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Benthos as a key driver of morphological change in coastal regions

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Abstract. Benthos has long been recognized as an important factor influencing local sediment stability, deposition and erosion rates. However, its role in long-term (annual-to-decadal scale) and large-scale coastal morphological change remains largely speculative. This study aims to derive a quantitative understanding of the importance of benthos in the morphological development of a tidal embayment (Jade Bay), as representative for tidal coastal regions. To achieve this, we firstly applied a machine learning-aided species abundance model to derive a complete map of benthos (functional groups, abundance and biomass) in the study area, based on abundance and biomass measurements. The derived data were used to parameterize the benthos effect on sediment stability, erosion/deposition rates, and hydrodynamics in a 3-dimensional hydro-eco-morphodynamic model, which was then applied to the Jade Bay to hindcast morphological and sediment change for 2000-2009. Simulation results indicate significantly improved performance with benthos effect included. Results suggest that the model is able to reproduce the main pattern of morphological change only when benthos impact is included, whilst abiotic drivers (tides, storm surges) alone would lead to an opposite pattern. Based on comparison among scenarios with various combinations of abiotic and biotic factors, we further investigated the level of complexity of hydro-eco-morphodynamic models that is needed to capture long-term and large-scale coastal morphological development. The accuracy in parametrization data was crucial for increasing model complexity. When the parametrization uncertainties were high, increased model complexity decreased model performance.

1. Introduction

Benthos includes flora such as sea grass and salt marsh species, which predominately stabilizes sediment (Corenblit et al., 2011; Zhang et al., 2012; Zhang et al., 2015) and fauna with more complex behaviors that can stabilize or destabilize sediment (Backer at al., 2010). Benthic in- and epifauna actively reworks sediment (so-called bioturbation) in order to increase the availability of resources for themselves (Jone et al., 1994; Meadows et al., 2012), and plays a critical role in modifying sediment properties such as grain size, porosity, permeability and stability at local scales in coastal environments (Backer et al., 2010 Arlinghaus et al., 2021; Murray et al., 2008).

The different behaviors of benthos and consequent impacts on sediment have been described in numerous studies and literature reviews (Arlinghaus et al, 2021; Andersen and Pejrup, 2011; le Hir et al., 2007). Major benthos behaviors include biomixing and bioturbation (Lidqvist et al., 2016; Queiros et al., 2013, Meyer et al., 2018, Weinert et al., 2022), bioirrigation (Wrede et al., 2017), biodeposition and -resuspension (Cozzoli et al., 2019; Graf and Roseberg, 1996), faecal pellet production (Andersen and Perjup 2011; Grant and Daborn, 1994; Troch et al., 2008) and biofilm stabilization (Le Hir et al., 2007; Stal et al., 2010). The impacts of benthos behaviors on sediments can individually or accumulatively lead to dramatic local morphological changes as demonstrated by defaunation experiments (Volkenborn and Reise, 2006; Volkenborn et al., 2008; Montserrat et al., 2008). However,

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most studies are limited to small temporal and spatial scales and it remains unclear whether such small-scale benthos-sediment interactions could affect long-term (annual-to-decadal scale) and large-scale (km-to-basin scale) coastal morphological change.

Over the past three decades, increasing efforts have been dedicated to upscale the impacts of benthos-sediment interactions to larger scales through the use of numerical modeling (Arlinghaus et al., 2021). Results indicate that benthos can induce erosion that is in the same order of magnitude as hydrodynamics (Wood and Widdows, 2002; Lumborg et al., 2006; Arlinghaus et al., 2022) and causes redistribution of sediments at large spatial scales, e.g. across tidal basins (Borsje et al., 2008) and coastal bays (Nasermoaddeli et al., 2017). Fine-grained, muddy sediments are especially sensitive to benthos impacts (Paarlberg et al., 2005; Knaapen et al., 2003; Smith et al., 1993). However, almost all modeling studies applied at large-scales are limited to qualitative results (Arlinghaus et al., 2021). Following the concept of Desjardins et al. (2018), numerical models can be categorized into three types corresponding to successive development stages, namely explorative, explanatory and predictive models. In explorative hydro-eco-morphodynamic models, processes and their parameterizations are varied within a certain range, creating an ensemble of possible final states to estimate and explore the impact range of a driver, e.g. benthos, on morphological evolution. In explanatory models, a certain final state is known and the model parameters are tuned in order to hindcast the change of the system from an initial state to the final state as accurate as possible, so that the simulation results can be used to understand the magnitude and relative importance of the involved processes contributing to the final state. Most hydro-eco-morphodynamic models are still at the explorative stage and have yet to reach the explanatory stage, and the reason is manifold. In general, benthic physical and biological processes are highly complex, involving many feedback loops and boundary conditions with large variability (Oreskes et al., 1994; French et al., 2015; Larsen et al., 2016), e.g. many biophysical functions such as the formation of biofilm and its impact on sediment stability remain still poorly understood (Stal, 2010; Van Colen et al., 2010; Chen et al., 2017). Interactions between different functional groups of benthos and between benthos and seabed morphology are important in coastal morphodynamics (Murray et al., 2008; Marani et al., 2010; Corenblit et al., 2011; Reinhardt et al., 2010; Zarnetske et al., 2017) but have rarely been incorporated in large-scale modeling (Arlinghaus et al., 2022, Brückner et al., 2021). Shortage of continuous field monitoring data (e.g. mapping of benthos and seabed morphology) with long-term coverage impedes a process-based understanding and mathematical description of benthic biophysical functions (Arlinghaus et al., 2021).

Explanatory models represent an intermediate stage of model development from exploratory toward predictive modeling (Desjardins et al., 2018). This study presents an effort to this end in hydro-eco-morphodyamic modeling. For this purpose, the Jade Bay, a tidal embayment located in the German Wadden Sea, was chosen to test the model. The reason for choosing the Jade Bay is that extensive datasets for both morphological evolution and biological parameters are available for the area, providing a unique opportunity for an explanatory modeling investigation.

Tidal embayments such as the Jade Bay are commonly found worldwide (Haas et al., 2017). They are among the most productive ecosystems in the Earth surface providing a variety of ecosystem functions (Mitsch and Gosselink 2007) and serve as important habitats for marine lifeforms (Levin et al., 2001). On the other hand, they are commonly utilized for fishing, navigation and tourism and endure strong population pressure (Duong et al., 2016).

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Depending on the effects of different biotic and/or abiotic drivers, tidal embayments may persist for centuries, be filled up or closed (Haas et al., 2017), or be drown (Plater and Kirby, 2011). Thus, understanding the morphodynamics of these systems is crucial for coastal mitigation and adaptation in response to climate change and human use.

In this study, an elaborate hydro-eco-morphodynamic model is used to hindcast the morphological development of the Jade Bay from 2001 to 2009. Jade Bay benthos data include infauna (>0.5 mm) and seagrass. By incorporating the impacts of these two types of benthos, we aim to address the following specific questions:

1. To what extent benthos accounts for the observed changes in the morphology and sediment composition in the study area? and
2. What are the individual and combined impacts of different functional groups on morphological development?

2. Study Area

Jade Bay is located in the inner part of the German Wadden Sea and connected to the outer part through a deep (>15 m) tidal inlet (Fig. 1). The tidal inlet and the Jade Bay have a combined length of ca. 36 km and vary in width between 4 and 15 km, covering around 370 km², with 160 km² inside the bay, and about 60 % of which is comprised of tidal flats (Lang et al., 2003). The Jade Bay is a meso-tidal system with a tidal range of ca 3.7 m (Svenson et al., 2009). The water depth of the main channel reaches up to 20 m below the mean sea level. The main channel penetrates Jade Bay and branches into three major basin channels which are permanently inundated (Stenckentief, Vareler Fahrwasser, Ahne, see Fig. 1a). The intertidal area has a mean water depth of 2.07 m during high tide (Von Seggern, 1980). Tidal currents transport an average volume of 0.4 km³ per tidal cycle with speed exceeding 1.5 m/s in the channels (Götschberg and Kahlfeld, 2008). A training wall guides tidal currents, leading to finer sediments towards the western and southern parts of the bay (Linke, 1939, Götschberg and Kahlfeld, 2008). The central part of the channel is characterized by medium to coarse sands, while towards the banks fine sands with increasing mud content are found (Reineck and Singh, 1967). Three bed types can be distinguished: sandflats, mudflats and mixed. The bay is inhabited by abundant benthic fauna and seagrass meadows (*Zostera noltii*).

3. Methods

3.1 Machine learning-aided mapping of benthos

According to the impacts of benthos on sediment dynamics and to achieve an appropriate level of model complexity, benthos are sorted into functional groups. A functional group comprises species from different taxa that impact their environment in similar ways (Kristensen et al., 2012). In this study, benthos is categorized into four major functional groups, namely bioturbators, stabilizers, filter/suspension feeders, and seagrass.

The existing field data set provides benthos abundance in the inter-tidal area and abundance plus biomass for the subtidal area at 160 stations in the Jade Bay (Senckenberg, Schückel and Kröncke, 2013; Schückel et al., 2015). Based on the intertidal abundance values and biomass averages from the subtidal, the intertidal biomass could be calculated. The total measured biomass in the Jade Bay is dominated by a few species which are widely distributed in the area. Since the metabolic rate of bioturbators is a useful indicator for bioturbation intensity (Cozzoli et al., 2019), which scales with biomass, we focus on five dominant species which make up 95% of benthos biomass in

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the area, namely *Cerastoderma edule* (filter feeder), *Peringia ulvae* (bioturbator), *Hediste diversicolor* (bioturbator), *Tubificoides benedii* (bioturbator) and *Macoma balthica* (suspension feeder and bioturbator). Complete mapping of benthos for the entire Jade Bay is done by extrapolation from the 160 field stations. Species distribution modeling (SDM) is commonly used for this purpose which produces probabilities of species occurrence.Various methods have been applied, spanning from statistical methods to machine learning (Waldock et al., 2022). Species abundance modeling (SAM) is developed from SDM and has an increased solution spacesince the output represents decimal values covering the whole range of measured abundance spectrum or biomass spectrum respectively. Existing studies show best results using decision trees (Luan et al., 2020; Waldock et al., 2022). For this reason we adopted a decision tree-based SAM to generate a complete map of benthos in the study area. Detailed description of the method and analysis of the applied dataset are provided in the supplementary material.

Six predictor variables at the stations, namely temperature, salinity, Chl-a content, inundation time, shear stress and mud content were used. The first three were derived via image analysis of the plots from the Jade Bay SDM results by Singer at al. (2016) and the latter three were extracted from the hydrodynamic model results. Abundance and biomass of the five dominant species are target variables. For each of the species a separate regression tree model was run for the Jade Bay area. In addition, the SAM model was extended to cover the inner and outer Jade. However, in this area there is no benthos field data for model validation and the number of predictor variables is reduced to three (mud content, shear stress and inundation time). Based on the field data, two SAM models were applied for each species, one for abundance and one for biomass, in order to calculate the mean individual biomass which is needed for the parametrization of benthos impacts on sediment. We used 90% of the species data points for model training and the rest 10% to test the model performance.

3.2 Mathematical description of benthos impact

Impacts of benthos on sediment are formulated through scaling functions between benthos abundance/biomass and model parameters for sediment dynamics (critical shear stress for erosion τ_c, erosion rate E_r and settling velocity W_s) and hydrodynamics (turbulence and bottom shear stress). For sediment erosion, the general approaches by Knaapen et al. (2003) for τ_c and Paarlberg et al. (2005) for τ_c and E_r are applied. An abiotic critical shear stress for erosion τ_c^0 and erosion rate E_r^0 are scaled by bioturbation functions p_d, g_d and stabilization functions p_s, g_s, respectively, which depend on abundance A and biomass B of these two functional groups:

$$\tau_c = \tau_c^0 \cdot p_d(B, A) \cdot p_s(B, A) \quad (1)$$

$$E_r = E_r^0 \cdot g_d(B, A) \cdot g_s(B, A) \quad (2)$$

3.2.1 Bioturbators

The main effect of bioturbators is sediment destabilization. However, bioturbating macrobenthos can also increase sediment stability when its biomass is small, which is attributed to hardening of mucus excreted during locomotion (Cozzoli et al., 2019). In our model, the formula from Cozzoli et al. (2019) are adopted to relate bioturbation effect with the overall metabolic rate M_{TOT}. The total eroded sediment per unit area in a given time, R_{TOT}, is described by:

$$R_{TOT} = \frac{a}{1+\exp\left(\frac{b-\tau_b}{c}\right)}, \quad (3)$$

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where the factors a and b are related to M_{TOT} and B, c is an empirical constant, and τ_b is the bottom shear stress. In order to calculate M_{TOT}, measurements from Cozzoli et al. (2019) are used to estimate the individual metabolic rate (M_{Indv}) from the individual biomass (B_{Indv}):

$$M_{Indv} = 0.0067 \cdot B_{Indv}^{0.835} \quad (4)$$

The SAM results for abundance and biomass are then used to calculate the mean individual biomass, which is fed into Eq. (4) to derive M_{Indv} and total metabolic rate M_{TOT}. The derived value of M_{TOT} is then used to calculate the factors a and b under bioturbation impact (a_{bio} and b_{bio}):

$$a_{bio} = 41.67 \cdot (1 + M_{TOT})^{0.34} \cdot (1 + M_{TOT})^{-0.09}, \quad (5)$$

$$b_{bio} = 0.1 + 0.01 \cdot \log(1 + M_{TOT}). \quad (6)$$

The total eroded sediment under bioturbation impact, R_{TOT}^{bio}, is calculated by feeding a_{bio} and b_{bio} into Eq. (3). The total eroded sediment under abiotic conditions R_{TOT}^{0} is calculated based on the formulation given in Cozzoli et al. (2019) and is used to derive the bioturbation function g_d:

$$g_d = \frac{R_{TOT}^{bio}}{R_{TOT}^{0}} \quad (7)$$

The other bioturbation function p_d is calculated following Brückner et al. (2021), which is also based on the data from Cozzoli et al. (2019). Abiotic (τ_c^0) and biotic critical shear stress for erosion (τ_c^{bio}) are defined based on the respective τ_b value at which a minimal erosion rate of 25 g m^{-2} s^{-1} is reached. p_d is then given by:

$$p_d = \frac{\tau_c^{bio}}{\tau_c^{0}} \quad (8)$$

g_d and p_d are calculated by adding up all bioturbating species considered in the SAM. For the Jade Bay, the derived values of g_d and p_d show a strong destabilizing effect on a vast part of the bay especially on the tidal flats, while the subtidal area is mainly stabilized (Fig. S3, supplementary material).

Macrobenthic oxygen consumption rate may decrease by a factor of 10 during winter compared to summer (Glud et al., 2003; Renaud et al., 2007) and thus bioturbation intensity may also decrease accordingly. To account for this seasonal variability, a sinusoidal variation of g_d and p_d was incorporated with maximum values in summer and minimum values (10% of maximum value) during winter.

3.2.2 Stabilizers

The stabilization functions p_s and g_s are related to MPB. According to measurements by le Hir et al. (2007) and Waeles et al. (2007), an increase of the critical shear stress for erosion by a factor of 4 (i.e. $p_s = 4$) is implemented for the summer months (from June to September) when MPB is present. For the rest of the year a factor of one is used. Erosion rate is assumed to be unaffected by MPB, i.e. g_s is set to 1 as a constant.

3.2.3 Filter/suspension feeders

The presence of suspension and filter feeders such as mussels effectively increases the settling velocity of sediment particles in the bottom water layer. The magnitude of resulting bio-deposition rate of sediments depends on the filtration rate and ingestion rate I of suspension/filter feeders which scale with biomass S. In this study, a simplified version of the filter feeder model from the US Army Corps of Engineers (2000) excluding the temperature effect was applied. Sediment particle settling velocity in the bottom most water layer (W_{sed}) is modified by:

$$W_{sed} = W_{sed}^{0} + I \cdot S \quad (9)$$

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where W_{sed}^{0} represents the settling velocity without the effect of filter/suspension feeders. Further details of the parametrization are provided in the supplementary material.

3.2.4 Seagrass

The impact of seagrass is incorporated by an additional drag term in the Reynolds-averaged Navier-Stokes equation and an additional source term for turbulent kinetic energy and mixing length, following the implementation of Cai (2018). The magnitude of these terms depends on the canopy height h, the stem diameter d, stem density N and the drag coefficient for vegetation c_D. The parameters were chosen according to the vegetation proof and the common densities of *Z. noltii* in the German Wadden Sea (Adolph, 2010) and are listed in the model setup section.

3.3 Hydro-eco-morphodynamic numerical model

The formula for benthos effect on sediment dynamics described in section 3.2 are integrated into a 3-dimensional modeling system SCHISM (Zhang et al., 2016) to simulate hydro-eco-mophodynamics. SCHISM solves the Reynolds-averaged Navier-Stokes equation on an unstructured horizontal grid employing a semi-implicit Galerkin finite element method (FEM). Vertical velocities and transport is computed with a finite volume method (FVM) approach for a flexible number of vertical layer, allowing for transition between regions of different depth and resolution (Zhang et al., 2008). Turbulence closure is implemented according to the k-kl closure scheme described in Umlauf and Burchard (2003). The original SCHISM framework includes a sediment module (SED3D, Pinto et al., 2012) which does not take into account the impacts of benthos. Sediment is divided into multiple classes, each with characteristic parameters including grain size, density, settling velocity, erosion rate and critical shear stress for erosion. Cohesive and non-cohesive sediments are distinguished. Non-cohesive sediments (sands) can be transported in both suspension and bed-load depending on the shear stress and settling velocity, while cohesive sediment (clay, silt and organic detritus) is transported in suspension. Transport of each pre-defined sediment class is computed independently.

3.3.1 Model setup for the study area

The model domain spans roughly from 53°23'N 8°35'E to 53°53'N 7°46'E (Fig. 1a). It is covered by unstructured triangular elements with a spatial resolution of ca. 800 m in the outer Jade and an increasing resolution toward the Jade Bay, with a resolution of ca. 200 m inside the bay. The vertical plane is divided into 11 sigma layers. The open boundary is forced by 15 tidal constituents (M2, K1, S2, O1, N2, P1, SA, K2, Q1, NU2, J1, L2, T2, MU2, 2N2) extracted from the global ocean tide atlas FES2014 (Florent et al., 2021) as well as observed storm surges (supplementary material) at a gauge station (Lighthouse Alte Weser) located at the open boundary (Fig. 1a). Discharge is specified for the Weser River at the south east boundary of the modeling domain according to Galbiati et al. (2008). Two sediment classes which are dominant in the study area (Fig. 1b) are included, namely fine sands with an initial settling velocity (W_{sed}^{0}) of 1 mm s^{-1} and mud with an initial settling velocity (W_{sed}^{0}) of 0.02 mm s^{-1}. A constant mud concentration of 40 mg l^{-1} is specified at the open boundary according to Pleskachevsky et al. (2005).

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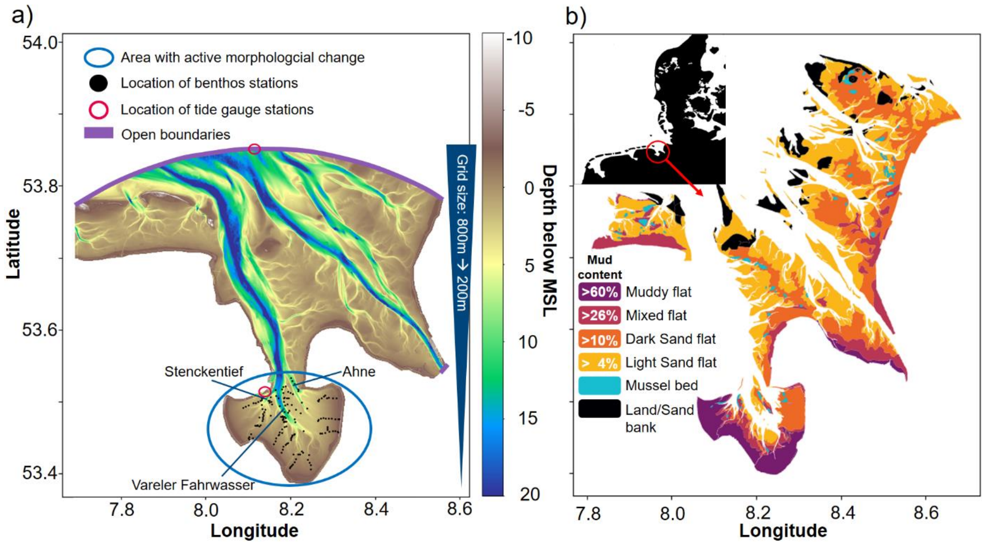

Figure 1. (a) Computational domain and its open boundary, including the initial morphology at 2001, the location of benthos data and tide gauge stations; (b) Distribution of sediment types including land and mussel beds (Meyer and Ragutski, 1999).

Datasets from various sources are used to initialize, parametrize and validate the model. A brief summary of these datasets is given in Table 1. The model is used to hindcast the change of morphology and sediment composition in the Jade Bay from July 2001 until December 2009. The measured morphology in 2001 serves as the initial condition. There are no sediment property measurement for periods around 2001, therefore measured data from 1996 (Fig. 1b) were used to specify the initial mud and sand contents. Default model parameters representing abiotic conditions are listed in Table 2.

Table 1. Data sources used for model initialization (Init.), parameterization (Param.), and model validation (Valid.).

Type	Use	Time	Description	Source/Provider
Benthos	Init.	2009	Abundance and biomass at 160 field stations	Senckenberg, Kröncke and Schückel (2013), Schückel et al. (2015)
Benthos	Param.	-	Laboratory erosion measurements with different species at different densities	Cozzoli et al., 2019
Benthos	Param.	-	Filter feeding rate	US Army Corps of Engineers, (2000)
Benthos	Param.	-	Estimated MPB impact	Le Hir et al., 2007
Benthos	Param.	-	Seagrass impact on hydrodynamics	SAV module of SCHISM, Adolph (2010)
Sediment	Init.	1996	Sediment map	Meyer and Ragutski (1999)

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Sediment	Valid	1996-2009	Map of sediment change	Ritzmann and Baumberg (2013)
Forcing: tides	Init.	2001-2009	Finite element global ocean tide atlas	FES2014 Florent et al., 2021
Forcing: storms	Init.	2001-2009	Observation data at the gauge station Lighthouse Alte Weser	Wasserstraßen- und Schifffahrtsverwaltung des Bundes (WSV)
Water level	Valid.	2001-2009	Observation data at the gauge station Wilhelmshaven	Wasserstraßen- und Schifffahrtsverwaltung des Bundes (WSV)
Morphology	Init. + Valid.	2001-2009	High-resolution morphology of the German Bight	Sievers et al., (2020)

Table 2. Configuration of default model parameters for abiotic conditions.

Parameter	**Configuration**
$\boldsymbol{h}$	25 cm
$\boldsymbol{d}$	0.2 cm
$\boldsymbol{N}$	400 m^{-2}
$\boldsymbol{c_D}$	1.13
$\boldsymbol{\tau_c^0}$	0.2 Pa
$\boldsymbol{E_r^0}$	$2 \cdot 10^{-5}$ s m^{-1}
$\boldsymbol{E_r^{10}}$	$2 \cdot 10^{-4}$ s m^{-1}
$\boldsymbol{W_{sed,mud}^0}$	$2 \cdot 10^{-5}$ m s^{-1}
$\boldsymbol{W_{sed,sand}^0}$	$1 \cdot 10^{-3}$ m s^{-1}

In order to disentangle the impacts of benthos, including effect of individual functional groups and combined effect of all functional groups, and abiotic drivers on morphological and sediment change of the study area, a total of 27 different model experiments have been performed (Table 3). The experiments were designed to include different levels of complexity in the variability of physical forcing (e.g. with and without storms) and benthos (e.g. with and without seasonality).

Table 3. Model experiments designed for combination of different functional groups and physical forcing. E0 denotes the standard erosion rate used in the original model formulation, while E10 denotes an enhanced erosion rate by a factor of 10. "Storm" denotes experiments including storm events. "Season_1" indicates an inclusion of seasonality in only one functional group, and "Season_2" indicates that seasonality is considered in all functional groups. Note that in the experiments with "All benthos", "Season_1" refers to bioturbators only.

	E0	E0 + Storm	E0 + Storm + Season_1	E0 + Storm + Season_2	E10	E10 + Storm	E10 + Storm + Season_1

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All benthos	All0	All1	All2	All3	--	--	--
Bioturbators	Des0	Des1	Des2	--	--	--	--
Stabilizers	Sta0	Sta1	Sta2	--	Sta0b	Sta1b	Sta2b
Filter/suspension feeders	Acc0	Acc1	Acc2	--	Acc0b	Acc1b	Acc3b
Seagrass	Gra0	Gra1	--	--	Gra0b	Gra1b	--
Abiotic drivers only	Ref0	Ref1	--	--	Ref0b	Ref1b	--

4. Results

4.1 Mapping of benthos

The performance of the decision tree-based SAM varies among the selected species and lies below 20% deviations from the measurements for the majority of the stations (Fig. S2, supplementary). Biomass and abundance distributions of all five species are shown in Fig. 2b-f.

For stabilizers, microphytobenthos (MPB) is considered, which is only distinguished by presence or absence in the field data. We applied a simple formulation relating the growth of MPB-based biofilm to the inundation period and mud content following the studies by Widdows and Brinsley (2002) and Daggers et al. (2018). In the Jade Bay, only the western and southern parts are inhabited by extensive biofilms (Fig. 2a).

Seagrass distribution in the Jade Bay is described for the years 2000-2008 in Adolph (2010) with vegetation density between 5-40% for the dominant species *Zostera noltii* (Fig. 2a).

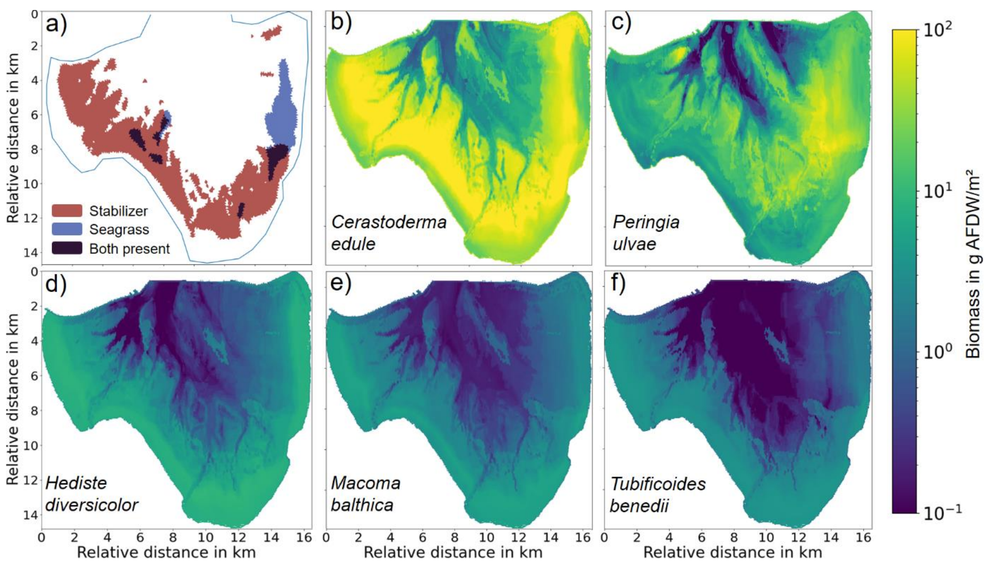

Figure 2. (a) Presence of stabilizers (MPB) and seagrass according to Adolph (2010); (b)-(f) Modeled biomass distribution of the five dominant benthic faunal species.

4.2 Assessment of hydro-eco-morphodynamic model performance

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The simulated change of sediment composition and morphology in all experiments are compared and evaluated. Firstly, simulation results are evaluated against observed changes to rank the performance of the experiments. Then, the impact of individual functional groups and their combined effect is analyzed based on the model results. In addition, the level of complexity of hydro-eco-morphodynamic models that is needed to capture long-term and large-scale coastal morphological development is investigated.

Simulated time series of water level in all experiments are quite similar, and exhibit differences only during storm periods between the experiments with and without storms. Comparison with measured water level at a tide gauge station in Wilhelmshaven, which is located at the inlet of the Jade Bay, shows a satisfactory model performance (Fig. 3). Taking the reference experiment Ref0 as example, the standard deviation is 1.34 m for the data measured at the gauge station compared to 1.33 m derived from model results. For the tide gauge station at the Lighthouse Alte Weser the values are 1.03 m and 0.99 m respectively. The correlation coefficient between modeled water elevation and measured data is 0.98 at Wilhelmshaven and 0.96 at Alte Weser station (Fig. 3b).

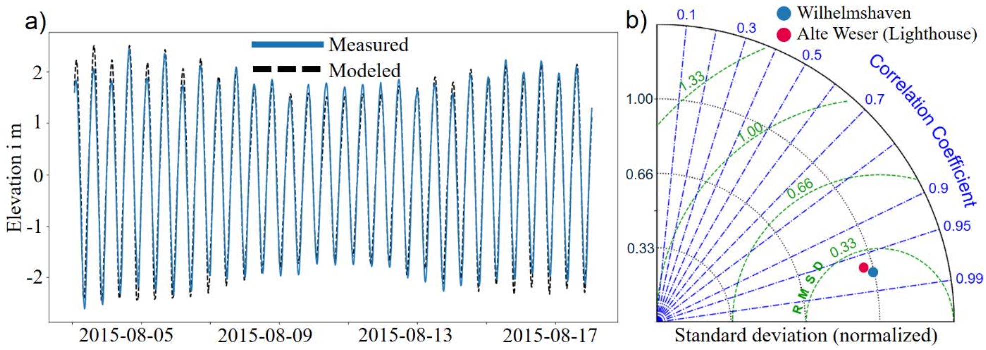

Figure 3. (a) Modeled and measured water elevation at the tide gauge station in Wilhelmshaven. (b) Comparison between model results and measurement at the gauge stations in Wilhelmshaven and the Lighthouse Alte Weser in a Taylor diagram.

The performance of all model experiments with regard to the morphological change of the Jade Bay is also evaluated. In order to minimize the effect of uncertainty in measurements, only the grid cells where the measured morphological change exceeds the standard deviation of difference between the 2001 and 2009 field data were chosen for comparison. Two indicators, namely the RMSE and the cosine similarity between the modeled and measured morphological change, were calculated for each of the experiments and shown in Fig. 4.

The RMSE (Fig. 4a) shows the best model performance in the group of experiments (Allx) which take into account the combined effect of all benthos functional groups, followed by the group of experiments (Desx) which include the effect of bioturbators only. The experiments (Accx) which include only the filter/suspension feeders show a better performance than the reference experiments (Refx) which consider only abiotic drivers, whist the experiments which include only seagrass (Grax) or stabilizers (Stax) do not show noticeable improvement compared to Refx. The difference in the RMSE between the model results with the best and the worst performance is about 15 cm, being about 150% of the average and 35% of the standard deviation of morphological change for the entire Jade Bay from 2001 to 2009. It is worth noting that within the group of experiments (Allx) which include all functional groups, better model performance is gained when storms are included (All1) and seasonality of the dominant functional group, namely the bioturbators, is included (All2). However, model performance decreases when seasonality of all functional groups is considered (All3). The decrease of model performance due to inclusion of seasonality is also seen in other experiments which consider only one functional group, whilst an inclusion of

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storms only slightly enhances or does not affect the performance of these experiments. On the other hand, an increase of erosion rate by a factor of 10 improves the performance of the simulations which considers only abiotic drivers (Refx) and those which include only one functional group (Grax, Accx, Stax), although their performance is still worse than the experiments with combined effect of all functional groups (Allx).

The cosine similarity between the modeled and measured morphological change provides further evaluation of the model performance in capturing the change in the main topographic units. In our evaluation, the cosine similarity is calculated for the main tidal channels (Stenckentief, Vareler Fahrwasser, Ahne, see Fig. 1). Results (Fig. 4b) show that in the experiments with all benthos (Allx) and with inclusion of only bioturbators (Desx), a positive correlation is found, suggesting that the modeled change is consistent with the measured change. On the contrary, a negative correlation is found in all other experiments, suggesting that an opposite pattern is produced in the model results compared to measurement. It is worth noting that an increase of erosion rate by a factor of 10 further strengthens the negative correlation in these experiments.

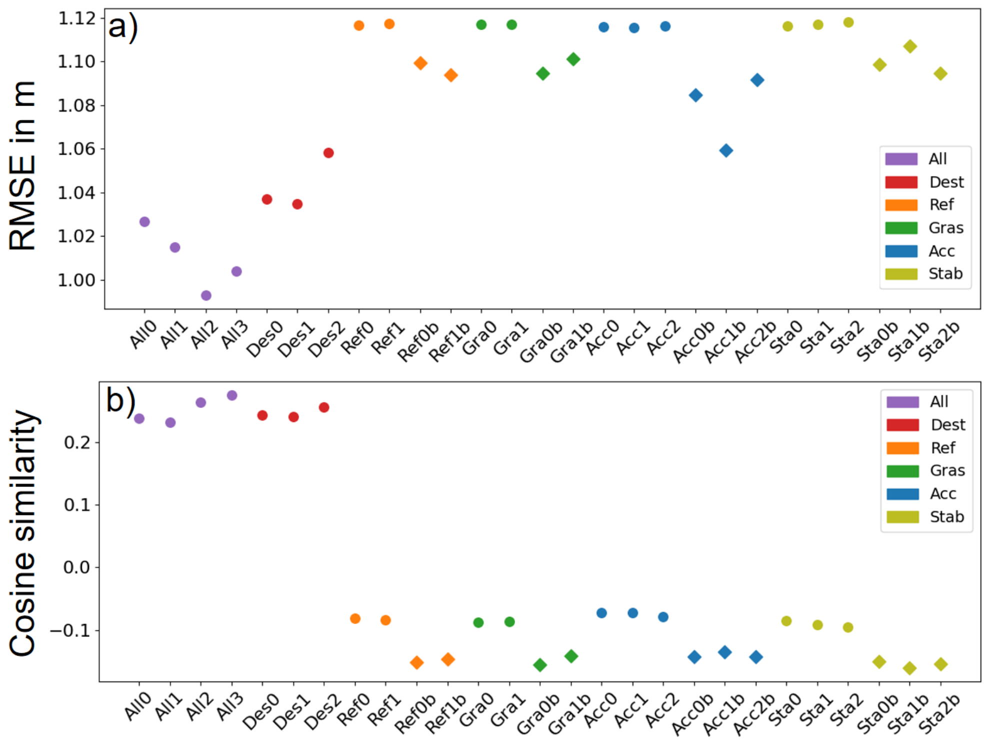

Figure 4. Performance of all simulations in terms of (a) RMSE between the modeled and measured water depth change over the entire bay and (b) cosine similarity in the main channels. The values 1, -1 and 0 indicate positive, negative and no correlation between modeled and measured depth change, respectively. Diamond markers indicate the simulations in which erosion rates were increased by a factor of 10. From left to right, for each experiment with an individual functional group, the model complexity is increased from a normal run without storms, to a run including storms, and lastly including seasonality of benthos effect (Table 3).

4.3 Morphological development

The spatial difference in the model results among the experiments and comparison with the measurement is shown in Fig. 5. Measured data indicate net deposition (up to 0.6 m) inside the main tidal channels accompanied by net erosion (up to 1.2 m) at adjacent flats from 2001 to 2009 (Fig. 5b). Compared to a dominant deposition pattern in the channels, the tidal flats exhibit both erosion and deposition in large parts, including various bar-like structures

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mostly within the range of ±0.2 m. However, these structures are likely attributed to artifacts caused by measurement uncertainties and data processing. Therefore we mainly focus on those apparent deposition and erosion patterns in the channels and adjacent flats that exceed the measurement uncertainties. As indicated in the cosine similarity analysis, only the experiments with all benthos (Allx) and with inclusion of only bioturbators (Desx) are able to reproduce the extensive deposition pattern in the tidal channels (Fig. 5a), whilst other experiments including those reference runs which consider only abiotic drivers show dominance of erosion in the main channels (Fig. 5c&d). The reference run based on the original formulation of erosion rate (Pinto et al., 2012) produces morphological change within the range of ±0.15 m (Fig. 5d), which is much smaller than the measured values (Fig. 5b). Only by an increase of the erosion rate by a factor of 10 the reference run is able to produce morphological changes that are at the same order of magnitude with the measurement (Fig. 5c).

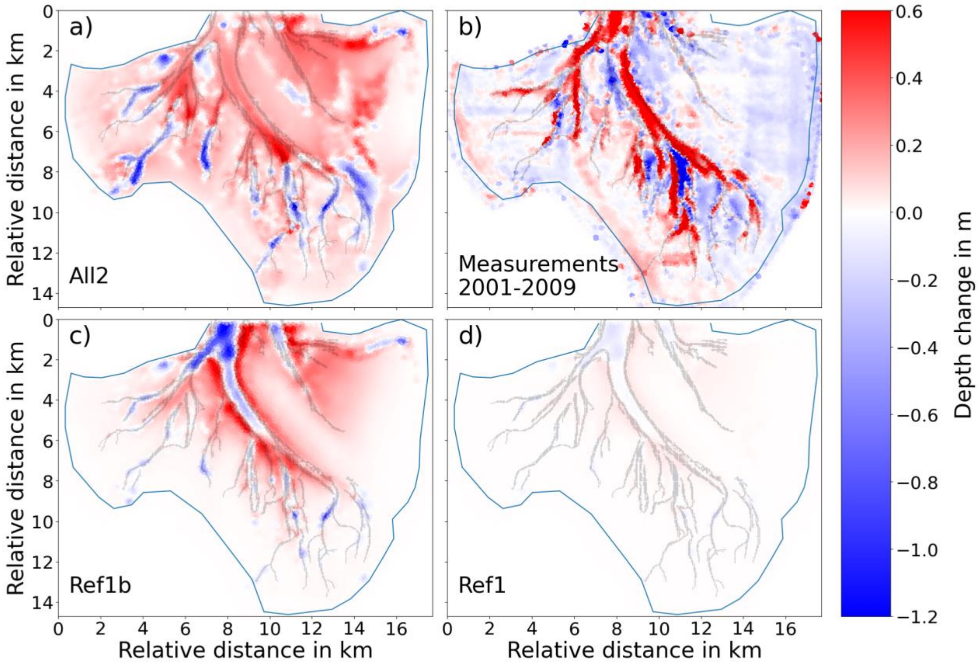

Figure 5. Comparison of morphological change from 2001 to 2009 between the model experiments and the measurement: (a) result of All2; (b) measurement; (c) result of Ref1b; (d) result of Ref1. Positive and negative values are for deposition and erosion, respectively.

There exists a net sediment input to the Jade Bay from 2001 to 2009, which is indicated by the measurement and captured by all model experiments. Increased sediment input into Jade Bay was also reported by Benninghoff and Winter (2019). However, most experiments overestimate the volumetric import compared to the measurement and the magnitude varies among the experiments (Fig. 6a), with largest value in the runs which include the combined effect of all benthos (Allx). Measurement data indicate that the net gain of sediment in the main channel exceeds the net import through the inlet of the bay, suggesting that the sediment accumulated in the channel originates not only from external sources outside the bay but also from internal sources, e.g. erosion at adjacent flats. Simulation results suggest that sands accumulated in the channels mainly come from internal sources whilst mud may originate from both internal and remote sources outside the bay (Fig. S4, Supplement material). Despite of an overestimation of net sediment import to the bay, the model experiments with all benthos included (Allx) produce less deposition in the main channel compared to the measurement (Fig. 6). Instead, much of the imported sediment is deposited over an extensive part of the tidal flats in these runs, as exemplified in Fig. 5a. The reference experiments which include only abiotic drivers (Refx) indicate little or none net sediment accumulation in the channel despite of net sediment import through the inlet. In these runs, imported and eroded sediments from the main channel are mostly deposited along the edges of the channels on the flats (Fig. 5c &d).

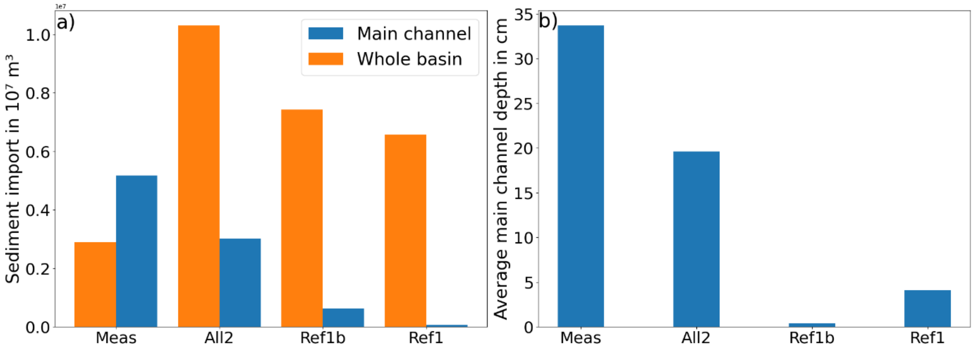

Figure 6. (a) Volumetric sediment import in the main channel and the entire bay, and (b) average depth change in the main channel calculated from the measured data (Meas.) and three representative model experiments between 2001 and 2009.

4.4 Change in sediment composition

There exists remarkable changes in sediment composition in the Jade Bay from 1996 to 2009 according to Ritzmann and Baumberg (2013). Comparison between the observed change and model results indicate that the changes are largely reproduced in the experiments but no experiment alone captures all observed changes (Fig. 7). The best performance is shown in the experiments which include all benthos (Allx). Most of the large-scale changes in sediment composition (indicated by ellipses with roman number I-V) are satisfactorily reproduced in All2, except for the area in the northwest part of the bay (I) where an opposite result is shown in the experiment (Fig. 7a&b). On the contrary, experiments which include only abiotic drivers are able to capture the observed change in this area (Fig. 7c), but with a worse performance in other areas. The experiment which includes only abiotic drivers and based on the original formulation of erosion rate (Ref1) produces only an increase of mud content but fails to capture the loss of mud (Fig. 7d).

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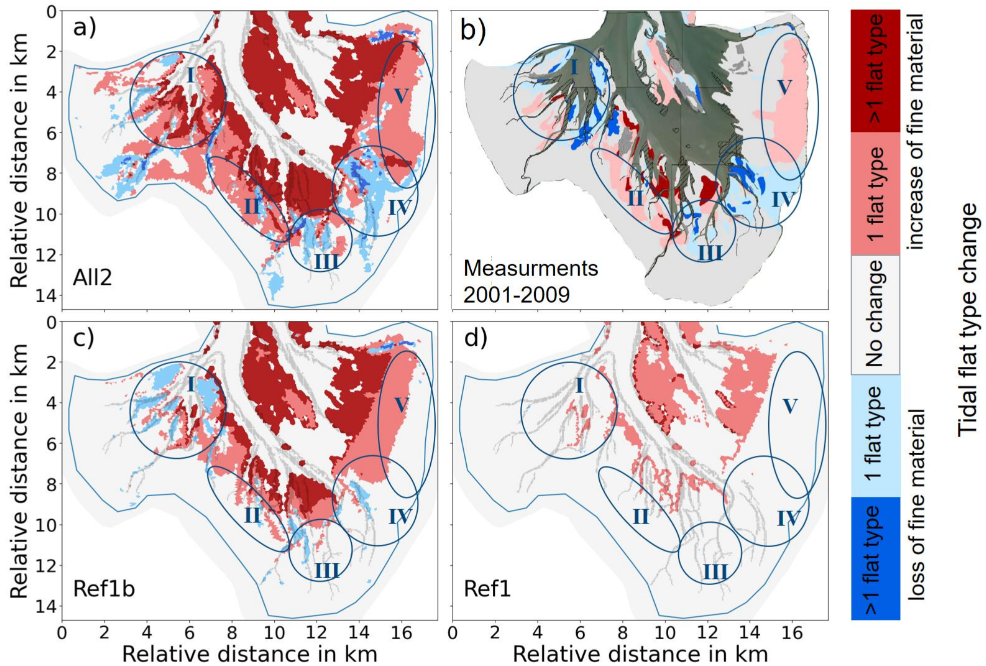

Figure 7. Comparison of change in sediment composition between 2001 and 2009 between model results and observation: (a) result of All2; (b) observation; (c) result of Ref1b; (d) result of Ref1. Pale red and pale blue show the areas where the amount of fine sediment increased or decreased respectively with a change by one tidal flat type (according to Fig. 1b). Red and blue show areas with changes by two or more tidal flat types. Areas featured by large-scale changes are marked by ellipses. (b) shows a modified version of a plot from Ritzmann and Baumberg (2013) and was kindly provided by the NLWKN.

4.5 Impact of benthos

To further figure out how the four functional groups of benthos contribute to changes in morphology and sediment composition, we compared the results of the model experiments which include the impact of individual functional groups with the reference experiments which include only abiotic drivers. Since each group of experiments consists of several runs with different complexity (Table 3), we chose the run from each group with the least RMSE for comparison, namely Ref1b, Des1, Acc1b, Gra0b and Stab0b.

4.5.1 Bioturbators

The difference in the depth change between the runs with benthos and the reference run Ref1b shows that the largest difference in the morphological change is caused by bioturbators (Fig. 8a), followed by filter/suspension feeders, seagrass and stabilizers (Fig. 8b, c & d). In particular, the extensive accumulation of sediment in the main channel, which is shown in the measurement (Fig. 5b), is associated to the impact of bioturbators. The impact of bioturbators also causes deposition over a large part of the shallow tidal flats, as well as erosion at the flats adjacent to the tidal channels. The joint effect leads to a smoothing of the depth gradients between the channels and adjacent tidal flats. Morphological changes caused by bioturbators are in the range of ±1 m compared to the reference run. It is worth noting that bioturbators account for not only the enhanced deposition in the main channel, but also the decrease of mud content in the southern and southeastern parts (III and IV) of the bay (Fig. 9a). These changes are in consistency with field data.

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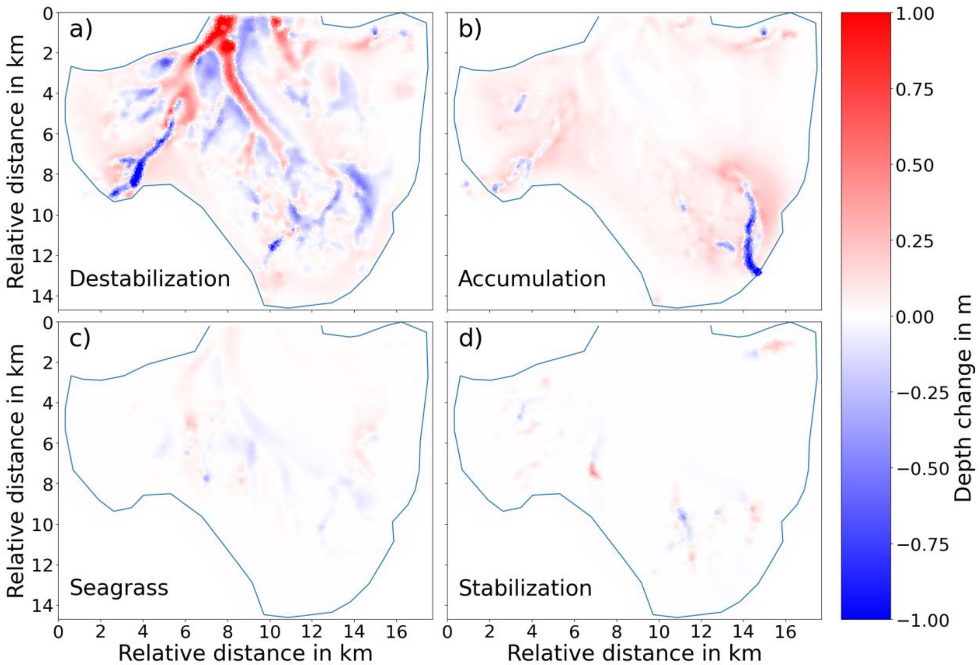

Figure 8. Difference in the depth change between the reference run Ref1b and (a) Des1, (b) Acc1b, (c) Gra0b and (d) Stab0b. Positive and negative values indicate increased deposition and erosion, respectively, in the runs with benthos compared to the reference run.

4.5.2 Filter/suspension feeders

The presence of filter/suspension feeders causes an overall enhanced deposition over a vast part of the tidal flats, with local values up to 0.5 m when compared to the reference run (Fig. 8b). In addition, enhanced erosion up to 1 m is seen in areas adjacent to the habitats of filter/suspension feeders. Filter/suspension feeders do not seem to directly impact the morphological change of tidal channels, however, model results show that they can lead to a significant increase of mud content in a vast part of the bay including the channels (Fig. 9b). In particular, the observed increase of mud content in the southwestern part (II) of the bay is attributed to the impact of filter/suspension feeders according to the model result.

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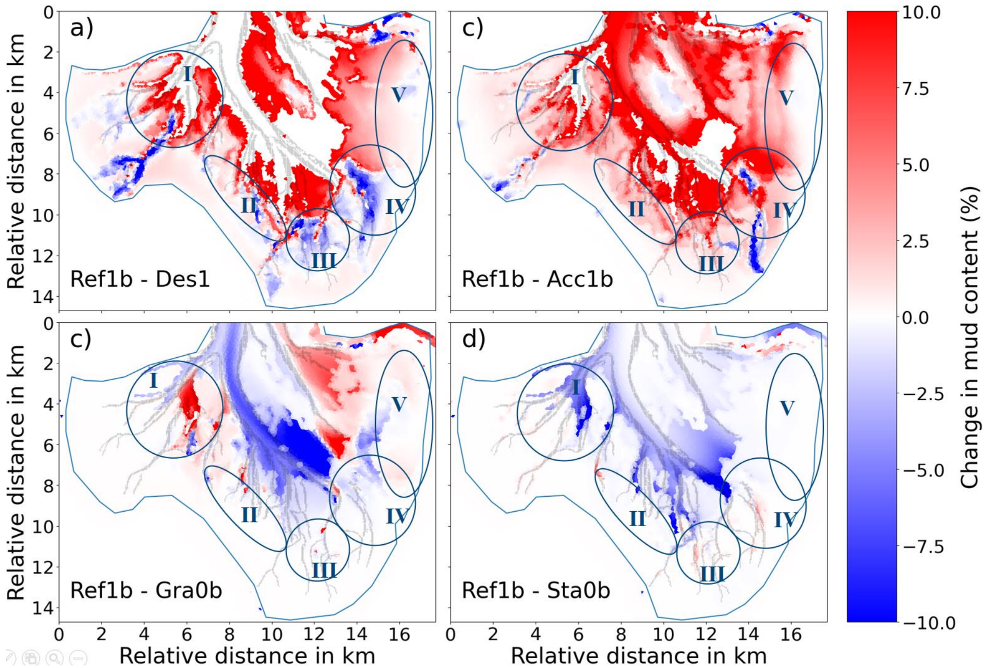

Figure 9. Difference in the mud content (%) between the reference run Ref1b and (a) Des1, (b) Acc1b, (c) Gra0b and (d) Stab0b.

4.5.3 Seagrass

Our simulation results suggest that the impact of seagrass on morphological change of the Jade Bay is smaller than that of bioturbators and filter/suspension feeders. In the eastern part of the bay where seagrass is present, a slight deposition in the range of 10-20 cm occurs at the edge and outer parts of the seagrass meadows (Fig. 8c). Meanwhile, mud content decreases in the same area, suggesting a winnowing process there (Fig. 9c). Interestingly, seagrass meadows affects not only sediment transport and morphodynamics at local scales around their habitats, but also causes far-reaching changes over the bay including the channels and other flats that are free of seagrass (Fig. 8c & 9c). This effect is through a feedback of seagrass meadows to larger-scale hydrodynamics. The ratio in the transported volume between the flooding and the ebbing phase calculated from the simulation results indicates that the majority of water enters the Jade Bay through its main channels during flooding phase and leaves it over the tidal flats during the ebbing phase (Fig. S5a). The spillway on the tidal flats in the east part of the bay (V), where seagrass meadows are located, experiences larger flow friction due to the presence of seagrass (Fig. S5b). As a consequence, more water is transported through the main channel, eroding more fine-grained sediments compared to the abiotic scenario (Fig. S5c).

4.5.4 Stabilizers

The impact of stabilizers on the morphological changes in Jade Bay is relatively minor according to our simulation results. The resultant morphological change is mostly local within the habitats of stabilizers and featured by both erosion and deposition (Fig. 8d). Sediment stabilization and consolidation in the areas where stabilizers exist lead to reduction of sediment sources for the distal ends of small channels, resulting in erosion in these parts. The impact of stabilizers on sediment composition is more prominent compared to the morphological change. In the

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subtidal area, a significant decrease of mud content is seen in the simulation result compared to the reference experiment (Fig. 9d), as a consequence of reduced mud input from stabilized areas.

5. Discussion

5.1 Model hindcast and implication

The model performance, both in terms of morphology and sediment distribution, are improved when biota is included in the simulation. In particular, the extensive deposition in the main channels is reproduced only by the experiments with either combined effect of all benthos (Allx) or with bioturbators (Desx), whilst other experiments produce an opposite pattern.

Our simulation results show that, among all four functional groups considered in the modeling, bioturbators are most impactful on morphological change of the Jade Bay, followed by filter/suspension feeders, seagrass and stabilizers. The morphological change of the bay over the 8.5-years period (2001-2009) is featured by distinct deposition inside the main channels and erosion at their adjacent flats (Fig. 5b). This feature and the amount of deposited sediment could be reproduced by modeling only when the impact of benthos, especially bioturbators, is included. The channel deposition can be explained by two factors related to macrobenthos. Firstly, the critical shear stress for erosion is increased by the presence of bioturbators (p_d>1 in Equation 1) in the channel leading to enhanced resistance to erosion. Secondly, enhanced erosion on the tidal flats by bioturbators (p_d<1, g_d>1) mobilizes sands which are partly deposited in the channel. Mud can hardly accumulate in the channel due to a low sinking velocity and low threshold for resuspension (before consolidation). The majority of the accumulated sands in the channels comes from the eroded tidal flats. The redistribution of sediments from the tidal flats, which become increasingly deeper, into the channels, which become shallower, represents a typical basin development pattern under the impact of biotic destabilization as demonstrated by Arlinghaus et al. (2022). This is the case for the Jade Bay where a shift of functional groups took place between the 1970s and 2000s with bioturbators increasing from ~ 20% to almost 70% in the field surveys (Schückel and Kröncke, 2013). Furthermore, the channel incision and sediment deposition at its edges in the model experiment which considers only abiotic drivers compare well with the abiotic scenario presented in Arlinghaus et al. (2022), in which deep and narrow channels develop with shallow tidal flats. The effect of unrealistically strong channel incision is known in morphodynamic modeling, although this problem is often overlooked (Baar et al., 2019). One practical solution that is often adopted in applications is an increase of the bed slope diffusion, e.g. by up to a factor of 100 (Van der Wegen and Roelvink, 2012; Schuurman et al., 2013; Braat et al., 2017). However, this solution does not represent a process-based understanding. An alternative solution is provided in our modeling study which proposes to include the impact of bioturbation instead of tuning the bed slope diffusion.

Compared to the remarkable impact of bioturbators which leads to deposition in the channels and erosion in the flats therefore a general widening of channels, other functional groups have less influence in the morphological change of the main channels according to our simulation results. Filter/suspension feeders mainly enhance sediment deposition on the tidal flats. Seagrass meadows can modify the flows not only within or adjacent to their habitats but also at a large-scale covering a vast part of the bay, which results in alternating erosion and deposition patterns in the main channel. The impact of stabilizers on the morphological change of the Jade Bay is the weakest among the four functional groups. This is attributed to their location. The shallow tidal flats in the south and west of Jade Bay where stabilizers are inhabited are subject to relatively weak tidal currents and small suspended sediment concentrations. The different impacts of the mentioned functional groups are depicted in simplified form in Figure 10. Our results suggest benthos as a critical driver determining sediment stability and morphological

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development of tidal embayments or basins, supporting an early study by Backer et al. (2010). A reference simulation, which considers only abiotic drivers and adopts formulation of erosion rates from laboratory experiments in which benthos is excluded, heavily underestimates the morphological change. An increase of the erosion rate by a factor of 10 allows the reference simulation to produce morphological changes that are at the same order of magnitude with the measurement, but still fails to capture the spatial pattern. This indicates that existing formulations for sediment resuspension rate that do not take into account benthos impact may be of limited use for application to real coastal systems that are inhabited by benthos.

As demonstrated in the model results, the major effect of benthos is sediment mobilization and redistribution, which was also found in Borsje et al. (2008) and Lumborg et al. (2006). Especially an import of mud into the bay is increased under the impacts of benthos, which is in line with other modeling results summarized in Arlinghaus et al. (2021). Our results show that filter/suspension feeders have the strongest impact on changes in sediment composition, followed by bioturbators, seagrass and stabilizers. The impact of filter/suspension feeders is mostly local, but this functional group is present over a vast part of the bay and thus jointly leads to a large-scale impact. By contrast, the impact of bioturbators extends beyond their habitats. Locally, sediment can be either stabilized or destabilized depending on the abundance of bioturbators. Non-locally, the enhanced erosion in large parts of the tidal flats by bioturbators increases the overall concentration of suspended sediment, especially on the flats outside the Jade Bay, which provides a sediment source for the bay. The impact of seagrass meadows also reaches beyond their habitats by altering the large-scale hydrodynamics and the ratio of the inflow to the outflow in the tidal channels and on the flats. The increased loss of mud content in the tidal channels in the stabilizers experiments (Stax) compared to the reference run can be explained by reduced supply of mud from the tidal flats which are inhabited by stabilizers. However, since mud content is small in the hydrodynamically active areas, the absolute change of mud content induced by stabilizers is minor.

The changes in sediment composition are reproduced more satisfactorily in four areas with the inclusion of benthos effects, namely the southern (III), the southeastern (IV), the eastern (V) and the southwestern (II) parts of the bay (Fig. 7). The loss of mud due to erosion in the southern (III) and the southeastern (IV) parts is mostly attributed to the impact of bioturbators which has a strong destabilization effect there. The eastern (I) part accumulates much more fine sediment compared to the reference run, which is attributed to the impact of seagrass and filter/suspension feeders (Fig. 9). The increase of mud content on the shallow tidal flats in the southwestern part is mainly due to the presence of filter/suspension feeders. At one site in the western part, the reference simulation yields better results with a loss of mud, which is not captured by experiments with benthos.

Overall, the increase of mud content is overestimated in all model experiments when compared to the field data. One possible explanation is that biomixing effect was not implemented in the model and thus all freshly deposited mud remains on the seabed surface before being eroded at a later stage or buried by further new deposits, whilst biomixing in a natural system would mix freshly deposited mud and organic matter with other coarser particles and lead to homogenization of sediment grain size in the upper 10-30 cm as pointed out by previous studies (Knaapen et al., 2003; Paarlberg et al., 2005; Arlinghaus et al., 2022).

5.2 Societal relevance

Similar to many other coastal bays/embayments worldwide, the Jade Bay serves important socio-economic functions for tourism, logistics and on the other hand provides important refuge for a variety of marine lifeforms. It is of critical importance to sustain the ecological functions of coastal bays such as the Jade Bay under the increasing pressure of human use and climate change. Our results indicate that benthos can significantly modify

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morphological change and sediment composition in tidal embayments, and can play a key role in the natural resilience of coastal systems against human and climate stressors. However, we also revealed that the impact on morphological development varies among different functional groups. Bioturbators tend to smooth the bathymetric gradients between channels and flats, whilst seagrass and filter/suspension feeders may counteract this to various extents. A combined effect of all functional groups leads to increased import of sediment, especially mud, to the bay. Our results support the hypothesis by Haas et al. (2018), who proposed that an abundance of mud and eco-engineering species often culminates in continuous embayment filling with fine sediment and the growth of intertidal and supratidal areas, eventually leading to closure of the embayment. However, on the other hand, there is growing concern on whether coastal systems such as the Wadden Sea including the Jade Bay can keep pace with the foreseeable sea level rise for the upcoming decades (Plater and Kirby, 2011). Our results show that the morphological development of the Jade Bay is able to sustain the impact of sea level rise, at least for the period 2001-2009, because of a net sediment import caused by a joint effect of abiotic and biotic drivers. But it is unclear how the drivers would change in future, especially how the different functional groups of benthos would react to human and climate stressors. For instance, chlorine inputs are expected to increase in the Jade Bay due to construction of liquefied natural gas (LNG) terminals, which will likely have an impact on the population, abundance and distribution of the different functional groups. This may result in a loss of sensitive species and functional groups as pointed out by studies in other regions (Chang, 1989; Wang et al., 2022). Extreme weather events, such as heat waves, also have a significant impact on benthos (Serrano et al., 2021). Intensity and frequency of extreme events are likely to increase in future due to climate change, but the consequent change in benthos remains largely unknown. To this end, explanatory and eventually predictive numerical models are of imperative value in exploring feasible nature-based solutions for sustaining both socio-economic and ecological functions of coastal regions.

5.3 Model limitations and future research needs

Earth system modeling and regional modeling inevitably comprise uncertainties, which originate from various sources including boundary conditions, numerical solvers, and parameterization of processes. This is especially true in modeling of coastal systems in which physical and biological factors may be of comparable importance in guiding the system evolution. Model refinement and/or inclusion of additional processes do not necessarily increase model accuracy since the uncertainties in parametrization of less-known processes (e.g. growth/decline of benthos, interactions between different species/functional groups) may exceed the gain in accuracy (Skinner et al., 2018, Pianosi et al., 2016). An earlier study found that it remains a challenge to get physically correct results for both sediment transport and morphodynamics simultaneously (Baar et al., 2019). Therefore, development of hydro-eco-morphodynamic models will always be limited to a certain tradeoff between complexity and accuracy. This is confirmed in our study, which indicates that an increase in model complexity by considering the benthos impact firstly increases model performance in approximating observed change, but model performance decreases when a higher complexity, i.e. seasonal change of benthos, is added by a simple parameterization. This points out a need for an accurate mapping of benthos including their temporal changes in field which can serve input for the modeling and/or process-based understanding and formulation of temporal change of benthos for modeling.

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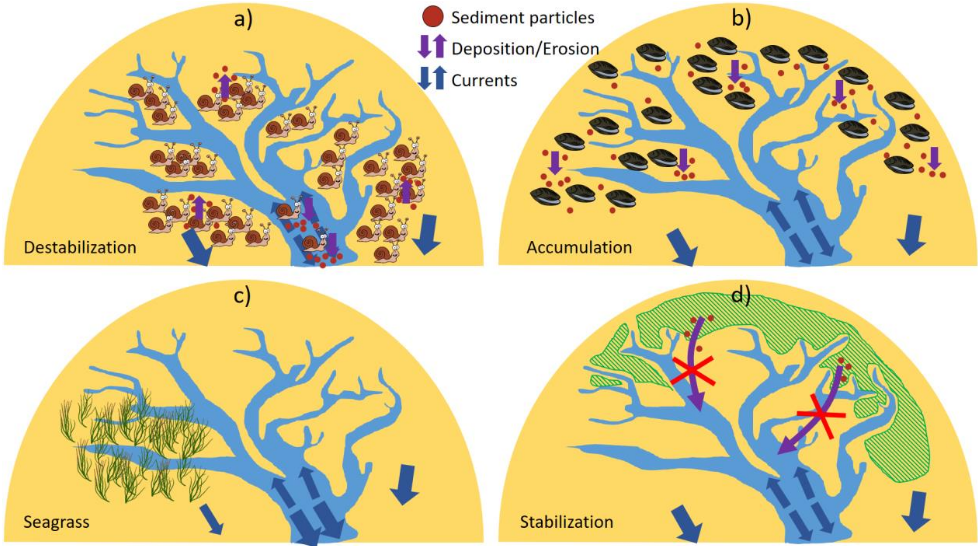

575 **Figure 10. Conceptual sketch of different effects of the four functional groups on sedimentation and hydrodynamics in tidal embayments: (a) destabilization in tidal flats caused by bioturbators, (b) accumulation caused by filter / suspension feeders, (c) modification of flooding / ebbing flows by seagrass meadows, and (d) sediment stabilization by MPB and reduced input to channels.**

6. Conclusions

We have presented an effort towards large-scale explanatory hydro-eco-morphodynamic modeling to explain
580 changes in both morphology and sediment composition observed in a real coastal system, thereby disentangling the impacts of biotic and abiotic drivers. The following conclusions are drawn from the study:

Benthos significantly reworks sediment, thereby mediating large-scale and long-term change of coastal morphology and seabed sediment properties well beyond their habitats. Compared to the scenarios which include only abiotic drivers, simulations with benthos included produced significantly improved results that are closer to
585 observation, and are able to explain some unique features in the historical change of morphology and sediment composition in the Jade Bay. The most impactful functional group regarding morphological change in the Jade Bay is bioturbators. The impact of bioturbators leads to prominent sediment accumulation in the main channels. Filter/suspension feeders mainly enhance sediment deposition on the tidal flats. Seagrass meadows modify the flows not only within or adjacent to the sites where they are located but also at a much larger scale beyond their
590 habitats, resulting in alternating erosion and deposition patterns in the main channels. Regarding the change of sediment composition in the Jade Bay, filter/suspension feeders have the strongest impact. The impact of filter/suspension feeders is mostly local, but this functional group is present over a vast part of the bay and thus jointly leads to a large-scale impact. By contrast, the impact of bioturbators, seagrass and stabilizers on sediment composition extends beyond their habitats. A combined effect of all functional groups leads to increased import
595 of sediment, especially mud, to the bay.

Our results further show that increasing model complexity does not necessarily lead to better model performance, especially when biotic drivers such as benthos is included. Including storm surges, which are precisely described by observational data, improves model performance. By contrast, adding seasonality in benthos impact through oversimplified parameterization decreases the general model performance. The reason is attributed to lack of

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observational data which can support a more accurate formulation of temporal changes of benthos behaviors. Therefore, the complexity of hydro-eco-morphodynamic models should be balanced at a certain level on which a tradeoff between complexity and accuracy can be obtained.

Coastal systems such as the Jade Bay have important socio-economic and ecological functions worldwide. Therefore, development of advanced numerical models which are able to explain and predict the states of coastal morphology and sediment properties and to develop measures for protection is of vital importance. To achieve this step, further effort in numerical modeling should explicitly include biotic drivers such as benthos and deepen the understanding on the interactions between different functional groups and between biota and abiotic drivers. In this sense, not only dedicated field measurements and lab experiments but also large-scale and long-term monitoring are indispensable.

Acknowledgements

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The benthic infauna dataset form 2009 was kindly provided by the Senckenberg am Meer.

Authors contribution

Peter Arlinghaus designed the study and performed numerical simulations. Wenyan Zhang designed and supervised the study. Peter Arlinghaus and Wenyan Zhang wrote the manuscript. Ingrid Kröncke provided the infauna dataset. All four authors were involved in manuscript revision.

Data statement

Publicly available datasets were analyzed in this study. Morphological data of the German Bight can be found at: https://datenrepository.baw.de/startseite. Sea level data at tide gauge station Wilhelmshaven can be found at: https://map.emodnet-physics.eu/platformpage/?platformid=9044&source=cp.

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