Benthos as a key driver of morphological evolution in coastal regions - exploration and explanation with numerical modeling

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Abstract

The study presented is about benthos and how it influences morphological evolution in coastal regions. Benthos is a group of organisms of different size and taxa that live in, on or in close proximity to the seabed. Directly directly or indirectly reworks the inhabited sediment which is termed bioturbation. Bioturbation affects the sediment in multiple ways and it is the aim of this study to unravel the impact of those small-scale processes on large-scale and long-term morphological evolution by using numerical models. A detailed review on benthic-morphodynamic modeling elucidates the processes involved in bioturbation, modeling approaches and limitations. Based on this an idealized tidal basin and a real tidal basin, namely Jade Bay are modeled. In the first study new insights in how species interactions may guide morphological evolution on basin scales are given. The second study highlights the key role of benthos in morphological development of Jade Bay and takes the next step toward predictive modeling in bio-morphodynamics.

Benthos impacts its environment in multiple ways. It induces particle fluxes within the sediment and at the sediment water interface. Sediment grains are transformed and their properties are modified. The own body, or assembled tubes and mounds protrude into the water and affect near bottom currents. During locomotion benthos and predominately microbenthoc excretes extracellular polymeric substances which coat the seafloor and changing its properties. Those processes can ultimately lead to changes in erosion, deposition and hydrodynamic conditions in the affected area and take place on small scales of cm and meters. However, benthos is very abundant especially in coastal regions and its biomass has increased over the last 50 years in the Wadden Sea. Many studies suggest that benthos is the most important driver determining sediment stability and that biota is a key driver in morphological evolution. However, it is largely unknown how the described small scale processes accumulate and ultimately are able to guide large-scale morphological evolution.

In the past 25 years many studies have tried to unravel the linkages between small-scale benthic activity and large-scale morphological development with the help of numerical models. They found that benthos can potentially change morphology in the range of several meters on the scale of decades and centuries. Benthos lead to sediment redistribution and was able trigger complex transport patterns. Fine grained sediment was shown to be specifically sensitive to benthic presence. However, all these models inherited great simplifications. One of those being the small number of implemented species and neglecting feedback mechanisms among them and the environment. Therefore, the impact of three main benthic functions (destabilization, stabilization and accumulation) on morphological evolution was investigated in an idealized tidal embayment setup. A species distribution model based on nutrient distribution was applied which enabled indirect species interaction. It was shown that all benthic functions have a profound impact on the evolution of the tidal basin. This regards the overall sediment budgets, suspended sediment concentrations, channel branching, channel deepening and tidal flat dynamics. It has been shown that these changes are due to feedback loops between the benthos and the morphological development of the basin. Benthos and basin exerted positive and negative control on each other by changed systems hydrodynamics, responsible for sediment redistribution and shifting the basin towards flood- or ebb-dominance. Feedback between different species arose due to habitat transformation. Accumulating and stabilizing species increased the growth and biomass for themselves and for destabilizing benthos. On the contrary destabilizers negatively controlled their own abundance and the abundance of the other species. This interplay lead to a balance showing more realistic biomass magnitude and channel features compared to the single species runs.

Despite the advances in numerical modeling, all current large scale models including benthos are limited to qualitative statement and yet, to my knowledge, no study has reach an explanatory stage so far. Three fundamental modeling stages can be distinguished. Explorative, explanatory and predictive models. In predictive models the processes guiding the system evolution are well known and are used to predict a future state. In contrast, the processes in explorative models are not well understood or cannot be quantified with the necessary accuracy. For this reason processes and parametrizations are scaled in a reasonable range leading to an ensemble of possible future scenarios in order to explore the possible scope of impact. This is the current stage of numerical benthic modeling. Explanatory models bridge the gap between predictive and explorative models. Here the final state of the system is well known and the processes are adjusted to each other in order to hindcast the final state most accurate. The purpose is to understand the impact and the balance between the involved processes leading to the final state.

To my knowledge this thesis is the first attempt of an explanatory large-scale benthic morphological modeling study. In a numerical simulation of Jade Bay, a tidal basin in the German Wadden Sea, three benthic functional groups and seagrass were implemented. An encompassing dataset of benthos occurrence combined with a state-of-the-art machine learning based species abundance model was used to estimate biomass and abundance in Jade Bay. Morphological changes between 2001 and 2009 were hindcasted. It was shown that benthos was the main driver of morphological change in Jade Bay. The morphological changes in Jade Bay could be much better depicted when benthos was included into the simulation. In the abiotic scenario, significant negative correlation with the characteristic feature of main channel accumulation was found, whereas in the biotic scenario this feature could be reproduced. Regarding morphological evolution destabilizing benthos was most impact. Regarding fine grained sediment redistribution accumulators and stabilizer were both of equal importance.

The results presented in this thesis, for the first time, show an explanatory benthic simulation, confirming model results on a basin scale. One more step toward predictive benthic models in the future could be made.

Zusammenfassung

In der vorgestellten Studie geht es um Benthos und seinen Einfluss auf die morphologische Entwicklung in Küstenregionen. Benthos bezeichnet eine Gruppe von Organismen unterschiedlicher Größe und Taxa, die im, auf oder in unmittelbarer Nähe zum Meeresbodens leben. Das besiedelte Sediment wird direkt oder indirekt umgestaltet, was als Bioturbation bezeichnet wird. Bioturbation wirkt sich auf verschiedene Weise auf das Sediment aus, und Ziel dieser Studie ist es, die Auswirkungen dieser kleinskaligen Prozesse auf die großskalige und langfristige morphologische Entwicklung zu entschlüsseln, mit Hilfe numerischer Modelle zu. In einem detailliertern Review über benthisch-morphodynamische Modelle werden die an der Bioturbation beteiligten Prozesse, deren Modellierungsansätze und Grenzen zusammengefasst. Auf dieser Grundlage werden eine idealisierte Meeresbucht und eine existierende Meeresbucht, nämlich der Jadebusen, modelliert. In der ersten Studie werden neue Erkenntnisse darüber gewonnen, wie Interaktionen zwischen verschiedenen Spezies morphologische Entwicklung in der Größenordnung von Meeresbuchten steuern können. In der zweiten Studie wird die Schlüsselrolle des Benthos bei der morphologischen Entwicklung des Jadebusens hervorgehoben und der nächste Schritt in Richtung prädiktiver Modellierung in der Biomorphodynamik unternommen.

Das Benthos beeinflusst seine Umwelt auf vielfältige Weise. Es induziert Partikelflüsse innerhalb des Sediments und an der Grenzfläche zwischen Sediment und Wasser. Sedimentkörner werden aufgebrochen, akkumuliert oder anderweitig umgewandelt was ihre Eigenschaften verändert. Der eigene Körper oder auch aufgebaute Röhren und Hügel ragen ins Wasser und beeinflussen bodennahe Strömungen. Während der Fortbewegung scheidet Benthos und vor allem Mikrobenthos extrazelluläre polymere Substanzen aus, die den Meeresboden überziehen und seine Eigenschaften verändern. Diese Prozesse können letztlich zu Veränderungen der Erosion, der Akkumulation und der hydrodynamischen Bedingungen in dem betroffenen Gebiet führen und spielen sich auf kleinen Skalen von Zentimetern und Metern ab. Das Benthos ist jedoch vor allem in Küstenregionen sehr abundant und seine Biomasse hat in den letzten 50 Jahren im Wattenmeer zugenommen. Viele Studien deuten darauf hin, dass das Benthos der wichtigste Faktor für die Stabilität der Sedimente ist und, dass Biota eine Schlüsselrolle bei der morphologischen Entwicklung spielt. Es ist jedoch weitgehend unbekannt, wie die beschriebenen kleinskaligen Prozesse zusammenspielen und letztlich großskalige morphologische Entwicklung steuern können.

In den letzten 25 Jahren haben viele Studien versucht die Zusammenhänge zwischen kleinräumiger benthischer Aktivität und großräumiger morphologischer Entwicklung mit Hilfe von numerischen Modellen zu entschlüsseln. Es wurde gezeigt, dass das Benthos potenziell die Morphologie in der Größenordnung von mehreren Metern auf einer Zeitskala von Jahrzehnten und Jahrhunderten verändern kann. Benthos führt zu einer Sedimentumverteilung und kann komplexe Transportmuster auslösen. Feinkörniges Sediment reagiert besonders empfindlich auf die Anwesenheit von Benthos. Alle bisherigen Modelle sind jedoch mit starken Vereinfachungen verbunden. Eine davon ist die geringe Anzahl der implementierten Spezies und die Vernachlässigung von Rückkopplungsmechanismen zwischen ihnen und der Umgebung. Daher wurden die Auswirkungen der drei wichtigsten benthischen Funktionen (Destabilisierung, Stabilisierung und Akkumulation) auf die morphologische Entwicklung in einer idealisierten Meeresbucht untersucht. Es wurde ein auf der Nährstoffverteilung basierendes Speziesverteilungsmodell angewandt, das indirekte Interaktionen ermöglicht. Es wurde gezeigt, dass alle benthischen Funktionen einen tiefgreifenden Einfluss auf die Entwicklung der Meeresbucht haben. Dies betrifft den Gesamtsedimenthaushalt, die Schwebstoffkonzentration, die Verzweigung der Strömungskanäle, deren Vertiefung und die Dynamik der Wattflächen. Es hat sich gezeigt, dass diese Veränderungen auf Rückkopplungsschleifen zwischen dem Benthos und der morphologischen Entwicklung der Meeresbucht zurückzuführen sind. Über

hydrodynamische Veränderungen konnten Benthos und Landschaft positive und negative Kontrolle aufeinander ausüben, die für die Umverteilung von Sedimenten und die Verschiebung der Meeresbuchtcharakteristik in Richtung Flut- oder Ebbe-Dominanz verantwortlich war. Rückkopplungen zwischen verschiedenen Spezies entstanden durch die erzeugte Veränderung des Lebensraums. Akkumulierende und stabilisierende Spezies erhöhten das Wachstum und die Biomasse von sich selbst und von destabilisierendem Benthos. Im Gegensatz dazu wirkten Destabilisierer eine negative Kontrolle auf die eigene Abundanz und auf die Abundanz der anderen Spezies aus. Dieses Zusammenspiel führte zu einem Gleichgewicht, das im Vergleich zu den Szenarien mit nur einer Spezies realistischere Biomasse und Strömungskanäle aufwies.

Trotz der Fortschritte bei der numerischen Modellierung beschränken sich alle derzeitigen großskaligen Modelle, die auch das Benthos mit einbeziehen, auf qualitative Aussagen, und meines Wissens hat bisher noch keine Studie ein erklärendes Stadium erreicht. Es lassen sich drei grundlegende Modellierungsstufen unterscheiden. Explorative, erklärende und prädiktive Modelle. Bei prädiktiven Modellen sind die Prozesse, die die Systementwicklung steuern, gut bekannt und werden zur Vorhersage eines zukünftigen Zustands verwendet. Im Gegensatz dazu sind die Prozesse in explorativen Modellen nicht gut verstanden oder können nicht mit der erforderlichen Genauigkeit quantifiziert werden. Aus diesem Grund werden Prozesse und Parametrisierungen in einem sinnvollen Bereich skaliert, was zu einem Ensemble möglicher Zukunftsszenarien führt, um den möglichen Umfang des Benthos Einflusses zu erkunden. In diesem Stadium der numerischen Benthosmodellierung befinden sich derzeitige Modelle. Erklärende Modelle schließen die Lücke zwischen prädiktiven und explorativen Modellen. Hier ist der Endzustand des Systems bekannt, und die Prozesse werden aufeinander abgestimmt, um den Endzustand möglichst genau abzubilden. Ziel ist es, die Auswirkungen und das Gleichgewicht zwischen den beteiligten Prozessen zu verstehen, die zum Endzustand führen.

Meines Wissens ist diese Arbeit der erste Versuch einer erklärenden großskaligen benthischen morphologischen Modellierungsstudie. In einer numerischen Simulation des Jadebusens, einer Meeresbucht im deutschen Wattenmeer, wurden drei funktionelle Benthos Gruppen und Seegras implementiert. Ein umfassender Datensatz über das Vorkommen von Benthos in Kombination mit einem modernen, auf maschinellem Lernen basierenden Modell zur Abundanzmodellierung von Arten wurde verwendet, um Biomasse und Abundanz im Jadebusen zu schätzen. Morphologische Veränderungen zwischen 2001 und 2009 wurden prognostiziert. Es zeigte sich, dass das Benthos der Haupttreiber der morphologischen Veränderungen im Jadebusen war. Die morphologischen Veränderungen im Jadebusen konnten viel besser widergespiegelt werden, wenn das Benthos in die Simulation einbezogen wurde. Im abiotischen Szenario wurde eine signifikante negative Korrelation zum charakteristischen Merkmal der Akkumulation im Hauptkanal festgestellt, während dieses Merkmal im biotischen Szenario korrekt reproduziert werden konnte. In Bezug auf die morphologische Entwicklung war das destabilisierende Benthos am einflussreichsten. Hinsichtlich der Umverteilung feinkörniger Sedimente waren Akkumulatoren und Stabilisatoren gleich wichtig.

Die in dieser Arbeit vorgestellten Ergebnisse zeigen zum ersten Mal eine erklärende Benthos-Simulation, die die Modellergebnisse in der Größenordnung einer Meeresbucht bestätigt. Damit konnte ein weiterer Schritt in Richtung prädiktiver Benthosmodelle in der Zukunft gemacht werden.

List of publications

1. Arlinghaus, P., Zhang, W., Wrede, A., Schrum, C., and Neumann, A. (2021). Impact of benthos on morphodynamics from a modeling perspective. Earth- Science Rev. 221. doi: 10.1016/j.earscirev.2021.103803

2. Arlinghaus, P., Zhang, W. and Schrum, C. (2022) Small-scale benthic faunal activities may lead to large-scale morphological change - A model based assessment. Front. Mar. Sci. 9:1011760. doi: 10.3389/fmars.2022.1011760

3. Arlinghaus, P., Schrum, C., Kröncke, I., and Zhang, W. (2024). Benthos as a key driver of morphological change in coastal regions, Earth Surf. Dynam., 12, 537–558, https://doi.org/10.5194/esurf-12-537-2024

Remarks on revised version

The version of the dissertation submitted on 31.01.2023 was revised. The present dissertation differs in the following points:

1. In the original version, there were five places that contained "[cite]", marking references that were forgotten to insert. The following 10 references have therefore been added to the Contextualization on page 1 and 2 retrospectively: Lalli and Parsons (1997), Jone et al. (1994), Hastings et al. (2007) Meysman et al. (2007), Kristensen et al. (2012), Friedrichs et al. (2009), Jimenez-Hornero et al. (2008), Stabili, L. (2019), Davies and Hawkins (1998), Coutinho et al. (2018).

2. The publication *Arlinghaus, P., Schrum, C., Kröncke, I., and Zhang, W. (2024). Benthos as a key driver of morphological change in coastal regions, Earth Surf. Dynam., 12, 537–558, https://doi.org/10.5194/esurf-12-537-2024* was submitted at the time of thesis submission but was published in 2024. The present dissertation contains the version published in 2024. References in the text of *Arlinghaus et al. (2023)* have therefore been changed to *Arlinghaus et al. (2024).*

3. The "Tag des Vollzugs der Promotion" (Date of completion of the doctorate) was previously the 31.01.2023. However, this is the day of thesis submission. The disputation was on the 20.06.2023. The Date of completion of the doctorate was therefore changed to 20.06.2023.

4. The page numbering was adjusted.

Contents

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1. Contextualization

The aim of this thesis is to understand the impact of benthos on large-scale morphological evolution. Benthos comprises a large group of animals living on, within or in very close proximity to the sea floor (Lalli and Parsons, 1997). It can be subdivided into microbenthos (<0.1mm) such as bacteria or diatoms, meiobenthos (0.1-1.0mm) such as the compepod and macrobenthos (>1mm) like the famous lug worm *Arenicola marina*. It is found in all world oceans from the deep sea to the continental shelf and coastal zones where it is especially abundant (Beukema and Dekker, 2020). Benthos takes part in many essential ecosystem functions such as biogeochemical cycling, carbon burial, food supply, oxygen regulation, sediment reworking and soil formation (Huettel et al., 2014; Middelburg, 2019; Lochte et al., 2011; Emerson and Hedges, 2003; Glud, 2008; Le Hir et al., 2007; Andersen and Pejrup, 2011).

This thesis consists of six parts including three research papers (part 2-4) that were written in the course of my PhD. Each paper is building up on the former and is subject to a certain research task (TX) with two subordinate research questions (TX.QY). The research task of the first paper is:

> **T1: Identify major functions of benthos in influencing coastal morphological evolution and comprise methods (results and challenges) which have been used to model this impact on large temporal and spatial scales.**

This paper is a review paper which provides the framework for the two subsequent studies and is in its essentials presented in this first chapter of contextualization. Research task T1 and the connected research questions which will finally lead up to research task 2 and 3 are presented and partially answered in this chapter. In chapter 5 the results of the three research papers will be discussed and the developed research questions be answered. Finally, in chapter 6, the relevance of this study for current and future research is discussed.

1.1 Benthos and its impact on sediment

Many benthic species are known as *ecosystem engineers* which modify the occupied habitat in a way which increases the availability of resources and by this increases the fitness for themselves or other species (Jone et al., 1994; Hastings et al., 2007). This is achieved in the so called bioturbation process. Bioturbation describes all ways in which benthos directly or indirectly reworks the inhabited sediment and changes its properties (Meysman et al., 2007; Kristensen et al., 2012). Ultimately, in the process of bioturbation 1. particle fluxes are induced within the sediment and at the sediment water interface 2. particle and grain size transformations take place 3. formed structures (allogenic) or the own body (autogenic) change the hydrodynamics and the transmission of hydrodynamic energy to the sea floor, and 4. coating the sediment floor with EPS (extracellular polymeric substances) (Arlinghaus et al., 2021). All four processes are interlinked and cannot completely be separated. Biomixing is one example for particle fluxes within the sediment. Due to foraging, burrowing and sheltering activities sediment particles are displaced which leads to a diffusion like mixing of different particles in the sediment column. Depending on the species the diplacement of particles can be local or non-local. For instance the sea urchin *Echinocardium cordatum* digs through the sediment in a bulldozing mode and displaces large amounts of particles. However the displacement is always in direct proximity and thus local. On the other hand upward or downward conveyers transport sediment either from the surface into sediment depth or the other way around which is called non-local mixing. This reworking process loosens up the sediment and increases its erodability which promotes sediment fluxes from the sea floor into the ambient water. Vice versa filter and suspension feeding species trap or imbibe particles from the seston in search for organic material which translates into fluxes from the water column to the sediment surface. Particles which are absorbed are either expelled as so called pseudo feces after the filtering process or are passed to the digestive tract and ultimately are excreted as fecal cast or

pellets and can form into a fluff layer. The cast which is created in this way differs in physical properties such as grain size, entrainment or settling velocity and biochemical properties like organic carbon content or microorganism colonization. Depending on where the fecal casts are deposited they can be prone to erosion and further entrainment or are buried and sheltered. New particle grains can also be formed from shell debris (Hyllberg et al., 1976). The shells of *gastropodae* or *bivalvia* species affects the close bottom currents. The same is true for mounds or tubes being assembled by benthos. At high densities all those structures protect the sediment bed from erosion, attenuates waves and trap particles due to the reduced current velocities. At low densities eddies form at the edge of those structures, releasing more turbulent kinetic energy to the sea floor and thus increasing erosion of ambient sediment (Jimenez-Hornero et al., 2008; Friedrichs et al., 2009). Finally many species, especially worms produce mucus which protects them and eases the movement through the sediment (Davies and Hawkins, 1998 ; Coutinho et al, 2018; Stabili, 2019). At small macrobenthic densities the mucus stabilizes the sediment (Cozzoli et al., 2019). Especially microphytobenthic (MPB) species produce mucus during locomotion in form of extracellular polymeric substances (EPS). Once the EPS is hardened the sediment stability is increased (Chen at al., 2017a). A complex mixture of MPB, EPS and bacteria, known as biofilm, can aggregate in patches covering large areas (Daggers et al., 2020).

A single species is able to bioturbate in multiple of the named ways. *Hediste diversicolor* for instance produces mucus while locomotion which potentially stabilizes the sediment. On the other hand it intensively reworks the sediment leading to destabilization. By the use of large branched galleries which are build, strong and rapid, non-local transport is possible. Further more, it may change between deposit feeding mode or filter feeding mode depending on which is more profitable. A new layer of complexity is added when interactions between species are added to this picture. If present in the same habitat one species may outcompete the other leading to a change in feeding type in order to find an ecological niche. Some species may improve the habitat conditions of other species such as mussel beds providing shelter to other macroinvertebrates or fecal pellets which are a preferable habitat for MPB. Vice versa grazing on biofilms will decrease its proliferation. The interaction between competition, predation, and physical drivers can create complex community patterns (Hart, 1992). Moreover other anthropogenic factors like pollution or even underwater noise influences bioturbation activity (Wang et al., 2022a). In view of this complexity the first research question arises:

T1.Q1: What are the main benthic functions to focus on to reduce complexity?

Many studies exist which describe the mentioned effects on small scales of cm to meters. Extensive reviews have been undertaken (Arlinghaus et al, 2021; Andersen and Pejrup, 2011; le Hir et al., 2007). Several data collections are available which are showing biomixing and irrigation rates (Lindqvist et al., 2016; Solan et al., 2019, bioturbation potentials (Queiros et al., 2013), erosion rates (Cozzoli et al., 2019), biodeposition and resuspension rates (Graf and Roseberg, 1996), filtration rate (Riisgard, 2001; Riisgard et al., 2014) fecal pellet production (Anderse and Perjup 20; Grant and Daborn, 1994; Troch et al., 2008) and biofilm stabilization rates (le Hir et al., 2007; Stal et al., 2010), documented for a variety of species and environments. Defaunation experiments show dramatic morphological and bio-chemical changes and even strong elevation differences, highlighting the significance of benthos (Volkenborn and Reise, 2006; Volkenborn et al., 2009; Montserrat et al., 2008). However little is known on how these local, small-scale effects, on a population level, interactively guide morphological processes on large spatial (basin and bigger) and temporal scales (decades to centuries).

Yet there are many indicators suggesting a strong large scale-impact. To name a few examples, a lower estimate of 21000 km³ of sediment are bioturbated worldwide (average global sea ice cover in 2022: 14300 km³ (PIOMAS)), suggesting an overarching role of benthos in morphological processes. Fecal pellet production can reach a level where up to 90% of the sediment in the uppermost centimetres are

composed of pellets (Andersen and Pejrup, 2011; Andersen, 2000; Austen et al., 1999). Filter feeders are potentially able to clear the entire water column within a few hours (Riisgard et al., 2007, Asmus and Asmus, 1991). And further more, the total deposited sediment in the Dutch Wadden Sea caused by only two species (*Cardium edule* and *Mytilus edulis*) accounts for at least 275000 tons of dry weight (Verwey, 1954) which is 10% of the average dredging and dumping in the dutch wadden sea (Nehls and Witte 2009). Finally, several studies suggest that the interaction and feedback between biota and geomorphology controls earth surface processes and landforms (Murray et al., 2008; Reinhardt et al., 2010). To elucidate the impact of benthos on morphological evolution the mentioned defaunation experiments could be repeated on e.g. a basin scale. However, this would be a very dangerous endeavor. A much more efficient and peaceful opportunity is to use numerical models. Recent advances in the development of numerical modeling have proven to be an efficient tool for studying coastal morphodynamics (Warner et al., 2008; Pinto et al., 2012; Deltares et al., 2020). Furthermore, increasing performance of processors according to Moore's law has enabled simulation capabilities on increasingly large areas of interest. One major advantage of numerical modeling is the full control over all input variables, which enables future prediction under changed environmental conditions such as sea level rise or climate change.

1.2 Benthos modeling and large scale impact

In the past 25 years less than 20 large scale morphological studies including benthos have been published (Arlinghaus et al., 2021). Summarizing these studies revealed that the main impact of benthos on morphology can be subdivided into erosion, sediment sensitivity and sediment redistribution:

Erosion

Numerical modeling studies including benthos indicate that while spatial patterns of erosion and deposition where mainly guided by hydrodynamics, the balance between these processes and their magnitude was strongly influenced by benthos (Wood and Widdows, 2002; Lumborg et al., 2006). Morphological changes caused by natural variations in benthic densities where shown to be in the same order of magnitude as changes caused by variations in physical drivers like tides (Wood and Widdows, 2002). Comparing bioturbated and non-bioturbated sediments, estimated sediment height changes were in the range of 5mm per tidal period (Lumborg et al., 2006), 2cm per month (Wood and Widdows, 2002), 20cm in half a year (Paarlberg et al., 2005), 5cm within seasons (Waeles, le Hir), a few millimeters in one year (Borsje et al., 2008), 40cm in 14 years (Orvain et al., 2012), a few meters within 50 years (Brückner et al., 2021) and within a few hundreds of years (Arlinghaus et al., 2022). The magnitude of deposition was changed up to a factor of 2 over different seasons when stabilizing MPB was added to the simulation (Wood and Widdows, 2002) while net erosion associated with interannual changes due to destabilizing benthos reached up to a factor if 5 (Wood and Widdows, 2002). Destabilizing benthos might in general facilitate the overall morphological drive of an inhabited system due to the considerate amounts of sediments which are mobilized leading to both higher peaks in deposition and erosion (Lumborg 2006; Arlinghaus et al., 2024). Suspended sediment concentration was locally increased by a factor of 2 under normal conditions and up to a factor of 3.5 during storm events (Sanford, 2008). Concentrations over large areas in the southern North Sea were estimated to reach 0.1 kg/m3 due to the presence of destabilizing macrobenthos (Nasermoaddeli et al., 2017) which is in the same range as the SSC peak values measured in the German Wadden Sea (Bartolomä et al., 2009).

Sediment sensitivity

All large scale modeling studies agree that fine-grained sediments are especially sensitive to benthic presence compared to sand or gravel classes. This has two reasons. First smaller particles are generally favored for ingestion compared to larger grains (Wheatcroft, 1992; Taghon, 2004; Gebhardt, 2019), since they are associated with organic material which can accumulate more effective on smaller particles because of the higher relative surface area (Burone et al., 2003). As a result muddy sediment are more intensively reworked. Higher bioturbation activities decreased the mud content compared to the non-biotrubated case by up to 20% (Knaapen et al., 2003) and even up to an order of magnitude in Paarlberg et al. (2005), Brückner et al. (2021) and Arlinghaus et al. (2022) due to an intensified biomixing between different sediment layers. The second reason is that finer grains usually have smaller sinking velocities which is why they travel longer distances before being deposited. This was evident in Nasermoaddeli et al. (2017) where fine silt classes (8-16 um) where strongly affected by destabilizing benthos compared to the almost unaffected sand classes.

Sediment redistribution

Benthic impact varies considerably over large areas especially in coastal shelf areas and facilitates redistribution of sediments. For most models the impact of benthos on morphology in general decreases offshore (Wood and Widdows, 2002; Wood and Widdows, 2003; Waeles et al., 2004; Le Hir et al., 2007; Orvain et al., 2012). Destabilizing benthos especially enhances erosion in intertidal areas (Brückner et al., 2021). Depending on the modeling domain different sediment transport patterns could be observed. Material which was predominately eroded around the mid-tide level by joint effects of destabilizers and physical forcing was transported and deposited in onshore direction. This deposition in shallow areas was facilitated by the stabilizing effect of MPB which was effective above mid-tide level (Wood and Widdows, 2002; Wood and Widdows ,2003; Waeles et al., 2004; Orvain et al., 2012). Transport of mobilized sediment in offshore direction could be observed in one study (Paarlberg et al., 2005). Brückner et al. (2021) showed that depending on community composition both import or export scenarios could be achieved. Despite these simple one directional transport pattern more complex transport pattern could also be facilitated by benthos with an active exchange of sediment between tidal flats and channels. During rough weather conditions and storm events sediment is eroded from the tidal flats and "stored" in the channels (Borsje et al., 2008). During calm conditions the sediment is transported back to the tidal flats. Overall net accumulation took place on the tidal flats and net erosion in the tidal channels. The latter might be facilitated by the fact that the effective impact of benthos is higher in hydrodynamic active regions even though the abundance might be very low due to less favorable living conditions in comparison to very habitable areas with low current velocities (Cozzoli, 2016). Not only is the benthic efficiency varying spatially with morphgical parameters but also the morphological impact varies over the inhabited domain and even reaches areas which are not inhabited with benthos. This can be easily comprehended when thinking of benthic mobilized sediment which is transported and deposited far beyond the inhabited zones (Borsje et al., 2008; Nasermoaddeli et al., 2017, Brückner et al., 2021). More complex linkages are also possible like benthic erosion changing the wave energy transmission in adjacent, unhabitated areas (Orvain et al., 2012).

Despite the advances in numerical modeling of benthos, the presented results are limited to qualitative statements and models inherit great simplifications. Including the second paper presented in this thesis only 20% of these studies apply 3-dimensional simulation of hydrodynamics and sediment

transport while the other 80% consist of 1D or 2D models. Usually only one or two species and respectively one or two species effects are considered at a time. Moreover model results are either not confirmed or not confirmed on a scale appropriate to the system size (table 2 in Arlinghaus et al., 2021). These shortcomings lead to the next research question:

T1.Q2: What are the current limitations of numerical benthic-morphological models?

The answer to this question is twofold and will lead to the development of the other research tasks and questions. The first sort of limitations are related to benthos modeling specifically, and the second to modeling in Earth-Sciences in general. Starting with the latter, the limitations are already implied in question T1.Q1. The high complexity of possible benthic processes and interactions make it impossible to combine all of those into one model while preserving a certain process accuracy. This *accuracy vs complexity problem* will more extensively be elaborated in the discussion section. However, one way for reducing model complexity is to use a functional group approach instead of a species level approach. A functional group describes a group of species which can involve different taxa and that impact its environment in a similar way and thus exert a similar effect on their environment. Functional groups can be defined from the standpoint of different distinguishing features among others the reworking mode of the sediment, feeding mode or species mobility (Kristensen et al., 2012, Lindqvist et al., 2016, Shull, 2001). Based on the modeling review paper (Arlinghaus et al., 2021) for the most fundamental functional groups we have decided for bio-stabilizers, bio-destabilizers and bio-depositers which were implemented in paper number two (Arlinghaus et al., 2022) with the following research task:

T2: Develop a numerical model to explore the potential long-term and large-scale impact of three main benthic functions and their interaction on morphodynamics.

For this purpose in the second paper an idealized tidal embayment setup was implemented. The geometry of this idealized embayment has been used in previous studies to investigate long term equilibrium behavior, tidal forcing, sea-level rise and the impact of mangroves (Marciano et al., 2005; Van Maanen et al., 2013a; Van Maanen et al., 2013b; Van Maanen et al., 2015; Zhang and Arlinghaus, 2022). In this paper however, it is the first time that the impact of benthos was incorporated in this setup, asking the research question:

T2.Q1: How and to what extent can benthic fauna modify embayment-scale coastal morphology?

In this study five different model scenarios were executed. One without any benthos, then one scenario with each of the three functional groups and one scenario with all functional groups together in one simulation. The aim was to understand the way and extent each of the functional groups modifies a coastal system on a tidal basin scale and how the different groups finally act together.

For the second sort of limitation (benthos modeling specific), again two major challenges can be distinguished which are related to process understanding on the one hand and data acquisition on the other. For instance, the impact of stabilizing biofilm on large-scale cohesive sediment dynamics is largely unquantified (Bastianon et al., 2022). The different stages of biofilm maturing, its penetration into depth, the grain induced propertiy changes and the many biotic and abiotic factors that influence its manifestation are poorly understood (Wal et al., 2010; Guarini et al., 2000; Chen et al., 2017a; Chen et al., 2017b; Andersen and Pejrup, 2011; Fang et al., 2017). It is for these reasons that the stabilization impact of biofilm is highly site specific and a reliable proxies does yet not exist (Riethmüller et al., 2000). Another important process is species interactions and interaction between species and their geo-morphological environment. Species interactions can lead to very complex and even counterintuitive behavior. For instance, two macrobenthic species, one slightly enhancing and one slightly decreasing microalgal cover, put together lead to a disappearance of algae (Boyer and Fong, 2005). Counteracting,

synergetic as well as no measureable effects were reported as results of interaction between ecosystem engineers (Passarelli et al., 2018). On large scales, so far only one modeling study has tried simulating such effects (Brückner et al., 2021). In this study ecosystem engineering determined habitat conditions and spatial species distribution. This was mediated by direct species interactions like grazing and competition and indirect feedback over eco-engineering of the habitat creating suitable area for co-existing species. The study highlighted that a combination of habitat suitability, species specific bioturbation and species interactions can guide large-scale morphological evolution. Several studies have suggested feedback and coevolution between landscape and ecosystem engineers as one of the important factors to understand geo-morphological evolution (Corenblit et al., 2011; Reihnardt et al., 2010; Murray et al., 2008). However, "*mathematical modeling of such systems is still in its infancy*" (Meadows et al., 2012). Tying on to these findings, the next research question was developed with the aim to reach puberty:

T2.Q2: How important is the role of species interaction in shaping morphological features?

This question aims to understand species-species and morphological feedback and to evaluate the importance of such feedback mechanisms. To answer this question, in the second paper a dynamic species distribution model was applied able to respond to system changes. This was achieved by implementing organic carbon with certain nutritional value, which would be imported from the open boundary with concentrations according to field measurements from the Wadden Sea. In short, deposited carbon increases the biomass and activity of bio-destabilizers and bio-stabilizers and suspended carbon likewise increases biomass and activity of bio-depositers. Inhabitet sediment will hence be bioturbated leading to sediment property changes which may lead to a redistribution of sediments and nutrients. In this way morphology and benthos distribution will dynamically adapt and excert a mutal feedback control on each other. To achieve a realistic species distribution however, it was necessary to incorporate flocculation processes depending on concentration and turbulence.

Finally, the remaining problem, putting limitations to benthos modeling is related to data acquisition. It can again be subdivided into parametrization data for benthic effects, species distribution data, and lastly morphological data for initialization and validation. The measurement setups inevitably contain errors which must be minimized. To generate parametrization data both laboratory and in situ experiments can be conducted. Reliable results are provided by in situ measurements, however the environmental parameters are not all accessible. On the other hand laboratory measurements have the advantage of control over all input and measurement parameters, but they come with scalability issues (Kleinhans et al., 2010). The challenge in acquiring benthos abundance data and morphological data are the large costs, effort, manpower and expert knowledge needed. Most often the data does not exist in the required spatial and temporal resolution. For this reason from the current large scale benthic-morphological models only two studies cover both spatial and temporal variations of benthos abundance by using a species distribution model. The other studies use constant estimated values, a distribution based on proxy parameters, or measurements for a limited amount of species which are extrapolated to large areas. Seasonal variations are only regarded by a small number of studies. Moreover large-scale studies either have no, or only a few data points in space or time to validate their results (table 2 in Arlinghaus et al., 2021).

It is for the reasons - high complexity, lack in process understanding, parametrization of benthic processes, species distribution and confirmation data - that all large-scale benthic-morphological studies are at an explorative stage, limited to qualitative statements (Arlinghaus et al., 2021). Following Desjardins et al. (2018) three fundamental modeling categories can be distinguished (Figure 1): Explorative, explanatory and predictive models. Essential elements of every numerical model are the definition of an initial stage (**I**), the implementation of internal processes (e.g. physical, biological (**P**) and the forcing of the system by external drivers (**E**) guiding the development towards a certain final state (**F**). In predictive models, **I**, **E** and **P** are well defined, and the aim is to ascertain the future state **F**. In explorative models external drivers, processes and their parameterization are tuned in a reasonable range, creating an ensemble of possible final states **F** to estimate and explore the impact range of benthos on morphological evolution. They are typically employed when the knowledge of **I, E** and **P** is limited. Lastly explanatory models bridge the gap between predictive and explorative models. In explanatory models, a certain final state is well known and **I, E** and/or **P** are tuned in order to hindcast the final state most accurate. The purpose of this model is to reconstruct the system evolution and to understand the relative importance of the involved processes contributing to reaching the final state.

To my knowledge, no large-scale bio-morphodynamic study has reached the explanatory stage yet. For this reason the next research task was undertaken to:
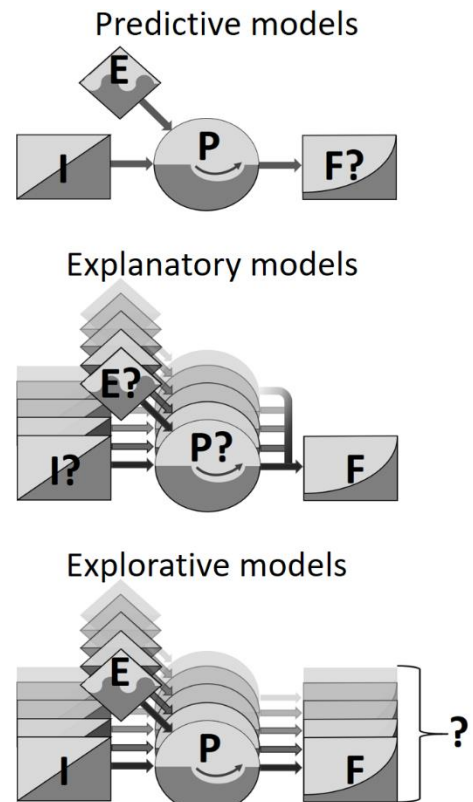

Figure 1. Conceptual image of the three general types of models. I and F indicate the initial and final state of the modeled system, respectively. P refers to the interacting processes and E represents external factors affecting the system. The question mark indicates the quantity in question (modified after Desjardins et al., 2018).

T3: Develop an explanatory model to hindcast recent morphological changes in the Jade Bay.

This task is processed in Arlinghaus et al. (2024). Morphological changes were hindcasted from 2001 to 2009 in Jade Bay including benthos. Reaching the explanatory modeling stage was possible because encompassing datasets for parametrization of benthic impact, benthos distribution and morphological data for model validation are available for the Jade Bay. Morphological data is compiled for the North Sea, provided by the *BAW* (*easyGSH files;* Sievers et al., 2020) and is available from 1996-2016. Based on the experience with tidal embayment setup (Arlinghaus et al., 2022) which has a similar shape as the Jade Bay, three major benthic functional groups were implemented plus the impact of sea grass which is present in Jade Bay. The impact of sea grass is available in the *submerged aquatic vegetation* (SAV) model of SCHISM (Zhang et al., 2016) which is based on Nepf and Vivoni (2000). The impact of bio-destabilizers was implemented based on measurements of Cozzoli et al. (2019) in a similar way as has been done in Brückner et al. (2021). The impact of bio-depositers was based on model and parametrization of the US Army Corps of Engineers (2000) and bio-stabilizers were regarded in a simplified manner as done in le Hir et al., (2007). The initialization of benthos is based on an encompassing dataset of benthos samples from 2009 (species, abundance and biomass) at 160 stations in the Jade Bay which was created by the Senckenberg Institute (Schückel and Kröncke, 2013).

To fill the unknown space between the stations with the respective species data an occurrence model can be used (Singer et al., 2016). However this study requires abundance and biomass values which is why a species abundance model (SAM) was developed, based on a random forest. Compared to species occurrence modeling, abundance modeling is a relatively unexplored field with best performing machine learning methods relying on decision trees (Waldock et al., 2021). Using the described data we were able to answer the question:

T3.Q1: Can including benthos to morphological models improve the model quality?

Different model setups were compared: abiotic, individual functional groups, and the combined effects of all functional groups. This gives us further insights into the roles of different species in creating certain features or morphological changes in Jade Bay. Then finally, the purpose of the explanatory model can be fulfilled, which is to explain:

T3.Q2: What is the impact of different functional groups on the morphological development in Jade Bay?

2. Impact of benthos on morphodynamics from a modeling perspective

This chapter contains a paper which was published in Earth Science Reviews as:

Impact of benthos on morphodynamics from a modeling perspective

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ABSTRACT

Benthic organisms and their bioturbation activities have a profound effect on a multitude of sediment properties. While many studies have already explored benthic impacts at small temporal and spatial scales, little is known on how the small-scale effects accumulate and interactively guide large-scale (km-scale) morphological evolution. Here we firstly summarize the most important processes of benthos affecting sediment stability and then explore existing biomorphodynamic modeling studies both at small- and large-scales. In general, microbenthos (body size <0.1 mm) mainly stabilizes sediments while meio- (0.1–1 mm) and macrobenthos (>1 mm) may stabilize or destabilize sediments. Among all types of sediment, fine-grained fraction (silt and clay) is most sensitive to the impact of benthos. Benthic organisms have the capability to mediate sediment transport and sedimentation patterns beyond their habitats on the long-term and over a large-scale. However, so far, numerical models evaluating benthic impact are limited to explorative studies and have not reached a stage where they can be used for predictive modeling. The barriers hindering a further development of biomorphodynamic models include not only limited understanding of fundamental biological/bio-physical processes affecting morphological development and dynamic feedback loops among them but also a shortage of data for model calibration and confirmation of simulation results. On the other hand, thriving for higher model complexity does not necessarily lead to better performance. Before conducting biomorphodynamic modeling, researchers must figure out which questions can be answered in a meaningful sense with simulation results that can be compared with observations and which level of modeling complexity is sufficient for that purpose.

1. Introduction

Benthos incorporates all animals living on or within the sea floor. Benthic communities contribute largely to marine biodiversity and sustain key functions and services such as biogeochemical cycling, carbon burial, food supply, oxygen regulation, sediment reworking and soil formation (Huettel et al., 2014; Haese, 2002; Middelburg, 2019; Lochte et al., 2011; Emerson and Hedges, 2003; Glud, 2008; Thorbergsdottir et al., 2004; Le Hir et al., 2007; Andersen and Pejrup, 2011). By modifying the inhabited sediment, benthic organisms are impacting morphodynamic evolution (Corenblit et al., 2011). Backer et al. (2010) proposed that benthos is the most important factor determining sediment stability in shallow waters such as tidal flats. Especially the so called engineer species strongly alter their environment towards an optimized fitness for themselves and even create new habitats for other

species (Jone et al., 1994; Hastings et al., 2007; Meadows et al., 2012). Morphodynamic and hydrodynamic conditions in turn are closely related to benthic abundance (Holzhauer et al., 2019; Shi et al., 2020). Understanding and quantifying the manifold linkages between benthos and morphodynamics is therefore a crucial task for studying not only sediment transport but also biogeochemical cycling (Zhang et al., 2019).

Benthic flora is well recognized to exert predominantly stabilizing effects of sediments. In coastal lands and marshes for instance plants are playing an antagonist role to erosion processes mediated by tides and wave action (Corenblit et al., 2011; Zhang et al., 2012; Zhang et al., 2015). The feedback between soil stabilization and sediment trapping due to flow attenuation by flora and resuspension by wind, waves and tides guide morphodynamic processes shaping the coastline (Marani et al., 2010; Murray et al., 2008). However, compared to benthic flora which has been extensively studied, the role of benthos in large-scale

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morphodynamics remains largely unexplored. In recent years the impact of micro-, meio- and macrobenthos has been increasingly incorporated into qualitative descriptions of coastal morphology (Murray et al., 2008; Reinhardt et al., 2010). Benthic fauna affects sediments in many different ways, including sediment being dug, swallowed, moved, paved, ventilated, etc. Such sediment reworking by benthos is generally unified in the expression of bioturbation (Meysman et al., 2007). Bioturbation behaviors are highly diverse and vary not only among species but also among individuals of the same species depending on the body size, age, and environmental factors such as depth, flow regime, nutrient availability and community structure (Andersen and Pejrup, 2011). Therefore, the impact of bioturbation on sediment stability can be manifold and it is a challenging task to incorporate it in deterministic models.

Le Hir et al. (2007) have summarized all potential impacts of bioturbation on sediments arising from different reworking activities of benthos into four distinct effects, namely, 1) change of sediment cohesion, 2) loosening up sediments due to locomotion of macrobenthos, 3) induction of matter fluxes between sediment and water column, and 4) changes in bottom roughness and flow field either by bare bodies or shells (autogenic structures) or by structures which are created during bioturbation including tubes, mounds and canopies (allogenic structures). The description of benthic activities and their impact is often focused on one or a few specific behaviors at small spatial and temporal scales. However, biological impacts on physical processes have been recognized to play a key role in landscape shaping and even local and short community disturbances can have potential impact on large spatial and temporal scales (Murray et al., 2008; Brückner et al., 2021). Further, each individual species may simultaneously exert several of the four above-mentioned effects on ambient sediment (Meadows et al., 2012). To predict landscape changes numerical models describing and differentiating the specific benthic activities and their impacts are required. Complexity of existing models falls into three categories. The first provides detailed descriptions for certain species of interest on specific subfields of morphodynamics (Willows, 1992; Borsje et al., 2008a; Borsje et al., 2009a; Borsje et al., 2014; Damveld et al., 2019), whereas the second uses simplified and general empirical relations linking benthos (e.g. abundance) to sediment stability parameters represented by critical shear stress for erosion and total erosion rate (Knaapen et al., 2003; Paarlberg et al., 2005; Lumborg et al., 2006; Borsje et al., 2007; Borsje et al., 2008b). The third category complements the second by deriving parameterization from species interaction and predicting suitable habitats and species distribution (Coco et al., 2006; Cozzoli, 2016; Brückner et al., 2021).It is important to identify the level of complexity best suited to address a certain ecosystem function in numerical modeling (French et al., 2015; Larsen et al., 2016). Generalized empirical models are easier to be implemented and applied on large-scale modeling than species-based models. However, they lack the level of refinement necessary to resolve the many-faceted species behavior as adaption to the environment. For application of species-based models to large-scale, so far we found at most four different species (Seifert et al., 2009) and three different possible impacts (Paarlberg et al., 2005; Lumborg et al., 2006) simultaneously included in numerical modeling. Although such models prove to better resolve individual species impact on sediment processes there is still no clear clue on the overall, combined impact of all coexisting species on a community level. To address this, a trend towards functional understanding of species and impact on general sediment processes becomes evident in recent years in morphodynamic modeling (Orvain, 2005; Orvain et al., 2012; Prooijen et al., 2011). Furthermore, most existing models just regard one-way control of benthos on morphodynamic, while Reinhardt et al. (2010) has however pointed out a mutual dependence between landforms and inhabiting species, which cannot be understood based on one side control but must rather be considered of as a co-evolution between a biological and a geomorphological system. Understanding the role of benthic bioturbation in these fundamental co-evolutionary processes is a major issue in biogeomorphodynamics and only until very recently a first step towards linking species interaction, habitat and morphological development has been undertaken (Brückner et al., 2021).

In this review, we try to build a clear link between small-scale bioturbation activities and large-scale morphodynamics. To do so we firstly provide an overview of bioturbation impact on small-scale morphodynamics. We then review existing modeling efforts including upscaling small-scale bioturbation to large scales (both spatially and temporally) and discuss their advantages and disadvantages. Based on the review, suggestions for future research needs are provided.

2. Bioturbation

Bioturbation summarizes all ways in which benthos affects the substratum where it inhabits (Kristensen et al., 2012). This includes processes of sediment reworking and bioirrigation (burrow ventilation of fluids and solutes). In this review we will focus on sediment reworking. Bioturbation mostly takes place in depth down to 20 cm (Holtmann et al., 1996) with higher bioturbator population densities in the upper sediment layers and lower in the deeper horizons (Touhami et al., 2018).

All bioturbators physically change their abiotic environment, either by building structures (allogenic engineering) or their activities (autogenic engineering). When in course of this the availability of resources for other species is modulated one speaks of an ecosystem engineer (Jone et al., 1994). Their impact on the environment is comparably high compared to other species and lasts beyond the lifetime of the engineers themselves (Hastings et al., 2007).

Bioturbating fauna can be classified by different criterions. In terms of size three major categories can be defined, namely microbenthos ($<$ 0.1 mm), micro and meiobenthos (0.1 mm - 1 mm) and macrobenthos ($>$1 mm) (Meysman et al., 2007). In terms of habitat it can be distinguished into epifauna inhabiting the sediment surface and infauna living below the surface within the sediment. Regarding sustenance benthos can be categorized into four major feeding types, namely suspension feeders filtering food from the ambient water (e.g. *Mytilus edulis, Crassostrea gigas*), deposit feeders feeding on living or dead deposited material, predators and parasites. Deposited material can be mixed into the sediment and is thus also available in deeper layers. Therefore, deposit feeders can be further distinguished in surface deposit feeders (e.g. *Hydrobia ulvae, Corophium volutator*) and subsurface deposit feeders (e.g. *Echinocardium cordatum, A. marina*). However, feeding type of some species may change depending on the in situ environmental conditions, e.g. switch between deposit feeding and suspension feeding. The complexity in trait expression (a trait is a distinguishing feature of an organism which can for example include the tolerance to environmental stressors, size or the feeding type) ultimately leads to the concept of functional groups of sediment reworking which is introduced in the following sections.

2.1. Small-scale and short-term impact

In this review, small scales refer to spatial scales from millimeters to meters and temporal scales from seconds to a few days. In contrast large scales span from months to decades in time and from a few kilometres (e. g. a tidal basin) up to an entire coastal shelf sea in space. In the following subchapters we will firstly review the most relevant small scale processes.

2.1.1. Biomixing

Sediment reworking by benthic animals comprises many different activities which are often driven by the need to forage and/or shelter (Meysman et al., 2007). All those activities may affect the sediment properties in diverse ways but all of them have in common that sediment grains get transported beyond chemical and compositional gradients. The sediment dislocation driven by benthic activity is called biomixing. To characterize benthic species contribution to biomixing they can be

divided into different reworking or functional groups. In general benthos can be classified into five major reworking modes (Kristensen et al., 2012), namely 1) upward conveyors which ingest food at depth and defecate at surface (e.g. *A. marina*) 2) downward conveyors which ingest food at surface and defecate at depth (e.g. *Cirriformia grandis*), 3) regenerators which constantly excavate burrows by tranporting sediment to the surface while ambient and suspended sediment is deposited in the burrow (*Neohelice granulata*, *Ocypode* spp.), 4) biodiffusors which constantly mix local sediments (e.g *Echinocardium cordatum*, *Uca* spp.) and 5) gallery diffusors such like burrow-dwelling organisms that conduct both diffusive mixing of local particles and rapid advective transport through galleries within the upper 10 to 30 cm of the sediment (e.g *Hediste diversicolor*). The different reworking modes are illustrated in Fig. 1. Depending on the reworking mode, the direction and rate of sediment bulk transport are different for each species (Lindqvist et al., 2016; Shull, 2001). Tracking the burial of chemical, radioactive or fluorescent tracers added to sediment surface is a common way of quantifying biomixing rates of those species (Lindqvist et al., 2016; Gebhardt, 2019). Biodiffusors for example randomly move sediment particles around on short distances of millimeters while conveying species can directly transport particles in the range of centimetres. Tracer profiles of the latter species are usually characterized by a subsurface peak in typical in depth of 10–15 cm (Kristensen et al., 2012). For regenerators or biodiffusors an initially surficial tracer will be distributed into deeper layers with decreasing concentration in a diffusion like manner. Especially large bioturbators have a stronger impact on biomixing compared to abundant but small bioturbators (Sandnes et al., 2000; Cozzoli et al., 2020). Wheatcroft et al. (1990) estimated a 10^4-fold increase in biomixing rates per individual (and a 20-fold increase per biomass unit) if animal body length is increased by 10 times. To exemplify the order of magnitude, the large bioturbator *Echinocardium cordatum* is able to displace massive amounts of sediment up to $0.02 \, \mathrm{m^3 m^{-2} d^{-1}}$ per individual which is 150 times the volume that it ingests. Given the reworking rate on a normal *Echinocardium* population level, Lohrer et al. (2005) concluded that the top 5 cm surface sediments are thoroughly reworked once every three days.

From a community-level perspective, a combined impact of various species may result in diffusion-like mixing of sediment particles (Rullkötter et al., 2003; Lecroart et al., 2010). In mathematical formulations based on advection- diffusion equations, the intensity of this mixing process is generally quantified by the diffusivity coefficient D_b and the related mixed layer depth L describing the length over which sediment mixing mostly occurs. Teal et al. (2008) have collected a considerable amount of studies calculating D_b ($n = 454$) and L ($n = 791$) and found a global mean of $D_b = 19.98 \pm 42.64 \, \mathrm{cm^2 a^{-1}}$ and $L = 5.75 \pm 5.67$ cm. Another earlier study estimated $L = 9.8 \pm 4.5$ cm (Boudreau, 1994). Based on the global mixed layer depth and conservative estimates of the ocean coverage area it was assumed that 20,700 $\mathrm{km^3}$ of sediments are bioturbated annually at a global scale (Teal et al., 2008).

Benthic reworking activity is mainly driven by food availability and temperature which lead to strong seasonal differences varying by one order of magnitude (Zhang and Wirtz, 2017; Gebhardt, 2019). Significant effects of seasonality, irrespectively of location, are supported by the large dataset collected by Teal et al. (2008) showing highest mixing rates D_b during summer and deepest mixing (L) in autumn. It is worth to note that the number of studies has been expanded to $n = 1281$ (for D_b) and $n = 1780$ (for L) during the past decade. Such dataset is now accessible under https://bioturbation.online/ (Solan et al., 2019).
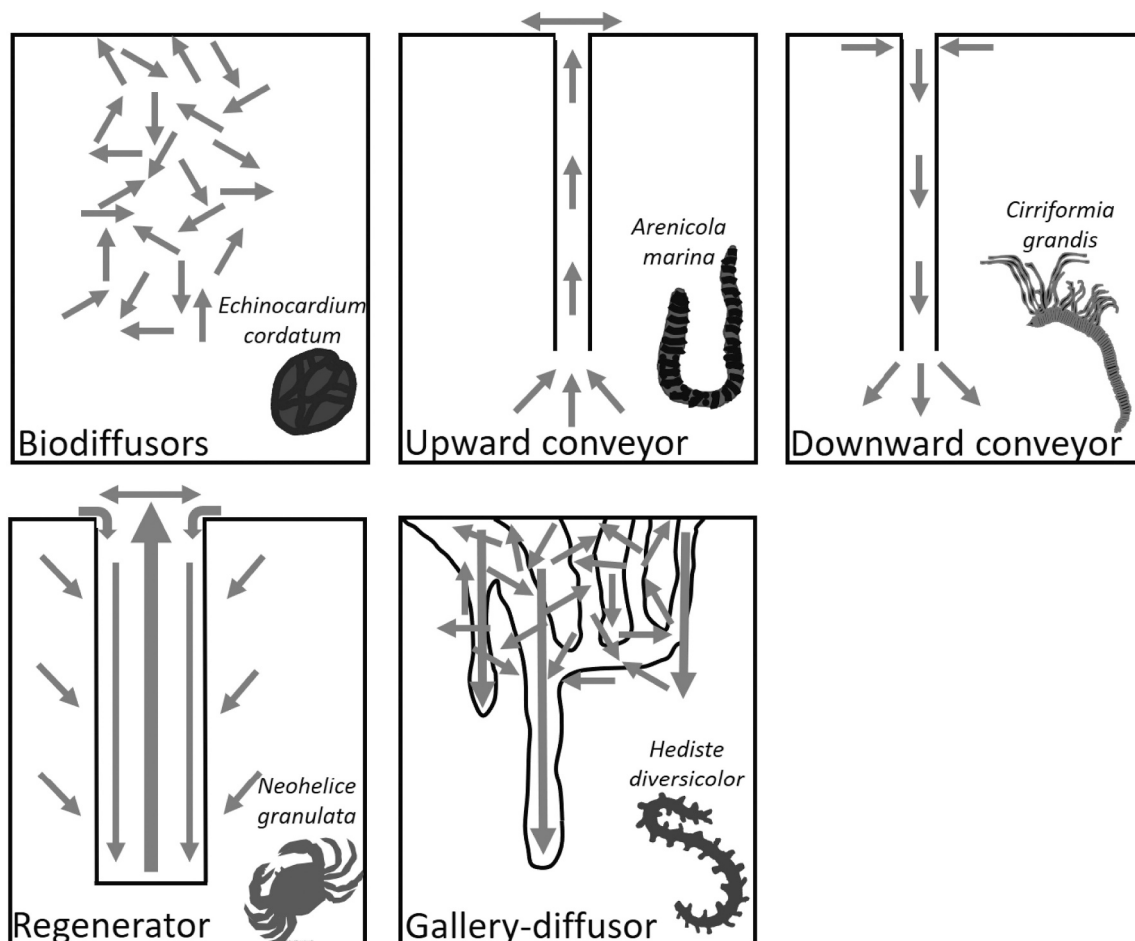

Fig. 1. Illustration of major functional modes of particle reworking with typical species (modified after Francois et al., 1997 and 2002).

Furthermore, D_b exhibits a generally decreasing trend towards deeper ocean (Henderson et al., 1999).

Persistent movement and particle mixing accompanied with the break up of biological and chemical bonds further loosen up sediments and prevent them from rapid consolidation. Although the combined effect of various mixing processes is difficult to quantify, these processes generally destabilize sediments and favor erosion/resuspension (Backer et al., 2010; Snelgrove, 2013). However, although typical animal behaviors have been described, certain movement patterns or biomixing rates have not been explicitly related to the amount of sediment destabilized or eroded. Until now we found only one numerical modeling study addressing destabilizing effect emerging from biomixing in simplified 1D plane (Sanford, 2008). Results of Sanford (2008) show that compared to non-bioturbated case in which an armoring sand layer emerges at the sediment surface and prevents strong erosion, bioturbation induces a mixing of sand grains and the critical shear stress for erosion into deeper sediment layers, making the surface less resistant to erosion. Suspended sediment was increased by a factor of two and during storm events even up to a factor of four when biomixing was included.

2.1.2. Particle flux mediation and grain transformation

Another important reworking activity is the processing of food which can be subdivided into ingestion, digestion and defecation. This has significant impact on particle flux and grain transformation. After ingesting and before passing into the digestive tract many species filter the swallowed sediment for particles of higher nutritional value. Regarding the particle size every species has its own preference but generally smaller particles are favored versus larger particles (Wheatcroft, 1992; Taghon, 2004; Gebhardt, 2019). Also low-density particles, which are associated with higher nutritional value and/or organic coatings are selected 10 to 100 times more often than other sediment particles (Smith et al., 1993). Similarly fine-grained particles with a higher relative surface area covered with organic material are selected more often than coarse particles (Burone et al., 2003). Those particles not selected may then be egested in form of pseudo faeces. Pseudo faeces are larger grain aggregates of smaller particles which are loosely bound by mucus substances. Together with sediment loosened up by superficial activities, pseudo faeces form a so-called fluff layer. In this case, sea bed erosion is featured by two distinct phases (Amos et al., 1997; Paterson and Black, 1999; Orvain et al., 2003). The first phase is named the supply-depending Type I erosion referring to erosion of to the fluff layer and the second Type II phase is the erosion of the subjacent sediment bed layer governed by excess shear stress.

Sediments which are passed on to the alimentary tract are digested and later deposited as faecal pellets, mounds or other kinds of faecal cast. Compared to pseudo faeces, faecal pellets constitute of more fine grains which are stronger bound leading to longer decay half-life. Usually faecal pellets are quite robust and long-lived and might even have been ascertained in geological records (Turner, 2002) but their resilience varies largely among different species (Austen, 1995, 1997).

If production rates are high and half-life is long enough, faecal and pseudo faecal pellets can fundamentally change physical properties and even comprise up to 80% or 90% of sediments in the upper sediment layers (Andersen and Pejrup, 2011; Andersen, 2000; Austen et al., 1999). Aggregations of pellets affect sediment properties mainly through enhanced particle sinking velocity and sediment cohesiveness (Forsberg et al., 2018). The larger size of faecal pellets compared to ambient sediments results in an increase in settling velocity by up to one or two orders of magnitude larger than the single pellet constituents (Andersen and Pejrup, 2011; Haven and Morales-Alamo, 1968). Because of smaller surface area, faeces are less cohesive than their fine grain constituents (Andersen and Pejrup, 2011). Their abundance may therefore lead to a gradual change of a muddy sea bed towards a less cohesive condition. This is accompanied by a general decrease in sediment stability and increased erosion rate (Andersen, 2001; Lanuru,

2004; Forsberg et al., 2018). However, opposite effects have also been observed where cohesive faecal pellets accumulate on a sandy bed (Le Hir et al., 2007). Faecal pellets produced by the amphipod *C. volutator* have been found to decrease erosion and increase critical shear stress for erosion (Grant and Daborn, 1994). Faecal pellets are not only a byproduct of nutrition and metabolism but they are also actively produced and used to achieve profitable environmental conditions (De Troch et al., 2008). For example, *Paramphiascella fulvofasciata* utilize faecal pellets as bait to, promote diatom growth on the pellets which are then re-ingested and expelled again for nourishment. A removal of faecal pellets from areas with abundant *P. fulvofasciata* subsequently increased faecal pellet production strongly, demonstrating an active role of benthos in terrain shaping (De Troch et al., 2008).

Production rate of faecal pellets strongly depends on species and available food but are not well documented. Le Hir et al. (2007) have collected observation data from different bivalvia, crustacea and polycheat worm species of different abundance in shallow water, and found particle mass transported to the sea bed surface ranging from 0.5 to 100 kg m^{-2}a^{-1}, comparable to the amount of sediment resuspended during a storm. Pseudo faeces are more frequently produced than faecal pellets and especially filter feeders contribute largely to pseudo faecal production. Hughes (1969) observed pseudofaeces production by *Scrobicularia plana* exceeding the defecation rate by 300 times.

Aside from the physical presence of faeces themselves, the uptake of sediment and deposition of faeces can further facilitate mixing, erosion and stratification processes (Cramer, 1991; Jone et al., 1994). Modeling results suggest that benthos is able to control the stratigraphic pattern (Jumars et al., 1981). Selective ingestion of certain sediment grains increases their mixing by the same order of magnitude of the selection preference. Depending on the depth of excretion in sediment, the selected grains are either burrowed and preserved or be exposed to erosion (Volkenborn et al., 2007). For example, sediments digested by *A. marina* are deposited as faecal mounds at the sediment surface where they are subject to erosion by bottom currents. This decreases the fine sediment compartment of the whole sediment bed. Under low hydrodynamic stresses, faeces decay and disaggreagte, leaving fine-grained sediment on the surface facilitating sediment stratification. *Echinocardium cordatum* is also known to select fine-grained particles more often than coarse ones. The former are then deposited in depth causing a heterogenous sediment distribution (Cramer, 1991). The formation of coarse shell debris layers was observed in depth of 20 cm (Hyllberg, 1976) and a doubling in grain size within the top five centimetres of the bed was observed with the presence of *A. marina* (Baumfalk, 1979). Jones and Jago (1993) found a distinct layer of coarse sand at the head level of *A. marina* in 70–100 mm depth. In the same study *Lanice conchilega* was shown to collect coarse sediment (predominately shell fragments) to pave its burrow walls which led to carbonate depletion in the surrounding sediment.

Among various functional groups, suspension feeders exert the most significant mediation on particle flux between the sediment-water interface. Suspension feeders use filtering organs to extract nutritious particles as well as phyto- and zooplankton from the water column. Various species are able to deploy suspension feeding such as polychaetes (e.g *H. diversicolor*), amphipods (e.g. *C. volutator*), bivalves (e.g. *Mytilus edulis*, *Cerastoderma edule*) and brittle stars (e. g. *Amphiura filiformis*). Suspension feeders can further be distinguished in 1) suspension feeders that are using their appendages or webs covered with mucus to stick organic matter from the passing water currents, and 2) filter feeders which actively inhale ambient fluid and filter nutrients from the water column (Lavaleye et al., 2018). With active suction the latter group is capable of utilizing the top few centimetres of the water column above the sediment. For example *M. edulis* can process the overlying water column with an effective feeding height of 3.5 cm and filtration height of 7 cm (Muschenheim and Newell, 1992). In shallow-water regions food resources can be depleted due to the impact of filter feeding. Under the combined influence of all ambient suspension feeders even

the entire water column can be cleared within a few hours (Riisgard et al., 2007, Asmus and Asmus, 1991). Suspended matter is cleared when water passes through the filtering organs, which leads to a decrease of turbidity. Part of the captured matter is ingested and the rest is rejected as pseudo faeces. To prevent re-ingestion, pseudo faeces often get expelled in a water jet created by filter feeders. Production rate of pseudo faeces is particularly high for filter feeders compared to other feeding types.

The high production of pseudo faeces and other faecal casts facilitates the incorporation of suspended material into the sediment bed (so-called biodeposition). Especially fine-grained materials with small sinking velocities, usually traveling long distances without deposition, can accumulate due to the presence of suspension feeders. The increase of fine-grained compartments typically changes the sediment bed towards more muddy and cohesive characteristics. Early estimates evaluated 275,000 tons of deposited dry weight per year in the Dutch Wadden Sea due to the presence of the bivalve species *Cardium edule* (36%) and by *Mytilus edulis* (64%) (Verwey, 1954). Large amount of biodeposits can raise the bed level. With the combined effect of high filtration rates and flow attenuation, mussel beds for instance trap sediment particles so effectively that they can elevate the ambient bed level by several decimeters within a few months, e.g. Dankers et al. (2004) reported a young mussel bed rising up by 30-40 cm in the first half year since its formation. Such control mechanisms on hydro- and morphodynamics and possible feedbacks between them are illustrated in Fig. 2.

2.1.3. Modification of sea bed roughness

Presence of macrobenthos may result in occurrence of roughness elements and structures on the seafloor. Autogenic structures are represented by a species own body or the shells encasing it, e.g. for bivalvia or gastropod species. Structures such as burrows, mounds, hollows, holes, tubes, tracks, faecel cast and pellets created by benthos are referred to as allogenic structures. Both autogenic and allogenic structures can potentially outlive their creator by many years (Hastings et al., 2007; Passarelli et al., 2018). Any morphological modification of the sea bed can influence the adjacent flow field. The resulting impact on the sediment can, depending on the flow regime, be either stabilization or destabilization. Sediment deposition can be facilitated due to mitigated flows and particles may be trapped in between structures. Large structures or agglomerates of smaller structures can shield the sea bed completely from currents and enhance wave attenuation (Donker et al.,

2013; Salvador de Paiva et al., 2018).

As an example of autogenic structures, *Lanice conchilega* creates tubes which protrude a few centimetres above the sea bed. At a certain tube density the dampened flow facilitates deposition especially of fine-grained sediment which elevates the inhabited area in the form of small mounds from 7.5 up to 80 cm (Alves et al., 2017; Borsje et al., 2014; Rabaut, 2009). Currents in between dense structures are too weak to induce sediment resuspension. Additionally, wave attenuation associated with roughness structures further more protect the sediment from erosion. Compared to the local effect of *Lanice conchilega*, mussel beds (Donker et al., 2013) and oyster beds (Salvador de Paiva et al., 2018) can shield the sea bed at a larger spatial scale and are thus object of ecosystem based coastal protection (Temmerman et al., 2013; Schotanus et al., 2020). Wave height may be significantly decreased over mussel or oyster beds (Borsje et al., 2011). Combined with their high filter feeding capacities, mussel beds are able to capture large amounts of sediment causing a rise of the mussel bed by several decimeters within half a year (Dankers et al., 2004). The ability of mussels to climb several centimetres per day ensures a rapid buildup of the mussel bed level (Widdows and Brinsley, 2002). Furthermore, an internal boundary layer (IBL) emerges that envelops mussel patches when subject to currents. Within that region longitudinal velocities are lower and turbulences are stronger compared to the ambient area (Nikora et al., 2002). The lower longitudinal velocities may have implications on sheltering the area in the direct vicinity which can be beneficial for other benthic species while increased turbulence would enhance vertical fluxes. The latter impacts deposition and resuspension of biodeposits which are rich in organic matter. With enhanced food availability combined with the refuge from predation, mussel beds also provide suitable habitat for other species (Nikora et al., 2002; Norkko et al., 2006).

Reidenbach et al. (2010) showed that compared to a completely smooth surface, turbulent mixing is enhanced on sand and cobble beds due to increased bottom bed roughness, leading to increased mass fluxes between sediment and water column by a factor of 1.3 and 7.5 for sand and cobble beds, respectively. The enhanced turbulent mixing is caused by turbulent vortices created downstream of the occurring obstacles and their size and location are dependent on the size and shape of the obstacles (Liao and Chen, 2015). For single objects this can result in an increase of destabilization by up to a factor of 20 (Amos et al., 2000). For an agglomerate of roughness objects however, depending on the density of the occurring structures the flow regime can either enhance or prevent erosion processes. In this regard one important parameter to
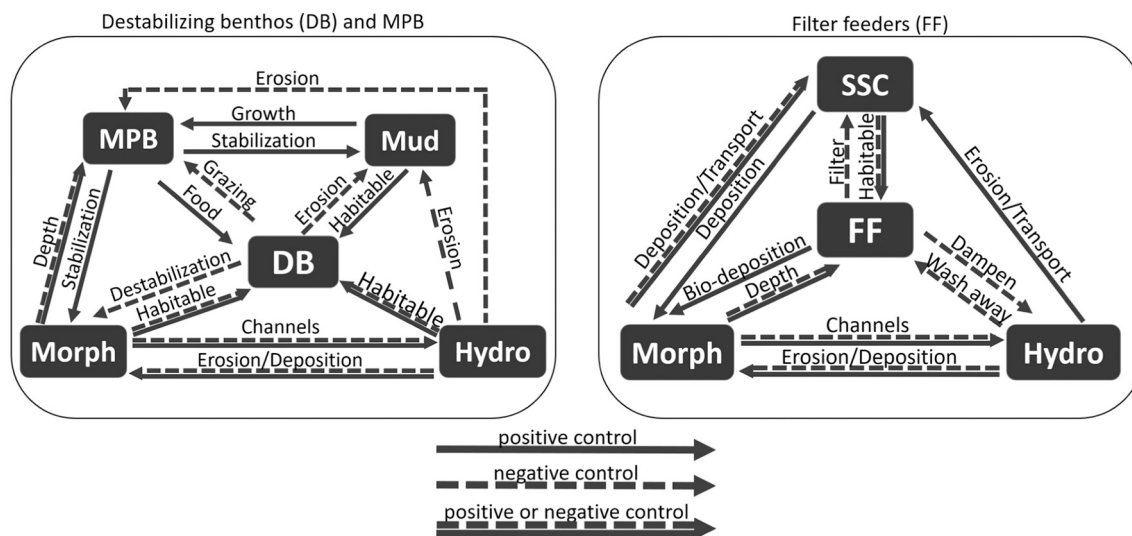

Fig. 2. Conceptual sketch of a few possible feedback mechanisms for three exemplary functional groups namely destabilizing benthos (DB), filter feeders (FF) and MPB with environmental variables such as hydrodynamics, morphology, mud content and SSC. Direct control, indirect control and feedbacks exist between benthos and environmental drivers.

characterize the flow regime surrounding the roughness structure is the aspect ratio H/W where H refers to the height and W is the width between occurring structures. Oke (1988) classified three different regimes in a 2D roughness geometry. Regime 1 refers to an isolated roughness flow ($H/W < 0.3$) for well separated roughness structures. Regime 2 is a wake interface flow ($H/W \approx 0.5$) with insufficient distance between the structures to reorganize the flow and Regime 3 represents a skimming flow regime ($H/W \approx 1$) (Jimenez-Hornero et al., 2008). Eddies adjoining the roughness element result in a release of turbulent energy into the sediment in the first two regimes while in the skimming flow regime there is only a weak intrusion into the gaps between the structures (Di Bernardino et al., 2015). In a flume study it was found that 8% surface coverage is a threshold for sediment stability (Nowell and Church, 1979). This general effect of destabilization in lower densities and stabilization in higher densities was shown for sea bed inhabited by mussels (Widdows and Brinsley, 2002) and for artificial tubes resembling worm tubes (Friedrichs et al., 2000). In a later study (Friedrichs et al., 2009) snail and mussel structures (including mounds, pits and cross-stream tracks) were tested, with the outcome of destabilizing effect at small densities and stabilizing effect at high densities. However, attention should be paid on roughness structures in situ. While the geometric laws defining the different flow regimes still apply, additional benthic activity can lead to stabilizing effects in destabilizing flow regimes and vice versa. For instance, tube worm studies come to contradictory results regarding tube related stabilization (Fager, 1964; Eckman et al., 1981). One possible explanation is mucus bindings created by animals, diatoms and bacteria (Eckman et al., 1981) whose growth is enhanced in the horseshoe vertex region surrounding tubes (Nowell and Jumars, 1984). Allogenic and autogenic structures generally facilitate growth of benthos. Close to tubes and galleries numbers of microphytobenthos are increased (Luckenbach, 1986). Furthermore, coarse and rough surfaces are much faster colonized by algae compared to smooth surfaces (Borsje et al., 2011).

2.1.4. Biofilm

Biofilm emerges due to benthic and especially microbenthic production. It is a complex mixture of the microorganisms themselves (around 10^9 microorganisms per cm^2 estimated in coastal sediments by Stal (2010) and extracellular polymeric substances (EPS) which are either produced during photosynthesis or excreted during locomotion of meio- and macrobenthos (Urban-Malinga, 2014). EPS are mucus substances consisting of mostly polysachharides and may also contain other components like lipids, proteins, lipposaccharides and nucleic acids (Hoagland et al., 1993; Hall-Stoodley and Stoodley, 2002; Bhaskar and Bhosle, 2008; Stal, 2010). It is produced by a large variety of species. Among them, there are tube building polycheata paving their tubes (S. Meadows et al., 2012), gastropos like *hydrobia ulvae* leaving EPS in their tracks, bacteria like cyanobacteria forming lamet like networks (Hoiczyk and Baumeister, 1998), and photoautotrophic microorganisms like diatoms (Stal, 2010). Two major functional types of EPS can be distinguished. Type 1 is the strong adhesive, stability enhancing b-EPS which is bound to the cell wall and Type 2 is the loosely bound colloidal c-EPS which is able to store large amounts of water (Chen et al., 2017a). Change of composition between these two types during biofilm maturing is relevant to sediment stabilization (Chen et al., 2017a). Biofilm composition is known to vary between bacterial and phytobenthic community structure (Van Colen et al., 2014). Diatoms for example can be divided into two groups, namely 1) sluggish or immobile episamic species, and 2) mobile epipelic species excreting EPS during locomotion (Andersen and Pejrup, 2011). Species from the latter group such as *Gyrosigma fasciola*, *Gyrosigma balticum*, or *Pleurosigma angulatum* produce more EPS than other species and therefore contribute largely to biofilm formation (Underwood and Smith, 1998). Both the community assemblage and the highly variable production of certain molecules depend on environmental factors such like light and nutrients, grain size, rhythms of vertical migration, interaction between microbial taxa

and hydrodynamic condition (Fang et al., 2017; Van Colen et al., 2014). Biofilm dynamically adapts to these environmental conditions and its characteristics change over hours depending on sunshine, tidal cycle and temperature (Guarini et al., 2000). On a seasonal scale biofilm growth is governed by the available light for photosynthesis, temperature, nutrients and wind speed (Wal et al., 2010). Both biomass and associated chl-α concentration peak in summer or early spring (Daggers et al., 2020; Staats et al., 2001; Stal, 2010; Chen et al., 2020). Biofilm typically aggregates in large patches. While the patch size is constant over the year the number of patches increases from winter to summer (Daggers et al., 2020). Although phytobenthos is bound to surface for photosynthesis, biofilm production is not solely a superficial phenomenon. It also occurs in sediment with decreasing concentration towards depth (Chen et al., 2017a; Chen et al., 2017b). There are multiple functions of biofilm for the organisms themselves. For instance, biofilm protects the organisms from UV rays, salinity changes, dewatering, predation, entrainment and serves as diffusion barrier against antibiotics and pollutants. It facilitates body movements and serves as carbon and energy storage (Le Hir et al., 2007; Stal, 2010). Enhanced cohesion facilitated by the excreted EPS, which protects the sediment and microbes from being washed away, is also one of the major functions of biofilm (Lageweg et al., 2017). The increase of critical shear stress due to EPS may be tide-dependent as mobile diatoms in tidal flats for instance are known to hide in sediment during submergence and move to the surface during low tide and produce EPS which increases the critical shear stress for erosion (Cartaxana et al., 2011; Stal, 2010). In the study by Stal (2010), critical shear stress was found to increase during a tidal period by a factor of 4–5 and return back to its initial value after inundation.

Biofilm impacts sediment in two ways. Due to the EPS which glues grains together, connecting them with threads or covering them with filaments, cohesive forces between the sediment particles are increased and the micro-morphology of the grains changes (Van Colen et al., 2014). A sketch of a biofilm is shown in Fig. 3. The increased cohesion results in a stabilization of the sediment and increased resistance to erosion and is considered the main effect of the biofilm on sediment stabilization (Dade et al., 1990; Underwood and Paterson, 1993; Yallop et al., 2000; Chen et al., 2020). A collection of different studies comparing the increase in sediment stabilization between bioturbated and non-bioturbated sediments indicates that a 2–10 fold increase in stabilization was found for non-cohesive sediments and 2–6 fold for cohesive sediments (Neumeier et al., 2006; Paterson, 1997). Stabilizing effects are especially significant in summer and usually disappear in winter (Chen et al., 2020). A positive feedback between the stabilization effect preventing erosion of fine-grained sediments and an enhanced growth of diatoms (see Fig. 2) on fine sediment grains (particularly silts)
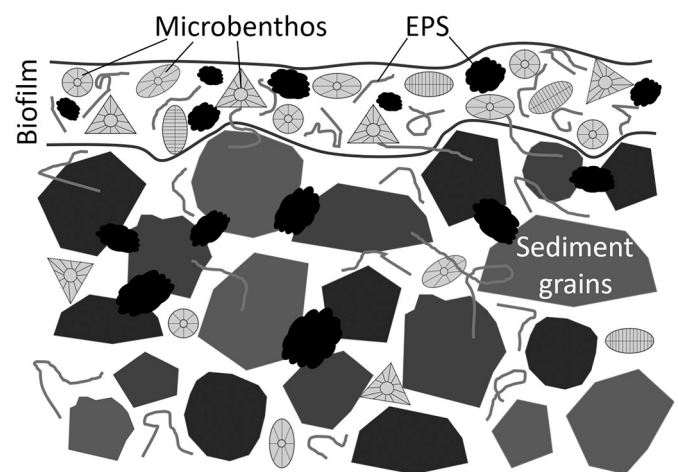

Fig. 3. A sketch of the biofilm with EPS excretion by microbenthos and EPS coatings.

facilitates the transition of non-cohesive sea bed towards cohesive sediment bed (van de Koppel et al., 2001; Chen et al., 2020). However, destabilizing effects have also been observed in developing phase of biofilm, while sediment is stabilized again when the biofilm is matured (Chen et al., 2017a; Chen et al., 2017b). This phenomenon may be due to a high amount of c-EPS and the associated increase in water content. It is worth to note here that a biofilm might never reach some kind of steady state as was shown by Fang et al. (2014) where the stabilization effect of biofilm decreased after seven weeks of maturing. Due to a vertical distribution of EPS the stabilization effect is not only limited to the uppermost sediment layer. It may lead to the emergence of an additional damped erosion phase in the transition between Type I (fluff layer erosion) and Type II (solid sediment layer) erosion which is termed hindered erosion (Chen et al., 2017a). After resuspension the eroded particles are still covered by mucus which influences subsequent deposition processes by altered sinking velocity and flocculation (Chen et al., 2017a; Chen et al., 2017b). For instance, floc size strongly increases when microbes are present (Shen et al., 2019). However, this effect remains largely unexplored.

Similar to microbenthos, mucus substances are excreted during locomotion of meio- and macrobenthos that stabilize the sea floor (Urban-Malinga, 2014). On the other hand meiobenthos grazes on diatoms and bacteria which destabilizes sediment. In general, meiobenthos facilitate biofilm growth due to selective feeding, mucus segregation and increasing food availability for lower trophic levels which is known as microbial gardening (Gerlach, 1978). Furthermore, same as for macrobenthos, sediment grains are reworked and structures are built by meiobenthos, like e.g. tubes which have the same effects as discussed before(Urban-Malinga, 2014).

3. Bioturbation modeling

In this section, a review of bioturbation modeling at small temporal and spatial scales is provided.

3.1. Biomixing

Mathematical models describing particle reworking and associated transport processes can be categorized into six different approaches according to Rullkötter et al. (2003), with each distinguished by a specific mechanistic criterion (local or non-local) and the mathematical form (discrete, semi-discrete and continuous). They all originate from the Chapman-Kolmogorov equation stating that the probability $p(i, n + 1)$ of finding a particle at an arbitrary lattice point i after $n + 1$ time steps Δt is given by:

$$p(i, n+1) = \sum_{j=1}^{n} a_{ij}\, p(j, m) \tag{1}$$

where a_{ij} is the transfer coefficient of one particle changing from grid point i to j which can also be expressed in a matrix form as $\mathbf{A} = [a_{ij}]$. The mechanistic criterion distinguishes the non-local transport models from the local transport models. Local models correspond to particle movement from one grid point to a neighbouring cell and non-local models from one grid point to any other grid point in the lattice. For local transport models the transfer coefficient matrix must be symmetric $\mathbf{A} = \mathbf{A^t}$. This symmetry criterion implies the directional randomness of the particle mixing process. The mathematical form can be discrete (in difference equations), semi-discrete (in ordinary differential equations) or continuous (in partial differential equations) for both local and non-local methods. A detailed description is given in Meysman et al. (2003). For both local and non-local models, the scale criterion and the frequency criterion must be satisfied:

$$\delta^m \ll \delta^t \tag{2}$$

$$\tau^m \ll \tau^t \tag{3}$$

where δ^m is the mixing length and δ^t is the tracer length, τ^m is the time between two tracer displacements caused by bioturbation and τ^t is the tracer life cycle. The scale criterion ensures that the sediment displacement given by δ^m is sufficiently small compared to δ^t (length over which the tracer concentration formulation and it's second order Taylor approximation deviate reasonably small). The frequency criterion ensures that bioturbation events occur sufficiently frequent compared to the life cycle of tracer being studied.

Out of the six approaches, the local biodiffusion model which assumes that bioturbation-induced particle mixing can be mathematically described as a Fickian diffusion process is commonly used to describe tracer profiles. The diffusion equation can be expressed as:

$$\frac{\partial C}{\partial t} = \frac{\partial}{\partial z}\left(D_b \frac{\partial C}{\partial z}\right) \tag{4}$$

where C is the tracer concentration, D_b is the diffusivity and z is the sediment depth. If D_b is not depth dependant, the above equation is simplified as:

$$\frac{\partial C}{\partial t} = D_b \frac{\partial^2 C}{\partial z^2} \tag{5}$$

A common way to quantify a species bioturbation activity is to derive D_b by fitting experimental tracer profiles in the biodiffusion model. An estimate $D_b = \frac{s^2}{2\Omega}$ was provided by Wheatcroft et al. (1990) where s resembles the distance of a particle step expressed as animal body length and Ω is the mean rest period of a particle. D_b in existing numerical models is termed differently, e.g. mixing intensity coefficient, bioturbation coefficient or simply biodiffusion coefficient and can be understood as the rate at which the variance of particle location changes over time. Biodiffusion models are commonly used but special care must be taken when and how to apply them and how to interpret the results. Sandnes et al. (2000) concluded that biodiffusion models generally underestimate biodiffusion rates. In a comprehensive study on mixing depth and intensity it was revealed that the chosen measuring method, rather than seasonality, has the strongest impact on variance of these quantities (Teal et al., 2008). Tracers with longer half-lives tend to result in lower D_b values and deeper mixing depth L than tracers with shorter half-lives. Sediment image analysis techniques consistently result in lower L values than tracer-based methods. It was concluded that the reason lies in a wrong use of short half-life tracers which violates inherent model criteria. This is supported by Rullkötter et al. (2003) confirming that many common reworking modes violate the assumptions of the biodiffusion model (scale and frequency criterion) particularly for short-lived tracers. Furthermore, by definition diffusion is a small-scale effect driven by spatial gradients but bioturbation on the other hand may lead to transport over chemical or compositional gradients. Besides, the assumption of a constant D_b, which is often applied in existing models, is problematic as abundance and total biomass decreases along with sediment depth (Jumars et al., 1981). Depth depending formulation should be preferred as shown by Boudreau (1997). The symmetry criterion is also violated for species with a preferred particle transport direction. Nevertheless, as reported by Rullkötter et al. (2003) and Lecroart et al. (2010), many down-core/in situ profiles of radioactive tracers suggest diffusive behavior for which biodiffusion models have proven to be valuable models. This contradiction is termed the bioduffusion paradox (Meysman et al., 2003; Rullkötter et al., 2003). To address this, Gebhardt (2019) suggested that differences between local and non-local models might often just reflect the time of observation. Given long time spans and an increasing number of displacement events, tracer peaks might be leveled out in a diffusion like manner especially on a community scale with a variety of different reworking types.

Sanford (2008) investigated the impact of biomixing on sediment erodibility by modeling. A detailed representation of the sedimentation/erosion, consolidation and sand armoring processes in a 1D plane with multiple sediment layers was implemented (Fig. 4a). As the bed mass of each layer is regarded constant during consolidation, the model used bed mass instead of depth as the vertical coordinate. For this reason the units of the bio-diffusion coefficient D_b were converted from (superscript z) into (superscript m):

$$D_b^m = D_b^z (\rho \bullet \phi)^2 \qquad (6)$$

where ρ is the sediment density and ϕ is the volume fraction of solute which varies over the bed layers. All layer variables such as E_r, τ_c, ϕ and sand fraction are resolved by a first-order diffusion equation between the bed layers. No specific species was considered but instead the potential impact of a constant biomixing of sediment representing a community level effect at long-term was explored. Results indicate that biomixing strongly enhances sediment erosion compared to the case without biomixing.

3.2. Particle flux mediation and grain transformation

The different fluxes and mixing rates of certain grains, accumulation in faecal pellets, disaggregation, erosion and particle burial can be implemented in transition matrix models (Jumars et al., 1981; Foster, 1985; Trauth, 1998; Shull, 2001). They belong to the non-local transport models and can directly be derived from the matrix representation of the transfer coefficient in the Chapman-Kolmogorov Eq. (1). Mechanisms representing the actual particle transport direction, quantity and depth are explicitly included in the model and can be expressed by the matrix coefficients for each individual group or species. Compared to bio-diffusion models, transition matrix models are better suited to resolve specific transport mechanisms on a species level such as characteristic subsurface tracer peaks which are not captured in diffusion models

(Shull, 2001). An advantage of transition matrix models is that sensitivity analysis can be easily performed to identify the dominant mixing processes contributing to particle burial, entrainment or accumulation. Matrix models therefore provide an explanatory tool for sediment stratification whose quality depends on measurements of sediment fluxes and transition probabilities.

Functional models that directly incorporate sediment flux terms, rates and directions by a few specific species have been incorporated in transport equations (Francois et al., 1997; Francois et al., 2002). These models also belong to the non-local transport models. For each functional group of e.g. biodiffusors, regenerators, upward-, downward-conveyors and gallery diffusors, an individual transport equation is set up which calculates transport rates between cells in a staggered grid (Francois et al., 1997; Francois et al., 2002). For example, the equation for the gallery diffusors consists of one term regarding biodiffusive mixing, one term for biotransport, one for physical mixing, one for output to the water column and one for tracer decay. With this approach a closer fit to experimental tracer profiles could be achieved compared to biodiffusion models. However, knowledge of species activities and associated variability is required, which hinders its application to a community level. A simplification was provided by Borsje et al. (2009b) who implemented a step function similar to an error function which increases fine particle selection probability in the upper part of the bioturbated area and decreases it by the same factor in the lower part in the presence of selective feeders (e.g. *E. cordatum*).

Biodeposition can be derived from the quantities of clearance rate (CR), filtration rate (FR), ingestion rate (IR) and absorption efficiency (AE) which are however not clearly discriminated in many studies (Fig. 5). CR describes the total volume of water passing through the animals filtering organ, which in case of mussels is the gill. It is usually measured as cleared volume per unit area and time which equals a velocity unit (Slavik et al., 2019). FR is the rate of removal of particles from the cleared water, IR is the rate of selection of the cleared particles for ingestion (others are rejected) and AE is the efficiency at which the
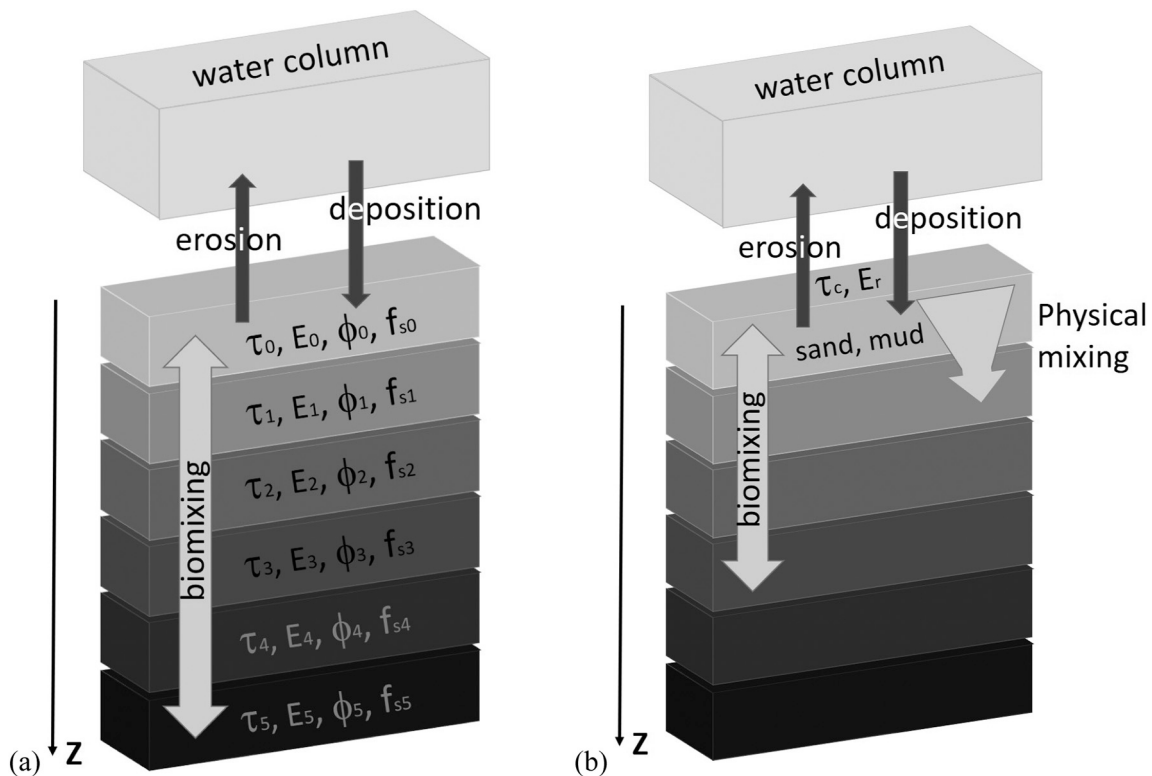

Fig. 4. Conceptual figure of bed layer and biomixing implementation in (a) Sanford (2008) and (b) Paarlberg et al. (2005). The former has been applied in small-scale modeling while latter has been used for large-scale modeling.
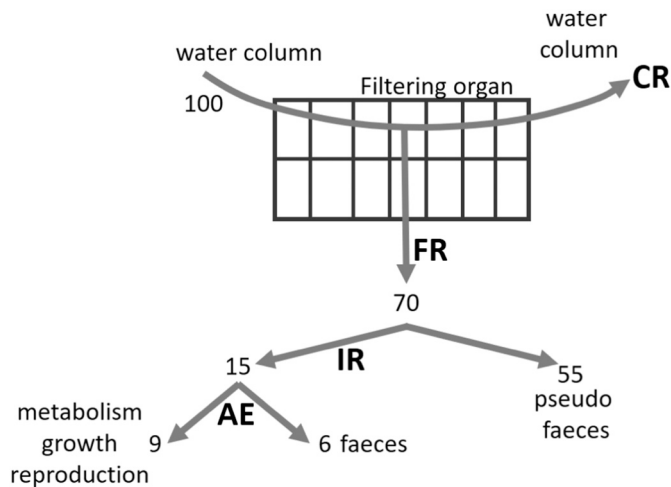
Fig. 5. Conceptual illustration of CR, FR, IR and AE with exemplary ratios of ingested suspended particles.

ingested particles are absorbed by the animal (Bayne et al., 1993, Slavik et al., 2019).

For individual mussels the clearance rate lies in the range of a few litres per day and is dependent on the mussel size, expressed as shell length L or mussel dry weight W. Larger individuals have higher CR in absolute values, but corresponding to body mass smaller individuals filter more effectively (Sylvester et al., 2005; Dankers et al., 1989). For *M. edulis* 2.0 $lh^{-1}ind^{-1}$ were measured for shell length around 40 mm (Van van Duren et al., 2006) and for 50 mm shells 3.84 $lh^{-1}ind^{-1}$ were derived (Kiørboe and Møhlenberg, 1981). Other studies found similar ranges (Widdows et al., 1979, Van Ledden, 2003). Allometric scale laws of type $CR(W) = aW^b$ and $CR(L) = cL^d$ with interpolation constants (a, b, c and d) are widely used to calculate the clearance rate. A list of allometric constants can be found in Riisgard (2001) and (Riisgard et al. (2014). The allometric exponents are in most studies in close range within the theoretical expected $b = 2/3$ and $d = 2$ (Riisgard et al., 2014). Due to seasonal mass variation shell length appears to be a more reliable proxy than dry weight and an empirical correction factor is used to adjust such under- and overestimation in CR(W) (Riisgard et al., 2014). Depending on food availability and temperature CR varies seasonally. CR increases with water temperature (Sylvester et al., 2005). Highest rates are normally measured in spring and summer, when diet quantity and quality are both high, and lowest rates in late autumn (November-December) characterized by low diet quantity and quality (Cranford and Hill, 1999; Marescaux et al., 2016). Also there seems to exist an upper limit of suspended particle mass which can be filtered. For low particle concentrations in the range of 10 mgl^{-1}, the clearance rate of *M. edulis* is highest with around 2 l/h and then linearly decreases with increasing particle concentration. At 300 mgl^{-1} the clearance rate is zero for most mussels (Widdows et al., 1979; Leeuwen et al., 2010). It is also worth to note that when estimating CR, the full clearance capacity of a filter feeder, which is rarely reached, and the actual exploitation of this capacity should be distinguished. It was shown that many studies greatly overestimate the in situ clearance rate by providing an optimal diet for the filter feeders while in contrast natural diet models appear to be more accurate (Cranford and Hill, 1999).

FR is highly dependent on the SSC in ambient water and the food concentration and lies in the order of magnitude of ca. 1% mussel biomass per hour (Bayne et al., 1993). In measurements from a 50 ha mussel farm for instance, 20% of the total biomass from a stream passing were consumed (Broekhuizen et al., 2002). For high particulate inorganic matter (PIM) to particulate organic matter (POM) ratios the filtration rate might decrease in order to select more organic material while for higher shares of POM the filtration rate can be increased.

Compared to the linear relation between CR and particle concentration, FR follows an upside down parabolic curve with a maximum of FR which decreases both for higher and lower particle concentrations (Widdows et al., 1979). According to measurements of (Widdows et al., 1979) this maximum shifts right (higher particle concentration) and up (higher FR) when the mussel shell size increases.

Utilization of organic material only refers to the amount of material being passed into the gut but doesn't mean it is all digested and fed into the metabolism. Therefore the absorption efficiency AE is used to describe the actually absorbed food (Cranford and Hargrave, 1994):

$$AE = \left(1 - \frac{TPM}{POM} \Big/ \frac{TFM}{FPOC}\right) \bullet 100 \qquad (7)$$

where TPM is the total particulate matter, TFM is the total faeces matter and FPOC is the fraction of POC in the faeces. According to the formulation Willows (1992) developed a mussel feeding model which expresses CR and the energy absorbed from the food depending on the gut residence time and a factor of so-called digestive investment representing the ability to enhance digestion efficiency at certain energy expenses. Changing AE is a common behavior for exploiter species which can decrease digestive investment and therefore AE during favorable nutritional conditions such like during phytoplankton bloom in order to optimally exploit resources and at minimal energy expenses (Bayne and Newell, 1983). By contrary, as adaption to low quantity and quality diets, metabolic losses to faeces were relatively low, indicating that the animals maximize energy gain by increasing the energy invested in digestive processes. AE gradually decreases at high diet quality and increases when quality is low.

Depending on the studied quantity, either CR, FR, IR or AE is used. In studies on consumption of the primary production by mussels (*Mytilus edulis*), FR was expressed as a power function of the phytoplankton carbon (C_{phy}) concentration in the ambient water (Slavik et al., 2019; Lemmen, 2018):

$$FR = 0.05 \bullet C_{phy}^{0.983} \qquad (8)$$

Based on this formulation, it was estimated that mussels consume 10% of the primary production in the entire southern North Sea and locally even up to 40% (Lemmen, 2018).

In studies addressing the transport of SSC, a constant value for CR (although termed as FR) was applied to calculate biodeposition (Forsberg et al., 2015; Forsberg et al., 2017; Leeuwen, 2008; Leeuwen et al., 2010).

$$m_{dep} = w_s \bullet SSC \qquad (9)$$

$$m_{bio} = CR \bullet SSC \qquad (10)$$

where m_{dep} is the deposited mass, w_s is the settling velocity, SSC refers to suspended sediment concentration, and m_{bio} is the mass of biodeposits. As the biodeposits mostly consists of loosely bound pseudofaeces the erosion rate E_r of biodeposits is increased (Leeuwen et al., 2010). It was shown that biodeposits mostly settled within a radius of around 400 m from a mussel bed (Forsberg et al., 2015). Artificially implemented mussel beds in two investigated coastal lagoons were able to reduce SSC between 5% and 22% (Forsberg et al., 2017).

Flume studies investigating the erosion of bioturbated fine-grained sediment usually demonstrate two distinct erosion phases. The first is supply limited erosion (type I) which is attributed to the presence of a fluffy and easily erodable layer, and the second phase (type II) refers to erosion of the subjacent and more resilient bed layer. Orvain et al. (2003) and Orvain (2005) investigated the formation and impact of a fluff layer emerging from the presence of two representative bioturbators *S. plana* and *H. ulvae* by modeling. As both bioturbators contribute to fluff layer emergence through different behaviors, their contribution to the mass of the fluff layer A was represented separately. *H. ulvae* contributes to fluff layer formation due to the tracks that are

formed during movement. Therefore the bioturbated mass A_{btb} is dependent on the track height h, fluff layer density ρ_{fluff} and the area covered by the fluff layer ϕ:

$$A_{btb} \sim h\rho_{fluff}\phi \sim h\rho_{fluff}(1 - e^{-n \cdot a \cdot t}) \qquad (11)$$

The area depends on the time that the sediment is bioturbated and the density n and movement speed a of the snails. In this approach sediment erosion is calculated separately but appears simultaneous in the fluff layer and the subjacent bed layer as illustrated in Fig. 6a. The fluff layer is featured by a specific critical shear stress for erosion τ_{fluff} which depends on a constant initial value and the amount of sediment which is left in the tracks after erosion of the fluff layer occurs.

The process of fluff layer formation is different for *S. plana*. This species is normally immobile and cannot move vertically. For this reason they can only reach and disturb ambient sediment which is within the siphon range, by which sediment is not only loosened but also the production of pseudofaeces contributes to fluff layer development. The associated mass of fluff layer A_t is therefore calculated based on the mass of expelled pseudofaeces PF and the frequency of ejection f:

$$A_t = t \cdot f \sum_{i=1}^{p} n_i \cdot PF_i \qquad (12)$$

Furthermore, the density of *S. plana* individuals (n_i) and the time for bioturbation (t) are important. They must be distinguished between individuals in different size classes (subscript i). For the expelled pseudofaecal mass an empirical exponential scale related to the shell size of the bivalves was used. .Unlike *H. ulvae* the impact of *S. plana* is not limited to the fluff layer formation alone, but also to the critical shear stress for erosion of the underlying bedlayer due to bioturbation (Table 1). The biophysical formula mentioned above were integrated into a 1DV model with multiple sediment layers.

A different approach to the fluff layer implementation was proposed by Prooijen et al. (2011). They re-analyzed the experimental results of Willows et al. (1998) and interpreted them in context of a fluff layer. Until then the two erosion phases had been considered by assuming a stratified bed with each sediment layer having a specific critical shear

Table 1

Erosion functions and scaling functions f and g for τ_c and E_r. M represents the macrobenthic density and C the chl-α concentration. X is the maximal tidal current velocity, u_c critical shear velocity and SCC the suspended sediment concentration. Other parameters represent empirical coefficients.

Erosion and scaling functions	Species	Publication
$SSC \sim 1 - \exp.(-M)$	mussel	Willows et al., (1998)
$SSC \sim 1 - \exp.(-M)$ $u_c(C) = 0.01 (0.4026C + 15.934)$	mussel, MPB	Wood and Widdows, 2002; Wood and Widdows, 2003
$f_s(C) = 0.2 + 0.014C + 1$ $f_d(M) = 0.00032 \ln(M^2) - 0.017 \ln(M) + 0.2$	mussel, MPB	Knaapen et al., 2003
$f_d(M) = 0.0016 \ln(M^2) - 0.085 \ln(M) + 1$ $f_s(C) = 0.07C + 1$ $g_d(M) = \dfrac{b_2\,\gamma}{(b_2 + \gamma b_1^M)}$ $g_s(C) = -0.018C + 1$	mussel, MPB	Paarlberg et al. (2005);
different but constant E_r and τ_c in different scenarios	snail, MPB	Lumborg et al. (2006)
$f_d(M), f_s(C), g_d(M)$ and $g_s(C)$ fitted from data. Function not given.	mussel, snail	Borsje et al. (2007); Borsje et al., 2008b
$\tau_c(M) = 0.35 \exp.(-0.0478 \cdot M) + 0.15$	mussel	Orvain et al., (2012)
$\Delta SSC = \dfrac{a_{bio}M^d X_{vel}^{bio}}{a_{contr}X_{vel}^{z.contr}}$ $f_d(M) = 0.0016 \ln^2(M) - 0.085 \ln(M) + 1$ $g_d(M) = \dfrac{b_2\gamma}{(b_2 + \gamma b_1^M)I}$	mussel, worm — mussel	Cozzoli, (2016) Nasermoaddeli et al., (2014); Nasermoaddeli et al., (2017)
E_r and τ_c are linearly scaled with biomass	worm, MPB, amphipod	Brückner et al., (2021)

stress for erosion as illustrated in Fig. 6a. By contrast, sediment layers which do not have a constant shear stress for erosion but rather a probability distribution of different thresholds were proposed by
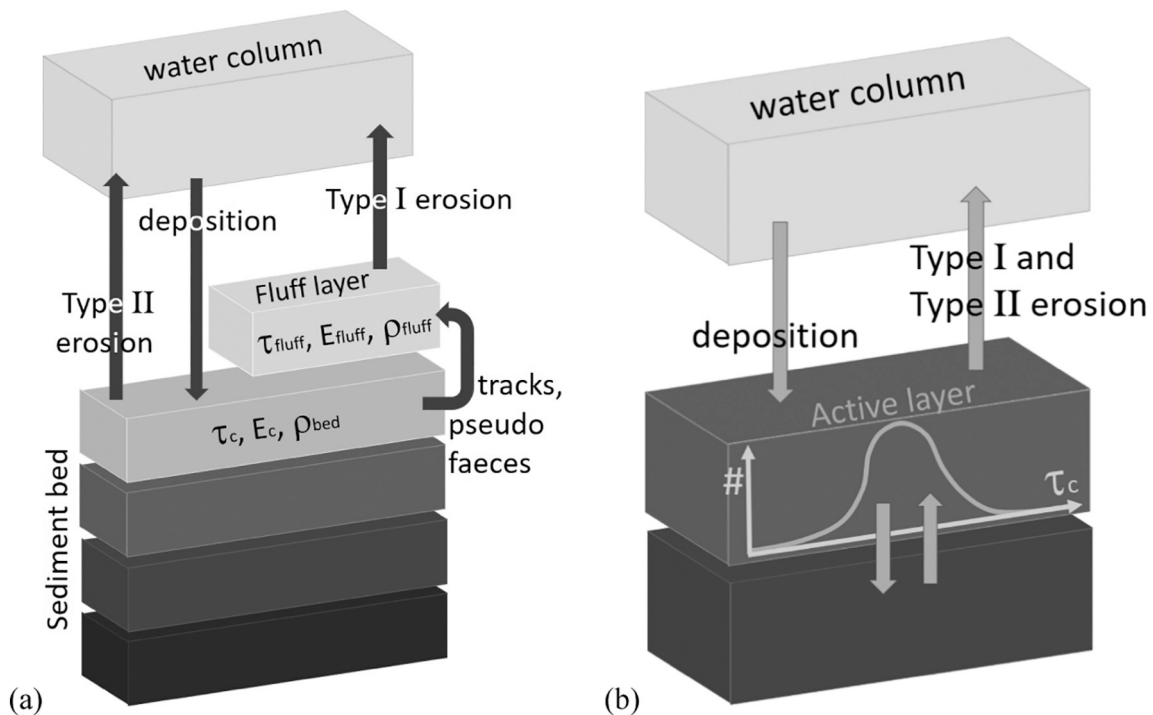

Fig. 6. (a) Conceptual figure of type I and type II erosion due to presence of fluff layer, redrawn after Orvain (2005). (b) Conceptual figure of layer implementation by Prooijen et al. (2011).

Prooijen et al. (2011). In this case several sediment layers with the uppermost layer being the so-called active layer were proposed. Only the active layer communicates with the pelagic part. As seen in Fig. 6, a fundamental difference to the fluff layer implementation proposed in Orvain et al. (2003) and Orvain (2005) is that the fluff layer and bed layer are not separated in Prooijen et al. (2011). Both layers are incorporated into the active layer. The probability distribution of the critical shear stress in the active layer can be described by a normal distribution depending on the density of species creating the fluff layer.

3.3. Modification of sea bed roughness

Sea bed modification by the presence of allogenic and autogenic structures can be described by the roughness length z_0 or the related quantity of bed roughness Ks or drag coefficient c_{100} which is linked to z_0 (Soulsby, 1997). Typical roughness length z_0 lies within the range of 1 mm (Forsberg et al., 2017). The roughness length determines bottom boundary fluid dynamics. Fluid velocity gradually approaches zero with decreasing distance to the sea bed and can be generally characterized by three different layers (Lorke and Macintyre, 2009). In the uppermost logarithmic layer flow velocity firstly decreases logarithmically towards the sea bed and then converts to linear progression in the so called viscous sublayer and finally ending up in the diffusive boundary layer. The latter two layers however are most pronounced above smooth surfaces and become virtually absent when the surface is hydrodynamically rough and turbulence induced by protruding grains disrupts the viscous layer (Friedrichs, 2004). Assuming an idealized case with uniform, steady flow and immobile bed material, the mean velocity in the near bed region can be approximated by a logarithmic profile known as the Karman-Prandtl equation:

$$u(z) = \frac{u_*}{\kappa} ln\left(\frac{z}{z_0}\right) \tag{13}$$

$$u_* = \sqrt{\frac{\tau_b}{\rho}} \tag{14}$$

where z denotes the height above the sea bed, κ is the Karman constant and u_* is the friction velocity which is again related to the bottom shear stress τ_b and the fluid density ρ. According to this equation the roughness length can be described as the height above the sea bed at which the flow speed becomes zero and it can be understood as the size of eddies generated by the bottom roughness (Vogel, 1994). On uneven surfaces covered by allogenic or autogenic structures, the logarithmic profile is raised by a certain height (z_1) so that the flow velocity becomes:

$$u(z) = \frac{u_*}{\kappa} ln\left(\frac{z + z_1}{z_0}\right) \tag{15}$$

The drag coefficient relates the flow speed at a specific elevation above the sea bed with the bed shear stress. To quantify the effect of autogenic and allogenic structures on flow field and sedimentation, their roughness length or drag coefficient is estimated. Depending on the investigated structure there are several empirical studies estimating the bottom roughness or the drag coefficient. Based on field measurements of different areas populated with horse mussels the drag coefficient could be formulated depending on the areal concentration λ (a dimensionless number relating the frontal area of roughness element and the average flat surface per element according to Wooding et al., 1973) of the horse mussels:

$$c_{100} = \left[\frac{\kappa}{ln(3000)/(g \cdot k \cdot} \lambda)\right]^2 \tag{16}$$

where k is the mussel height and g is an empirical constant with an approximate value of 100 (Green et al., 1998). Empirical functions from Friedrichs (2004) were used to scale bottom roughness with the abundance of four important bioturbators in the Baltic Sea by Bobertz et al.

(2009). z_0 of crustacean mounds can be calculated depending on their size (Rowden et al., 1998), and for mussels an empirical roughness length $z_0 = d_s/10$ with d_s being the height of shells can be used (Hofland, 2005). The latter was applied in a mussel bed study in Leeuwen et al. (2010). Furthermore, biodeposition due to filter feeding and subsequent change in bed properties were incorporated. An area of several hundred meters around the mussel bed was found subject to increased deposition elevating the sea bed level by a few centimetres within 60 days, meanwhile the implemented mussel bed elevated itself by around 10 cm (Leeuwen et al., 2010).

The effect of worm tubes were investigated in Borsje et al. (2014) in which L. conchilega tubes were simulated as solid cylindric piles affecting flow field and turbulent kinetic energy. Results show that decreased flow velocity within the 2×2 m^2 worm tube patches led to accretion of sediment reaching an equilibrium height of up to 70 cm after 160 days. The mound height was mainly controlled by tube length and population density. The mound effect spread over an area which is 20 times of the area where the worm tube patches are located. Without the presence of L. conchilega these mounds still persisted for more than 100 days illustrating how structures formed by benthic animals can surpass their spatial and temporal extent.

3.4. Biofilm

Several models and methods describing biofilm growth exist (Garrett et al., 2008; Lodhi, 2010; Wanner et al., 2006). But yet we found no model connecting growth with stability of sediments. Due to lack of mechanistic connection between biofilm and sediment stability, all existing modeling approaches rely on proxy methods to quantify the stabilizing effect of biofilm. The biostabilizing effect can be largely attributed to the amount of produced EPS and a linear relationship between them exists (Lageweg et al., 2017). The microbenthic communities producing EPS are known to correlate significantly with chl-α content and colloidal carbohydrate (Andersen and Pejrup, 2011). Besides EPS, chl-α and water content have been found to be the most reliable proxies for estimating sediment stability which were combined by Yallop et al. (2000) in the form:

$$\tau_c = -12 + 0.0179 C_{chl-\alpha} + 0.0311 C_{EPS} + 26.8 P_{water} \tag{17}$$

where τ_c is the critical shear stress for erosion and $C_{chl-\alpha}$, C_{EPS} and P_{water} represent concentration of chl-α and EPS and the water content relative to the volume, respectively. Since it is easier to measure chl-α content by spectral analysis than to measure the EPS content, chl-α is generally used as a proxy for microphythobenthic biomass and therewith as a proxy for EPS and sediment stability. Chl-α can also be detected using remote sensing, e.g. from satellite images. In a remote sensing study by Riethmüller et al. (1998), the general stabilizing effect associated with chl-α was confirmed and was found most pronounced in clayey mud but did not occur in sand or muddy sand sediments. Further, Riethmüller et al. (2000) found the relation between chl-α content and critical shear stress for erosion to be highly site specific and characterized by large variations within the same observed site. The complexity in the relationship between sediment stability and chl-α content remains to be addressed. In fact the processes involved in biostabilization are barely understood yet which is why all existing formulations rely on proxy parameters and are generally site specific. Riethmüller et al. (2000) concluded that erosion parameters cannot be derived solely from chl-α content and instead they promoted a more inclusive view incorporating benthos abundance, sediment surface reworking and microphythobenthic community assemblage. Regarding the latter factors, recent studies were able to predict microphythobenthic biomass and community assemblage from air-borne observations based on hyperspectral models and laboratory measurements of various microphythobenthic species (Launeau et al., 2018). Studies to this end may guide the path into a comprehensive understanding of biofilm stabilization effects.

4. Large-scale morphodynamic modeling

While benthic activities have been extensively investigated at small scales, extrapolation and upscaling of benthos impact to large spatial and temporal scales have been tackled by only a few researchers so far and are thus still in the fledgling stage. We found less than 20 numerical modeling studies in the past two decades explicitly addressing the impact of benthos on sediment transport processes and morphodynamics at scales larger than $\mathcal{O}(1\ km)$ (Table 2). The impact of benthic activity can be included in large-scale models in two ways: 1) empirical parameterization of impact of certain species by simplified relationships, and 2) process-based models resolving the impact of functional groups or community in a mechanistic manner. All different benthic effects are expressed in terms of critical erosion threshold, erosion rate and particle settling velocity. To provide a comprehensive overview of large-scale modeling, this section is structured into three parts. The first two subsections (4.1 and 4.2) introduce the two types of models, respectively. Main outcomes of model application are then introduced in Section 4.3.

4.1. Empirical parameterization models

Empirical parameterization models often rely on field survey or flume experiments to obtain empirical relationships between certain species of interest and the resulting impact on sediment transport. These formulations usually represent simplified relationships based on proxy methods to link the species abundance with some key parameters (e.g. sea bed roughness, critical shear stress for sediment resuspension). The simplicity of such approach allows a straightforward implementation of these models in 2D or 3D space for large area coverage.

4.1.1. Sediment stability

Most parameterizations of sediment stability (i.e. stabilization or destabilization) are built on the assumption that macrobenthos solely destabilizes sediment and the extent is proportional to the abundance or density of the species, while microphytobenthos (MPB) solely stabilizes sediment and the extent is proportional to the chl-α content which serves as a proxy for MPB biomass.

The first study to investigate benthic impact on large-scale sediment transport was done by Willows et al. (1998) who incorporated the effect of destabilizing mussels on SSC in a 1D cross-shore model. For model calibration mussels were placed into a flume and SSC was measured. The feeding area and sediment which is disturbed is limited to the siphon radius of the bivalves. At high densities where feeding areas of individuals overlap, the area of disturbed sediment does not increase proportionally to the number of individuals. This is reflected in the exponential relationship between *M. balthica* density (represented by M) and SSC reaching a saturation for large M (Table 1). In follow-up studies the model was extended to include morphological analysis with bed level changes (Wood and Widdows, 2002; Wood and Widdows, 2003). An empirical formulation relating *M. balthica* density to sediment grain size and bed height was applied. In addition, stabilization induced by microphytobenthic biofilm was included by assuming a constant chl-α concentration over the tidal basin and a rapid decrease below the mid tide level. The critical velocity for erosion was linearly linked to chl-α concentration in sediments.

Instead of linking SSC and benthos which requires measurements at different benthic densities and under different flow conditions, later studies almost exclusively rely the expression of critical shear stress for erosion τ_c and the erosion rate E_r on benthic density. In this context, Knaapen et al. (2003) introduced a simple concept assuming that every biological effect can be parameterized independently and expressed as a scaling factor f or g for the erosion parameters:

$$\tau_c(M, C) = \tau_c^0 \cdot f_d(M) \cdot f_s(C) \tag{18}$$

$$E_r(M, C) = E_r^0 \cdot g_d(M) \cdot g_s(C) \tag{19}$$

where the superscript 0 denotes the value of the critical erosion threshold and the erosion rate without bioturbation. These parameters are scaled by both a destabilizing function (with subscript d) depending on the macrobenthic density M and a stabilizing function (with subscript s) depending on the chl-α concentration C. The respective scaling functions are listed in Table 1. Paarlberg et al. (2005) used the same

Table 2

Models relevant for large scale morphodynamic changes induced by benthos. Abbreviations: dest = destabilization, stab = stabilization, fluff = fluff layer, pellets = pelletization, mix = biomixing, rough = bottom roughness, x = space, t = time.

Size	Time	Model	Environment	Number of species	Modeled process	Species distribution	Confirmation	References
$\mathcal{O}(10^0 km)$	$\mathcal{O}(10^0 d)$	1DH	Tidal flat	1	dest.	x, t: const	flume	Willows et al., 1998
$\mathcal{O}(10^0 km)$	$\mathcal{O}(10^0, 10^1 d)$	1DH	Tidal flat	2	dest., stab.	x: proxy t: const	x: one point t: few points	Wood and Widdows, 2002
$\mathcal{O}(10^0 km)$	$\mathcal{O}(10^0, 10^2 d)$	1DH	Tidal flat	2	dest., stab.	x: proxy t: const	no	Wood and Widdows, 2003
–	$\mathcal{O}(10^2 d)$	1DV	Tidal flat	2	dest., stab.	x: const, t: measured	x: three points t: few points	Knaapen et al., 2003
$\mathcal{O}(10^1 km)$	$\mathcal{O}(10^3 d)$	1DH & 1DV	Tidal flat	2	stab.	x: const t: increase summer	no	Waeles et al., 2004, Le Hir et al., 2007
$\mathcal{O}(10^1 km^2)$	$\mathcal{O}(10^2 d)$	3D & 1DV	Estuary	2	dest., stab., mix	x, t: const	no	Paarlberg et al., 2005
$\mathcal{O}(10^2 km^2)$	$\mathcal{O}(10^1 d)$	2DH & 1DV	Tidal flat	2	dest., stab., pellets	x, t: const	x: two points t: time series	Lumborg et al., 2006
$\mathcal{O}(10^3 km^2)$	$\mathcal{O}(10^2 d)$	2DH & 1DV	Shelf	3	dest., stab.	x, t: measured	x: several points t: few points	Borsje et al., 2007, Borsje et al., 2008b
$\mathcal{O}(10^4 km)$	$\mathcal{O}(10^1 d)$	3D	Shelf	4	rough	x: measured, proxy t: const	no	Bobertz et al., 2009; Seifert et al., 2009
$\mathcal{O}(10^1 km)$	$\mathcal{O}(10^3 d)$	1DH & 1DV	Tidal flat	2	dest., fluff, pellets	x: measured, t: sinus	flume	Orvain et al., 2012
$\mathcal{O}(10^2 km^2)$	$\mathcal{O}(10^3 d)$	2DH	Estuary	2	dest., stab.	x, t: species distribution model	no	Cozzoli, 2016
$\mathcal{O}(10^5 km^2)$	$\mathcal{O}(10^2 d)$	3D	Shelf	1	dest.	x: measured, interpolated, t: const	x: large area t: time series	Nasermoaddeli et al., 2017
$\mathcal{O}(10^2 km^2)$	$\mathcal{O}(10^0 d)$	2DH	Estuary	1	dest.	x: measured, t: const	no	Angeletti et al., 2018
$\mathcal{O}(10^2 km^2)$	$\mathcal{O}(10^4 d)$	2DH	Estuary	3	dest., stab.	x, t: species distribution model	no	Brückner et al., 2021

approach as Knaapen et al. (2003) and further added the erosion rate E_r to the parameters influenced by bioturbation. Besides implementation of erosion parameters, a biomixing coefficient was additionally applied. It was also the first effort to implement benthos impact on sediment transport in a 3D hydrodynamic model. Borsje et al. (2007), Borsje et al. (2008b), and Nasermoaddeli et al. (2017) applied the same scaling function approach but at a much larger scale than previous models. In the former two studies, temporal and spatial variations of benthos based on measurements were introduced for the first time. Compared to the two earlier studies, Nasermoaddeli et al. (2017) laid more emphasis on the sediment composition and resuspension over a large spatial scale covering the southern North Sea. Three different sediment fractions, namely very fine, fine and coarse sediments were implemented with size-dependant erosion and settling parameters.

The scaling function approach introduced by Knaapen et al. (2003) can be easily incorporated into numerical models to account for multiple species (Nasermoaddeli et al., 2014). For this reason it is widely adopted in morphodynamic simulations. There is however one study using an alternative approach which does not directly rely on species mapping (Cozzoli, 2016). As introduced in the previous section, Cozzoli (2016) applied an allometric scaling approach to account for stabilization and destabilization effects. Individual body size and abundance and the maximum tidal current velocity jointly determine the change of SSC (ΔSSC) compared to the control case (contr.) which excludes bioturbation (Table 1). This parameter (ΔSSC) is termed potential ecosystem engineering effect on landscape. Another novelty in Cozzoli (2016) is that the species biomass density was modeled in a species distribution model (SDM). The SDM is driven by environmental variables including current velocity, inundation time, salinity and salinity range. Similar to Cozzoli (2016), a species distribution model was applied in Brückner et al. (2021). Based on a literature scan, suitable ranges of three parameters (inundation time, flow velocity and mud fraction) were identified for each investigated species. Presence or absence of a specific species depends on whether these parameters fall within the suitable range. Biomass is estimated by a suitability range of the parameters. E_r and τ_c are jointly determined by biomass and sediment properties based on measurements by Cozzoli et al. (2019). It is worth to note that this study is the first large-scale biomorphodynamic modeling study to incorporate species interactions including grazing, competition and coexistence.

4.1.2. Sea bed roughness

The impact of benthos-induced change in bottom roughness has been studied in an exemplary study of the Baltic Sea by Seifert et al. (2009), which was built on earlier studies investigating the transport of fine material including the effect of fluff layer. In the study, a detailed sediment map with four grain size classes compiled by Bobertz et al. (2009) was used to estimate bottom roughness. Sediment erosion, transport and deposition including the redistribution of fine material which initially evenly cover the whole model domain in a form of fluffy layer was modeled by a 3D hydrodynamic model. Four classes of fine material with different sinking velocities were considered. Change in the bottom roughness due to reworking of four major species of bioturbators in the Baltic Sea were incorporated using a target proxy method from Bobertz et al. (2009) which relates the bottom roughness to bioturbator abundance based on the relationship derived from flume experiments by Friedrichs (2004).

4.2. Process-based models

Process-based models assume that the impact of benthos on sediment can be separated into different physical and/or bio-physical processes that can be mechanistically described. Unlike empirical parameterization models in which the impact of benthos on sediment stability is often site-dependant, process-based models adopt consistent mathematical formulation with only a few tunable parameters.

4.2.1. Fluff layer

Fluff layer formation and erosion was modeled by Orvain et al. (2012). One stationary bivalve and one mobile snail species were implemented. Both species affect fluff layer formation but sediment bed erosion is only affected by the bivalve species. Once a fluff layer is formed, erosion is divided into two phases as described in Section 3.2.

4.2.2. Pelletization

Sinking of bio-aggregates including faecal pellets and pseudo faeces was investigated by Lumborg et al. (2006) using a 2D hydrodynamic model. A concentration-based flocculation model was introduced. Four scenarios characterized by different community structures of a destabilizing and pellet producing species (*H. ulvae*) and stabilizing MPB were modeled. Biophysical effects were implemented in the erosion parameters and sinking velocity. For instance, increased individual numbers of pelletizers are reflected in a decrease in critical shear stress for erosion, higher production of bioaggregates, higher erosion rate and increased flocculation and sinking velocity. Orvain et al. (2012) also implemented pelletization associated with enhanced sinking velocities but without flocculation.

4.2.3. Biomixing

A horizontally varying biomixing coefficient was implemented in Paarlberg et al., (2005). Biomixing effect was coupled with the stabilizing effect of MPB and destabilizing effect of macrobenthos. In contrast to the former study only sediment grains are mixed between the bed layers by applying a diffusion coefficient D_{mix} which is the sum of the a varying physical mixing D_p (depending on bottom current shear velocity and grain size) and the constant benthos-induced mixing D_b. The latter assumes that D_b scales with the biomass of bioturbators. Six sediment layers, each with 5 cm-thickness, were implemented. Biomixing D_{mix} is limited to the top 20 cm, i.e. the top 4 sediment layers as shown in Fig. 4b. Physical mixing D_p decreases exponentially in depth. A critical mud content 20% was set to mark the transition between cohesive and non-cohesive bed.

4.3. Results

4.3.1. Deposition and erosion

Results of large-scale modeling suggest that while the spatial pattern of erosion and deposition are mainly determined by hydrodynamics, their magnitude is strongly influenced by benthos (Wood and Widdows, 2002; Lumborg et al., 2006). A parameter scan of different physical and biological drivers (tide heights, offshore sediment supply, densities of destabilizing bioturbators and stabilizing MPB) revealed that changes in deposition and erosion caused by naturally varying benthos were in the range of the changes caused by physical drivers (Wood and Widdows, 2002).

Due to seasonal variations the impact of stabilizing MPB is smaller compared to that of destabilizing macrobenthos. In Wood and Widdows (2002) the difference in bed level changes between bioturbated and non-bioturbated scenarios is ~2 cm per month. Seasonal variations of stabilizing MPB was shown to change the magnitude of deposition locally by a factor of 2, while net erosion associated with interannual change in *M. balthica* distribution even reached up to a factor of 5. In Paarlberg et al. (2005) bed level variations in half a year are in the range of a few centimetres in case of a solely stabilizing scenario and up to 20 cm for a destabilizing scenario. In a 1-D cross shore profile developing towards a morphological equilibrium, stabilizing MPB shows a mild long-term impact with seasonal bed level change in the range of 5 cm (Waeles et al., 2004; Le Hir et al., 2007). In a similar study including the impact of destabilizing benthos, sea bed was locally eroded by about 40 cm (Orvain et al., 2012). Incorporating fluff layer processes increased the erosion only slightly because the material which was converted into fluff accounted only for around 15% of the total eroded material. The additional inclusion of faecal pellets with enhanced sinking velocities

reduced erosion by ~5%. It was concluded that morphological equilibrium is not sensitive to pelletization. In contrast, in Lumborg et al. (2006) a comparison of different model scenarios showed highest deposition for the scenario including pelletization. Model results further indicate that the physically-driven temporal peaks in deposition and erosion are both enhanced due to destabilizing effects. This effect is attributed to the large amount of sediment which is mobilized and amplified by pelletization. By contrast stabilization dampened the amplitudes in both erosion and deposition. Bed level changes are in the order of 5 mm per tidal period. The combined effects of two destabilizing bioturbators and stabilizing MPB were found to lead to bed level changes in the range of meters at different locations of an estuary over the course of 50 years (Brückner et al., 2021). In contrast to the former studies which highlighted the impact of benthos, Borsje et al. (2008b) found bioturbation-induced bed level changes just in a range of a few mm over the course of a whole year.

Beside bed level changes, benthos-induced fluxes of erosion and deposition as well as change in large-scale SSC have also been investigated. In the first study to investigate benthos impact on large-scale sediment transport by Willows et al. (1998), it was shown that up to 0.42 kgm^{-2} of sediment were resuspended during one tidal cycle at above the mid tide level by destabilizing bioturbators (*M. balthica*) appearing in natural population density. In two follow-up studies changes in sediment deposition caused by different benthic community compositions ranged between 0.1 and 1 kgm^{-2} over one month (Wood and Widdows, 2002) and 10–100 kgm^{-2} over one year (Wood and Widdows, 2003). Comparably, changes in erosion and deposition of fluff layer due to benthos-induced bottom roughness were in the order of 0.1 kgm^{-2} and locally up to 1–5 kgm^{-2} in the Baltic Sea (Seifert et al., 2009). SSC was locally increased by a factor of two and during storm events even up to a factor of 3.5 when biomixing was included (Sanford, 2008). Increase of SSC by destabilizing bioturbators was estimated to reach up to 0.1 kg/m^3 at a large-scale (south North Sea) according to Nasermoaddeli et al. (2017).

The magnitude of erosion and deposition was proposed to be proportional to the abundance of benthos (Wood and Widdows, 2002; Wood and Widdows, 2003). However, Cozzoli (2016) suggested that the relationship might not be linear. He found that the accumulated impact of bioturbators is larger in less habitable regions with more dynamic flow conditions compared to shallower and favorable habitation environment with high abundance of bioturbators. The reason for this complexity is that although both hydrodynamics and benthos positively influence sediment resuspension, a negative control of hydrodynamics on benthos in the applied SDM effectively leads to an inverse relationship between bioturbators abundance and biomass and the ecosystem engineering impact (see Fig. 2). This is one of the only two studies we found by now incorporating feedback mechanisms between benthos and its environmental drivers. The other study by Brückner et al., (2021) which implemented both morphological feedback and species interaction confirmed such nonlinear relationships and came to the conclusion that bioturbation efficiency rather than species abundance determines morphological changes.

It is worth to note that the order of magnitude of modeled bed level changes due to stabilization and destabilization is roughly the same. Existing results further indicate that different bioturbation activities may impact erosion and deposition on the same order of magnitude. This is the case for sediment resuspension and deposition caused by destabilization, stabilization, biomixing and roughness modification. Such results imply that these various benthos-induced processes are of comparable importance for morphological evolution.

4.3.2. Spatial sediment redistribution

Benthos can significantly redistribute sediment. Wood and Widdows (2002) and Wood and Widdows (2003) found that sediment eroded jointly by destabilizers and physical forcing was transported and deposited onshore. Combined with stabilizing impact of MPB, net

deposition occurs in shallow areas while areas around the mid tide level is subject to net erosion. This result is in line with Waeles et al. (2004) who found that MPB is able to stabilize areas above the mid tide level. The same effect was also seen in Orvain et al. (2012). By contrast, Paarlberg et al. (2005) did not detect the onshore transport of eroded sediment. Borsje et al. (2008b) described a more complex transport pattern with an active exchange of sediment between the tidal flats and channels. Eroded sediment from tidal flats is stored in the channels during rough weather and transported back to the tidal flats under calm conditions. Over the simulation of a year, net accumulation occurred on the tidal flats while at the tidal channels more material was eroded compared to the non-bioturbated scenario. This finding is in line with observations from the Northern Wadden Sea showing net accumulation in shallow parts of the Wadden Sea (tidal flats) and net erosion in the deep parts (channels) during the last decades (Benninghoff and W. C., 2019).

The impact of benthos on morphology in general decreases offshore (Wood and Widdows, 2002; Wood and Widdows, 2003; Waeles et al., 2004; Le Hir et al., 2007; Orvain et al., 2012). However, benthic impact is not restricted to the inhabited areas. For example, Orvain et al., (2012) revealed that bioturbation-induced erosion on the upper shore may lead to enhanced wave energy in the mid- and low-shore. As a consequence the mid- and low-shore are subject to enhanced erosion, despite that macrobenthos was absent there. Furthermore, eroded material by destabilizers can be transported over long distances and deposit in regions where no bioturbators are present (Borsje et al., 2008b). In a large-scale study of the southern North Sea, Nasermoaddeli et al. (2017) concluded that the benthos-mediated SSC spreads far beyond the simulated inhabited zones. This effect appears most pronounced during storm conditions but is also present over a spring-neap cycle. Sediment transport over a large distance into uninhabited areas was also recognized in an estuary where offshore transport of bioturbated sediment was modeled (Brückner et al., 2021). Depending on the composition of benthic community, transition from a mud-importing scenario for a stabilizing case and a mud-exporting scenario for destabilizing or mixed case was observed. Furthermore, presence of bio-destabilzers enhances erosion in intertidal areas and leads to a widening of the estuary and a smoothening of the hypsometric curve. Because of a combined effect of mud content in the specific habitat and bioturbation efficiency, efficient bioturbators were found most impactful in upstream and center reach of the estuary while less efficient bioturbators mainly affected the mouth of the estuary. Less efficient bioturbators and MPB generally have local impacts while efficient bioturbators can influence the morphological evolution of an entire estuary.

4.3.3. Sensitivity of sediment types

The grain size of sediment determines its sensitivity to benthos impact. In Nasermoaddeli et al. (2017) three different silt classes (coarse, fine, very fine) were implemented spanning three orders of magnitude in sinking velocity, with decreasing sinking velocity and τ_c for finer particles. While very fine material can be washed away readily by small shear stress, coarse sediment is resistant and the fine silts class (8–16 μm) turns out to be most sensitive to the presence of macrobenthos. The difference in suspended material between bioturbated and non-bioturbated cases is largest for fine silt, small for coarse silt and not visible for very fine silt. Knaapen et al. (2003) applied hydrodynamic modeling incorporating both cohesive and non-cohesive sediment behaviors distinguished by a critical mud content. Two sediment classes, mud and sand, were regarded. Compared to the reference run (non-bioturbation), mud content over three different study sites becomes significantly lower (10–20% instead of 30%) when bioturbation is considered. This effect is even more pronounced in an estuary where stabilizing and destabilizing benthos was found to increase and decrease the mud content by up to one order of magnitude, respectively (Brückner et al., 2021). In line with the above-mentioned studies, Paarlberg et al. (2005) revealed a strong control of benthos on mud distribution.

Their results indicate that in a scenario which destabilizing effect dominates, biomixing facilitates the change of the initially cohesive sediment layer (initial mud content 20%) into non-cohesive sediment layer featured by a mud content of 2% after around 50 days of simulation. However, in another scenario which stablizing effect prevails, mixing of mud content between the sediment layers was overwhelmed by mud accretion and the mud content in all layers persistently rise until the end of simulation. Such results suggest that biomixing and MPB could both exert a systematic change of sediment properties. It was concluded that while destabilizing organisms always decrease the mud content, stabilizing organisms can, but not necessarily, increase the mud content. In the study of Sanford (2008), distinct layers of high and low sand content emerge in a sand-mud mixture case without biomixing. As a result the sand layer armors the sea bed and strongly inhibits resuspension of mud. In contrast, biomixing prevents the emergence of a homogeneous sand layer. As a result, critical shear stresses for erosion are mixed between the sediment layers which significantly increases the resuspension of mud compared to the non-biomixing case.

5. Discussion

Regarding the type of research questions that can be answered with numerical models in earth sciences, three different kinds of numerical models, namely predictive models, explanatory models and explorative models can be distinguished (Desjardins et al., 2018). Depending on the initial state of the modeled system (represented by I) and external driving factors (represented by E), certain processes such like physical interactions (represented by P) lead the system to a final state (represented by F, see in Fig. 7). In predictive models, I, E and P are well defined, and the aim is to ascertain the future F. In explanatory models, I, E and P lie in a certain range, and the aim is to understand how a system reaches a known state F by testing all possible combinations of I, E, P that might finally lead to F. By contrast, I, E and P each contains a large degree of freedom in explorative models, and such models seek to evaluate potential development of the investigated system under different circumstances. In explorative models typically a set of scenarios and parameters for I, E and P is tested to assess temporal and spatial patterns, thresholds, sensitivities or plausible ranges of F (Desjardins et al., 2018).

The three kind of models represent different levels of understanding of the system complexity. So far all presented large-scale morphodynamic models can be classified as explorative models. There are three reasons to explain why so far development of large-scale morphodynamic models has not followed the common progression from exploration over explanation to prediction (Desjardins et al., 2018). First and most important is that we still lack a comprehensive understanding of fundamental biological/bio-physical processes affecting morphological development and dynamic feedback loops among them. Second is that data for model calibration of biological/bio-physical processes are scarce, and last but not least is that data for confirming model results are difficult to obtain. We believe that addressing these three issues are crucial for future development of large-scale biogeomorphodynamic models.

5.1. Process understanding

There are three major points that need to be addressed in order to improve our understanding of processes and implementation in numerical models. These include deepening of understanding of 1) effects on a species and functional group level, 2) feedback and interaction between co-existing species and functional groups, and 3) benthic morphological feedback mechanisms. Considerable progress has been made for the first point so far (as described in previous sections) whereas little attention has been paid on the last two points.

As for the first point, some fundamental processes and functions of benthos affecting sediment stability and morphodynamics remain
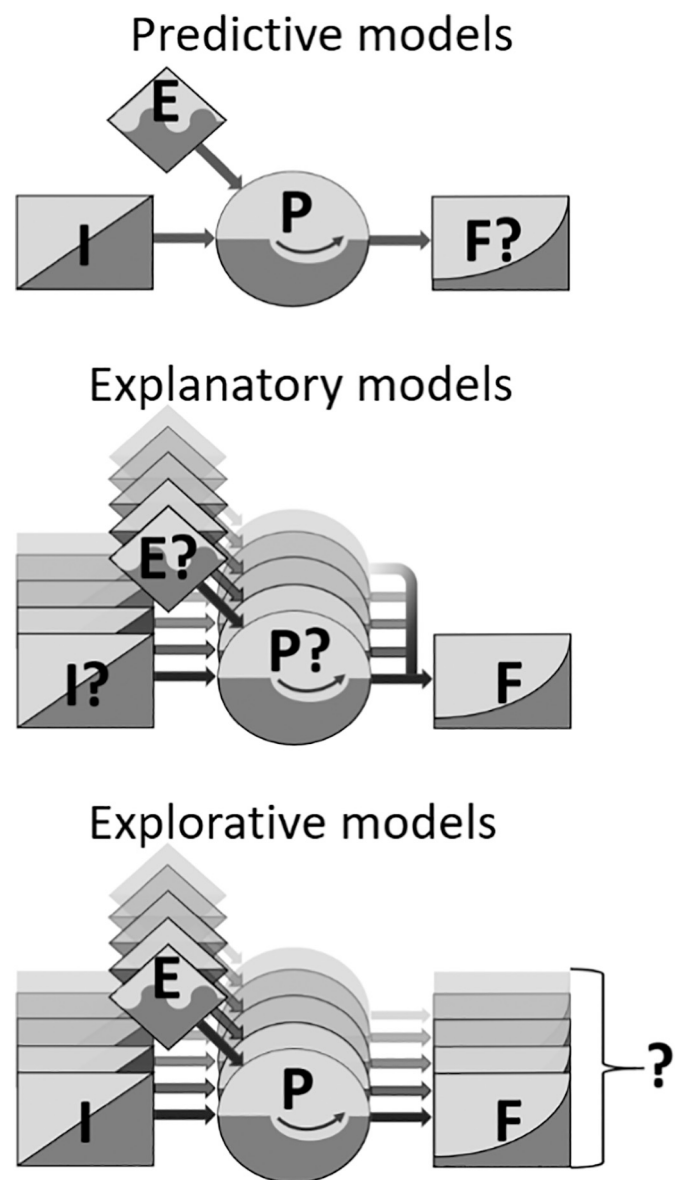

Fig. 7. Conceptual image of the three general types of models. I and F indicate the initial and final state of the modeled system, respectively. P refers to the interacting processes and E represents external factors affecting the system. The question mark indicates the uncertain quantities (modified after Desjardins et al., 2018).

underexplored. For example, biofilm maturing and EPS penetration into sediment and consequences on erosion have barely been investigated. The effect of EPS coating to sediment flocculation is largely unknown and the proxy parameter of chl-α proves to be a over-simplification for biofilm stability. On this aspect, recent progress in airborne identification of biofilm assembly (e.g. Launeau et al., 2018) and a further understanding of its mechanistic linkage to ecosystem drivers and sediment properties might help to advance the integration of biofilm dynamics in large-scale modeling in near future. A better understand the functioning of meio- and macrobenthos is also needed. Studies connecting general movement patterns, burrow activity or burrowing depth with sediment stability are still scarce. The implementation of biomixing and fluff layer demonstrates the use of data-driven parameterization in process-based models. Biomixing had been usually parameterized as a constant diffusion coefficient in the advection-diffusion equation in process-based models, only until recently has its temporally and spatially-varying feature been emphasized by Zhang and Wirtz (2017)

through mechanistically linking biomixing with its drivers (foraging of food and sheltering from predators) and applied to large-scale modeling (Zhang et al., 2019). The level of representation of fluff layer dynamics seems promising according to existing model studies (Orvain, 2005; Prooijen et al., 2011), which prove to correctly resolve formation and destruction processes associated with two typical functional groups (one for mobile and track-creating species and the other for sessile and pseudofaeces-producing species). Still, further research is needed in order to include other functional groups concerning their influence on fluff layer.

As for the second and third points, feedback mechanisms between co-existing species and/or functional groups and between benthos and morphology have been recognized as key mechanism for development of complex morphological features (Murray et al., 2008; Corenblit et al., 2011; Reinhardt et al., 2010) and to determine species survivability (Coco et al., 2006). As described in Fig. 2, the interactions between benthos and environmental drivers can have many implications. For instance, positive feedback between MPB and mud content may increase abundance and content of both. Negative feedback between destabilizers and mud content may lead to a reduction of habitable area of destabilizers. However, sustainability can be maintained if MPB is involved in the feedback loop. Subsequent changes in morphology and hydrodynamics would also feed back on the inhabiting species. A first step towards implementing feedback mechanisms on large scales was made by Cozzoli (2016) where species distribution was controlled by hydrodynamics. Results suggested that the combined effect of bioturbators and hydrodynamics creates a complex pattern of sediment erodability. Interactions between different species have only until recently been considered in large-scale morphological modeling. Different but co-existing species are usually investigated separately rather than in a combined manner. In most cases only one or two species are modeled and we found only one study considering the impact of four species (Seifert et al., 2009). Most studies emphasize one effect per species but in fact every species impacts the sediment in multiple ways. There is no study yet considering multiple functional groups or multiple effects for individual species. Species interactions such as varying trait expression, positive and negative feedback loops (e.g. grazing on biofilm, see Fig. 2) are rare. The first study to incorporate both benthic morphological feedback and species interactions showed promising results (Brückner et al., 2021). Species interaction was implemented in a simplified way with grazing, competition and coexistence included. Their results show how a combination of habitat suitability, species specific bioturbation and species interactions can guide large-scale morphological evolution. Results also indicate that large morphological impact is not necessarily related to species abundance but more to ecosystem efficiency. In this perspective, an implementation of species interaction may also enable the simulation of ecological succession in future studies.

5.2. Data for model calibration

With regard to process implementation, the difference between empirical parameterization and process-based models is the level of complexity in presenting benthos impact. Despite such difference both types of models require parameterization which is not readily available for all benthic effects. For upscaling of macrobenthic destabilization, controlled flume experiments provide a valuable tool which has been used in many studies (Willows et al., 1998; Wood and Widdows, 2002; Wood and Widdows, 2003; Orvain et al., 2012; Prooijen et al., 2011). However, most of the flume experiments are designed for a specific purpose and targeted on a small number of selected species. Recently Cozzoli et al. (2019) carried out an elaborate flume study investigating a large amount of different species with the aim to relate sediment resuspension with metabolic rate and bed shear stress. Data derived from such experiments are useful for calibration of numerical models. Investigations by Lindqvist et al. (2016) on particle reworking by

different species in a glass aquarium mimicking natural environments can be similarly used for calibration of biomixing. Modeling in general benefits from the use of controlled experiments (Kleinhans et al., 2010). Especially when thinking of future scenarios laboratory experiments can help to gain insights into the behaviors of species in response to e.g. more frequent occurrence of heat waves (Román et al., 2020), and thus make such data available for model calibration. However, a major drawback of laboratory experiments is the question of scalability of an idealized system to reality. Obtaining a realistic species distribution is still challenging even when a limited number of species and effects are considered. Typically, species distribution is considered either as constant or simplified through proxy parameterization (e.g. Lumborg et al., 2006; Orvain et al., 2012; Paarlberg et al., 2005; Wood and Widdows, 2003). Temporal variations are often simplified by applying either constant scaling factor with seasonality (Le Hir et al., 2007) or a sinusodial scaling for an annual cycle (Orvain et al., 2012), while spatial variations are approximated by proxy parameters (Wood and Widdows, 2002; Wood and Widdows, 2003). Table 2 shows that most models are not able to represent realistic temporal and/or spatial species distributions, despite that both spatial and seasonal variability of the species distribution have proven critical for achieving realistic results (Borsje et al., 2008b). This is later supported by Cozzoli (2016) who revealed possible feedback mechanisms between hydrodynamics and benthos distribution leading to a large impact of benthos even at low densities. Only three studies have so far incorporated both spatial and temporal variability of benthos (Borsje et al., 2008b; Cozzoli, 2016; Brückner et al., 2021).

In this context, it is important to firstly define the level on which parameterization is needed, i.e. whether it is on species or functional group/community level, and then to target on data for model calibration. The species level parameterization can be derived from lab or field experiments with a few selected key species, while the functional group/community level should be built on meta-analysis that combines various datasets covering as many species as possible that function in similar ways. For modeling a single tidal basin or estuary the species level parameterization might be sufficient, while representing the integrative effect of benthos on the level of functional groups/community appears to be one crucial task for larger-scale morphodynamic modeling, despite that a clear strategy to group the benthos is still lacking and relevant calibration data are scarce.

Trait-based formulation of bioturbation has been used as predictor for benthos impact on ecosystem functions (Solan et al., 2004; Queirós et al., 2015; Wrede et al., 2017). Species sharing the same or similar traits can be categorized into functional groups. One early example is the categorization of feeding guilds, summarizing species that exploit the same food resources in a similar way without regard to their taxonomic position (Root, 1967). A widely-cited study by Fauchald and Jumars (1979) reviewed a considerable amount of polycheat studies and matched the worms a priori to one of several different feeding types. Later studies have listed up to 20 different feeding guilds (Rosenberg, 2001). However, the feeding guild concept has not been widely applied and those applied studies could hardly see a clear benefit (Gallagher, 2008). In contrast to the feeding guild concept, the functional group concept classifies all organisms affecting their habitat in a similar way without solely focusing on the modes in which the resources are exploited (Woodin and Jackson, 1979). In fact this rather broad definition has been interpreted in different ways and there is no commonly accepted convention on how to group species and how to evaluate their behavior regarding a certain impact, e.g. geographically distinct populations of intertidal sediment dwelling invertebrates may have no constancy in species traits manifestation (Wohlgemuth et al., 2017). Some species are known to adapt their feeding mode to environmental conditions such as hydrodynamics or nutrient availability and change e. g. between suspension and deposit feeding behavior (Lange et al., 2018). Besides, two species might positively or negatively affect each other's trait expressions in order to fit in a certain niche. Parasites for example

were found to change trait expression of bioturbators and decrease destabilizing effects of macrobenthos (Dairain et al., 2019; Dairain et al., 2020). Also a system perturbation history may influence trait expression (Murray et al., 2017). Murray et al. (2014) concluded that the membership of a species in a functional group and the number of functional groups should depend on the investigated ecosystem process and functioning. Every benthos-mediated sediment process may require a specific grouping of functional types which lead to the circumstance that one species can be categorized into different groups. Most existing models simplify the system to a dominant functional group and refer to abundance as the criterion for dominance, which proves to be questionable as there can be large difference in the impact between different ecosystem engineers (see Section 2). For instance results by Brücker et al., (2021) indicate that bioturbation efficiency rather than spatial abundance of a species determines its impact on morphodynamics. Furthermore, as explained in Section 2, the function or trait expression may vary depending on the environmental conditions and community assemblages. Existing research suggests that functional trait expression may have advantage over species abundance in characterizing the response of benthic community to environmental stressors such like bottom trawling, in which circumstance abundance might change significantly on a species level while the same functional trait is maintained by adaption on the community level (Muntadas et al., 2015). Observations and mechanistic approaches linking a function or trait expression of benthos with dynamic environmental drivers might provide a solution to account for this (e.g. Cozzoli, 2016; Cozzoli et al., 2019; Zhang et al., 2019; Brückner et al., 2021).

5.3. Data for model confirmation

Existing modeling studies on large-scale morphological change induced by benthos are often only partly validated, e.g. by flume experiments (Willows et al., 1998; Wood and Widdows, 2002; Wood and Widdows, 2003; Orvain et al., 2012; Prooijen et al., 2011). Comparisons between model result and field measurement are usually limited to a few points in space and time (Wood and Widdows, 2002; Wood and Widdows, 2003; Knaapen et al., 2003; Lumborg et al., 2006; Borsje et al., 2008b; Borsje et al., 2007). Only one study combined measuring stations and satellite data to assess model results at larger spatial and time scales (Nasermoaddeli et al., 2017). On the other hand, it is difficult to discern morphological changes induced by benthos, which are often superposed on the first-order changes by pure physical forcing (currents and waves).

Accumulation of high-resolution data in both space and time allowing for obtaining a wide spectrum of possible combinations of I, E, P and F are necessary in order to disentangle the benthos impact from the complex mosaic of observed morphological development. It is particularly worth to note that with accumulation of observation data and the improvement in computing power, machine learning (ML) has been increasingly applied to develop inductive statements and optimized predictions directly from data sets (Goldstein et al., 2019). Several types of supervised ML approaches, including Artificial Neural Networks (ANN), Genetic algorithms (GA), Bayesian networks (BN) and Regression trees (RT), have been applied to predict sediment transport (Goldstein and Coco, 2014), small-to medium scale coastal morphodynamics (López et al., 2017; Plomaritis et al., 2018) and embedded in process-based morphodynamic models to improve predictability (Limber et al., 2014; Lin and Sheng, 2017). ML has also become popular for high-resolution mapping of benthic habitats and sediment properties in recent years (Diesing et al., 2014; Mohamed et al., 2020). Although we have not found any application of ML to discern benthos impact on sediment and morphodynamics yet, there is a good reason to believe that large-scale biomorphodynamic modeling can greatly benefit from data-driven parameterizations optimized by ML (e.g. identification and grouping of functional types) as well as confirmation data derived by ML in near future.

5.4. Complexity in modeling - how far we can/should go?

Despite the progress in numerical modeling it should be noted that all numerical models in earth sciences inevitably contain uncertainties because the nature system is not closed (Oreskes et al., 1994). In this sense numerical models cannot be fully validated. Instead modelers must thrive to confirm their models as good as possible. For this reason numerical modeling should always go hand in hand with observations recorded in field data, laboratory and field experiments to gain and improve understanding of processes (Kleinhans et al., 2010). Furthermore, when constructing a numerical model the question of appropriate complexity of modeled interactions must be answered (French et al., 2015; Larsen et al., 2016). For example, in early climate modeling two modeling philosophies emerged with one relying on incorporating more complex processes on a smaller scale to ensure eddy-resolving capability and the other implementing processes with less complexity (e.g. eddy-permitting) but on a larger scale (Mcguffie and Henderson-Sellers, 2001). Similarly, the ability to resolve certain benthos effects is constrained to the applied model complexity and refinement. For example, unraveling the sensitivity of sediments to bioturbation requires distinguishing various sediment classes (Nasermoaddeli et al., 2017). Idealized forcing might be sufficient to achieve a rough estimate on the amount of sediment eroded by destabilizers (Willows et al., 1998), but subsequent transport and deposition processes must be taken into account to assess the impact of stabilizing species on bed level changes especially at large-scale (Wood and Widdows, 2002; Wood and Widdows, 2003). To assess biomixing effects, a more realistic sediment bed representation with multiple layers instead of a single layer should be adopted (Paarlberg et al., 2005; Sanford, 2008). For studying formation and erosion associated with fluff layer, production processes (e.g. production of pseudo faeces) and the two-phase erosion need to be resolved (Orvain et al., 2003; Orvain, 2005), and resolving the effect of faecal pellets further requires flocculation modeling (Lumborg et al., 2006).

Despite limitations in computational power the omission or simplification of certain processes in favor of appropriate model complexity is also relevant in terms of accuracy and realistic results. Increasing the number of implemented processes often means an increase in the number of parameters which need to be either measured, estimated from proxy data or theoretical considerations or derived empirically. Uncertainties in parameters arise especially from the latter three sources. Accumulation of uncertainties in parameterization may strongly affect model results, necessitating studies investigating how variations in output are attributed to input factors and which factors have the greatest impact on it (Skinner et al., 2021, Pianosi et al., 2016). For instance Baar et al. (2019) have tested five different morphodynamic scenarios and found that it was impossible to calibrate the magnitude of sediment transport and the morphological change simultaneously. A high sensitivity of morphological development to sediment transport parameterization and even to model spin-up time has also been reported by other authors (Diaz et al., 2020). In this respect, thriving for higher model complexity does not necessarily lead to better performance. Therefore, before conducting numerical modeling, researchers must figure out which questions can be answered in a meaningful sense with simulation results that can be compared with observations and which level of modeling complexity is sufficient for that purpose. This is especially relevant for biomorphodynamic modeling since our current understanding and knowledge is still quite limited.

6. Conclusions

Interaction between benthos, morphodynamics and other environmental drivers is highly dynamic involving a large range of feedback loops which remain poorly understood. So far, four major functions of benthos affecting sediments and morphodynamics have been identified, namely (1) biomixing which transports and mixes sediment particles horizontally and vertically through foraging and sheltering behaviors.

Biomixing is depth dependant and can be further classified into five major functional modes. From a community-level and long-term perspective, biomixing exhibits a diffusion-like mixing of sediment particles and can be implemented in process-based advection-diffusion models. In general, biomixing promotes sediment erosion; (2) mediating particle flux and grain transformation through processing of food. This function can be further classified into three modes which not only significantly affect particle deposition, burial, resuspension and transport but also transform particles towards more muddy and cohesive characteristics or the opposite way. Among various processing ways, biodeposition remarkably promotes deposition. In addition, processed particles (e.g. pseudo faeces) may form a fluff layer in the immediate vicinity of the sea bed which alters the erosion process. This function can either enhance erodibility or stability of the sea bed depending on the abundance of processed particles and local sediment properties (e.g. ratio of sand to mud); (3) change of sea bed roughness through allogenic and autogenic structures. The increased sea bed roughness may significantly affect the overlying flow regime. The resulting impact can either promote erosion or deposition, depending on the density of the created structures and the altered flows; (4) coating on sediment grain surface by biofilm. Biofilm is generated mainly by microbenthic production but is also produced during locomotion of meio- and macrobenthos. Biofilm mainly stabilizes sediments and reduce erosion.

Among different types of sediment, fine-grained classes (silt and clay) are most sensitive to the impact of benthos. The degree of morphological change is governed by an interplay between physical processes such as tides, wind and waves on the one hand and biological impact on the other hand. While erosion and deposition are mainly driven by hydrodynamics, benthos influences the degree and balance of these processes on seasonal and spatial scales. Existing modeling studies show that the degree of benthos-induced change can be in the same order of magnitude as that by the hydrodynamic processes. MPB is acting as a stabilizer reducing erosion processes especially on the upper shore above mid-tide level. Due to a pronounced temporal variation it is mainly responsible for seasonal variations of sediment transport. Its overall effect on bed level changes is smaller than that of macrobenthos whose influence persists over the year and controls spatial variations in sediment transport. Benthic organisms have the capability to mediate sediment transport and sedimentation patterns beyond their habitats on the long-term and over a large-scale. Morphological evolution is guided by bioturbation efficiency rather than species abundance.

The current development of large-scale biomorphodynamic models is still in an explorative stage. The reason can be attributed to (1) lack a comprehensive understanding of fundamental biological/bio-physical processes affecting morphological development and dynamic feedback loops among them, (2) scarcity in data for model calibration of biological/bio-physical processes, and (3) data for confirming model results are difficult to obtain. We believe that addressing these issues are crucial to advance the development of large-scale bio-geomorphodynamic models. Furthermore, thriving for higher model complexity does not necessarily lead to better performance. Before conducting biomorphodynamic modeling, researchers must figure out which questions can be answered in a meaningful sense with simulation results that can be compared with observations and which level of modeling complexity is sufficient for that purpose.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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3. Small-scale benthic faunal activities may lead to large scale morphological change – A model based assessment

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Small-scale benthic faunal activities may lead to large-scale morphological change- A model based assessment

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A novel 3-dimensional numerical model resolving dynamic interactions between environmental drivers and benthic fauna was applied to an idealized domain as analogous to typical tidal embayments. The aim is to derive insights into the role of benthic fauna in guiding long-term (decadal to centennial) coastal morphological evolution at a system scale. Three major functions by benthic fauna on sediment dynamics, namely bio-destabilization, bio-deposition and bio-stabilization, were incorporated. Results indicate that each of the three functions is able to guide a unique and profound long-term change of the embayment morphology. Bioturbation-induced sediment mixing and bio-destabilization may result in net sediment export out of the embayment, whilst bio-deposition and bio-stabilization tend to alter the embayment toward a net sediment import environment. Benthic fauna is able to modify large-scale hydro-morphology toward a state favorable for living. A combined effect of the three functions is not just a simple neutralization of the opposing impacts between sediment stabilization and destabilization. Rather, it leads to a unique response of the embayment morphology due to interactions between different benthic functional groups. Comparison with a real tidal embayment (Jade Bay from the Wadden Sea) justified a general validity of the model results in terms of statistics in both morphology and benthic fauna, and suggested an equal importance of interactions between benthic fauna and bed morphology and between different benthic functional groups in guiding morphological development of complex coastal systems.

KEYWORDS

mophological evolution, benthos, bioturbation, tidal basin, modeling, functional groups

Introduction

Morphological evolution of coastal systems is jointly controlled by physical, biological and anthropogenic processes (Angamuthu et al., 2018). While the impacts of physical and anthropogenic drivers on coastal morphological development have long been acknowledged and extensively studied, the role of biota in guiding evolution of coastal landscapes is often overlooked and has become another focal point only until recent decades (Fagherazzi et al., 2004; Murray et al., 2008; Wang and Temmerman, 2013; Shi et al., 2020; Viles, 2020; Chen et al., 2021). The interaction between biota and environment is twofold. On one hand, coastal morphology, associated environmental forcing (e.g. tides, waves) and food availability exert a first-order control on the type of habitats as well as abundance and trait expression of biota (Murray et al., 2008; Holzhauer et al., 2019; Shi et al., 2021). On the other hand, biota in turn actively modify their environment to attain an optimized fitness for their living conditions (Jones et al., 1994; Hastings et al., 2007; Li et al., 2021). Understanding such dynamic interactions between environmental parameters and biota is essential in management and optimization of many coastal systems against present and future climate and anthropogenic threats (Murray et al., 2008; Viles, 2020).

Biota in coastal systems include flora and fauna. The former is well recognized to exert predominantly stabilizing effects on sediments and coastal morphology. In coastal lands and marshes, for instance, plants play an antagonist role to erosion by dampening tidal currents and waves, and trapping sediment (Möller et al., 2014; Zhang et al., 2015; Leonardi et al., 2018). Benthic fauna incorporates all animals living on or within the sea floor. Benthic faunal behaviors are highly complex and variable (Murray et al., 2014; Murray et al., 2017; Dairain et al., 2019), and can influence the stability of coastal morphology in either positive or negative ways depending on a variety of parameters such as age, biomass, community composition, sediment type, hydrodynamics (Arlinghaus et al., 2021). Benthic fauna is known to actively rework sediments and promote soil formation at small spatial scales (from millimeters to meters) within the habitat (Craft, 2000; Valdemarsen et al., 2018), which is *via* four main functions, namely (1) biomixing which transports and mixes sediment particles horizontally and vertically through foraging and sheltering behaviors (Kristensen et al., 2012; Lindqvist et al., 2016), (2) mediating particle flux over chemical and compositional gradients and grain transformation through processing of food (Andersen and Pejrup, 2011), (3) change of sea bed roughness through allogenic and autogenic structures (Alves et al., 2017), and (4) coating on sediment grain surface by biofilm (Stal, 2010).

An understanding of how small-scale benthic faunal behaviors may accumulatively lead to long-term and large-scale (km-scale) coastal morphological change is not trivial since benthic fauna may cause sediment deposition and erosion of the same order of magnitude as changes caused by natural physical drivers such as tides, waves, and sediment supply (Wood and Widdows, 2003). It requires an extension of current knowledge from species level to an integrated system level since many species may co-exist and interact among each other in a natural coastal system. In addition, variation in ecological traits may lead to large differences in bio-morphodynamics mediated by different species in different circumstances (Viles, 2020). Focus on only a few selected species but omission of other interacting species and feedback mechanisms among themselves and the environment may lead to incomplete or even biased knowledge (Reinhardt et al., 2010; Arlinghaus et al., 2021; Brückner et al., 2021). Despite of an increasing consensus that benthic fauna plays an important role in mediating morphological evolution at spatical scales much larger than its habitat (Nasermoaddeli et al., 2017; Brückner et al., 2021), development of numerical models quantifying associated bio-morphodynamics is still at an explorative stage. The hindering factors include not only limited understanding of fundamental biological/bio-physical processes affecting morphological development and dynamic feedback loops among them but also a shortage of data for model calibration and confirmation of simulation results especially at a large spatial scale (Arlinghaus et al., 2021).

Tidal embayments represent one of the most dynamic coastal systems which are persistently shaped by hydro-morphodynamics and bio-morphodynamics. Disentangling respective impact of individual abiotic and biotic drivers as well as their dynamic interactions and combined effects on morphological development of tidal embayments is difficult. For example, an investigation by Benninghoff and Winter (2019) of the German Wadden Sea, which consists of a series of tidal embayments and associated ebb deltas, barrier islands, salt marshes and estuaries, found that the region has undergone net sediment deposition in most tidal flats whilst net erosion in subtidal channels based on comparison of bathymetric data between 1998 and 2016. On the other hand, several abiotic (e.g. mean sea level rise, tides, waves and boundary sediment supply) and biotic (e.g. flora and fauna) factors can individually or jointly cause erosion in tidal channels and/or deposition in tidal flats (Marciano et al., 2005; Van Maanen et al., 2013a; Van Maanen et al., 2013b; Van Maanen et al., 2015; Zhang and Arlinghaus, 2022) and the exact mechanisms explaining the observed changes of the Wadden Sea have yet to be explored (Benninghof and Winter, 2019).

In this study, we intend to bridge part of the knowledge gap by quantifying the importance of benthic fauna in guiding long-term (decadal to centennial) coastal morphological evolution at a large and regional scale and disentangling its impact from abiotic drivers. To achieve this, we applied a novel 3-Dimensional numerical model, which resolves dynamic interactions between environmental drivers (hydrodynamics, morphodynamics, temperature), food availability and benthic

fauna to an idealized domain as analogous to typical tidal embayments. Benthic fauna is represented by three functional groups according to its major impacts (bioturbation, bio-deposition and bio-stabilization) on sediment dynamics. Specifically, we aim to address the following questions:

I. How and to what extent can benthic fauna modify embayment-scale coastal morphology?

II. How and to what extent can interactions between different functional groups of benthic fauna influence long-term morphological development of tidal embayments?

Material and methods

In order to derive a general understanding of the importance of benthic fauna in guiding long-term and large-scale morphological development of tidal embayments, we have adopted an idealized initial coastal morphology which is composed of an offshore area, a tidal inlet and a tidal basin to mimic typical tidal embayments such as the Wadden Sea tidal basins (Figure 1). The similar initial morphology has been used in various studies to understand the sensitivity of morphological evolution to bottom slope, tidal current strength and sediment properties (Marciano et al., 2005), sea level rise (Van Maanen et al., 2013b) and coastal vegetation (mangroves, Van Maanen et al., 2015).

Hydrodynamic module

The 3-dimensional semi-implicit modeling system SCHISM was used to simulate hydrodynamics (Zhang et al., 2016). It solves the Reynolds-averaged Navier-Stokes equation on an unstructured grid employing a Garlekin finite element method (FEM) for horizontal and a finite volume method (FVM)

approach for vertical velocities. Turbulence closure is implemented according to the k-kl closure scheme described in Umlauf and Burchard (2003).
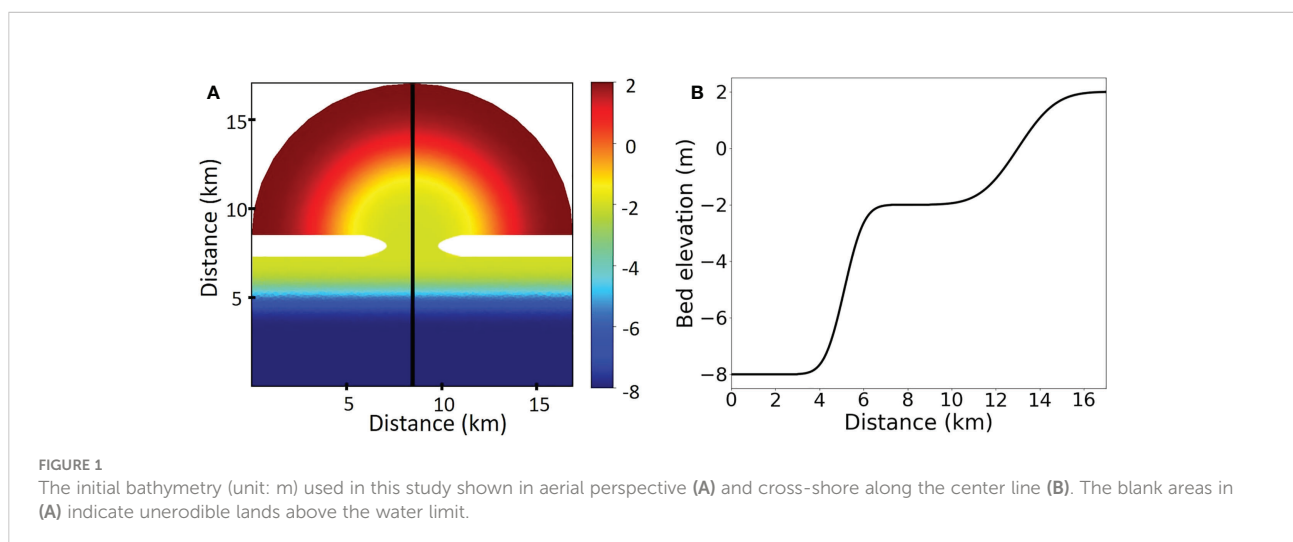
Sediment module

The sediment model SED3D (Pinto et al., 2012) is part of SCHISM. Sediment is divided into multiple classes, each with a characteristic grain size. 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.

Due to the cohesion arising from electrochemical surface charges and extracellular polymeric substances (EPS) secreted by benthic organisms including diatoms and bacteria, fine-grained particles can aggregate into flocs with settling velocity increased by orders of magnitude (Mikkelsen and Pejrup, 2000). The processes of flocculation depend on a variety of parameters including salinity, suspended sediment concentration (SSC), turbulence shear , organic matter component and temperature (Manning et al., 2011; Klassen, 2017; Zhang et al., 2020). In this study, the impact of flocculation on sediment settling velocity is considered. Settling velocity of cohesive sediment is calculated by the following Equation 1, which has been proven robust in capturing sediment dynamics in the Ems and Weser estuaries (Malcharek, 1995; Weilbeer, 2005):

$$\omega = \omega_0 \frac{1 + mG}{1 + nG^2} \qquad (1)$$

where w_0 is a reference settling velocity in still water depending on the particle grain size, $m=1$ and $n=100$ are empirical constants, and G is the turbulence shear.

FIGURE 1
The initial bathymetry (unit: m) used in this study shown in aerial perspective **(A)** and cross-shore along the center line **(B)**. The blank areas in **(A)** indicate unerodible lands above the water limit.

To account for morphodynamics, the seabed is represented by a dynamic layered system adopted from the model ROMS (Warner et al., 2008). Sediment layers (thickness, age, fraction of each sediment class) at each grid cell are modified at each computational time step according to deposition or erosion fluxes.

In mixed seabed with both sandy and muddy particles, sediment stability changes dramatically when a certain critical mud content p_{crit} is exceeded which marks the transition from non-cohesive to cohesive seabed (Van Ledden, 2001). The value for the critical mud content is highly dependent on the lithology of clay and ranges between 5% to 30% of mud (Van Ledden, 2002). The formulation by Van Ledden (2003) was adopted to calculate the *in situ* critical shear stress T_c:

$$\tau_c = \begin{cases} \tau_{c,s}(1 + p_m)^{\gamma}, & p_m < p_{crit} \\ \frac{\tau_{c,s}(1+p_{crit})^{\gamma} - \tau_{c,m}}{(1 - p_{crit})}(1 - p_m) + \tau_{c,m}, & p_m > p_{crit} \end{cases} \quad (2)$$

where p_m is the mud content, $T_{c,s}$ and $T_{c,m}$ are the critical shear stress for resuspension of sands and mud, respectively, and $\gamma=1$ is an empirical constant.

Benthic fauna module

The benthic fauna module represents a novel component in the 3D model system (Figure 2). It incorporates (1) growth/decline functions of benthic fauna in response to environmental drivers food availability, (2) bioturbation and related effect in vertical transport of particulate organic carbon in sediments as well as effects in sediment stability (bio-destabilization), (3) bio-

deposition, and (4) bio-stabilization. Major model functions relevant to this study are introduced in the following sub-sections, with technical details (numerical implementation schemes) provided in the Supplement Information.

Benthic infauna and bioturbation

Algorithms for calculating the growth/decline of benthic infauna and associated bioturbation intensity are adopted from the Total Organic Carbon-Macrobenthos Interaction Model (TOCMAIM) developed by Zhang and Wirtz (2017). The model mechanistically links benthic infaunal biomass and bioturbation intensity to food quantity and quality as well as constraint by stressors (mortality caused by predators and oxygen deficiency). Food quantity and quality are represented by the content and lability of particulate organic carbon (POC), respectively. The theoretical basis of the model is built on the hypothesis that (a) the community structure of benthic infauna is mainly dependent on the quality of POC settled on the seafloor, which further controls the intensity of bioturbation; (b) bioturbation in turn affects the vertical transport of POC in sediments; and (c) the vertical positioning of benthic infaunal biomass reflects a trade-off between benefits (i.e., quantity and quality of food) and costs (i.e., respiration and mortality). Details of model principles and mathematical descriptions, sensitivity analysis of model parameters and application to station data are elucidated in Zhang and Wirtz (2017). Model applications to case study areas (North Sea) were introduced in Zhang et al. (2019) and Zhang et al. (2021).

In the model, POC is divided into three pools depending on the degradability, namely, labile (i.e., of high quality nutrient), semi-labile (i.e., of intermediate quality nutrient), and refractory
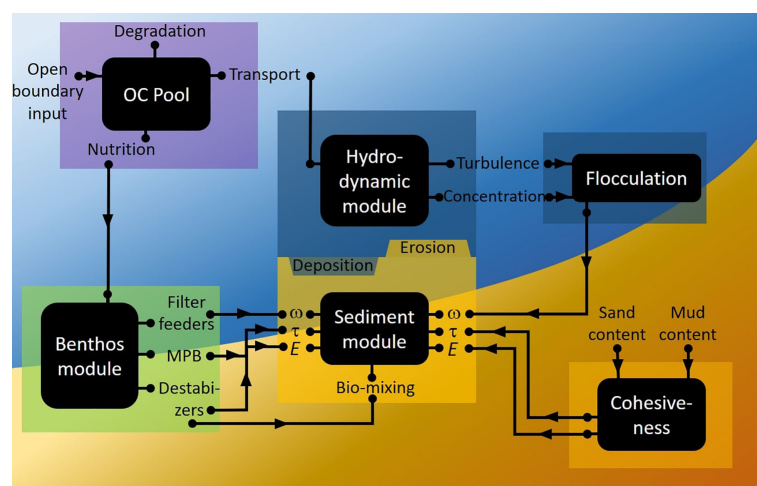

FIGURE 2
Schematic overview of numerical model components and their coupling. The hydrodynamic and sediment modules are from the SCHISM model, while other components were integrated to the SCHISM model as module (benthic fauna module) or subroutines (flocculation of cohesive sediments and organic detritus). Exchange of parameters between the model components is indicated by the arrows.

(i.e., of low-quality nutrient). These three POC pools are modeled as cohesive sediment classes, with each characterized by a first-order degradation rate (representing a sink term). Degraded POC provides a source for inorganic cohesive sediment class. The mass balance equation of each sediment class in seabed taking into account the impact of bioturbation, deposition/erosion caused by bottom currents and degradation of POC is calculated by:

$$(1-p)\frac{\partial C_{s,i}}{\partial t} = -\frac{\partial w(1-p)C_{s,i}}{\partial z} + \frac{\partial}{\partial z}\left(D_b(1-p)\frac{\partial C_{s,i}}{\partial z}\right)$$
$$+ \, Source - Sink \quad (3)$$

where $C_{s,i}$ is the mass concentration of class i in sediment depth z, p is the sediment porosity, w is the deposition/erosion rate, and D_b is the bioturbation diffusivity. The source term on the right hand side of the equation refers to the transformation of organic sediment to inorganic sediment (i.e., $Source = 0$ for all organic cohesive sediment and sand classes, and > 0 for inorganic cohesive sediment class), and the sink term refers to loss of organic cohesive sediment due to degradation and uptake of benthic infauna. Temporal change of benthic infaunal biomass B is calculated by:

$$\frac{\partial B}{\partial t} = (G - L)B \quad (4)$$

where G and L represent the rate of gain and loss, respectively. The former is dependent on available food resources and temperature, and the latter is controlled by respiration and mortality (Zhang and Wirtz, 2017).

Bioturbation diffusivity D_b scales with the local benthic infaunal biomass through a power law and inversely proportional to local food resource (i.e., the three POC pools):

$$D_b = \beta B^b \left(\sum_{i=1}^{3} a_i C_{s,i}\right)^{-1} \quad (5)$$

where β, b are empirical parameters linking body-size and abundance to biomass (Zhang and Wirtz, 2017). a_i (i=1, 2,3) are coefficients representing the efficiency of the POC pool in terms of gaining benthic infaunal biomass, with higher quality POC gaining biomass more efficiently as expressed by $a_1 > a_2 > a_3$. The above formulation explicitly links the bioturbation diffusivity with (1) the body-size and abundance of benthic infauna (through scaling with biomass), and (2) the local food resource which determines the intensity of vertical movements of benthic infauna to derive enough nutrition for metabolism and growth.

TOCMAIM is coupled to the sediment module adopting the same dynamic seabed layer scheme (section 2.2) so that a two-way exchange between hydro-morphodynamics and benthic faunal functioning is ensured (Figure 2). In this study, all empirical parameters and coefficients of the benthic infauna module including those in Equation 3-5 are adopted from the field application in Zhang et al. (2021) listed in Table 2. As shown in Equation 3, bioturbation is considered as a diffusive

process in the seabed sediment module. Not only the mass of each sediment class but also associated properties (e.g. median grain size and mud content) are mixed by bioturbation, which consequently modify the critical shear stress for sediment resuspension. Such mixing effect in sediment properties is termed biomixing. Biomixing has a destabilization effect in sediment because it loosens the upper-most sediment layers (normally up to 20-30 cm deep in sediments) where bioturbation exists (Sanford, 2008). The numerical scheme to implement the destabilization effect of biomixing in sediments and the empirical constants is explained in Supporting Information.

Bio-deposition

The benthic infauna model (section 2.3.1) provides estimates on the growth and decline of biomass in response to deposition and erosion of POC caused by bottom currents but does not account for deposition induced by benthic fauna themselves (so-called bio-deposition). The presence of suspension and filter feeders such as mussels effectively increases the settling velocity of sediment particles in the bottom most water layer. The magnitude of resulting bio-deposition of sediments depends on the filtration rate, ingestion rate and biomass of suspension/filter feeders. To account for bio-deposition, the suspension feeder model from the (US Army Corps of Engineers, 2000) was added as part of the benthic fauna module (Figure 2). Temporal change of the biomass S of suspension/filter feeders is given by:

$$\frac{dS}{dt} = (g - r - \varphi S)S \quad (6)$$

where g is the growth rate, r and φ are the loss rates cause by respiration and predation, respectively. The growth rate depends on the ingestion rate I, the concentration of suspended POC in bottom water, and respective nutritional value a_i for the POC class i as defined in Equation 5. Parameterizations of g, r and β are provided in Supporting Information. The rate of bio-deposition is then calculated by:

$$dep_{bio,i} = I \cdot S \cdot C_{s,i} \quad (7)$$

Bio-stabilization

A major contribution to sediment stabilization is made by extracellular polymeric substances (EPS) secreted by benthic organisms including microphytobenthos (e.g. diatoms) and bacteria that are correlated with Chlorophyll-a content in the sediment (Arlinghaus et al., 2021). The approach from Paarlberg et al. (2005) was adopted to include bio-stabilization by relating the critical shear stress for erosion and erosion rate E_r to the stabilization functions f_T and f_E associated with EPS:

$$\tau_c^b = \tau_c \cdot f_\tau, \quad (8)$$

$$E_r^b = E_r \cdot f_E \tag{9}$$

where T_c and E_r are the reference values of the critical shear stress for erosion (see Equation 2) and the erosion rate without biological impact, respectively. Chl- normally degrades with a decay constant between 7/yr and 30/yr (Stephens et al., 1997), which is close to that of the labile POC class (20/yr) (Zhang and Wirtz, 2017). Therefore, it is assumed that Chl- is contained only in the fresh, labile POC class in our model. A constant ratio of labile carbon (unit: g) to Chl- (unit: μg) as 40 found by (Jakobsen and Markager, 2016) is used to estimate the content of Chl-a in sediments, which is then used to calculate f_T and f_E (Paarlberg et al., 2005) given by:

$$f_\tau = 0.07 \cdot Chl - \alpha + 1 \tag{10}$$

$$f_E = -0.018 \cdot Chl - \alpha + 1 \tag{11}$$

Model configuration

The total domain size is 17 by 17 km² (Figure 1). The horizontal resolution of each grid cell is about 150 m in the tidal inlet and the basin, and gradually decreases offshore to 300 m at the seaward boundary. Eleven equidistant vertical layers using the Generalized sigma coordinates (Song and Haidvogel, 1994) were used. Configuration of key model parameters is given in Table 1.

The initial seabed material consists of uniform sands with D_{50} = 120 μm. Cohesive sediments (inorganic and organic classes) are imported from the seaward boundary (30 mg L^{-1} for inorganic mud and 10 mg L^{-1} for labile POC). This concentration of suspended particulate matter (SPM) represents a typical value in coastal waters (Pleskachevsky et al., 2005). In total five sediment classes are considered in the study and their corresponding

TABLE 1 Configuration of model parameters.

Parameter	Configuration
Domain size	17x17 km²
Grid spacing	150-300 m
Grid type	Triangles
Hydrodynamic layers	11 (sigma coordinates)
Bed layers	300
Bed layer height	1-6 cm
Sediment classes	5
Time step	120 s
Morphological acceleration factor	40
Forcing	M2 tide
Input mud open boundary	30 mg L^{-1}
Input labile POC open boundary	10 mg L^{-1}

reference values of settling velocity, critical shear stress for erosion and erosion rate are listed in Table 2.

The model is forced by a semidiurnal tide at its seaward boundary with an amplitude of 1.5 m. Higher-order components are produced by bottom friction and current-topography interaction during the propagation of the tidal wave through the model domain. The chosen value for the tidal amplitude at the open boundary is comparable to the average tidal amplitude of 1.42 m at the mouth of a tidal embayment (Jade Bay) in the German Wadden Sea measured by *Bundesanstalt für Gewässerkunde* (BfG). Morphological acceleration in updating the bed level change is used to save the computational time so that a stable state of coastal morphology can be reached more rapidly. Sensitivity runs using an acceleration factor of 10 indicate similar results to that of 40 but requires much longer computational time. Larger values produced spurious features such as random pockmarks and mounds. Therefore an acceleration factor of 40 was used in all simulations presented in this study. Benthic fauna induced bed level change is added up to the hydrodynamics induced change in the same grid cell at every time step. Wind-waves, Coriolis force, effect of temperature and seasonality on growth and decline of benthic fauna were excluded in order to reduce complexity of the model.

Channel detection and extraction

Morphological change of the embayment driven by tides is characterized by development of complicated channel network, as is the case in nature. In order to quantify the morphological changes, a channel detection method was developed based on image analysis inspired by Passalacqua et al. (2010). The stepwise procedure is illustrated in Figure 3 and utilizes the *python* library *OpenCV* (Gracia et al., 2015; Guillen, 2019). As a first step the raw image was converted into a greyscale image with pixel values between 0 and 255. In order to remove background noise while preserving the channel structures, anisotropic diffusion (Perona and Malik, 1990; Borroto-Fernandez et al., 2013) was applied to the greyscale image. Next, an adaptive thresholding method was used to create a binary image depending on the averaged local pixel values. Some channels might get disconnected after the adaptive thresholding. To solve this problem, a correction algorithm was then performed to reconnect those channels and remove irrelevant features (e.g. islands at both sides of the tidal inlet). The new image was then turned into a one-pixel-width representation. Intersections and end points of all channels were subsequently identified by counting the non-zero neighbors of each pixel. All intersecting pixels were then changed to zero to identify different branches. The total number of channels as well as the length of each channel branch were finally quantified as the last step in the procedure (Figure 3). The derived values serve as a database for our analysis of simulation results.

TABLE 2   Parameter setting of five sediment classes in this study.

Sediment class	W_0	$T_{c,s}$ or $T_{c,m}$	E_r
Very fine sand	0.5 mm s^{-1}	0.2 Pa	4.15 10^{-3} s m^{-1}
Inorganic mud	0.01 mm s^{-1}	0.4 Pa	1.15 10^{-3} s m^{-1}
Labile POC	0.01 mm s^{-1}	0.4 Pa	1.15 10^{-3} s m^{-1}
Semi labile POC	0.01 mm s^{-1}	0.4 Pa	1.15 10^{-3} s m^{-1}
Refractory POC	0.01 mm s^{-1}	0.4 Pa	1.15 10^{-3} s m^{-1}

Scenarios for modeling

Previous studies have revealed a significant control by bottom slope, tidal current strength and sediment properties (Marciano et al., 2005), sea level rise (Van Maanen et al., 2013b), coastal vegetation (Van Maanen et al., 2015), initial bathymetry and tidal forcing (Van Maanen et al., 2013a) on morphological development of tidal embayments. In this study, we focus on the impact of benthic fauna which has not been investigated yet in tidal embayment systems. Benthos is represented by three major functional groups (as described in section 2.3) instead of specific species. To this end, simulation results of an abiotic scenario by switching off the benthic fauna module in the 3D model system are used as the reference results. Four other simulations which include the benthic faunal impacts individually or jointly, named as Bio_destabilization, Bio_stabilization, Bio_deposition and Bio_all, are then compared with the reference results (named as Reference) for a quantitative analysis.

Results

Morphological development

Starting from the initial bathymetry (Figure 1), all simulations show a quick morphological development in the first 100 years especially in the first few decades (Figure 4A). Sediment scouring in the tidal inlet due to accelerated flood currents leads to a massive redistribution of sediment over the entire tidal basin within the first few years. During ebb-tides large amounts of sediment are transported offshore and exported out of the embayment through the inlet, subsequently deposited and forming an ebb tidal delta (Figure 5). The development of channel network in the embayment starts with the formation of two main channels at the inlet, which become increasingly deeper and gradually extend into the basin. During the extension of the main channels, secondary channels in the form of bifurcations appear, and further develop into more bifurcations when they extend to shallower area, ultimately

FIGURE 3
A step-by-step procedure of the channel extraction method is shown starting from a color image leading to the identification and extraction of all channel branches. The *python* library *OpenCV* is utilized.
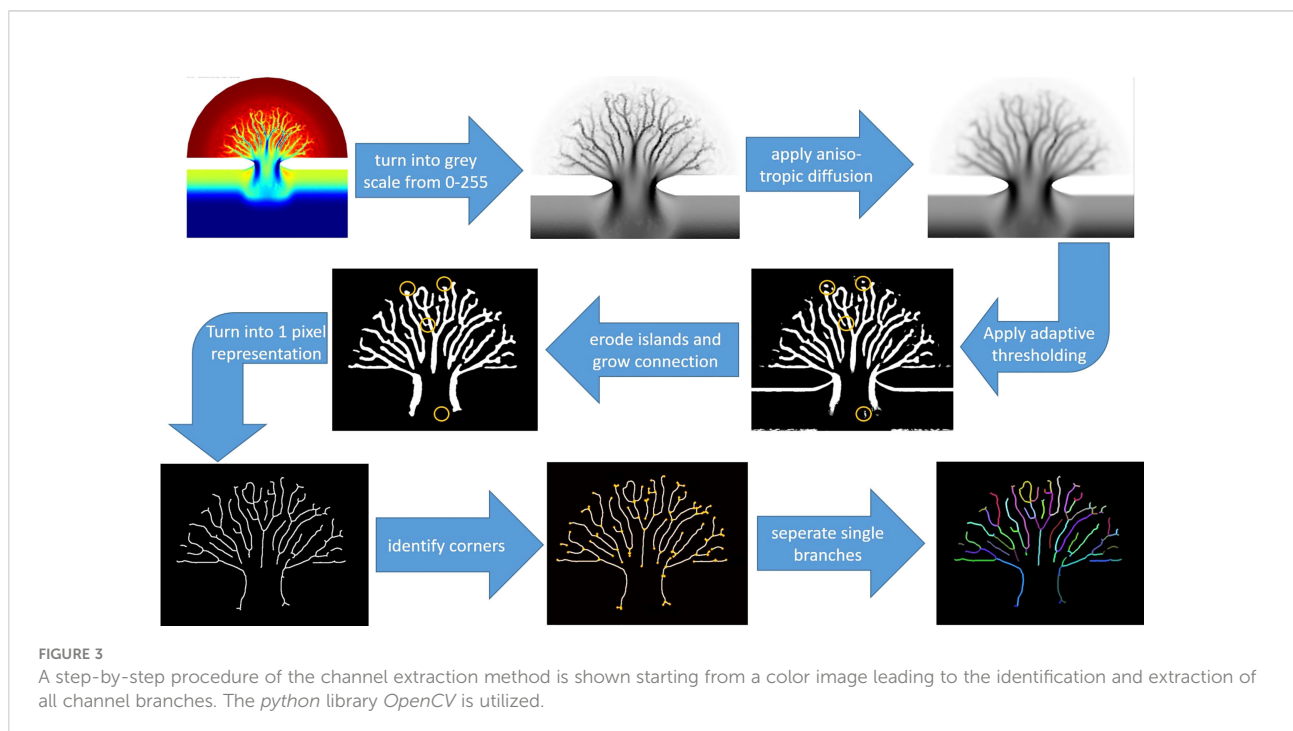
forming a complex of channel network in all simulations (Figure 5). Following a rapid morphological development in the first few decades, a general pattern of the channel network is established and the speed of development slows down. In the scenarios Bio_stabilization, Bio_deposition and Bio_all, a stable state in which sediment import and export through the inlet are balanced is reached after simulation of 500 years (Figure 4A). In the other two scenarios (Reference and Bio_destabilization) a stable state is not yet reached after simulation of 500 years and the embayment is still governed by a net sediment export (i.e. erosion). However, statistical results indicate that a clear spatial distribution pattern of channels is established at this time and shows only minor changes afterwards in both scenarios (Figure 6). Based on the relatively stable morphology established after year 500 in all scenarios, and for the sake of affordable computational effort, the simulation results till year 500 were analyzed to understand the role of benthic fauna in mediating long-term coastal morphological evolution at an embayment-scale.

Channel network

Statistics of channels in all simulations shown in Figure 6A indicate that the relationship between channel length and number of channels in each of the scenario follows an exponential function, which is consistent with the concept proposed by Horton (Horton, 1945; Strahler, 1953). Along with a consistent decrease in channel length with distance from the tidal inlet, the number of channels increases until a maximum is reached, and then start to decrease with further distance from the inlet (Figure 6B). The average channel depth shows an increasing trend when moving away from the inlet until a maximum is reached at a distance between 0.8-1.1 km

from the inlet, and then decreases gradually with further distance from the inlet (Figure 6C). Temporal change of the mean channel depth shows that the value rises rapidly in the first 100 years in all simulations, and gradually slows down afterwards. In three scenarios (Reference, Bio_deposition and Bio_all) the mean channel depth still continue to increase at year 500 with a small rate, while in the other two scenarios (Bio_destabilization and Bio_stabilization) the values approach a stable level (Figure 6D).

Reference result – abiotic scenario

Both the simulated morphology and statistics of channel networks (Figures 4–6) indicate significant differences among the simulations. In the abiotic scenario (Reference run), two similarly long and deep channels develop in the inlet (Figure 5A). Tides passing through the narrow inlet creates strong currents reinforcing the deepening of the main channels. They extend into the tidal basin and bifurcate into various channels which become smaller and shallower along a landward extension. The average channel depth in the entire basin is 4.5 m at year 500 (Figure 6D). The maximum number of channels is reached at approximately 4 km from the tidal inlet which is similar to the result in Van Maanen et al. (2013b). The highest order in the channel network is four, which is also in line with the study by Marciano et al. (2005).

The scenario is ebb-dominated with a net export of sediment over the whole course of the simulation period (500 yrs, see Figure 4A). Due to a lack of biomixing between sediment layers, all deposited mud accumulates on the seabed surface until being resuspended or buried beneath new deposits. As consequence, mud content is very high in the surface sediment layer at the tidal flat (outside the channels). At year 500, mud content takes
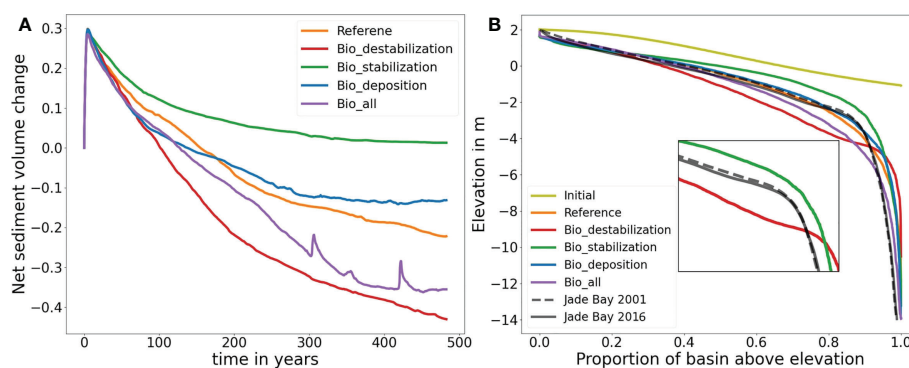

FIGURE 4
(A) Temporal evolution of the tidal embayment in all simulations with regard to the net sediment volume change at the basin (normalized by the initial total water volume in the basin; negative value implies export). **(B)** Hypsometric curves of all simulation results after 500 years. Note that the hypsometry curve of a real tidal embayment (Jade Bay in the Wadden Sea) for two different years 2001 and 2016 (data source: Sievers et al., 2020) are also plotted in **(B)** for comparison.
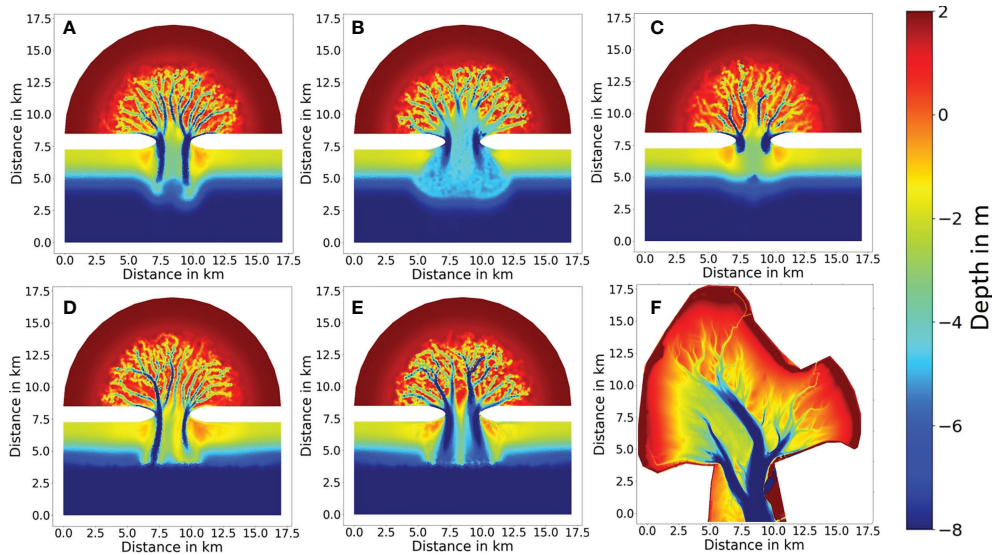
Simulated morphology at year 500 in **(A)** Reference run, **(B)** Bio_destabilization, **(C)** Bio_stabilization, **(D)** Bio_deposition, and **(E)** Bio-all. Bathymetry of a real tidal embayment (Jade Bay) is shown in **(F)** (data source: Sievers et al., 2020). Unit is m. Note that the belt-like deposition on the offshore side of the unerodible islands in all simulations is due to an exclusion of alongshore transport in the model.

up more than ~10% in most tidal flats and at some places even close to 100% (Figure 7A). In contrast, mud content is normally within a few percentage in the channels due to energetic tidal currents which impede deposition. As mud content increases, the seabed sediment becomes more resilient to hydrodynamic erosion (see Equation 2), which further facilitates accumulation of mud and stabilizes the morphology of the embayment.

Impacts of benthic fauna

Bioturbation and biomixing

Simulated morphological development of the tidal embayment with a destabilization effect caused by benthic fauna through bioturbation (i.e. the Bio_destabilization scenario) shows a remarkable difference with the reference result (Figures 5A, B). Compared to the reference scenario in which the two main channels at the inlet are deep, with a large depth gradient at their banks and long extension offshore, the two main channels in the Bio_destabilization scenario appears less distinctive with a relatively small depth gradient at the banks and much shorter in their length. The average channel depth in the entire basin is 3.7 m, being the smallest among all scenarios. The spatial gradient of depth in the channel network is also lowest among all scenarios. On the other hand, the channels are wider than the reference result. The embayment area within 2.5 km from the inlet is featured by erosion which makes the channels less distinctive and the first channel bifurcations occur further onshore than the reference results (Figure 5B).

Compared to the reference results, less long channels (length > 1.5 km) whilst shorter channels (length < 1.5 km) develop in the Bio_destabilization scenario (Figure 6A). The hypsometric curve of Bio_destabilization in Figure 4B shows that the basin as a whole is deeper although the main channels are shallower than the reference result. This is accompanied by a decrease in area of intertidal flats. A unique feature in the hypsometric curve of the Bio_destabilization scenario is a plateau indicating a considerable portion (~15%) of the embayment area within water depth between 4 and 5 m (Figure 4B), which corresponds to the erosional semicircle area within 2.5 km from the inlet (Figure 5B).

The above-mentioned differences are attributed to a reworking of sediments by benthic fauna. Input of organic carbon driven by tides through the inlet and subsequent deposition in the embayment (Figure 8B) fosters a growth of benthic fauna with biomass between a few tens and a few hundred g C m^{-2} in the tidal flat (Figure 9A). In contrast, benthic faunal biomass is persistently low (<10 g C m^{-2}) in the channels due to lack of deposition. Mud and POC are vertically mixed into deeper layers of sediment by benthic fauna through bioturbation (Figures 7B and 8B). As consequence, mud content in the upper-most surface sediment layer is generally below 10% over a major part of the tidal flat, much smaller than the reference result (Figure 7B). Reduction of mud content together with a loosening effect on the sediment caused by biomixing leads to a decrease of critical shear stress for resuspension, which makes surface sediment more susceptible to erosion and transport. To adapt to the impact of bio-
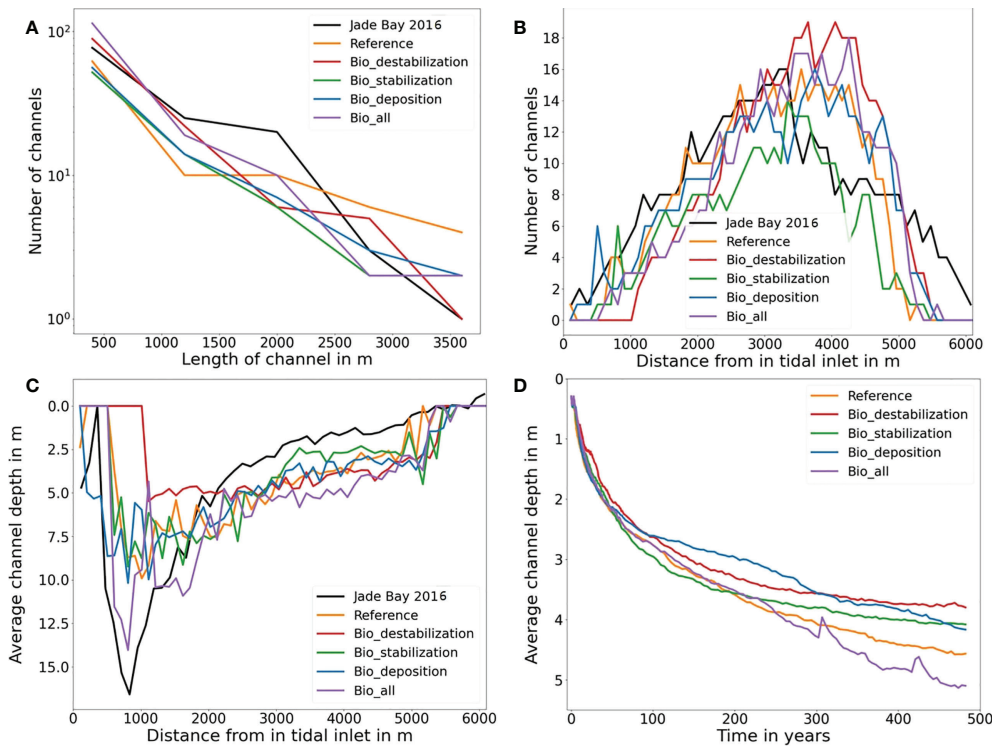
FIGURE 6
Statistics of channels in all simulations at year 500. **(A)** Number of channels in relation to the channel length. Note that the y-axis is in logarithmic scale. **(B)** Number of channels in relation to the distance from the inlet. **(C)** Average channel depth in relation to the distance from the inlet. **(D)** Change of average channel depth with simulation time. Note that statistics of channel in a natural tidal embayment (Jade Bay) are also included in **(A–C)**.

destabilization, the basin morphology evolves in a way that less mud and POC are imported to the basin (so that benthic fauna becomes less leading to less bio- destabilization) and more sediment is exported out of the basin compared to the reference result (Figure 4A). The channel widening in the Bio_destabilization scenario is also caused by a dynamic feedback between deposition, benthic facilitated erosion and hydrodynamics. In the tidal flat area that is in a direct vicinity of the channels, a reduction of current velocities allows deposition of mud and POC, which feeds a growth of benthic fauna there. However, subsequent bio-destabilization caused by benthic fauna facilitates sediment resuspension, causing an erosion at the channel banks. As consequence, the channels become wider instead of deeper compared to the reference result. Deposition of mud and POC as well as resultant benthic faunal biomass are spatially re-organized until a balance between deposition and erosion is established. This feedback mechanism is responsible for creation of the erosional area within 2.5 km from the inlet (Figure 5B) and accounts for wider but shallower channel morphology than the reference result. Bio-destabilization also leads to generation of more short and lower order channels (Figure 6A).

Bio-stabilization

Bio-stabilization caused by benthos and POC on sediment also has a profound impact on long-term morphological development of the tidal embayment (Figure 5C). The effect is opposite to the Bio-destabilization scenario. Time series of calculated net sediment volume change suggest that in this scenario a stable state is met before year 500 (Figure 4A). The hypsometric curve of this scenario (Figure 4B) indicates that the tidal basin exports much less sediment than other scenarios, resulting in a higher overall elevation of the tidal embayment compared to other scenarios and a larger intertidal flat area. Import of mud from offshore area and subsequent deposition increases both the mud content and bio-stabilization effect associated with POC content. These jointly lead to a higher threshold for sediment resuspension and seabed becomes more resilient to erosion. Therefore, the two main channels at the inlet are much shorter compared to the reference result (Figure 5C). The entire embayment becomes increasingly stable along time and impedes the development of low-order bifurcations. This explains why the total number of channels in this scenario is smallest among all scenarios (Figures 5C and 6B). Since tidal currents are confined in fewer major channels, enhanced current
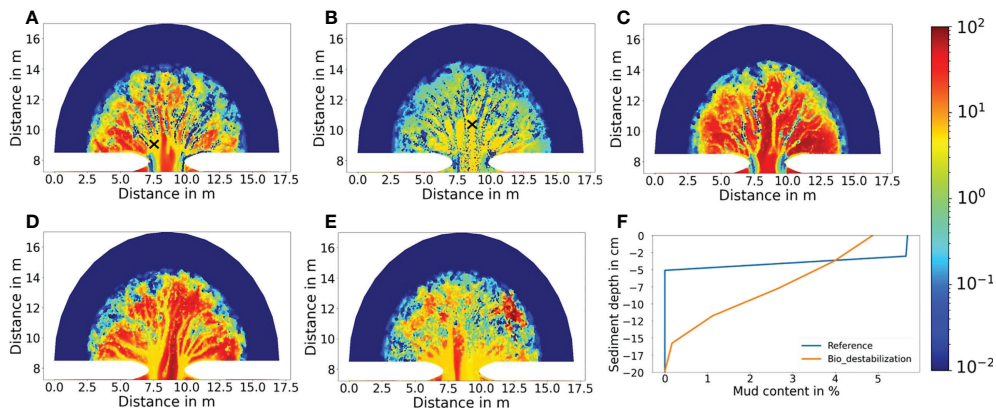
FIGURE 7
Simulated mud content (in percentage) at year 500 for the **(A)** Reference result, **(B)** the Bio_destabilization scenario, **(C)** the Bio_stabilization scenario, **(D)** the Bio_deposition scenario and **(E)** the Bio_all scenario. **(F)** Comparison of typical vertical profile of mud content in seafloor sediment at tidal flats between the reference result (exclusion of benthic faunal impact) and the Bio_destabilization scenario (inclusion of bio-mixing). Locations of the sites are indicted by X mark in **(A)** and **(B)**, respectively.

velocity during peak tidal flows leads to a scouring in the channels. The average channel depth is 4.1 m at year 500 (Figure 6D). However, this value is smaller than the reference result (4.7 m). This is mainly due to the stabilization effect which is also present in lower order channels, where tidal currents are less energetic and allow more deposition of mud and POC than in higher order main channels (Figure 7C).

Benthic stabilization exerted by deposited mud and POC gradually changes the embayment geometry. Due to the stabilization effect less sediment is eroded in the basin and meanwhile deposition of imported mud and POC in the tidal flats is increasingly facilitated. Furthermore, altered hydrodynamics

increase the overall concentration and import of mud and POC to the basin compared to the reference scenario (see Supplement Information). These jointly lead to a net sediment import to the embayment, and an increased basin elevation. Both mud content and POC content are strongly increased in the seabed surface sediment compared to the reference scenario (Figures 7C and 8C). In a large portion of the tidal flats mud content even approaches 100% in the surface sediment layer at year 500.

Bio-deposition

The impact of bio-deposition caused by suspension and filter feeders on morphological development of the embayment
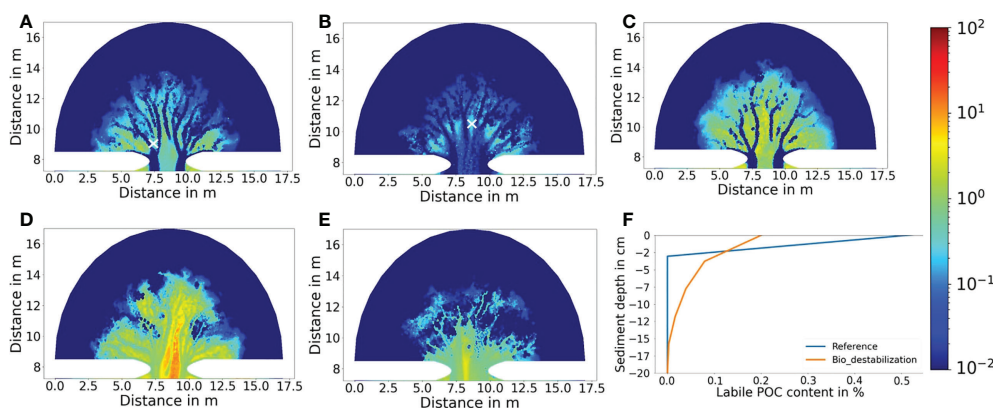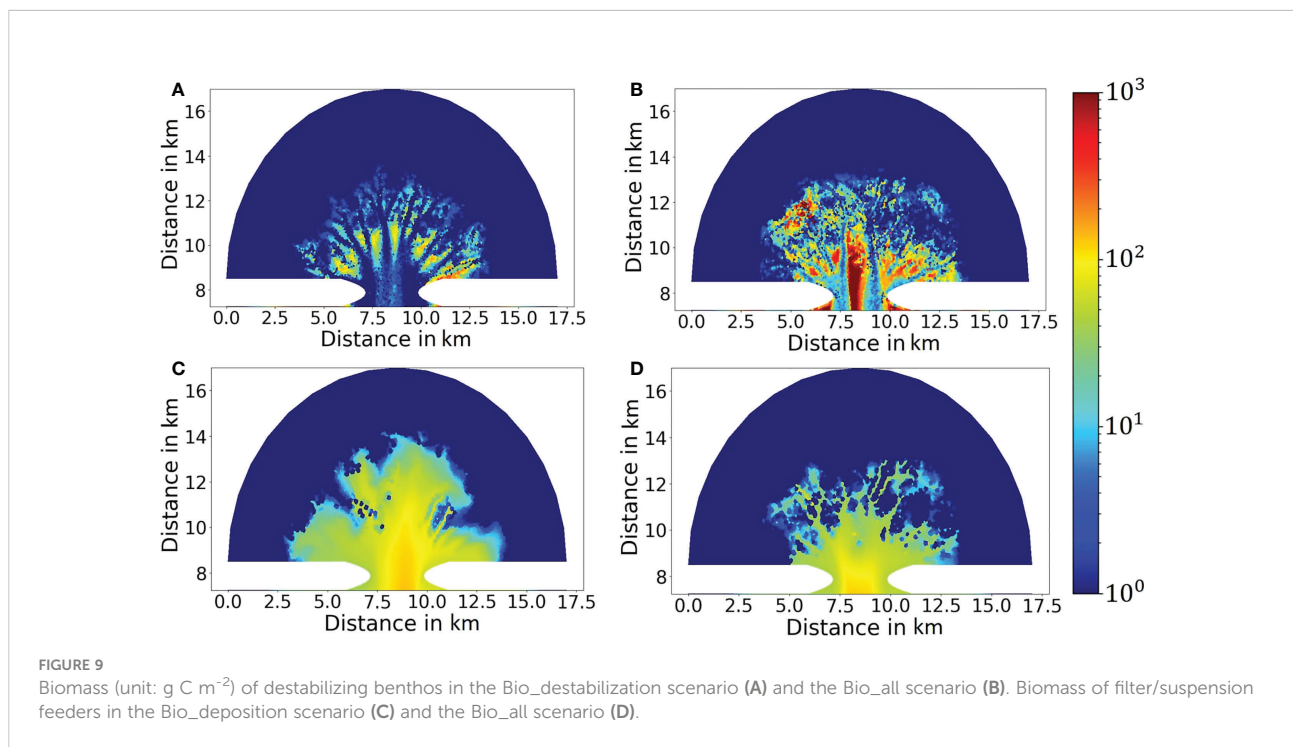

FIGURE 8
Simulated labile POC content in percentage at year 500 for the **(A)** reference result, **(B)** the Bio_destabilization scenario, **(C)** the Bio_stabilization scenario, **(D)** the Bio_deposition scenario and **(E)** the Bio_all scenario. **(F)** Comparison of typical vertical profile of labile POC content in seafloor sediment at tidal flats between the reference result (exclusion of benthic faunal impact) and the Bio_destabilization scenario (inclusion of bio-mixing). Locations of the sites are indicted by X mark in **(A, B)**, respectively.

FIGURE 9
Biomass (unit: g C m^{-2}) of destabilizing benthos in the Bio_destabilization scenario **(A)** and the Bio_all scenario **(B)**. Biomass of filter/suspension feeders in the Bio_deposition scenario **(C)** and the Bio_all scenario **(D)**.

(Bio_deposition scenario) shows both similarities as well as significant differences to the Bio_stabilization scenario. The average channel depth is 4.15 m at year 500 in this scenario (Figure 6D), being very close to the result (4.1 m) in the Bio_ stabilization scenario. High mud and POC content are also seen in a large portion of the tidal flats (Figures 7D and 8D). The hypsometric curve of this scenario lies in between the curves of the reference result and the Bio_stabilization scenario (Figure 4B), indicating that bio-deposition is able to elevate the overall bed level of the embayment, increase the intertidal area and reduce net sediment export compared to the reference result. The statistics of number of channels with regard to the distance to the inlet (Figure 6B) shows a similar channel development pattern to the reference results within a distance of ~3.5 km from the inlet, but with more channels developed further away from the inlet. This indicates that bio-deposition may facilitate bifurcations in low-order channels.

A clear feature in the sedimentation of mud and POC in the Bio_deposition scenario, which marks its major difference with previously mentioned scenarios, is that mud and POC also accumulate inside the channels (Figures 7D and 8D). Mud content ranges from a few up to 10% in the main high-order channels and slightly decreases in secondary low-order channels. POC content shows a similar pattern with maximum value of ~2% in the main channels. Such abnormally high mud and POC content in the channels, in comparison to other scenarios, is attributed to bio-deposition. The simulated biomass of filter/suspension feeders ranges between 20 and 100 g C m^{-2} in the main channels as well as over the tidal flats between the channels (Figure 9C). The high

biomass ensures a high ingestion rate of suspended particles in the bottom water layer and results in a high rate of bio-deposition (as implemented in Equation 7). The spatial distribution of filter/ suspension feeder biomass shows a clear difference with that of bioturbating infauna (Figure 9A). This is because that the latter depends on abiotic (only related to bottom hydrodynamics) deposition of POC, which is favored in tidal flats but impeded in channels due to energetic tidal currents, while the former depends on the amount of suspended POC in the bottom water, which shows small difference between tidal flats and channels.

Combined effects of benthic fauna

In a natural embayment environment, all biological impacts are combined and interact with physical drivers. The hypsometric curve of the scenario which combines all biological impacts (Bio_all) lies in between the curves of the reference result and Bio_destabilization, indicating that in this scenario more sediment is exported out of the embayment than the reference result but the amount is less than that in Bio_destabilization (Figure 4B). Unlike the hypometric curve of Bio_destabilization which is characterized by a plateau corresponding to a similar depth (4-5 m) in the erosional semicircle area within 2.5 km from the inlet (Figure 5B), such pattern is not seen in the Bio_all scenario. Another clear difference is also seen in the channel morphology (Figure 5E). The two main channels at the inlet are deep and wide in this scenario, with relatively sharp boundary (large gradient in bathymetry) with adjacent tidal flats. The number of channels developed within 3.5 km from the inlet is similar to that of the Bio_destabilization scenario and smaller than the reference result. However, more

channels develop further away from the inlet (> 3.5 km) in this scenario than the reference result, although being less than the Bio_destabilization scenario (Figure 6B).

The average channel depth is 5.1 m at year 500, being largest among all scenarios (Figure 6D). This is attributed to interactions between different benthic functional groups (bioturbators and filter/suspension feeders, Figure 11). The coexistence of bioturbators (which destabilize sediments) and filter/suspension feeders (which stabilize sediments) has a profound impact on the embayment morphology. Bioturbators are mainly distributed in the tidal flats while filter/suspension feeders are located in both tidal flats and channels (Figures 9B, D). However, biomass of bioturbators in this scenario is significantly higher than that in the Bio_destabilization scenario (Figure 9A), whilst biomass of filter/suspension feeders is remarkably lower than that in the Bio_deposition scenario (Figure 9C). This result indicates that filter/suspension feeders promote the growth of bioturbators (positive feedback), whilst bioturbators in turn would lead to a decline of filter/suspension feeders (negative feedback). Such feedback is caused by a change of food (POC) availability. Mud and POC content in surface sediments in the Bio_all scenario is higher than that in the Bio_destabilization scenario but lower than the Bio_deposition scenario (Figures 7, 8). This indicates that more food (POC) is transferred into sediment through bio-deposition compared to the Bio_destabilization scenario which excludes this process. The increased POC facilitates an increase of bioturbators in terms of biomass in both tidal flat and channel area. At some parts of the tidal flats (e.g. area between the main channels) the biomass of bioturbators is even increased by an order of magnitude (Figures 9A, B). As the biomass increases, bioturbators exert an increasing destabilization impact on sediment at both the channel edges and within the channel, leading to a widening and deepening of the channels (Figure 5E) compared to the Bio_deposition scenario. Cozzoli (2016) found that in strong hydrodynamic conditions, benthic bioturbation impact may increase at lower density of abundance because of a mutual feedback between hydrodynamics and benthic fauna. This is confirmed in the simulation results showing that the average channel depth is largest in the Bio_all scenario among all scenarios. A widening and deepening of the channels caused by bioturbators lead to a decrease of current velocity and sediment transport rate in the channels. As a consequence, POC availability to filter/suspension feeders is reduced, leading to a decline of their biomass compared to the Bio_deposition scenario (Figures 9C, D).

Discussion

Comparison with existing literature and real environments

Since our simulation results are based on idealized model domain and simplified forcing, a direct point-to-point validation of our simulation results against a real coastal system is not feasible. To assess the reliability of the model results, we divide the model domain into two zones, namely sub-tidal and inter-tidal zones, and compare the simulation results in these two zones with existing literature and data from the Jade Bay in the German Wadden Sea that shares similar environmental configuration (hydrodynamic forcing, domain size, sediment composition) with the idealized model setup in a qualitative and statistical manner. In particular, we focus on comparison of parameters that are relevant to benthic faunal impact, including the spatial distribution of biomass, functional groups, bioturbation intensity, bio-depositional rate and the magnitude of erosion/deposition thickness caused by benthic fauna.

Statistics of the Jade Bay exhibits similar distribution in channel network (Figure 6) and hypsometric curve (Figure 4B) with the simulation results. Biomass of benthic fauna in tidal embayments of the Wadden Sea is found to range between 1 and 100 g C m^{-2} (Beukema, 1974; Dekker, 1989; Essink et al., 1998). In the Jade Bay, measurements conducted in 1930s, 1970s and 2009 show that the spatially averaged biomass of benthic fauna varied between 12 and 20 g C m^{-2} (Schückel et al., 2015a). In 2009, the spatially averaged biomass in the Jade Bay was 19.2 g C m^{-2}, with ~7 g C m^{-2} from filter/suspension feeders and ~12 g C m^{-2} from bioturbators (Schückel et al., 2015a). Compared to the measurement data in the Jade Bay, our simulation result (Bio_all) shows a larger spatially averaged biomass over the entire embayment area (~40 g C m^{-2}), with local peak values up to a few hundred g C m^{-2} (Figure 9). However, although being larger than the measured value in the Jade bay, our simulation result is comparable to data from other tidal embayments. Measurements in the western and northern parts of the Wadden Sea show seasonal fluctuation of spatial average biomass between 10 and 90 g C m^{-2} (Reise et al., 1994; Beukema and Dekker, 2020). In local sites with high abundance of filter/suspension feeders such as mussel beds of *M. edulis*, biomass can reach to 2000 g C m^{-2} (Büttger et al., 2008). Therefore, the predicted biomass of benthic fauna in our simulation results lies in a reasonable range when compared to real tidal embayments. With regard to spatial distribution pattern of functional groups, existing literature suggested its correlation with environmental variables. In the Jade Bay, abiotic variables most strongly correlated to benthic faunal communities are tidal current velocity, water depth, mud and TOC contents, which together account for 35% of the total variation (Schückel et al., 2015b). In addition, Chlorophyll-content, which is correlated with fresh POC, appears to be another important variable significantly correlated with some bioturbating species (e.g. *Peringia ulvae*, *Retusa obtusa*) (Singer et al., 2016). These major influencing variables are taken into account in our model (section 2). The species distribution maps in the Jade Bay compiled by Singer et al. (2016) show that the inter-tidal flats are mainly dominated by bioturbating species (*Tubificoides benedii*, *Peringia ulvae*, *Retusa obtusa*), whilst sub-

tidal channels are inhabited by both bioturbators (*Tubificoides benedii, Scoloplos armiger*) and filter/suspension feeders (*Macoma balthica*). Such distribution pattern is also reproduced in our simulation results (Figure 9).

Bioturbation diffusivity derived by fitting observed vertical distributions of tracers varies over 3 orders of magnitudes (10^{-2}– 10 cm^2 day^{-1}) among different seafloor settings in the North Sea including the Wadden Sea (Boon et al., 1998; Teal et al., 2008; Jørgensen and Parkes, 2010). In addition, bioturbation may vary by more than one order of magnitude even at the same site because of seasonal changes in food supply and in the metabolism of benthic organisms (Brown et al., 2004; Zhang et al., 2019). Compilation of existing measurements by Teal et al. (2008) indicates that the mean value of bioturbation diffusivity in the North Sea is 0.16 cm^2 day^{-1}. Given that the average biomass of benthic fauna in the southern North Sea is ~8 g C m^{-2} according to the ICES survey in 2000 (Rees et al., 2007), the higher abundance of benthic fauna in the Jade Bay (19 g C m^{-2}) should result in higher bioturbation intensity than in the southern North Sea. Therefore a mean value of bioturbation diffusivity larger than 0.16 cm^2 day^{-1} is expected in the Jade Bay, despite that actual field measurements in the Jade Bay are absent. Our simulation results indicate that the bioturbation diffusivity ranges between 0.01 and a 10 cm^2 day^{-1} in the tidal embayment with a spatial mean value of 0.41 cm^2 day^{-1} (Figure 10A), which may serve as a reference value for the Jade Bay and other embayments in the Wadden Sea to assess a regional impact of bioturbators in mediating particle fluxes. Modeled bio-deposition rates range from 0.1 to 100 g m^{-2} day^{-1} (Figure 10B). This value range is in line with studies of *Mytilus edulis* with bio-deposition rates between 0.2 – 1.2 g m^{-2} day^{-1} for sparsely populated small patches (Kautsky and Evans, 1987). Oyster beds of *Cassostrea gigas* are reported with rates of 40-180 g m^{-2} day^{-1} (Mitchell, 2006). Mussel beds in the North and Wadden Sea can reach several 100 g m^{-2} day^{-1} (Dittmann, 1987; Flemming and Delafontaine, 1994).

A comparison of hypsometric curves of the Jade Bay between 2001 and 2016 (Figure 4B) suggests that the area underwent slight erosion during 2001-2016. The curve of 2016 shows a plateau at water depth of ~2 m which is the transition

depth between intertidal (tidal flats) and subtidal (channel) areas. Such plateau is a characteristic of the scenario Bio_destabilization as described previously. On the other hand, this feature is not evident in the curve of 2001. A remarkable shift in proportion of functional groups between 1970s and 2009 was observed in the Jade Bay, with bioturbating deposit feeders (destabilizers) increased from ~ 20% to almost 70% (Schückel and Kröncke, 2013). Such increase of bioturbators might explain the plateau feature and decrease in the hypsometric curve of 2016, which is supported by our simulation results (Bio_destabilization).

Former bio-morphological modeling studies indicate that changes in deposition and erosion caused by benthic fauna can be in the same order of magnitude as changes caused by hydrodynamic drivers (Wood and Widdows, 2002). This is confirmed in our results. Existing investigations on short-term (monthly to decadal scale) impact indicate that the average thickness of deposition and erosion caused by benthic fauna ranged from a few cm (Wood and Widdows, 2002; Paarlberg et al., 2005; Lumborg et al., 2006) to a few tens of cm on a monthly scale (Paarlberg et al., 2005), from a few mm (Borsje et al., 2008) to a few tens of cm on an annual scale (Orvain et al., 2012) and several m on a decadal scale (Brückner et al., 2021). Such order of magnitude in morphological change and its time scale dependence are also seen in our simulation results. Further, our results indicate that the difference in average thickness of deposition or erosion between bioturbated and non-bioturbated scenarios is around 1 m at both the channel and tidal flats at year 500 (Figure 6). Such results imply that on a long-term (centennial) scale, the most significant impact of benthic fauna on large-scale coastal morphological development is a re-organization of the channel network and hypsometric distribution, rather than an absolute change in elevation.

Future research needs

Dynamic interactions between biota and landform have been recognized as a critical mechanism in controlling
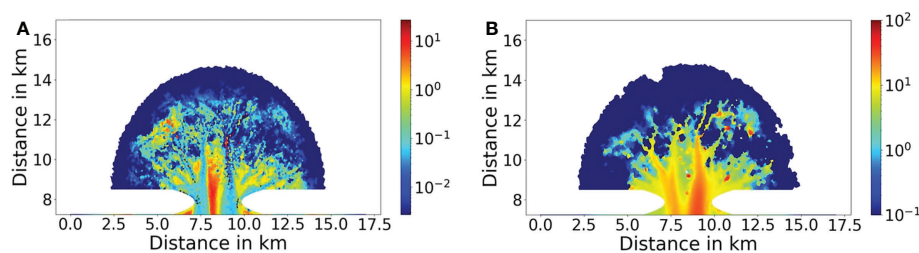

FIGURE 10
Bioturbation diffusivity (**A**, unit: cm2 day-1) by bioturbators and bio-deposition rate (**B**, unit: g m-2 day-1) by filter/suspension feeders in the Bio_all run.

morphological evolution of complex coastal systems (Murray et al., 2008; Reinhardt et al., 2010; Marani et al., 2010). On the other hand, a recent review by Arlinghaus et al. (2021) pointed out that the development of bio-morphodynamic numerical models remains still at an initial stage and these models are of limited use for explanation and prediction of natural systems. The authors attributed the reasons to (1) lack of understanding of fundamental biological/bio-physical processes affecting morphological development and especially dynamic feedback loops among them, (2) scarcity in data for model calibration of biological/bio-physical processes, and (3) scarcity in data for confirming model results. An appropriate model complexity needs to be found in order to reconcile the limitations of process understanding on one hand and the ability to calibrate and validate the model on the other hand (French et al., 2016; Larsen et al., 2016). For this reason, most existing modeling studies only regard one-way control of benthic fauna on morphodynamics, and are focused on species level with a few species and small spatial scale (Arlinghaus et al., 2021). Some recent studies underline the necessity of differentiating between species of the same functional group and focusing on their mutual interactions (such as competition and grazing) and interaction with the environment (Brückner et al., 2020; Brückner et al., 2021). In an estuarine environment, Brückner et al. (2021) found that morphological change can be mainly driven by efficient bioturbators albeit with a small abundance, whilst highly abundant but less effective species only have minor impact. Direct interactions between these species determine each other's abundance and indirect feedback over eco-engineering of the habitat creates suitable area for co-existing species. These results clearly highlight the importance of feedback control and implementation of species interaction in numerical modeling.

In this study, we propose a simplified implementation of multi-functional groups instead of species. Although no direct species interaction was implemented in the model, indirect feedback was mediated *via* the availability of food (POC). A negative feedback from erosion to bioturbators is a shortage of food that limits the increase of biomass and therefore would lead to a decrease of bioturbation and bio-destabilization. Sedimentation of mud and POC promoted by EPS and filter/suspension feeders is a positive feedback increasing the biomass of bioturbators. In addition, a geomorphological feedback arises between the benthos and the altered hydrodynamic conditions of the system towards a higher or lower sediment and POC import. This geomorphological feedback is guided by the relative expansion (Bio_stabilization, Bio_deposition) and reduction (Bio_destabilization) of tidal flats seen in the hypsometry (Figure 4B) which favors flood dominance and subsequent sediment import in the first case and ebb dominance and sediment export in the latter case (Zhou et al., 2017). Such indirect feedbacks between functional groups and between functional groups and morphology are illustrated in Figure 11. The positive geomorphological feedback of species promoting

bio-deposition and stabilization may thus lead to a continuous growth of tidal flats which become increasing shallower over time, while at the same time the benthic faunal biomass continuously increase. Adding the negative feedback control of bioturbators may counteract this trend by preventing tidal flat expansion and reducing the food supply to deposition- and stabilization-promoting species. Therefore, the hypsometric curve of the Bio_all scenario lies in between the purely destabilized scenario on the lower limit and the purely stabilized scenario on the upper limit (Figure 4B). Furthermore, bio-stabilization and deposition may facilitate growth of bioturbators in hydrodynamically active regions, resulting in a larger channel depth (Figure 6D) and width (Figure 5E) when comparing Bio_all with the other scenarios. Clearly, more research efforts are needed to incorporate dynamic interactions between biota and landform as well as interactions between different functional groups of biota in quantitative analysis and modeling of coastal systems.

Conclusions

By application of a novel 3-dimensional numerical model resolving dynamic interactions between environmental drivers and benthic fauna to a simplified tidal embayment configuration, this study aims to understand (1) the quantitative importance of benthic fauna in guiding long-term (decadal to centennial) coastal morphological evolution at a large and regional scale, (2) the individual and combined impact of multiple benthic functional groups in shaping coastal morphology and (3) interaction between benthic fauna and hydro-morphodynamics. Comparison with a real tidal embayment (Jade bay in the Wadden Sea) and existing literature justified the general validity of the model results, leading to the following conclusions.

Each of the investigated benthic faunal impacts, namely bio-destabilization caused by bioturbators, bio-deposition by filter/suspension feeders, and bio-stabilization associated with EPS secreted by benthic organisms including microphytobenthos and bacteria, may lead to a profound change of the embayment morphology in terms of development of channel network (channel depth, width, length and bifurcations) and overall elevation of adjacent tidal flats. Bioturbation-induced sediment mixing and bio-destabilization may result in a net sediment export out of the embayment, whilst bio-deposition and bio-stabilization tend to alter the embayment toward a net sediment import environment. A combined effect of these biophysical processes leads to a unique response of the embayment morphology due to interactions between different benthic functional groups. While bioturbators promote erosion which has a negative feedback (reduction of food) to their growth, a positive feedback exerted by suspension/filter-feeders increased the biomass and spatial abundance of bioturbators. In addition, a negative geomorphological feedback by bioturbators through enhanced
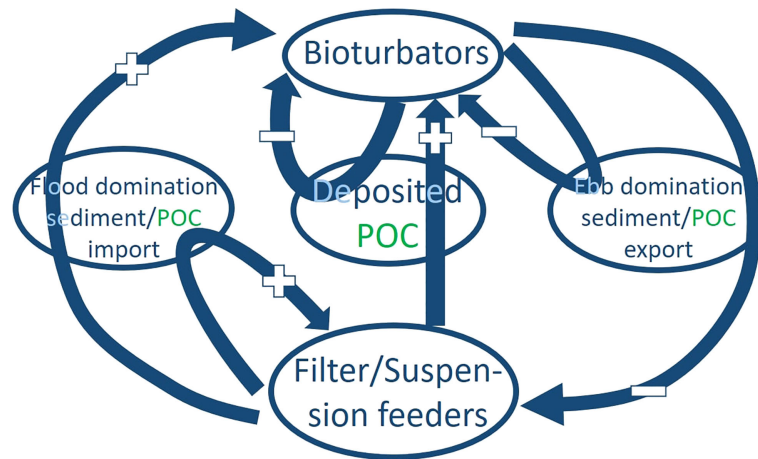
FIGURE 11
Illustration of feedback between two major functional groups in terms of growth ("+") or decline ("-") in biomass. Internal feedback within each of the group is also indicated.

erosion decreases the biomass of suspension/filter-feeders compared to the case in which bioturbators are absent.

From a modeling perspective, development of bio-morphodynamic models should consider not only dynamic interactions between biota and landform but also interactions between different benthic lifeforms, which is equally important in guiding morphological development of complex coastal systems.

Data availability statement

Publicly available datasets were analyzed in this study. This data can be found here: https://datenrepository.baw.de/startseite.

Author contributions

All authors conceived and designed the study. Numerical simulations were supervised by WZ and carried out by PA. PA and WZ analyzed results and wrote the paper. All authors contributed to manuscript revision. All authors approved the final version of the manuscript and agree to be held accountable for the content therein.

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Conflict of interest

Publisher's note

Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fmars.2022.1011760/full#supplementary-material

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4. Benthos as a key driver of morphological change in coastal regions.

This chapter contains a paper which was published in Earth Surface Dynamics:

Earth **Surface**
Dynamics

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 of tidal coastal regions. To achieve this, we first 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 rates and deposition rates, erosion and hydrodynamics in a 3-dimensional hydro-eco-morphodynamic model, which was then applied to Jade Bay to hindcast the morphological and sediment change for 2000–2009. Simulation results indicate significantly improved performance with the benthos effect included. Simulations including benthos show consistency with measurements regarding morphological and sediment changes, while abiotic drivers (tides, storm surges) alone result in a reversed pattern in terms of erosion and deposition contrary to measurement. Based on comparisons among scenarios with various combinations of abiotic and biotic factors, we further investigated the level of complexity of the hydro-eco-morphodynamic models that is needed to capture long-term and large-scale coastal morphological development. The accuracy in the parameterization data was crucial for increasing model complexity. When the parameterization uncertainties were high, the increased model complexity decreased the model performance.

1 Introduction

Benthos includes flora such as seagrass, kelp, and salt marsh species, which predominately stabilize sediment (Corenblit et al., 2011; Zhang et al., 2012, 2015), and fauna with more complex behaviors that can stabilize or destabilize sediment (Backer et al., 2010). Benthic in- and epifauna actively rework sediment in order to increase the availability of resources for themselves (Jone et al., 1994; Meadows et al., 2012) and play a critical role in modifying sediment prop-

erties 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 the 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 (Lindqvist et al., 2016; Queiros et al., 2013; Meyer et al., 2019; Weinert et al., 2022), bioirrigation (Wrede et al., 2017), bio-deposition and bio-resuspension

(Cozzoli et al., 2019; Graf and Roseberg, 1997), faecal pellet production (Andersen and Pejrup, 2011; Grant and Daborn, 1994; Troch et al., 2008), and biofilm stabilization (Le Hir et al., 2007; Stal, 2010). All of the ways in which benthos changes and modifies the sediment directly or indirectly are termed bioturbation (Meysman et al., 2007). The impacts of bioturbation on sediments can individually or accumulatively lead to dramatic local morphological changes, as demonstrated by defaunation experiments (Volkenborn and Reise, 2006; Volkenborn et al., 2009; Montserrat et al., 2008). However, 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 (kilometer to basin scale) coastal morphological change.

Over the past 3 decades, increasing efforts have been dedicated to upscaling 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 can cause the 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, the 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 in the system from an initial state to the final state as accurately 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 reasons are 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., 2014; 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-morphodynamic modeling. For this purpose, Jade Bay, a tidal embayment located in the German Wadden Sea, was chosen to test the model. The reason for choosing 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 Jade Bay are commonly found worldwide (Haas et al., 2018). They are among the most productive ecosystems on the Earth's surface, providing a variety of ecosystem functions (Mitsch and Gosselink, 2007) and serving as important habitats for marine life-forms (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). 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., 2018), or be drowned (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 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 does benthos account for the observed changes in the morphology and sediment composition in the study area?

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 Jade Bay have a combined length of approx. 36 km and vary in width between 4 and 15 km, covering around 370 km^2, with 160 km^2 inside the bay, about 60 % of which is comprised of tidal flats (Lang, 2003). Jade Bay is a meso-tidal system with a tidal range of ca 3.7 m (Svenson et al., 2009). The water depth
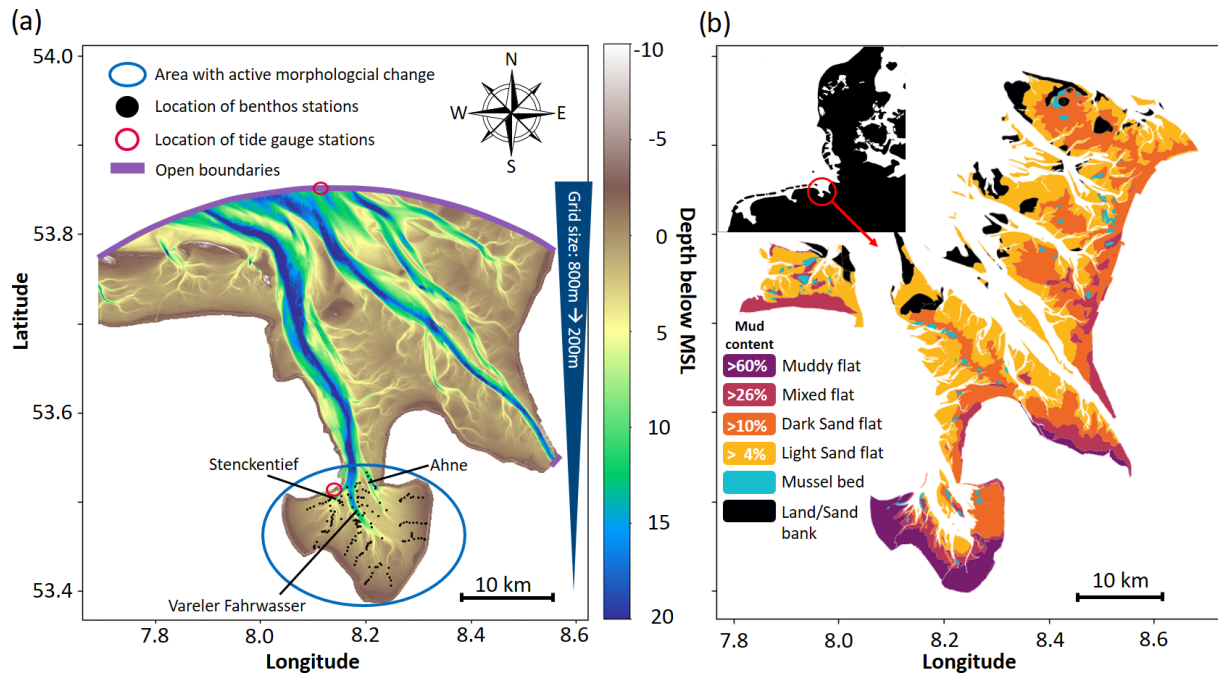
Figure 1. (a) Computational domain and its open boundary, including the initial morphology at 2001, the location of benthos data, and tide gauge stations. **(b)** Distribution of sediment types, including land and mussel beds (Meyer and Ragutski, 1999).

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, and 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 $0.4\,\text{km}^3$ per tidal cycle with speeds exceeding $1.5\,\text{m\,s}^{-1}$ in the channels (Götschenberg 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*). In terms of biomass, the most abundant organisms are Bivalvia (*Cerastoderma edule* and *Macoma balthica*), Gastropoda (*Peringia ulvae*), and Polychaetes (*Arenicola marina, Hediste diversicolor*, and *Tubificoides benedii*), with a spatially averaged biomass of $20\,\text{g\,C\,m}^{-2}$ according to Schückel et al. (2015b). Typical values of benthic biomass range between 1–$100\,\text{g\,C\,m}^{-2}$ in the Wadden Sea (Beukema, 1974; Reise et al., 1994; Beukema and Dekker, 2020).

3 Methods

3.1 Machine-learning-aided mapping of macrobenthos

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 biomixers, stabilizers, accumulators, and seagrass. Biomixers and accumulators consist of macrobenthos, while stabilizers are represented by a biofilm which is mainly assembled by microphytobenthos (MPB) of all contributing species. The seagrass present in Jade Bay belongs to the species *Zostera noltii* (Adolph, 2010).

The existing field dataset provides macrobenthos abundance in the inter-tidal area and abundance plus biomass for the subtidal area at 160 stations in Jade Bay (Senckenberg; Schückel and Kröncke, 2013; Schückel et al., 2015a). Based on the intertidal abundance values and biomass averages from the subtidal measurements, the intertidal biomass could be calculated (Fig. 2b–f). The total measured biomass in Jade Bay is dominated by a few species which are widely distributed in the area. Since the metabolic rate of biomixers 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 the area, namely the mussels *Cerastoderma edule* (accumulator) and *Macoma balthica* (accumulator and biomixer),

the snail *Peringia ulvae* (biomixer), and the worms *Hediste diversicolor* (biomixer) and *Tubificoides benedii* (biomixer). Complete mapping of benthos for the entire Jade Bay is done by extrapolation from 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., 2021). Species abundance modeling (SAM) is developed from SDM and has an increased solution space, since the output represents decimal values covering the whole range of measured abundance spectrum or biomass spectrum, respectively. Existing studies show the best results when using decision trees (Luan et al., 2020; Waldock et al., 2021). For this reason, we adopted a decision-tree-based SAM to generate a complete map of benthos in the study area. A detailed description of the method and an analysis of the applied dataset are provided in the Supplement.

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 Jade Bay SDM results by Singer et 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 Jade Bay area. In addition, the SAM was extended to cover the inner and outer Jade. However, in this area there are 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 SAMs were applied for each species, with one for abundance and one for biomass, in order to calculate the mean individual biomass which is needed for the parameterization of benthos impacts on sediment. We used 90 % of the species data points for model training and the remaining 10 % to test the model performance.

Although the field dataset of benthos abundance and biomass is uniquely comprehensive for a tidal basin in the Wadden Sea, seasonal variations were not covered. To take into account seasonal variations in the benthos impact, a simple sinusoidal function describing the change in the biomass and related bioturbation intensity (see details in Sect. 3.2.1) was used in some of the model experiments described in Table 3.

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, namely the critical shear stress for erosion τ_c (Pa), the erosion rate E_r (kg m^{-2} s^{-1}), the sediment-settling velocity W_{sed} (mm s^{-1}), and hydrodynamic parameters for 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 the erosion rate E_r^0 is scaled by dimensionless biomixing functions p_d, g_d and stabilization functions p_s, g_s, respectively, which depend on the abundance A (number of individuals) and biomass B (milligrams of ash-free dry weight (AFDW)) of these two functional groups:

$$\tau_c = \tau_c^0 \cdot p_d(B, A) \cdot p_s(B, A), \tag{1}$$

$$E_r = E_r^0 \cdot g_d(B, A) \cdot g_s(B, A). \tag{2}$$

Changes in hydrodynamics by the effect of seagrass are incorporated using the submerged aquatic vegetation model (SAV) of SCHISM (Zhang et al., 2016), and changes in W_{sed} by the effect of accumulators are applied according to a filter-feeder ingestion rate model (US Army Corps of Engineers, 2000). Both are explained in the following sections. No direct control between different functional groups is considered in the presented simulations.

3.2.1 Biomixers

The main effect of biomixers is sediment destabilization. However, biomixing macrobenthos can also increase sediment stability in certain conditions of the metabolic rate, bottom shear stress, and sediment composition (Cozzoli et al., 2019), which is attributed to hardening of mucus excreted during locomotion (Orvain, 2002; Le Hir et al., 2007). In our model, the formulae from Cozzoli et al. (2019) are adopted to relate biomixing effect with the overall metabolic rate M_{TOT} (mW). In this study, measurements of the total eroded sediment per unit area in a given time, R_{TOT} (g m^{-2}), were taken. Assuming that the erosion rate (kg m^{-2} s^{-1}) over the given time is constant, it can be described by

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

where the factors a (g m^{-2}) and b (Pa) are related to M_{TOT} and B, c (Pa) is an empirical constant, and τ_b is the bottom shear stress. In order to calculate M_{TOT}, measurements from Cozzoli et al. (2019) (Table 1) are used to estimate the individual metabolic rate (M_{Indv} (mW)) from the individual biomass (B_{Indv} (milligrams of AFDW)):

$$M_{Indv} = 0.0067 \cdot B_{Indv}^{0.835}. \tag{4}$$

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 the total metabolic rate M_{TOT} by multiplying it with the abundance A. The derived value of M_{TOT} is then used to calculate the factors a and b under the biomixing impact (a_{bio} and b_{bio}):
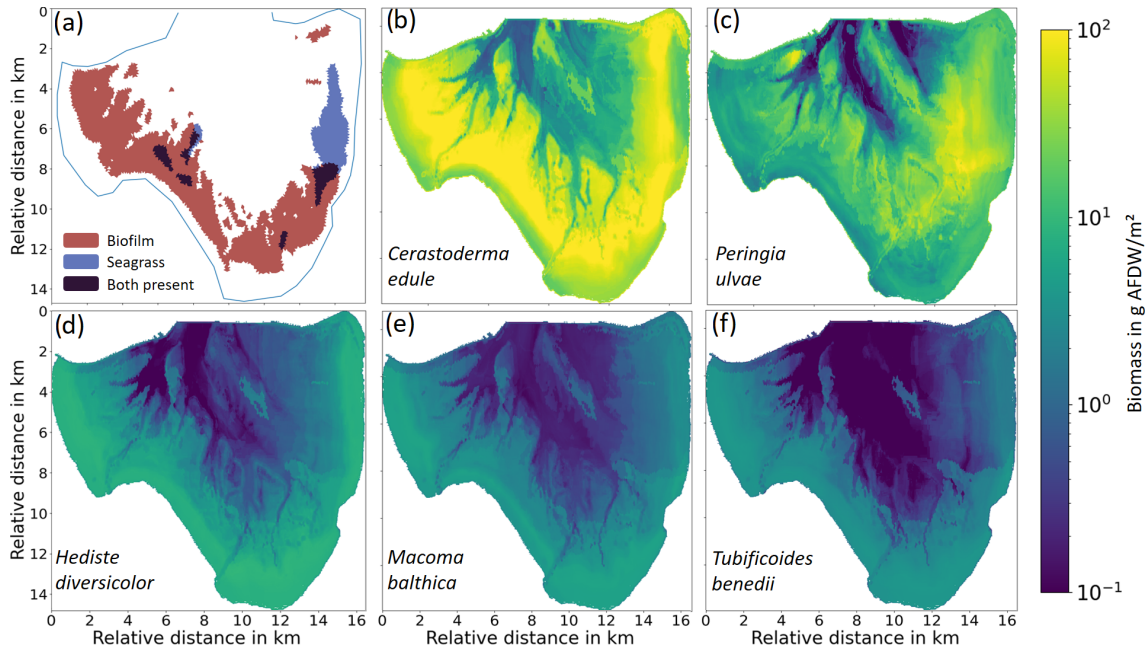
Figure 2. (a) Presence of stabilizers and seagrass according to Adolph (2010). **(b–f)** Modeled biomass distribution of the five dominant benthic faunal species.

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

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

The total eroded sediment under biomixing 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 biomixing function g_d:

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

The other biomixing 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 $25\ \mathrm{g\,m^{-2}}$ is reached. This is done by converting Eq. (3) into

$$\tau_c = b - c \cdot \log\left(\frac{a - R_{25}}{R_{25}}\right). \quad (8)$$

τ_c^0 is calculated using a_0, b_0, and c_0, which are constants for the defaunated control experiments given in Table 1 in Cozzoli et al. (2019). For τ_c^{bio}, a_{bio}, b_{bio}, and c_0 are used. p_d is then calculated via

$$p_d = \frac{\tau_c^{bio}}{\tau_c^0}. \quad (9)$$

g_d and p_d are calculated by adding up all biomixing species considered in the SAM. For 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).

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, biomixing intensity may also decrease accordingly. To account for this seasonal variability, a multiplication factor for M_{TOT} was introduced according to a sine function with a period of 1 year, reaching the maximum value of 1.0 in summer and the minimum value of 0.1 during winter.

3.2.2 Stabilizers

The stabilization functions p_s and g_s are related to biofilm, which is primarily built by microphytobenthos (MPB). According to measurements by le Hir et al. (2007) and Waeles et al. (2004), an increase in the critical shear stress for erosion (τ_c) by a factor of 4 ($p_s = 4$) is implemented for the summer months (from June to September) when MPB is present. For the rest of the year, a factor of 1 is used because MPB is mostly not present in winter and thus has no effect ($p_s = 1$). The erosion rate (E_r) is assumed to be unaffected by MPB; thus, g_s is set to 1 as a constant.

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. (2015a)
Benthos	Param.	–	Laboratory erosion measurements with different species at different densities	Cozzoli et al. (2019)
Benthos	Param.	–	Filter feeding rate for accumulators	U.S. 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)
Sediment	Valid.	1996–2009	Map of sediment change	Ritzmann and Baumberg (2013)
Forcing: tides	Init.	2001–2009	Finite-element global ocean tide atlas	FES2014 Lyard et al. (2021)
Forcing: storms	Init.	2001–2009	Observed water elevation data at the gauge station Alte Weser Lighthouse	Wasserstraßen- und Schifffahrtsverwaltung des Bundes (WSV, 2023)
Water level	Valid.	2001–2009	Observation data at the gauge station Wilhelmshaven	Wasserstraßen- und Schifffahrtsverwaltung des Bundes (WSV, 2023)
Morphology	Init. + Valid.	2001–2009	High-resolution morphology of the German Bight	Sievers et al. (2020)

3.2.3 Accumulators

The presence of accumulators (mainly 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 ($\mathrm{L\,mg^{-1}}$) of accumulators, which scales with biomass B_{acc} ($\mathrm{mg\,AFDW\,m^{-2}}$). In this study, a simplified version of the filter-feeder model from the U.S. 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

$$W_{\mathrm{sed}} = W_{\mathrm{sed}}^0 + I \cdot B_{\mathrm{acc}}, \qquad (10)$$

where W_{sed}^0 represents the settling velocity without the effect of accumulators. Further details of the parameterization are provided in the Supplement.

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 (mm), stem diameter d (mm), stem density N ($\mathrm{m^{-2}}$), and drag coefficient for vegetation c_{D}. The parameters were chosen according to the vegetation cover and the common densities of $Z.\ noltii$ in the German Wadden Sea (Adolph, 2010) and are listed in the model setup section (after Sect. 3.3). Seasonal change in the seagrass is not included in this study due to a lack of field data support for parameterization.

3.3 Hydro-eco-morphodynamic numerical model

The formulae for the benthos effect on sediment dynamics described in Sect. 3.2 are integrated into a 3-dimensional modeling system SCHISM (Zhang et al., 2016) to simulate hydro-eco-morphodynamics. 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 are computed with a finite-volume method (FVM) approach for a flexible number of vertical layers, allowing the transition between regions of different depth and resolution (Zhang and Baptista, 2008). Turbulence closure is implemented according to the k–kℓ closure scheme described in Umlauf and Bur-

chard (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 bedload, 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.

3.4 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 approx. 800 m in the outer Jade Bay and an increasing resolution toward Jade Bay, with a resolution of approx. 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, and 2N2) extracted from the global ocean tide atlas FES2014 (Lyard et al., 2021), as well as observed storm surges which were implemented in terms of water level changes (see the Supplement). These changes are based on measurements at a gauge station (Alte Weser Lighthouse) located at the open boundary (Fig. 1a). Discharge is specified for the Weser River at the southeastern 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). Seasonal variability in the suspended sediment concentration (SSC) at the open boundary was not implemented due to the lack of measurement data. Turbidity and sediment concentration measurements from Jade Bay typically cover one or a few points measured over one or a few tidal cycles (Götschenberg and Kahlfeld, 2008; Becker, 2011), while longer and larger-scale measurements were absent. SSC values in the presented simulations are in the same range as the measurements from Jade Bay (Becker, 2011) and comparable to another simulation study in Jade Bay (Kahlfeld and Schüttrumpf, 2006). A map of the simulated SSC is provided in the Supplement (Fig. S7).

Datasets from various sources are used to initialize, parameterize, and validate the model. A brief summary of these datasets is given in Table 1. The model is used to hindcast the change in the morphology and sediment composition in Jade Bay from July 2001 until December 2009. The measured morphology in 2001 serves as the initial condition. There are no sediment property measurements for the periods around

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

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

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.

In order to disentangle the impacts of benthos, including the effect of individual functional groups and the combined effect of all functional groups and abiotic drivers on morphological and sediment change in 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 in the physical forcing (e.g., with and without storms) and benthos (e.g., with and without seasonality). In addition, an increased erosion rate was applied to some experiments that excluded biomixers for comparability reasons. Biomixers strongly enhance SSC, which leads to an increase in the impact of other functional groups such as accumulators. To achieve comparable SSC levels in simulations excluding biomixers, the basic erosion rate (E0) was increased by a factor of 10 (E10), which helps to distinguish the effects of certain functional groups from scenarios with all benthic groups included.

4 Results

4.1 Mapping of benthos

To assess the performance of the decision-tree-based SAM, the measured data were split into training and validation datasets. The training dataset was used for training the model, and the validation dataset was checked against the resulting estimations of biomass and abundance. The performance of the SAM varies among the selected species. For the majority of the points, the estimated value deviates from the measured value by less than 20 % (Fig. S2). Biomass and abundance distributions of all five species are shown in Fig. 2b–f.

For stabilizers, biofilm built by MPB is considered, which is only distinguished by its presence or absence in the field data. We applied a formulation relating the growth of MPB-based biofilm to the inundation period and mud content, fol-

Table 3. Model experiments are designed for a combination of different physical forcing and functional groups which are abbreviated as mix (biomixers), *acc* (accumulators), *sta* (stabilizers), *gra* (seagrass), all (inclusion of all functional groups), and *abio* (abiotic model run without consideration of any benthos effect). Seasonal variations in benthos impact are abbreviated as *no* (followed by the abbreviation of a specific functional group) if they were excluded or included. Hydrodynamic forcing excluding or including storm surges is abbreviated as T or TS, and a default erosion rate or an erosion rate scaled by a factor of 10 is abbreviated as 1 or 10. The experiments are named by combination according to the different model features, separated by an underscore, and read as modeled functional groups_seasonality_hydrodynamics_erosion rate. For example, in the model experiment acc_acc_TS_10, accumulators are the simulated functional group, seasonality of accumulators was considered, both tides and storm surges were considered hydrodynamic forcing, and the erosion rate was scaled by a factor of 10.

	E0	E0 + storm	E0 + storm + seasonality	E0 + storm + seasonality all	E10	E10 + storm	E10 + storm + seasonality
All benthos	all_no_T_1	all_no_TS_1	all_mix_TS_1	all_all_TS_1	–	–	–
Biomixers	mix_no_T_1	mix_no_TS_1	mix_mix_TS_1	–	–	–	–
Stabilizers	sta_no_T_1	sta_no_TS_1	sta_sta_TS_1	–	sta_no_T_10	sta_no_TS_10	sta_sta_TS_10
Accumulators	acc_no_T_1	acc_no_TS_1	acc_acc_TS_1	–	acc_no_T_10	acc_no_TS_10	acc_acc_TS_10
Seagrass	gra_no_T_1	gra_no_TS_1	–	–	gra_no_T_10	gra_no_TS_10	–
Abiotic drivers only	abio_no_T_1	abio_no_TS_1	–	–	abio_no_T_10	abio_no_TS_10	–

lowing the studies by Widdows and Brinsley (2002) and Daggers et al. (2020). In Jade Bay, only the western and southern parts are inhabited by extensive biofilms (Fig. 2a).

Seagrass distribution in 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).

4.2 Assessment of hydro-eco-morphodynamic model performance

Simulated time series of the water level in all experiments are quite similar and exhibit differences only during storm periods between the experiments with and without storms. A comparison with measured water level at a tide gauge station in Wilhelmshaven, which is located at the inlet of Jade Bay, shows a satisfactory model performance (Fig. 3). Taking the reference experiment abio_no_TS_10 as an 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 Alte Weser Lighthouse, the values are 1.03 and 0.99 m, respectively. The correlation coefficient between the modeled water elevation and measured data is 0.98 at Wilhelmshaven and 0.96 at Alte Weser station (Fig. 3b).

The simulated change in the sediment composition and morphology in all experiments is compared and evaluated. First, 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.

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 the comparison in Fig. 4. Two indicators, namely the RMSE and the cosine similarity between the modeled and measured morphological change, were calculated for each of the experiments and are shown in Fig. 4.

The RMSE (Fig. 4a) shows the best model performance in the group of experiments (all_x) which takes into account the combined effect of all benthos functional groups, followed by the group of experiments (mix_x) which includes the effect of biomixers only. The experiments (acc_x) which include only the accumulators show a better performance than the reference experiments (abio_x) which consider only abiotic drivers, while the experiments which include only seagrass (gra_x) or stabilizers (sta_x) do not show noticeable improvement compared to abiotic scenarios. The difference in the RMSE between the model results with the best and the worst performance is about 15 cm, which is 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 (all_x) which includes all functional groups, better model performance is gained when storms are included (all_no_TS_1) and the seasonality of the dominant functional group, namely the biomixers, is included (all_mix_TS_1). However, model performance decreases when the seasonality of all functional groups is considered (all_all_TS_1). The decrease in the model performance due to the inclusion of seasonality is also seen in other experiments which consider only one functional group, while an inclusion of storms only slightly enhances or does not affect the performance of these experiments. On the other hand, an increase in the erosion rate by a factor of 10 improves the performance of the simulations which considers only abiotic drivers (abio_x) and those which include only one functional group (gra_x, acc_x, and sta_x), although their performance is still worse than the experiments with combined effect of all functional groups (all_x).
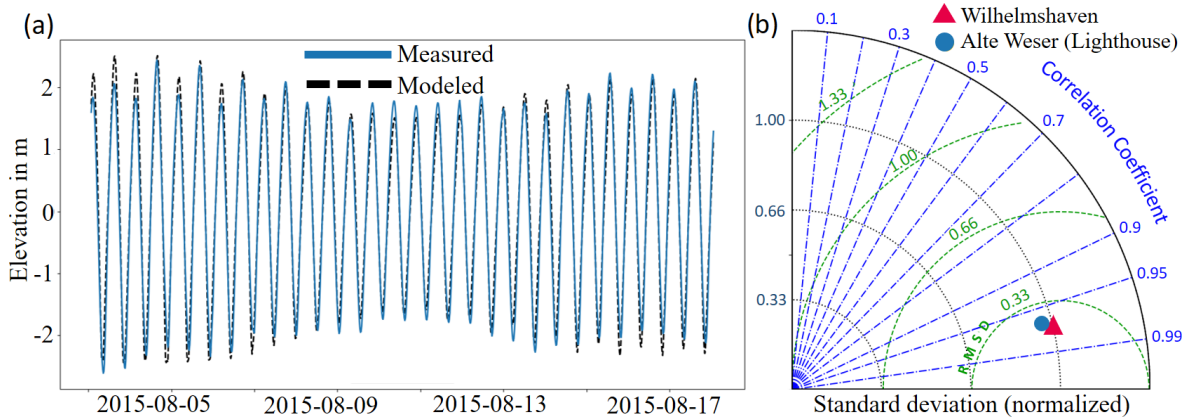
Figure 3. (a) Modeled and measured water elevation at the tide gauge station in Wilhelmshaven. **(b)** Comparison between model results and measurement at the gauge stations in Wilhelmshaven and the Alte Weser Lighthouse in a Taylor diagram.
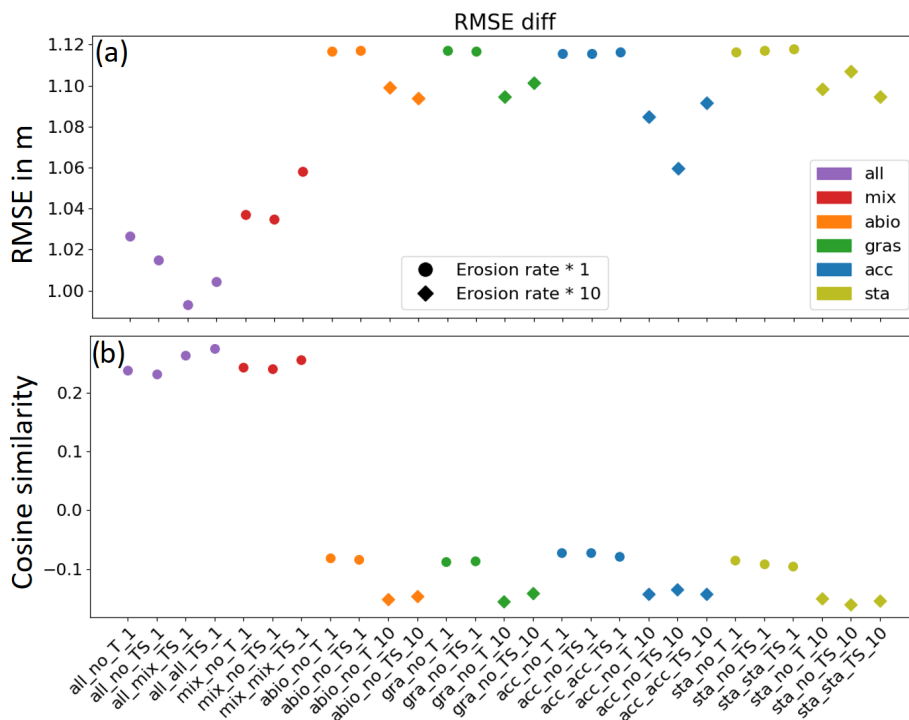

Figure 4. Performance of all simulations in terms of **(a)** RMSE between the modeled and measured water depth change over the entire bay and **(b)** cosine similarity in the main channels. The values 1, −1, and 0 indicate positive, negative, and no correlation between modeled and measured depth change, 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 and a run including storms to a run including the seasonality of the benthos effect (Table 3).

The cosine similarity between the modeled and measured morphological change provides a further evaluation of the model performance in capturing the change in the main to-pographic units. It is a measure of similarity between two non-zero vectors which can be derived from the Euclidean dot product. In our evaluation, the cosine similarity is calculated for the main tidal channels (Stenckentief, Vareler Fahrwasser, and Ahne; see Fig. 1). Results (Fig. 4b) show

that in the experiments with all benthos (all_x) and with the inclusion of only biomix (mix_x), 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 the measurement. It is worth noting that an increase in the ero-

sion rate by a factor of 10 further strengthens the negative correlation in these experiments.

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 0.8 m) inside the main tidal channels accompanied by net erosion (up to 1.2 m) at adjacent flats from 2001 to 2009 (Figs. 5b and 6). 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 mostly within the range of ± 0.2 m. However, these structures are likely attributed to artifacts caused by measurement uncertainties and data processing which partly explain the discrepancy in the average depth of tidal flats between measurement and model simulations (Fig. 5). 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 (all_x) and with inclusion of only biomixers (bio_x) are able to reproduce the extensive deposition pattern in the tidal channels (Figs. 5b and 6), while other experiments including those reference runs which consider only abiotic drivers show the dominance of erosion in the main channels (Figs. 5c and d and 6). The reference run based on the original formulation of erosion rate (Pinto et al., 2012) produces morphological change within the range of ± 0.1 m (Fig. 5c), which is much smaller than the measured values (Fig. 5a). Only following an increase in the erosion rate by a factor of 10 is the reference run able to produce morphological changes that are at the same order of magnitude as the measurement (Fig. 5d).

There os a net sediment input to Jade Bay from 2001 to 2009 ($\sim 0.7 \times 10^7$ m^3), which is indicated by the measurement and captured by model experiments to various extent (Fig. 5). 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, especially on the tidal flats, and the magnitude varies among the experiments (see the Supplement), with largest values in the runs which include the combined effect of all benthos measurement data indicating that the net gain of sediment in the main channel exceeds the net import through the inlet of the bay and suggesting that the sediment accumulated in the channel originates not only from sources external to 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, while mud may originate from both internal and remote sources outside the bay (Fig. S4). Despite an overestimation of net sediment import to the bay, the model experiments with all benthos included (all_mix_TS_1) produce less deposition in the main channel compared to the measure-

ment (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 (abio_x) indicate little or no net sediment accumulation in the channel, despite 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 and d).

4.4 Change in sediment composition

There were remarkable changes in sediment composition in Jade Bay from 1996 to 2009, according to Ritzmann and Baumberg (2013). A comparison between the observed change and model results indicates 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 (all_x). Most of the large-scale changes in sediment composition (indicated by ellipses with roman number I–V) are satisfactorily reproduced in all_mix_TS_1, except for the area in the northwestern part of the bay (I) where an opposite result is shown in the experiment (Fig. 7a, b, and e). On the contrary, experiments which include only abiotic drivers are able to capture the observed change in this area (Fig. 7d and e) but with a worse performance in other areas. The experiment which includes only abiotic drivers and is based on the original formulation of erosion rate (abio_no_TS_1) produces only an increase in the mud content but fails to capture the loss of mud (Fig. 7c and e). Figure 7a illustrates changes in the flat type according to changes in mud content. Since the original mud content change data were not available, the flat-type change instead of the mud content change was compared in this study, which restricts the comparison to a qualitative manner.

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 levels of complexity (Table 3), we chose the run from each group with the smallest RMSE and same hydrodynamic conditions for comparison, namely abio_no_TS_10, mix_no_TS_1, acc_no_TS_10, gra_no_TS_10, and sta_no_TS_10.

4.5.1 Biomixers

The difference in the depth change between the runs with benthos and the reference run abio_no_TS_10 shows that the largest difference in the morphological change is caused by
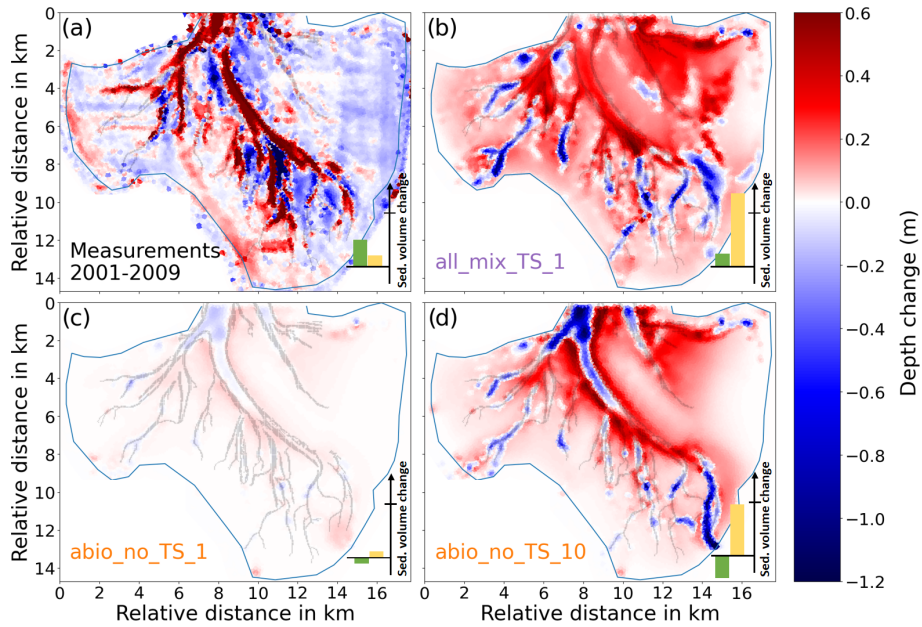
Figure 5. Comparison of the morphological change from 2001 to 2009 between the model experiments and the measurement. **(a)** Results of all_mix_TS_1. **(b)** Measurement. **(c)** Results of abio_no_TS_1. **(d)** Results of abio_no_TS_10. Positive and negative values are for deposition and erosion, respectively. The bars in the lower-right corner represent the total sediment volume change in the main channel (green bar) and the basin excluding the channel (yellow bar). Negative/positive values indicate erosion/deposition. The line across the y axis indicates $10^7\,\mathrm{m}^3$. In the measured data, only the grid cells for which the morphological change exceeds the measurement uncertainty (standard deviation of difference between the 2001 and 2009 field data) were included in the sediment budget analysis.
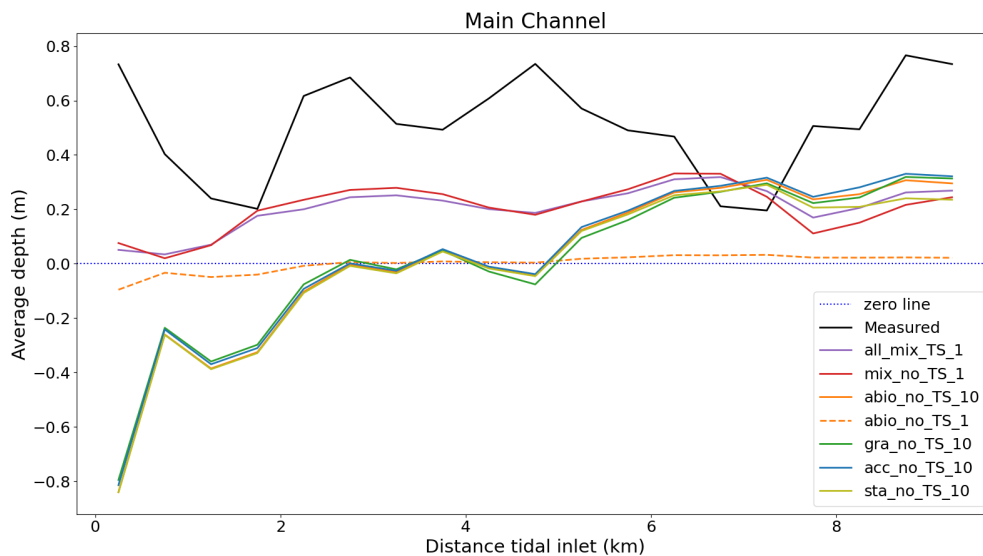
Figure 6. Average depth change in the main channel calculated from the measured data and seven representative model experiments between 2001 and 2009. The point at 0 km on the x axis marks the position of the inlet directed into the basin.

biomixers (Fig. 8a), followed by accumulators, seagrass, and stabilizers (Fig. 8b–d). In particular, the extensive accumulation of sediment in the main channel, which is shown in the measurement (Fig. 5a), is associated with the impact of biomixers. The impact of biomixers also causes deposition over a large part of the shallow tidal flats, as well as ero-

sion 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 biomixers are in the range of ± 1 m compared to the reference run. It is worth noting that biomixers account for not only the enhanced deposition in the main channel but also the
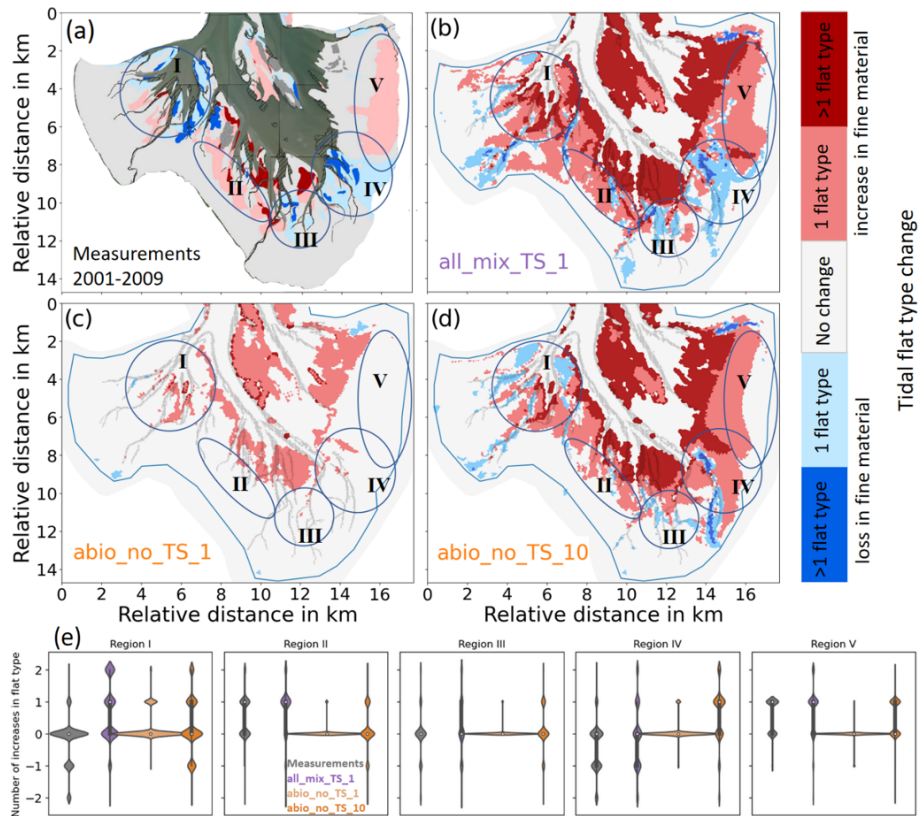
Figure 7. Comparison of change in sediment composition between 2001 and 2009 between model results and observation. **(a)** Result of all_mix_TS_1. **(b)** Observation. **(c)** Result of abio_no_TS_1. **(d)** Result of abio_no_TS_10. Pale red and pale blue show the areas where the amount of fine sediment 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 featuring large-scale changes are marked by ellipses. Panel **(a)** shows a modified version of a plot from Ritzmann and Baumberg (2013) and was kindly provided by the NLWKN (Niedersächsischer Landesbetrieb für Wasserwirtschaft, Küsten- und Naturschutz). The dark gray area in panel **(a)** marks the area where Ritzmann and Baumberg (2013) could not obtain data due to permanent inundation. The roman numerals indicate areas to compare the measurements with the simulations. Panel **(e)** shows the violin plot of the five denoted regions in panels **(a)** to **(d)** for each of the scenarios. The width of the violin plot shows the probability distribution, and the white dot indicates the median.

decrease in the mud content in the southern and southeastern parts (III and IV) of the bay (Fig. 9a and e). These changes are consistent with the field data.

4.5.2 Accumulators

The presence of accumulators 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). The average deposition over at the tidal flats is highest compared to other simulations (Fig. S6b). Accumulators do not seem to directly impact the morphological change (I) the tidal channels; however, model results show that they can lead to a significant increase in the mud content in a vast part of the bay including the channels (Fig. 9b and e). In particular, the observed increase in the mud content in the southwestern part (II) of the bay is attributed to the impact of accumulators according to the model result.

4.5.3 Seagrass

Our simulation results suggest that the impact of seagrass on morphological change in Jade Bay is smaller than that of biomixers and accumulators when looking at the overall depth change (dark red and blue bars in Fig. 8). However, local changes might be higher compared to the accumulator scenarios (Fig. 8b and c). Furthermore, instead of tidal flats, channels and areas adjacent to seagrass meadows are particularly under high impact. In the eastern part of the bay where seagrass is present, a slight deposition in the range of 20 cm occurs at the edge and at the outer parts of the seagrass meadows (Fig. 8c). Meanwhile, mud content decreases in the same area, suggesting a winnowing process there (Fig. 9c and e).

Interestingly, seagrass meadows not only affect sediment transport and morphodynamics in the direct vicinity around their habitats but also cause far-reaching changes over the bay, including the channels and other flats that are free of
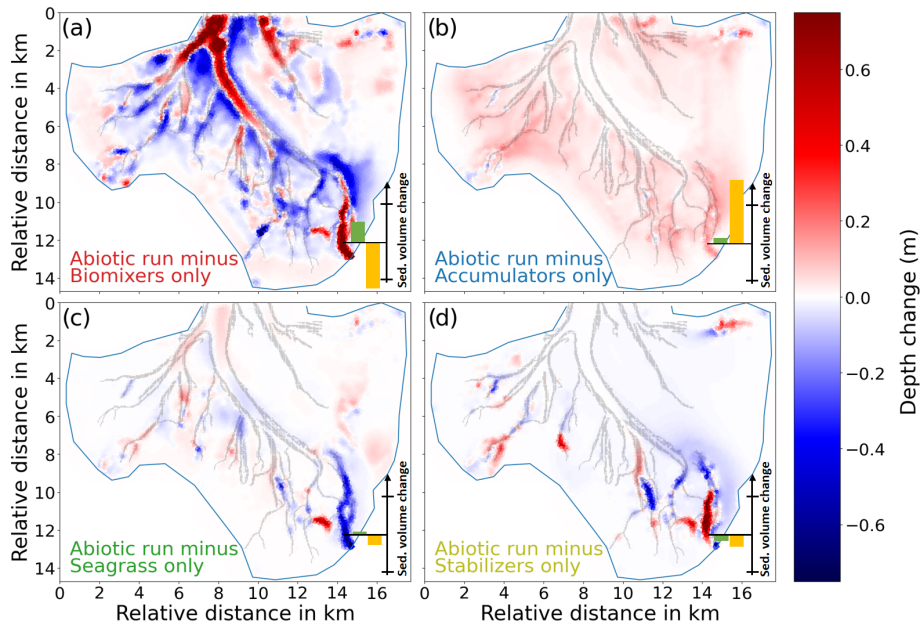
Figure 8. Difference in the depth change between the reference run abio_no_TS_10 and **(a)** mix_no_TS_1, **(b)** acc_no_TS_10, **(c)** gra_no_TS_10, and **(d)** sta_no_TS_10. Positive and negative values indicate increased deposition and erosion, respectively, in the runs with benthos compared to the reference run. The bars in the lower-right corner represent the total sediment volume change in the main channel (green bar) and the basin excluding the channel (yellow bar). Negative/positive values indicate erosion/deposition. The lines across the y axis indicate $\pm 3 \times 10^{6}\,\mathrm{m}^{3}$.

seagrass (Figs. 8c and 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 Jade Bay through its main channels during the flooding phase and leaves it over the tidal flats during the ebbing phase (Fig. S5a). The spillway on the tidal flats in the eastern 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). Thus, the increased loss of fine-grained sediment in the main channel (Fig. 9c and e) correlates significantly with the changed water flux in the main channel (Fig. S5c).

4.5.4 Stabilizers

The impact of stabilizers on the morphological changes in Jade Bay is comparable to that of seagrass in magnitude. 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 in the sediment sources for the distal ends of small channels, preventing the mobilization of sediments in these parts. Compared to the abiotic run, the sediment budget in the tidal flat is negative

(Fig. 8d). This is attributed to the stabilization of tidal flats outside of Jade Bay, leading to less erosion there and thus less sediment transport from outside into Jade Bay. The impact of stabilizers on sediment composition is more prominent compared to the morphological change. In the subtidal area, a significant decrease in the mud content is seen in the simulation result compared to the reference experiment (Fig. 9d and e) as a consequence of reduced mud input from stabilized areas that are predominantly on the distant tidal flats.

5 Discussion

5.1 Model hindcast and implication

The model performance, both in terms of morphology and sediment distribution, is improved when biota are 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 (all_x) or with biomixers (mix_x), while other experiments produce an opposite pattern.

Our simulation results show that, among all four functional groups considered in the modeling, biomixers are most impactful on morphological change in Jade Bay, followed by accumulators, seagrass, and stabilizers. The morphological change in the bay over the 8.5-year period (2001–2009) features distinct deposition inside the main channels and erosion at their adjacent flats (Fig. 5a). This feature and the
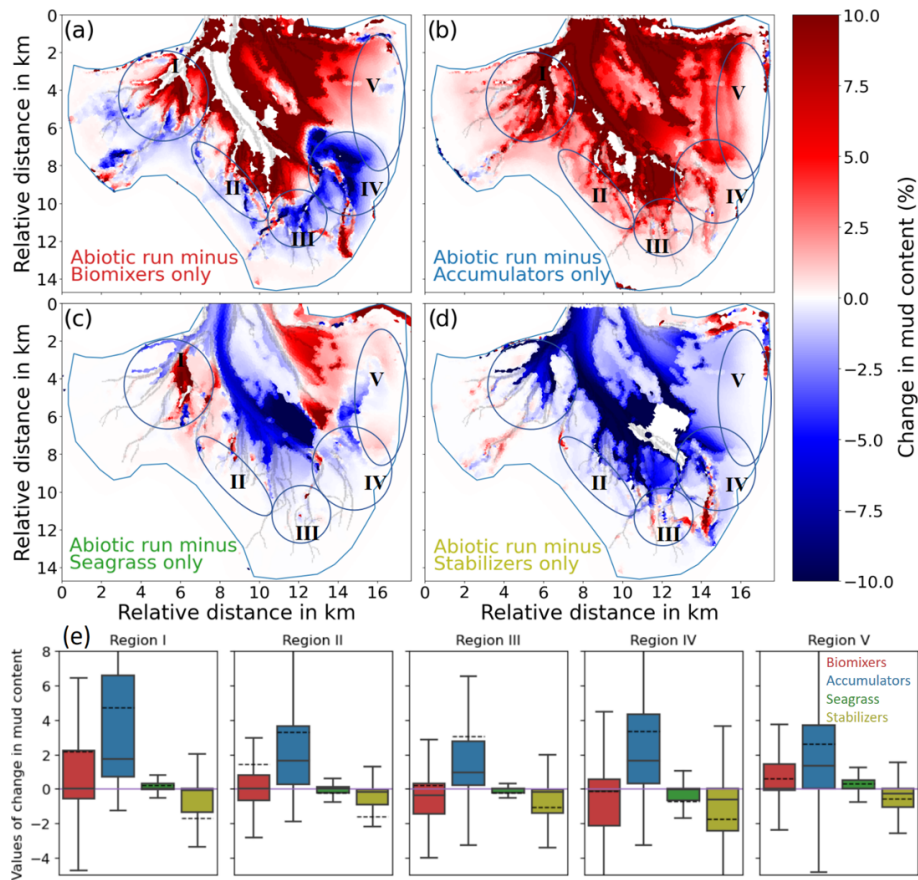
Figure 9. Difference in the mud content (%) between the reference run_abio_no_TS_10 and **(a)** mix_no_TS_1, **(b)** acc_no_TS_10, **(c)** gra_no_TS_10, and **(d)** sta_no_TS_10. Panel **(e)** shows the box plot diagram of the five denoted regions in panels **(a)** to **(d)** for each of the scenarios. The zero line is indicated in purple. The median (solid black line) and the mean (dashed black line) are shown in the box plot.

amount of deposited sediment could be reproduced by modeling only when the impact of benthos, especially biomixers, is included.

The impact of biomixers on sediment is mainly destabilization (Arlinghaus et al., 2021) but can, under certain circumstances, exert stabilization as well (Cozzoli et al., 2019). This depends on the metabolic rate, bottom shear stress, and sediment composition. Muddy sediment particles in general have a higher organic matter content and therefore higher nutritional value than sands and are hence more intensively reworked and bioturbated by benthic fauna (Arlinghaus et al., 2021). In sandy sediments, benthos-produced mucus exerts a stabilization impact which often exceeds the destabilization impact because of less bioturbation (Orvain, 2002; Le Hir et al., 2007). For this reason, the channel deposition can be explained by two factors related to macrobenthos. First, the critical shear stress for erosion is increased by the presence of biomixers ($p_d > 1$ in Eq. 1; Fig. S3) in the sandy channels, leading to enhanced resistance to erosion. Second, enhanced erosion on the tidal flats by biomixers ($p_d < 1$, $g_d > 1$) 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 Jade Bay, where a shift in the functional groups took place between the 1970s and 2000s with biomixers 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 only considers abiotic drivers, compare well with the abiotic scenario presented in Arlinghaus et al. (2022), who asserted that 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 in 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 biomixers which leads to deposition in the channels and erosion in the flats and therefore a general widening of channels, other functional groups have less influence on the morphological change in the main channels according to our simulation results. Accumulators 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 in Jade Bay is small compared to biomixers and accumulators. This is attributed to their location. The shallow tidal flats in the south and west of Jade Bay which are inhabited by stabilizers are subject to relatively weak tidal currents and low SSC. The different impacts of the mentioned functional groups in Jade Bay are depicted in a simplified form in Fig. 10, where sediment redistribution (e.g., from tidal flats to channels) and vertical erosion/deposition patterns are distinguished. Our results suggest benthos as a critical driver determining sediment stability and morphological development of tidal embayments and basins, supporting an earlier 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 in 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 the fact that 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 the 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 accumulators have the strongest impact on changes in sediment composition, followed by biomixers, seagrass, and stabilizers. The impact of accumulators 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 biomixers extends beyond their habitats. Locally, sediment can be either stabilized or destabilized, depending on the abundance of biomixers and other factors elucidated previously. Non-locally, the enhanced erosion in large parts of the tidal flats by biomixers increases

the overall concentration of suspended sediment, especially on the flats outside Jade Bay, which provides a sediment source for the bay. The impact of seagrass is prominent in close vicinity to the meadows but not so much within the meadow itself. One explanation is that the effect of organic sediment accumulation due to primary and detritus production and root and rhizome formation, which are main sources for sediment production (Gacia et al., 2003), was not considered in this study. The found changes close to the meadows are in line with measurements indicating differences in bed level elevation between vegetated and nonvegetated areas in the range of $3\,\mathrm{cm\,yr^{-1}}$ (Potouroglou et al., 2017). 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 compared to the reference run can be explained by the reduced supply of mud from the tidal flats which are inhabited by stabilizers. However, since the mud content is small in the hydrodynamically active areas, the absolute change in the 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 biomixers, which has a strong destabilization effect there. The eastern (V) part accumulates much more fine sediment compared to the reference run, which is attributed to the impact of seagrass and accumulators (Fig. 9). This impact might even be enhanced in reality due to the organic sediment accumulation explained above. The increase in the mud content on the shallow tidal flats in the southwestern part is mainly due to the presence of accumulators. 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 in the mud content is overestimated in all model experiments when compared to the field data. One possible explanation is that mixing between sediment layers, which gets enhanced by biomixers, 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, while mixing in the sediment column 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).

It should be noted that the dominant impact of biomixers and accumulators is related to their widespread abundance and high biomass in Jade Bay. In other environments, different functional groups may dominate. For instance, some
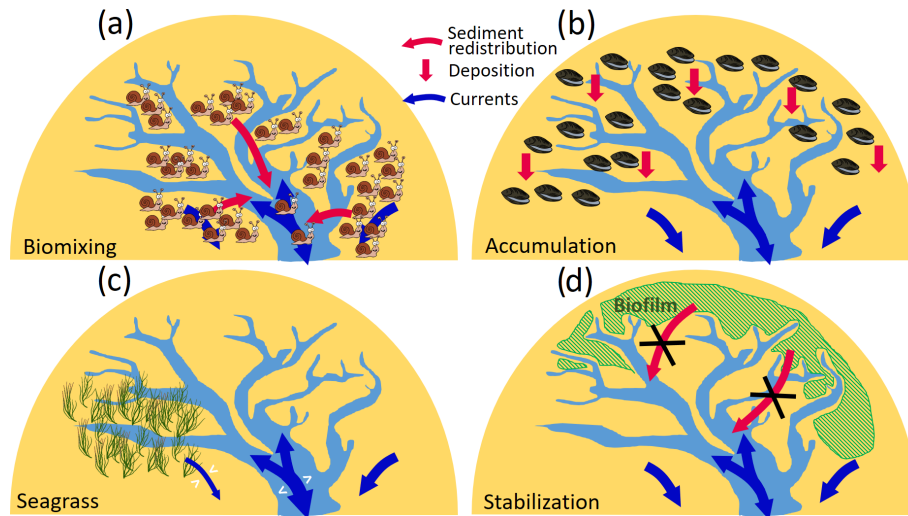
Figure 10. Conceptual sketch of different effects of the four functional groups on sedimentation and hydrodynamics in tidal embayments. **(a)** Destabilization in tidal flats caused by biomixers. **(b)** Accumulation caused by filter/suspension feeders. **(c)** Modification of flooding/ebbing flows by seagrass meadows. **(d)** Sediment stabilization by MPB and reduced input to channels.

modeling studies show a significant impact of seagrass on the morphodynamics of tidal basins (Mohr, 2022), barrier islands (Reeves et al., 2020), and estuaries (Walter et al., 2020). Seagrass impact may further complicate when their effect interacts with other plants such as salt marshes (Carr et al., 2018). Unfortunately, a quantitative comparison of the impact normalized to biomass between the different functional groups cannot be made in this study due to a lack of biomass data for seagrass and stabilizers in the study area, which points out a need for future studies.

5.2 Societal relevance

Similar to many other coastal bays/embayments worldwide, Jade Bay serves important socioeconomic functions for tourism and logistics, and on the other hand, Jade Bay provides important refuge for a variety of marine life-forms. It is of critical importance to sustain the ecological functions of coastal bays such as Jade Bay under the increasing pressure of human use and climate change. Our results indicate that benthos can significantly modify 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. Biomixers tend to smooth the bathymetric gradients between channels and flats, while seagrass and accumulators may counteract this to various extents. A combined effect of all functional groups leads to the 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 about whether coastal systems such as the Wadden Sea and including 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 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 with respect to how the different functional groups of benthos would react to human and climate stressors. For instance, chlorine inputs are expected to increase in Jade Bay due to the 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 heatwaves, also have a significant impact on benthos (Serrano et al., 2021). The intensity and frequency of extreme events are likely to increase in the future due to climate change, but the consequent change in benthos remains largely unknown. To this end, explanatory and eventually predictive numerical models are imperative for exploring feasible nature-based solutions for sustaining both socioeconomic 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 the parameterization of processes. This is especially true in the 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 parameterization of less-known processes (e.g., growth/decline in benthos and 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, the 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 first increases model performance in approximating observed change but that model performance decreases when a higher complexity, i.e., seasonal change in benthos, is added by a simple parameterization. This points out a need for an accurate mapping of benthos, including the temporal changes in the field which can serve input for the modeling and/or process-based understanding and formulation of the temporal change in benthos for modeling.

6 Conclusions

We have presented an effort towards large-scale explanatory hydro-eco-morphodynamic modeling to explain changes in both the 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 in the 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 observation and are able to explain some unique features in the historical change in the morphology and sediment composition in Jade Bay. The most impactful functional group regarding morphological change in Jade Bay is biomixers. The impact of biomixers leads to prominent sediment accumulation in the main channels. Accumulators 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 habitats, resulting in alternating erosion and deposition patterns in the main channels. Stabilizers locally prevent the mobilization of sediments on the distant tidal flats. Regarding the change in the sediment composition in Jade Bay, accumulators have the strongest impact. The impact of accumulators 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 biomixers, seagrass, and stabilizers on sediment composition extends beyond their habitats. A combined effect of all functional groups leads to the increased import of sediment, especially mud, to the bay. Also, results indicate that the impacts of functional groups can both counteract and enhance each other. An increased SSC level by biomixers, for instance, enhances the impact of other functional groups. On the other hand, biomixing-induced sediment erosion on the tidal flats is partly offset by the bio-deposition of accumulators.

Our results further show that increasing model complexity does not necessarily lead to better model performance, especially when biotic drivers such as benthos are included. Including storm surges, which are precisely described by observational data, improves model performance. By contrast, adding seasonality to the benthos impact through an oversimplified parameterization decreases the general model performance. The reason is attributed to a lack of observational data which can support a more accurate formulation of temporal changes in 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 Jade Bay have important socioeconomic and ecological functions worldwide. Therefore, the 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 of 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.

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5. Discussion

T1.Q2: What are the current limitations of numerical benthic-morphological models?

There are generally two types of limitations for the presented and analyzed modeling studies. One regards numerical modeling in earth sciences in general and the other is more specific to large-scale benthic-morphodynamic modeling. The general problem in earth science is that real systems, compared to their numerical modeling counterparts, are not closed and inherit a multitude of boundary conditions which can never be all known or only to a certain accuracy (Oreskes et al., 1994). Trying to increase model complexity as much as possible can never ultimately solve this problem. Because increasing the number of implemented processes comes with an increase in required parametrizations which need to be obtained empirically, by theoretical considerations or further models. All three sources will always inherit uncertainties. Accumulation of uncertainties in parameterization may equalize or even revert the advantages of model refinement (Skinner et al., 2018, Pianosi et al., 2016). This phenomenon was shown in Arlinghaus et al. (2024) where a trend of increased model performance was found for model refinement which was reverted when model complexity become too high. This phenomenon may even lead to conflicts when multiple effects are modeled at the same time. For instance, Baar et al. (2019) have tested multiple morphodynamic setups and found that it was impossible to correctly model both magnitude of sediment transport and morphological changes simultaneously. For either of the target observables a special calibration was required which led to unrealistic results in the other observable. Despite high sensitivity to measurable quantities like sediment parametrization, morphodynamic models can also be highly sensitive to the chosen model spin-up time (Diaz et al., 2020) or the choice of the computer or compiler even if the code and numerical model is identical (Geyer at al., 2021). For these reasons, thriving for higher model complexity does not necessarily lead to better performance.

The second type of limitations regards uncertainties specific to large-scale benthic-morphodynamic modeling, namely 1. process understanding, 2. species distribution data plus modeling, 3. calibration data and 4. morphological and sedimentological data. Each of the identified factors will be explained with an example from the presented thesis.

Due to the high complexity the processes understanding of sediment stabilization due to biofilm is still limited (Arlinghaus et al., 2021; Bastianon et al., 2022). All large scale modeling studies have treated biofilm as an superficial phenomenon. However it penetrates the sediment column up to a few centimetres and influences sediment erosion beyond the erosion phase of the upper most layer. It changes the micro-morphology of sediment grains and affects their properties like settling velocity and flocculation (Chen et al., 2017a; Chen et al., 2017b; Van Colen et al., 2014). During the maturation process, it goes through several stages of varying stability which are influenced by community composition and environmental conditions like hydrodynamics, temperature, nutrients, tidal cycle or sunshine and might change on the scale of hours (Wal et al., 2010; Guarini et al., 2000; Chen et al., 2017a; Andersen and Pejrup, 2011; Fang et al., 2017). Feedback processes add further complexity to this picture. For instance, the positive mutual feedback between fine grained sediment (especially silt) and microphytobenthic growth or the negative control of grazing on diatoms (van de Koppel et al., 2001; Chen et al., 2020). For these reasons its impact on stabilization is highly site specific and yet a reliable model or proxy for biofilm stabilization needs to be found (Riehtmüller et al., 2000).

Knowledge of species abundance is essential to spatially and temporally quantify bioturbation impact. The limiting factor to generate species abundance data is the large effort, manpower and high required expertise. For the used macrofauna dataset from Jade Bay (Arlinghaus et al., 2024) cylindrical core

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samplers were used in the field, their content sieved, and benthos was counted and taxonomically classified (Schückel und Kröncke, 2012). Wet weight was measured for all species found in the sublittoral. Since in the eulitoral only abundance was measured, the biomass needed to be calculated based on averages from the species present in the sublittoral, which was not possible for all species. Further more the sampling design was not well suited to determine the occurrence of the important bioturbator *Arenicola marina* (Singer at al., 2016). Moreover the samples were taken once per station from spring to summer time and thus only serve as a snapshot of benthic distribution without including seasonal or interannual variations. Although the used dataset is uniquely comprehensive, with 160 sampling stations over ca. 160 km² and around 300000 classified benthic individuals, the measurement design inevitable introduces inaccuracies for species modeling. Nevertheless, with different methods, the mentioned shortcomings could be fixed and prediction accuracy between 20-40% could be achieved with the applied SAM model (Arlinghaus et al., 2024).

Bioturbators destabilization parametrization was based on an idealized laboratory flume setup (Cozzoli et al., 2019). It had the advantage of testing a variety of benthic species in different densities and under the same controlled conditions which would not be possible in situ. On the contrary it might be difficult to scale the results of laboratory measurements to realistic environments (Kleinhans et al., 2010). For instance, no mixed sediments where presented to the species and the impact on erosion was only measured for single species. Also the measurements where limited to an initial time period of species sediment colonization. Therefore no interactions between species themselves, between species and different environmental parameters and long term impact could be captured with these measurements. It has been shown that measurements of critical shear stress and erosion rates can vary considerably between laboratory and in situ studies (Andersen et al., 2002). Hybrid solutions, such as laboratory experiments with sediments taken from the field also have their limitations since the sediment properties change during transport (Tolhurst et al., 2000; Tompkins et al., 2008). Moreover, depending on the applied technique the same observables can have different values. In Stal (2010) uncertainties in measurement technique were larger than seasonal variation of the observable. Despite the simplifications used, with the used erosion formulation the main morphological patterns in Jade Bay could be depicted. The framework in Cozzoli et al. (2019) is very comprehensive and provides a simple, but yet effective, proxy parameter (metabolic rate).

Morphological data for model initialization and verification on the scale required for this study are often mergers of different datasets. The used data was compounded from different surveys, at different times, applying different mapping techniques (Sievers at al., 2020). Uncertainties of the morphological data in the years from 1996 to 2000 was larger than the morphological changes in Jade Bay which is why the simulation starts with 2001.

T1.Q1: What are the main benthic functions to focus on to reduce complexity?

The answer to the question for main benthic functions depends on the scales and the quantity that shall be modeled. For instance, if morphological changes shall be modeled, the destabilizing and stabilizing impact of bioturbators should be considered first (Arlinghaus et al., 2024). If a correct depiction of sediment changes is the goal, biomixing (Arlinghaus et al., 2022) and bio-accumulation (Arlinghaus et al., 2024) are the more important functions. The functions mentioned can be broken down into several processes. For example, every benthic species can contribute differently to the biomixing process and facilitate particle transport upward or downward, over long and short distances, selective or randomly. On small scales each of these processes has its justifications and is required to confirm measurements. On the larger scales however, it is not feasible to follow these processes on a species level. Firstly because spatial and temporal variations of species abundance and effects are not available with the required accuracy and secondly the computational effort will be much higher. Instead, the different small-scale effects should be condensed into a formulation that works on a

community level. For biomixing, given a long enough time span, directed transport processes of a variety of species will accumulate into a diffusion like mixing (Arlinghaus et al., 2021). The impact of all species with sediment transport traits can then be described by one much simpler diffusion equation for sediments. Clustering a variety of species with similar traits is called functional group modeling. It is an effective way to reduce model complexity and can potentially be done for all benthic functions.

The challenge is to unify different small scale benthic functions in a meaningful way, reducing the number of required parameters, while preserving a certain model accuracy. For destabilization impact of bioturbators most current models have used biomass (Arlinghaus et al. 2021). A more accurate predictor might be the overall metabolic rate (Cozzoli et al., 2019; Arlinghaus et al. 2021). For stabilizing biofilm most studies have used the chlorophyll-α content, although this proxy is not very reliable. (Riethmüller et al., 2000; Arlinghaus et al. 2021). Except for the presented study (to my knowledge) there exist no large scale benthic-morphological study including the impact of bio-accumulators (Arlinghaus et al., 2021). In Arlinghaus et al. (2022, 2024) an accumulation formulation was used, depending on biomass, suspended sediment and nutrient concentration. The formulation is specific to mussels and does not cover effects of other suspension feeders which don't rely on filtration. Thus a confirmed functional group model comprising all bio-accumulating species does yet not exist. The same is true for pelletization, autogenic/allogenic structure and benthic roughness impact. For each of the named effects one publication was found. All studies showed significant impact for the respective functional group, but development is still on an initial stage (Arlinghaus et al., 2021). Also Arlinghaus et al., 2022 showed that destabilizers, stabilizers and accumulators had a comparable strong impact compared to a reference scenario. However, looking at all existing modeling studies, on average destabilizers were the most impactful group regarding morphological development. Therefore more research is needed to better classify the impact of all functional groups in relation to each other.

5.3 T2.Q1: How and to what extent can benthic fauna modify embayment-scale coastal morphology?

Most large-scale benthic morphological modeling studies have investigated the impact of stabilizers and destabilizers (Arlinghaus et al., 2021). The impact of accumulation, biomixing and pelletization was only investigated by a few studies and is thus not well understood. For pelletization for instance, both little and strong impact on sediment dynamics was found (Lumborg et al., 2006; Orvain et al., 2012). However, potentially all presented benthic main functions can have significant impact on morphology (Arlinghaus et al., 2021). All functional groups investigates in Arlinghaus et al. (2022), namely destabilizers, stabilizers and accumulators, had a profound impact on tidal basin morphology in terms of development of channel network (channel depth, width, length and bifurcations) and overall elevation of adjacent tidal flats.

Bio destabilizers are most impactful in intertidal areas and lead to a widening of estuarines, tidal inlets and tidal channels together with a smoothening of the hypsometric curve (Arlinghaus et al., 2021, 2022, 2024). Compared to a reference scenario tidal channels were shallower and adjacent tidal flats deeper (Arlinghaus et al., 2022, 2024). Enhanced erosion triggers the development of new tidal channels resulting in strong channel branching. Bioturbation induced destabilization and biomixing may result in a net sediment export. On the contrary the impact of stabilizers and accumulators tend to alter the system toward a sediment importing scenario. In the one case sediment accumulation on tidal flats, and in the other case stabilization and thus lower net erosion of tidal flats led to current concentration and increased channel incision. Similar effects have also been reported for seagrass (Mohr, 2022). In case of accumulators the channels become deep and long and in case of stabilization deep but much shorter. Stabilization also prevented branching of tidal channels (Arlinghaus et al., 2022). The hypsometric curve in the accumulation case was similar to the reference scenario while in the stabilization case the highest hypsometric curve was reached. Compared to the reference scenario all functional groups lead to elevation changes in the range of meters over the course of 100 years.

5.4 T2.Q2: How important is the role of species interaction in shaping morphological features?

Large scale modeling studies addressing species interaction are rare and with the exception of the presented thesis only one study was found. It highlighted that direct interactions between these species determined each other's abundance and indirect feedback over eco-engineering of the habitat creates suitable area for co-existing species (Brückner et al., 2021). Similar effects were found in Arlinghaus et al. (2022). Unlike Brückner et al., 2021 no direct feedback was hardcoded but instead indirect feedback was mediated via the availability of nutrients entering the system and being redistributed by benthos. Two kind of feedback mechanisms could be distinguished. First an indirect feedback between benthos and the inhabited area and second an indirect feedback between benthos and overall morphological change. Destabilizers for example increased erosion in the inhabited areas and thus decreased net deposition of nutrients which created a negative feedback, controlling the biomass of destabilizers. Vice versa, stabilizers increased deposition of nutrients, which in turn increased stabilization impact, leading to a positive feedback loop of increased deposition and stabilization. Accumulators were not impacted directly by deposited sediment since they only utilize nutrients from the seston. Instead a positive feedback between accumulators and morphology arose where flow concentration with channel incision and elevation of tidal flats changed the systems hydrodynamics toward a flood dominated scenario. This increased suspended sediment and nutrient concentrations which increased the biomass of accumulators. The same positive morphological feedback works for stabilizers, since higher concentration leads to higher deposition. For destabilizers inlet and channel widening shifted the hydrodynamics of the basin toward ebb domination leading to lower sediment and nutrient import into the basin which is another negative feedback control, limiting destabilizers biomass.

In a simulation including all three functional groups the different control mechanisms influenced spatial species distribution and biomass. Sediment erosion and the shift toward sediment export, triggered by destabilizers, decreased the abundance and biomass of stabilizers and accumulators. On the contrary, deposition and shift toward sediment import increased the biomass of destabilizers. Stabilization of the tidal inlet prevented its strong widening as seen in the destabilization run. Further more accumulation and stabilization allowed the presence of destabilizers in hydrodynamic active areas such as the channels and their direct vicinity, leading to a widening of the tidal channels. Compared to the narrow channels in the accumulation and stabilization scenario and the wide inlet in the purely destabilized scenario a much more sound result, comparable to the channels in Jade Bay was achieved. This highlights the importance of incorporating multiple functional species into morphological modeling. In the case of the presented work in Arlinghaus et al. (2022) simulation of single species might lead to unrealistically high or low biomasses. Moreover, species interactions are needed to develop certain morphgical features. This is supported by Arlinghaus et al. (2024) where the impact of accumulators was only significant because sediment was mobilized by destabilizing benthos.

5.5 T3.Q1: Can including benthos to morphological models improve the model quality?

The answer is yes.

Current morphological models including benthos were limited to qualitative results. They explored potential impacts of benthos and there was hardly any study confirming model results on a large spatial scale (Arlinghaus et al., 2021). This problem of result confirmation is a general problem in coastal morphological modeling (Amoudry et al., 2011). A previous morphological modeling study in Jade Bay concluded that *"(…) the model did not reproduce the observed morphological changes very well."* (Chu et al., 2011). In line with the findings presented in my thesis, Chu et al. (2011) see the main reason in

an insufficient parametrization. As demonstrated, besides parametrization issues, a main factor for morphological development in Jade Bay is biota which was neglected in the named study. Overall the results presented in Arlinghaus et al. (2024) are far from being perfect, but they depict the most prominent pattern evident in the bathymetric measurements. Especially compared to the abiotic scenario a clear difference in the main channel development is seen. Cosine similarity shows positive correlation for the bioturbated scenario and negative correlation in the abiotic case. Also sediment redistribution was much more realistic when benthos was integrated into the simulation. Four out of five areas in Jade Bay showed the same sedimentation pattern with benthos. The overall overestimated sediment concentration in the top sediment layer can be attributed to the lack of biomixing which was neglected in this study.

This study demonstrates the possibility to hindcast morphological changes on a basin scale and it can be confirmed that an explanatory stage could be reached. The results clearly show the importance of benthos in guiding large scale morphological development. The first two papers leading up to this study provided the necessary process understanding and model experience to attain these results. Two factors of special importance should be highlighted here. First the destabilization/stabilization formulation as introduced by Cozzoli et al. (2019). The divergent behavior for lower and higher benthic metabolic rates was the reason for the characteristic main channel development. Secondly the extensive benthos dataset, available for Jade Bay, in combination with the machine learning species abundance model. With both factors together a realistic spatial distribution of benthic impact could be estimated.

5.6 T3.Q2: What is the impact of different functional groups on the morphological development in Jade Bay?

Regarding morphological changes *bioturbators* are most impactful followed by accumulators, seagrass and lastly by stabilizers (Arlinghaus et al., 2024). In this study the term *bioturbator* was specifically used for macrobenthos which generally destabilizes the sediment, but under certain conditions exerts stabilizing impact on the sediment. The morphological changes showed a very distinctive feature of sediment accumulation in the main channel over the selected time span with more than 1 meter difference compared to the abiotic scenario. The accumulation can be explained by two factors related to *bioturbators*. First an increase of critical shear stress for erosion is created by the presence of *bioturbators* in the channel which dampens erosion and second a sediment redistribution is initiated. Strong erosion on the tidal flats mobilizes sediment which is then deposited in the channel. The redistribution of sediment from the tidal flats, which are becoming deeper, into the channels, which are becoming shallower, might be a typical basin development under the presence of strong biotic destabilization (Arlinghaus et al., 2022). This is actually the case for Jade Bay where a shift of functional groups took place between the 1970s and 2009 with bioturbating deposit feeders (destabilizers) increasing from ca. 20% to almost 70% (Schückel and Kröncke, 2013). The development of a plateau, characteristic for destabilizers can be seen in the development of the hypsometric curve in Jade Bay (Arlinghaus et al., 2022).

The morphological impact of accumulators was mostly limited to the tidal flats which were elevated up to several tens of cm compared to the abiotic scenario. Despite not destabilizing impact, some channel areas were significantly deeper compared to the abiotic case. One explanation is, that the suspended sediment is deposited by the presence of accumulators, before it can reach the areas that experience strong erosion. Regarding the fine grained sediment distribution accumulators a more impactful than *bioturbator.* However, this impact is only evident when the overall erosion rate is increased. This highlights the importance of *bioturbators* in Jade Bay by mobilizing large amounts of sediment from the tidal flats. Accumulators are only impactful in combination with *bioturbators*. These

results are in line with Borsje et al. (2008) and Lumborg et al. (2006) where sediment mobilization by destabilizers both increased total deposition and erosion magnitude.

The impact of seagrass regards the area in its direct vicinity and the three main channels in Jade. The part of the seagrass meadow and especially the area immediately in front of it, which is facing the incoming tide accumulates sediment. It attenuates the currents and traps suspended sediment particles. Beyond this local effect it serves as a big patch of enhanced friction preventing a rapid run off in the eastern part of Jade Bay. This part is usually subject to strong ebb currents which are now partially diverted into the main channel, which explains the increased erosion in the main channel compared to the abiotic scenario.

The impact of stabilizers on morphology in Jade Bay is hardly visible. A possible reason is that it is too distant from areas of high shear stress and deposition. The shallow tidal flats in the south and west of Jade Bay are neither subject to strong currents nor is the suspended sediment concentration high in those areas. The highest suspended sediment concentrations in Jade Bay are found in the east. Another factor might be the strong seasonal pattern of stabilizer.

6. Outlook

The presented work has demonstrated the ability to hindcast morphological evolution and sediment redistribution on a basin scale incorporating biota. The results were much better compared to abiotic modeling scenarios. To achieve this, ecompassing data sets where combined with state-of-the-art machine learning techniques for species biomass distribution and a functional group level representation of benthos, based on an elaborate paper review. Results indicate a profound impact of benthos on guiding long term and large scale morphological evolution especially in coastal zones such as the presented tidal basin Jade Bay.

Jade bay is an economically, ecological and cultural important basin. On the one hand Jade Bay is a major spot for tourism. The Jade-Weser-Port is Germany's only deep sea port able to accommodate ships of the PANAMAX class and hosts the first German LNG terminal and regasification facility. On the other hand it is part of the UNESCO world heritage and an important refuge for a variety of marine lifeforms. Yet it is subject to a multiude of stressors including sea level rise, climate change, dredging and pollution. Sea level rise will likely increase the imported sediment into the basin (Plater and Kirby, 2011). Pollutants, especially increased inputs of chlorine in context of the LNG terminal will likely change the benthic community distribution (Chang 1989; Wang et al., 2022b). Climate change was shown to increase the numbers and biomass of on tidal flats (Beukema and Dekker, 2020). Depending on different biotic and abiotic parameters tidal inlets may persist for centuries in a quasi equilibrium state or might fill up and close (Haas et al., 2017). Muddy embayments with large numbers of ecosystems engineers, as it is the case for Jade Bay, are hypothesised to close on time scales of centuries (Haas et al., 2017). It is thus of vital importance for policy makers and stakeholders to be able to predict future basin developments incorporating changing benthic communities. This studies adds to developing such abilities.

Beyond Jade Bay and tidal embayments the presented work can be useful for evaluating measures for coastal protection. Globally more than 600 million people live in coastal areas that are less than 10m above the sea level (McMichael et al., 2020). At least 18 million people and 3000 billion US dollar assets are directly endangered by sea level rise today and are expected to rise to 150 million people and 35000 billion US dollar by 2070 (Nicholls et al., 2007). In order to protect those areas, typically engineered coastal protection measures were implemented such as gryones, embankments, dykes, sea walls and dredging and dumping. However such measures are generally static and oversized, require a high maintenance effort and cost and may lead to unforeseeable impacts on ecosystems on large scales (Borsje et al., 2011; Cozzoli et al., 2016; Temmermann et al., 2013). Further more, because conventional engineering approaches are challenged by climate change, sea level rise, land subsidence and sediment supply, ecosystem-based coastal protection measures might be more sustainable (Temmermann et al., 2013). On the contrary costal defense measures based on ecological engineers are less expensive to implement and maintain, will dynamically adapt to system changes, have the ability to self repair and can help to restore and preserve ecosystem function (Spalding et al. 2013). Those include vegetation based solutions like salt marsh cultivation, seagrass planting, willow floodplain construction and mangroves (Unsworth et al., 2019; Temmermann et al., 2013, 2023; Borsje et al., 2011). Benthos based approaches are also under investigation (Borsje et al., 2011). Mussel beds which can grow on stable artificial structures attenuate waves and storm surges, reduce current velocities, trap sediment particles and bioaccumulate (Borsje et al., 2011). In context of hybrid solutions between conventional and ecological coastal defense measures, changing the texture of constructions e.g. drilling pits and holes into seawalls proved to increase the number of algae and macrobenthos (Martins et al., 2010). Optimized textures were colonized much stronger by algae, barnacles, mussels and macrobenthic snails compared to unchanged surfaces (Borsje et al., 2011; Gregory et al. 2021). Thus, depending on environmental variables like salinity, temperature or inundation time, it is possible to place certain functional groups specifically in the coastal area such as stabilizers, destabilizers, accumulators and vegetation. However, it is difficult to evaluate the

prospective success of such measure because so far long term studies don't exist (Temmermann et al., 2013) and bio-morphodynamic computer simulations assessing ecological protection measures were at a fledging stage (Borsje et al., 2011). The presented study added more stones for paving the way leaving the explorative stage of benthic-morphodynamic studies into the explanatory and predictive stage and thus may contribute in evaluating the use and application of ecosystem based coastal adaption and protection measures in the future.

Due to the presented limitations all coastal management measures should be conducted with care and study sites must be carefully selected (Temmermann et al., 2013) and simulations should always go hand in hand with laboratory and field experiments (Kleinhans et al., 2010). In this way, in order to enhance model capabilities further research is needed. Four factors were identified limiting the model validity which were 1. process understanding, 2. species distribution data plus modeling, 3. calibration data and 4. morphological and sedimentological data. Following ideas and state-of-the-art techniques which were not or only partially used in this study might help to improve on these points in the future.

1. Studies investigating direct species interaction on sediment parameters are rare. A few are collected in Passarelli et al. (2018) and Albertson et al. (2014). However a more systematic analysis and quantification is needed.
   The processes involved in biofilm assembly and the reason for its strong site specific variations are also underexplored. Most modeling studies have used the unreliable proxy of chlorophyll-α to estimate the stabilization effect of biofilms (Arlinghaus et al. 2021). Bastionen et al. (2022) carried out a biofilm modeling study for investigating growth and feedback on morphodynamic development depending on a variety of parameters. Continuing in this direction might help to complete the picture of biofilm maturing and to find more reliable sediment stabilization proxies.

2. Recent advances in machine learning and the ability to generate and process high resolution satellite, aerial or underwater images provide many opportunities for species abundance and biomass mapping. For instance, applying a hyperspectral optical model, biofilm reflectance from high resolution airborne images can be utilized to determine diversity, taxonomic group and biomass of microphytobenthos (Launeau et al., 2018). Multispectral remote sensing combined with a machine learning approach enables mapping of microphytobenthos abundance on intertidal mudflats and determination of its primary production with classification accuracy >90% (Meleder et al., 2020; Brunier et al., 2022). Such measures can easily be applied over large areas and require much less effort and manpower compared to sampling and subsequent laboratory analysis. Data might be acquired more frequently to cover seasonal and interannual cycles in biofilm development.
   Taxonomic classification of macro- and meiobenthos, as performed for acquiring the used Jade Bay benthos data set, is a tedious task. Species image analysis based on machine learning methods, especially convolutional neural networks, is a promising approach to reduce classification effort (Weinstein, 2018). It has proven to work well for plants (Wäldchen and Mäder 2018a, 2018b) and benthos (Lytle et al., 2010; Borba et al., 2021; Singh and Mumbarekar) and has reached a stage where it outperforms non-expert humans in classification accuracy (Raitoharju et al., 2018). Similar techniques, utilizing machine learning and image analysis were used for benthic habitat mapping on a large scale in coral reefs (Pavoni et al., 2021; Schürholz and Chennu 2022) and may be transferable to other ecosystems. Recent progress in species prediction has focused on occurrence modeling rather than species abundance and biomass modeling. Most of present abundance modeling papers concern birds and reef fish while – with the exception of the presented thesis - there are hardly any benthos studies (Waldock et al. 2022). As a key element to benthos-morphological modeling, for future research more reliable benthos abundance models need to be developed.

In order to enable such models long term and large scale benthos monitoring should be conducted. The most encompassing dataset is provided by the Ministry of Infrastructure and Environment, The Netherlands, (2018), recording nearly 60000 occurrence samples with a total count of around 9 million macrobenthic individuals in the Dutch continental economical zone from 1991 to 2015. To be able to utilize such datasets for benthic-morphological modeling this effort should be supported by extending studies that provide species specific bioturbation and functional group classification (Queiros et al., 2013) and conversion factors between wet-weight, dry-weight and ash-free-dry-weight (Gogina et al., 2021).

3. To generate species effect calibration data field and laboratory measurements can be deployed. For field measurements typically mobile devices such as the *shear vane* or the *cohesive strength meter* (Tolhurst 1999; Watts 2003) are used to measure sediment erosion rates or stability while laboratory measurements generally rely on flume experiments (Cozzoli et al., 2019). Regarding laboratory experiments, the advantage of full control over the input and measuring parameters is opposed by scaling problems which is the other way around for in situ measurements. However, modern devices are potentially able to combine the advantages of both methods. One example is the *TiDyWAVE* device which resembles a portable flume. Compared to other in situ devices it is not limited to unidirectional currents and is able to mimic near-bed water motion of waves and storm conditions (de Smit et al., 2020). For future research it is conceivable to recreate other processes in situ such as heat waves.

4. Traditional bathymetric surveys used big and expensive hydrographic vessels. Recent advances in bathymetric survey are going in two directions: Airborne/spaceborne and in situ measurement techniques. The former comprises a variety of techniques relying on satellite remote sensing, laser scanning (LiDAR) or aerial images. The latter uses unmanned autonomous vehicles (Benet et al., 2019), underwater drones or remotely operating vehicles. All methods have their individual field of application depending on required spatial resolution, depth and distance from the coastline (Leder et al. 2020).

Despite the mentioned issues in parametrization, process understanding and validation the recognition of the relevance of large-scale benthic-morphodynamic studies, which is reflected in the small number of studies in the past 25 years (table 2 in Arlinghaus et al., 2021) is the main factor limiting progress. 80% of the existing studies were exploring the impact of stabilization and destabilization. Parametrization of destabilization has proven to be sufficient while stabilization processes require a more profound process understanding. However, for other fundamental benthic functions such as, biomixing, bio-accumulation, autogenic/allogenic structures and maybe even pelletization, a sufficient level of process understanding is available. But yet only 20% of the existing studies deal with one of those. One explanation is the simple implementation for destabilization and stabilization compared to the other functions. Scaling critical shear stress and erosion rate via a scaling function, as proposed by Knaapen et al. (2003), has proven a straight forward and reliable solution. More complex solutions are required for the other benthic functions. Perhaps, the dominating impact of destabilizers on morphological evolution only reflects the smaller experience and ability of implementing the other benthic functions in large scale models (Arlinghaus et al., 2024). How parametrization uncertainties could diminish model performance was clearly shown in Arlinghaus et al. (2024). Thus more effort is needed in future studies to implement all main benthic functions and understand their impact on large temporal and spatial scales.

By actually proving the validity and importance of biota, not only qualitatively, but also quantitatively with measurements, this study may contribute to increasing the required attention for this field of research. The prospective importance of benthic-morphodynamic modeling is further highlighted by

the overall increasing trend of benthic biomass in the Wadden Sea in the past 50 years (Beukema and Dekker, 2020). This study was made possible in proceeding of excellent research in benthic-morphodyanamic modeling in the recent decades and hopefully other studies can tie on presented results and conclusions. Therefore a special emphasize was put on current model limitations and suggestions for future development. However, not all limitations can be overcome. Thus, before conducting bio-morphodynamic modeling, researchers must determine which questions can be answered in a meaningful sense with simulation results that can be compared to observations and choose an appropriate level of complexity for that purpose (French et al., 2015, Larsen et al., 2016).

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Versicherung an Eides statt – Affirmation on Oath

Hiermit erkläre ich an Eides statt, dass ich die vorliegende Dissertationsschrift selbst verfasst und keine anderen als die angegebenen Quellen und Hilfsmittel benutzt habe.

I hereby declare upon oath that I have written the present dissertation independently and have not used further resources and aids than those stated.

Hamburg, 31.01.2023

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