., et al. (2012). Numerical models of salt marsh evolution: Ecological, geomorphic, and climatic factors. Reviews of Geophysics, 50, RG1002. https://doi.org/10.1029/2011RG000359

FitzGerald, D. M., & Hughes, Z. (2019). Marsh processes and their response to climate change and sea-level rise. Annual Review of Earth and Planetary Sciences, 47, 481–517.

Friedrichs, C. T., & Perry, J. E. (2001). 3D tidal salt marsh morphodynamics: A synthesis. Journal of Coastal Research, 27, 6–36.

Friend, P. L., Clavola, P., Cappucci, S., & Santos, R. (2003). Bio-dependent bed parameters as a proxy tool for sediment stability in mixed habitat intertidal areas. Continental Shelf Research, 23(17–19), 1899–1917.

Gill, J. A., Norris, K., Potts, P. M., Gunnarsson, T. G., Atkinson, P. W., & Sutherland, W. J. (2001). The buffer effect and large-scale population regulation in migratory birds. Nature, 412(6845), 436.

Graßmeier, B., Dam, G., & Taal, M. (2013). Actualisatierapport Delft3D Schelde-estuarium (in Dutch).

Grémare, H. P. M. J., Middelburg, J. J., & Heip, C. H. R. (2001). Benthic community structure and sediment processes on an intertidal flat: Results from the ECOFLAT project. Continental Shelf Research, 21(18–19), 2055–2071.

Holling, C. S. (1973). Resilience and stability of ecological systems. Annual Review of Ecology and Systematics, 4, 23.

Hu, Z., Van Der Wal, D., Cai, H., Van Belzen, J., & Bouma, T. J. (2018). Dynamic equilibrium behaviour observed on two contrasting tidal flats from daily monitoring of bed-level changes. Geomorphology, 311, 114–126.

Huckel, J. M., Potter, J. A., & Marrs, R. H. (2000). Influence of environmental factors on the growth and interactions between salt marsh plants: Effects of salinity, sediment and waterlogging. Journal of Ecology, 88(3), 492–505.

Hughes, A. M. K., Wilson, A. M., & Morris, J. T. (2012). Hydrologic variability in a salt marsh: Assessing the links between drought and acute marsh dieback. Estuarine, Coastal and Shelf Science, 111, 95–106.

Ides, S. J., Plancke, Y., & Peters, J. J. (2007). A new approach for managing the Western Schelde’s morphology and ecology (Vol. 1, pp. 233). Venice, Italy: IAHR 32th Congress.

Jones, C. G., Lawton, J. H., & Shackach, M. (1994). Organisms as ecosystem engineers. Oikos, 69(3), 373–386.

Kirwan, M. L., & Megońial, J. P. (2013). Tidal wetland stability in the face of human impacts and sea-level rise. Nature, 504(7478), 53.

Kleinhehs, M. G., de Vries, B., Braat, L., & van Oorschot, M. (2018). Living landscapes: Muddy and vegetated floodplain effects on fluvial pattern in an incised river. Earth Surface Processes and Landforms, 43(14), 2948–2963.

Le Hir, P., Monbet, Y., & Orvain, F. (2007). Sediment erodability in sediment transport modelling: Can we account for biota effects? Continental Shelf Research, 27(8), 1116–1142.

Leonard, L. A., & Luther, M. E. (1995). Flow hydrodynamics in tidal marsh canopies. Limnology and Oceanography, 40(8), 1474–1484.

Lesser, G. R., Roelvink, J. V., Van Kester, J. A. T. M., & Stelling, G. S. (2004). Development and validation of a three-dimensional morphological model. Coastal Engineering, 51(8–9), 883–915.

Leys, E., Plancke, Y., & Ides, S. (2006). Shallow-shaller-shallowest: Morphological monitoring Wals江东岸.

Lokhorst, I., Braat, L., Van Kester, J. A. T. M., & Stelling, G. S. (2004). Development and validation of a three-dimensional morphological model. Coastal Engineering, 51(8–9), 883–915.

Lesser, G. R., Roelvink, J. V., Van Kester, J. A. T. M., & Stelling, G. S. (2004). Development and validation of a three-dimensional morphological model. Coastal Engineering, 51(8–9), 883–915.

Lokhorst, I., Braat, L., Van Kester, J. A. T. M., & Stelling, G. S. (2004). Development and validation of a three-dimensional morphological model. Coastal Engineering, 51(8–9), 883–915.

Lokhorst, I., Braat, L., Van Kester, J. A. T. M., & Stelling, G. S. (2004). Development and validation of a three-dimensional morphological model. Coastal Engineering, 51(8–9), 883–915.

Macleay, J., Baas, J. H., Hope, J. A., Aasplein, R. J., Parsons, D. R., Pealkall, J., et al. (2015). The pervasive role of biological cohesion in bedform development. Nature Communications, 6, 6257.
Matth, K. J., Persua, T., & Elner, B. W. (2018). Shorebirds as integrators and indicators of mudflat ecology. In P. Beninger (Ed.), Mudflat ecology, Aquatic Ecology Series (Vol. 7, pp. 309–338). Cham: Springer.

Maximova, T., Ides, S., De Mulder, T., & Mostaert, F. (2009a). LTV O en M thema veiligheid - deelproject 1: Verbetering hydrodynamisch nevia model ten behoeve van scenario-analyse (in Dutch), Flanders Hydraulics Research & Deltare, Antwerp, Belgium.

Maximova, T., Ides, S., Vanlede, J., De Mulder, T., & Mostaert, F. (2009b). Verbetering 2D randvoorwaardenmodel. Deelrapport 3: kalibratie bovenlopen (in Dutch), Flanders Hydraulics Research, Antwerp, Belgium.

Meire, P., Ysebaert, T., Van Damme, S., Van den Bergh, E., Maris, T., & Struyf, E. (2005). The Scheldt estuary: A description of a changing ecosystem. Hydrobiologia, 540(1–3), 1–11.

Mendelssohn, I. A., & Morris, J. T. (2002). Eco-physiological controls on the productivity of Spartina alterniflora Loisel. In M. P. Weinstein & D. A. Keever (Eds.), Concepts and Controversies in Tidal Marsh Ecology (pp. 59–80). Dordrecht: Springer.

Mitchener, H., & Torfs, H. (1996). Erosion of mud/sand mixtures. Coastal Engineering, 29(1-2), 1–25.

Morris, J. T., & Haskin, B. (1990). A 5-yr record of aerial primary production and stand characteristics of Spartina alterniflora. Ecology, 71(6), 2209–2217.

Morris, J. T., Sundareswaran, P. V., Nietch, C. T., Kjerfve, B., & Cahoon, D. R. (2002). Responses of coastal wetlands to rising sea level. Ecology, 83(10), 2669–2677.

Nehring, S., & Hesse, K.-J. (2008). Invasive alien plants in marine protected areas: The Spartina anglica affair in the European Wadden Sea. Biological Invasions, 10(6), 937–950.

Partheniades, E. (1965). Erosion and deposition of cohesive soils. Journal of the Hydraulics Division, 91(1), 105–139.

Paterson, D. M. (1994). Biological mediation of sediment erodibility: Ecology and physical dynamics. Burt, Neville; Parker, R. and Watts, Jacqueline H. eds. (1997) Cohesive sediments.

Plancke, Y., Schrijver, M., Meire, D., & Mostaert, F. (2017). Overleg flexibel storten: Deelrapport 22 analyse van de waterbeweging, het sedimenttransport en de morfologie nabij de plaat van waalsoonen (in Dutch). Versie 3.0. WI Rapporten 00_031_22.

Poppema, D. W., Willemsen, P. W. J. M., DeVries, M., Zhu, Z., Borsje, B. W., & Hulscher, S. J. M. H. (2017). Experiment-supported modeling of salt marsh establishment: Applying the Windows of opportunity concept to the Marconi pioneer salt marsh design (Master’s thesis). University of Twente.

Pott, D. R., Filditch, C. A., Lohrer, A. M., & Thrush, S. F. (2014). The effects of short-term increases in turbidity on sandflat microphytobenthic productivity and nutrient fluxes. Journal of Sea Research, 92, 170–177.

Reed, D. J. (1990). The impact of sea level rise on coastal salt marshes. Progress in Physical Geography, 14(4), 465–481.

Riethmüller, R., Heineke, M., Kühl, H., & Keuper-Rüdiger, R. (2000). Chlorophyll a concentration as an index of sediment surface stabilisation by microphytobenthos? Continental Shelf Research, 20(10-11), 1351–1372.

Saenrijn, H. H. G. (2006). Salinity and tides in alluvial estuaries. Amsterdam, The Netherlands: Elsevier.

Schrijversh, R., & Vroom, J. (2016). Effecten van realistische (extreme) stortstrategieën in de Westerschelde (in Dutch). Deltare.

Schuur, M., Dolph, T., Reise, K., & Vafedînî, A. T. (2014). Unravelling interactions between salt marsh evolution and sedimentary processes in the Wadden Sea (southeastern North Sea). Progress in Physical Geography, 38(6), 691–715.

Ser, J., Catarino, F., et al. (1999). Fortnightly light and temperature variability in estuarine intertidal sediments and implications for microphytobenthos primary productivity. Aquatic Ecology, 33(3), 235–241.

Silinski, A., Fransen, E., Bouma, T. J., Meire, P., & Temmerman, S. (2016). Unravelling the controls of lateral expansion and elevation change of pioneer tidal marshes. Geomorphology, 274, 106–115.

Staats, N., De Deckere, E. M. G. T., Kornman, B., van der Lee, W., Terwindt, J., & de Winder, B. (2001). Observations on suspended particulate matter (SPM) and microalgae in the Dordai Estuary, The Netherlands: Importance of late winter ice cover of the intertidal flats. Estuarine, Coastal and Shelf Science, 53(3), 297–306.

Steele, J. H., Thorpe, S. A., & Turekian, K. K. (2001). Encyclopedia of ocean sciences.

Suykerbuyk, W. (2019). Watching grass grow: Bottlenecks in seagrass survival.

Temmerman, S., Govers, G.,artel, S., & Meire, P. (2003). Spatial and temporal factors controlling short-term sedimentation in a salt and freshwater tidal marsh, Scheldt estuary, Belgium, SW Netherlands. Earth Surface Processes and Landforms: The Journal of the British Geomorphological Research Group, 28(7), 739–755.

Temmerman, S., Govers, G.,artel, S., & Meire, P. (2004). Modelling estuarine variations in tidal marsh sedimentation: Response to changing sea level and suspended sediment concentrations. Marine Geology, 212(1-4), 1–19.

Van Belzen, J., van de Koppel, J., Kirwan, M. L., van der Wal, D., Herman, P. M. J., Dakos, V., et al. (2017). Vegetation recovery in tidal marshes reveals critical slowing down under increased inundation. Nature Communications, 8, 15811.

Van Dijk, W. M., Hiatt, M. R., van der Werf, J. J., & Kleinhans, M. G. (2019). Effects of shoal margin collapses on the morphodynamics of a tidal flat. Estuarine, Coastal and Shelf Science, 201, 1–19.

Van Ledden, M., Van Kesteren, W. G. M., & Winterwerp, J. C. (2004). A conceptual framework for the erosion behaviour of sand–mud mixtures. Continental Shelf Research, 24(1), 1–11.

Van Rijn, L. C., Walstra, D. J. R., & Ormond, M. (2004). Description of TRANSPOR2004 and implementation in Delft3D-online. Z3748.

van de Koppel, J., Herman, P. M. J., Tholen, P., & Heip, C. H. R. (2001). Do alternate stable states occur in natural ecosystems? Evidence from a tidal flat. Ecology, 82(12), 3449–3461.

van de Lageweg, W. I., Braat, L., Parsons, D. R., & Kleinhans, M. G. (2018). Controls on mud distribution and architecture along the fluvial-to-marine transition. Geology, 46(11), 971–974.

Van der Wal, D., Forster, R. M., Rossi, F., Hummel, H., Ysebaert, T., Roose, F., & Herman, P. M. J. (2011). Ecological evaluation of an experimental beneficial use scheme for dredged sediment disposal in shallow tidal waters. Marine Pollution Bulletin, 63(1), 99–108.

Van der Wal, D., & Herman, P. M. J. (2012). Ecosystem engineering effects of Aster tripolium and Salicornia procumbens salt marsh on macrofaunal community structure. Estuaries and Coasts, 35(3), 715–726.

Van der Wal, D., Herman, P. M. J., Forster, R. M., Ysebaert, T., Rossi, F., Knaeps, E., et al. (2008). Distribution and dynamics of intertidal macrobenthos predicted from remote sensing: Response to microphytobenthos and environment. Marine Ecology Progress Series, 367, 57–72.

Van der Wegen, M., & Roelvink, J. A. (2012). Reproduction of estuarine bathymetry by means of a process-based model: Western Scheldt case study, the Netherlands. Geomorphology, 179, 152–167.

Vos, P. C., DeBoer, P. L., & Madoop, R. (1998). Sediment stabilization by benthic diatoms in intertidal sandy shoals: qualitative and quantitative observations. In P. L. de Boer et al. (Eds.), Ten-influenced sedimentary environments and facies, Extended versions of papers
presented at the Symposium on Classic Tidal Deposits, held August 1985 in Utrecht, Netherlands (pp. 511–526). Dordrecht: D. Reidel Publishing.

Vroom, J., de Vet, P. L. M., & van der Werf, J. (2015). Validatie waterbeweging delft3d-nevla model westerschelde monding (in Dutch). Deltares.

Waeles, B., Le Hir, P., Lesueur, P., & Delsinne, N. (2007). Modelling sand/mud transport and morphodynamics in the Seine river mouth (France): An attempt using a process-based approach. *Hydrobiologia*, 588(1), 69–82.

Wang, Z. B., Langerak, A., & Fokkink, R. J. (1999). Simulation of long-term morphological development in the Western Scheldt. Genova, Italy: Symposium of the International Association for Hydraulic Research.

Wang, C., & Temmerman, S. (2013). Does biogeomorphic feedback lead to abrupt shifts between alternative landscape states?: An empirical study on intertidal flats and marshes. *Journal of Geophysical Research: Earth Surface*, 118, 229–240. https://doi.org/10.1029/2012JF002474

Wang, C., Vanlede, J., Vandenbruwaene, W., Plancke, Y., & Temmerman, S. (2015). Historical evolution of mud deposition and erosion in intertidal areas of the Scheldt estuary. In *Scheldt estuary physics and integrated management: Proceedings of the 36th IAHR World Congress, 28 June–3 July 2015* (pp. 61–64). Delft & the Hague, the Netherlands: IAHR World Congress.

Wiberg, P. L., Fagherazzi, S., & Kirwan, M. L. (2019). Improving predictions of salt marsh evolution through better integration of data and models. *Annual Review of Marine Science*, 12, 389–413.

Widdows, J., & Brinsley, M. (2002). Impact of biotic and abiotic processes on sediment dynamics and the consequences to the structure and functioning of the intertidal zone. *Journal of Sea Research*, 48(2), 143–156.

Winterwerp, J. C., Jeuken, M. C. J. L., Stive, M. J. F., & De Vriend, H. J. (2000). Lange termijnvisie westerschelde: Cluster morfologie. Deltares (WL).

Xiao, D., Zhang, L., & Zhu, Z. (2009). A study on seed characteristics and seed bank of Spartina alterniflora at saltmarshes in the Yangtze Estuary, China. *Estuarine, Coastal and Shelf Science*, 83(1), 105–110.

Yallop, M. L., de Winder, B., Paterson, D. M., & Stal, L. J. (1994). Comparative structure, primary production and biogenic stabilization of cohesive and non-cohesive marine sediments inhabited by microphytobenthos. *Estuarine, Coastal and Shelf Science*, 39(6), 565–582.

Yallop, M. L., Paterson, D. M., & Wellsbury, P. (2000). Interrelationships between rates of microbial production, exopolymer production, microbial biomass, and sediment stability in biofilms of intertidal sediments. *Microbial Ecology*, 39(2), 116–127.

Zhu, Q., van Prooijen, B. C., Maan, D. C., Wang, Z. B., Yao, P., Daggers, T., & Yang, S. L. (2019). The heterogeneity of mudflat erodibility. *Geomorphology*, 345, 106834.