Weathering the storm
How benthic macrofauna respond to dynamic intertidal sediment

Lauren E. Wiesebron

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De storm doorstaan
Hoe benthische macrofauna reageren op dynamische intergetijden sedimenten
(met een samenvatting in het Nederlands)

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Summary

Benthic macrofauna in the dynamic intertidal

Benthic macrofauna are a key component of intertidal ecosystems. Not only do they provide food for birds and fish, their mobility and behavior determine processes like nutrient cycling and the biogeomorphic development of intertidal flats. Local environmental conditions shape benthic macrofauna assemblages as well as the functions these perform. Because benthic macrofauna assemblages and behavior underpin many ecosystem services, it is vital to know how they respond to the highly variable environment of the intertidal.

While benthic macrofauna are adapted to living in their constantly shifting intertidal habitat, unsuitable conditions can test the limits of their tolerance. Beyond the daily and seasonal cycles of sediment erosion and deposition caused by waves and tides, intertidal sediments may undergo extreme sediment dynamics during storms. Sudden and severe sediment erosion can have devastating consequences for benthic macrofauna. Environmental extremes, including the frequency and magnitude of storms, will only increase with climate change.

In addition to facing increasing climactic extremes, the intertidal environment also experiences sustained anthropogenic stress. Restoration initiatives are used to counteract the degradation of benthic macrofauna habitat. Even though restoration initiatives are intended to have beneficial outcomes for benthic macrofauna, they can be highly disruptive. Such measures will bring about concurrent rapid change in abiotic and biotic characteristics of an intertidal system.

This thesis seeks to address how benthic macrofauna respond to dynamic sediment drivers in an era of increasing climactic and anthropogenic pressure. Individual responses, such as behavioral adjustments, will vary depending on the resilience traits of different species and life-cycle stages. These responses will affect population trajectories and the composition of intertidal benthic macrofauna assemblages. By exploring the effects of sediment dynamics on benthic macrofauna, we can help clarify the complex animal-sediment interactions that occur on intertidal flats which underpin their ecosystem services. Finally, the findings of this thesis can be applied towards improving the design of restoration initiative for benthic macrofauna habitat and increasing our understanding of the resilience of benthic macrofauna assemblages to climate change.

Sediment bulk density effects on benthic macrofauna (Chapter 2)

Benthic macrofauna assemblages change composition depending on physical attributes of their local environment, such as sediment grain size, or the strength of hydrodynamics. Sediment bulk density (dry sediment weight per sediment wet volume) is an important characteristic of intertidal geomorphology, but its effects on benthic macrofauna are poorly studied. In **Chapter 2**, we performed a mesocosm experiment where we investigated the effect of bulk density on the burrowing rate, burrowing depth, bioturbation activity, and oxygen consumption of bivalves (*Macoma balthica*, *Scrobicularia plana*, *Cerastoderma edule*) and polychaetes (*Hediste diversicolor,* and *Arenicola marina*). Overall, we found that bulk density had a strong effect on benthic macrofauna behavior. Benthic macrofauna burrowed faster and bioturbated more intensely in soft sediments with low bulk density, regardless of grain size.

Bivalve resilience to storm-induced erosion (Chapters 3 & 4)

The intensification of extreme climactic disturbances, like winter storms, will alter the erosion dynamics of tidal flats. Slow-moving bivalves may be particularly impacted by storms due to their limited ability to escape extreme storm-induced erosion. In **Chapters 3 and 4**, we explore species and size-dependent traits that may confer resiliency on bivalve species against storm erosion. In both chapters, we use a novel flume method to examine the erodibility of bivalves (*Cerastoderma edule*, *Ruditapes philippinarum*, and *Macoma balthica*) in an experimental setting.

Chapter 3 concerns native vs. invasive species adaptations to storm-induced sediment erosion. Invasive species are highly adaptable to a wide range of abiotic characteristics, and this adaptability may make them better able to withstand erosion events. In this chapter, we concluded that the native *C. edule* and non-indigenous *R philippinarum* have different strategies to avoid mortality by severe storm erosion: *C. edule* avoided being surfaced and *R. philippinarum* avoided being transported. In this case, it appears that extreme storms favor the specific adaptations of a native species over the broad adaptability of a non-indigenous one. Indeed, *C. edule* may be more likely to survive moderately extreme storms than *R. philippinarum*, though the most extreme storms would be equally devastating to both species.

In **Chapter 4**, we examined how size-dependent vulnerabilities towards storms may impact population recovery after such storms. We uncovered a size-dependent bivalve erosion relationship in the flume and applied it to an age-structured model of *M. balthica* populations in the Scheldt, which revealed that the total impact of a single extreme storm event is much greater in a population with size-dependent storm mortality than in one without. Storm-induced erosion events could change the diversity of tidal flat communities by selecting for species that can better tolerate such disturbances. Due to localized extreme storm-induced sediment erosion and high larval dispersal, bivalve population resilience to extreme storm-induced sediment erosion may persist on a landscape scale, while on a local scale we may expect a larger contrast in bivalve population trajectories and viability between wave-exposed and unexposed tidal flats.

Improving benthic macrofauna habitat with human intervention (Chapter 5)

Creating physical modifications which are beneficial to an intertidal system's ecology necessitates a good understanding of the relationships between the abiotic and biotic components of a given intertidal habitat. In **Chapter 5**, we evaluated how abiotic characteristics drive the development of the benthic macrofauna community during the first five years following engineering measures to enhance benthic macrofauna biomass and diversity at three case studies in the Western Scheldt, the Netherlands, from project initiation in 2015 or 2016, until 2020. We examined the concurrent development of the hydrogeomorphology and benthic macrofauna community using multivariate methods. We conclude that while a low-dynamic habitat may harbor more diverse assemblages of benthic macrofauna than a high-dynamic one, extremely high silt content, which is typical for low-dynamic habitats, may slow the benthic community development.

Key management implications

Our studies support the value of low-dynamic (calm, sheltered) habitats for benthic macrofauna assemblages. We found that low-dynamic habitat may increase the biomass and diversity of benthic macrofauna assemblages that perform desirable ecosystem functions, such as feeding migratory birds (**Chapter 5**). While the difference between low-dynamic and high-dynamic habitat is typically defined by hydrodynamic conditions (e.g. current velocity more or less than 0.6 m/s), our studies suggest that erosion events play a key role in driving the differences between assemblages of benthic macrofauna in these habitats (**Chapter 3 and 4**). Indeed, low-dynamic habitat conditions may provide shelter for slow-moving benthic macrofauna species against sudden and severe sediment erosion produced by increasingly severe storm events (**Chapter 3 and 4**). However, sediments in low-dynamic habitat tend towards extremely high silt content (**Chapter 5**). This could slow the development of benthic macrofauna biomass (**Chapter 5**), perhaps due to stress caused by extreme sediment bulk density (**Chapter 2**). Finally, though low-dynamic habitat provides benefits for certain benthic macrofauna assemblages, restoration efforts shouldn't only target one set of conditions because habitat homogeneity decreases the assemblage diversity, and thus the resilience, of intertidal systems (**Chapter 5 and discussion in Chapter 6**).

Samenvatting

Benthische macrofauna in het dynamische intergetijdengebied

Benthische macrofauna zijn een essentieel onderdeel van intergetijdenecosystemen. Ze leveren niet alleen voedsel voor vogels en vissen, maar hun mobiliteit en gedrag beïnvloeden ook processen als de nutriëntencyclus en de biogeomorfologische ontwikkeling van intergetijdengebieden. Lokale milieuomstandigheden bepalen de bentische macrofauna samenstellingen en de functies die deze vervullen. Aangezien de samenstelling en het gedrag van benthische macrofauna de basis vormt voor veel ecosysteemdiensten, is het van groot belang te weten hoe zij reageren op de sterk wisselende milieuomstandigheden in het intergetijdengebied.

Hoewel benthische macrofauna zijn aangepast aan het leven in hun voortdurend veranderende intergetijdenhabitat, kunnen ongeschikte omstandigheden de grenzen van hun tolerantie op de proef stellen. Naast de dagelijkse en seizoensgebonden cycli van erosie en accretie van sediment door golven en getijden, kan extreme sedimentdynamiek plaatsvinden in intergetijdengebieden tijdens stormen. Plotselinge en extreme sedimenterosie kan verwoestende gevolgen hebben voor benthische macrofauna. Extreme milieuomstandigheden, waaronder de frequentie en omvang van stormen, zullen door klimaatverandering alleen maar toenemen.

Het intergetijdengebied wordt niet alleen geconfronteerd met toenemende klimaatextremen, maar ook met aanhoudende antropogene stress. Herstelinitiatieven kunnen worden gebruikt om de degradatie van de habitat van benthische macrofauna tegen te gaan. Hoewel herstelinitiatieven bedoeld zijn om gunstige resultaten op te leveren voor de bentische macrofauna, kunnen zij zeer verstorend zijn. Dergelijke maatregelen leiden tot een gelijktijdige snelle verandering van de abiotische en biotische kenmerken van een intergetijdensysteem.

Deze thesis tracht na te gaan hoe benthische macrofauna reageren op sedimentdynamiek in een tijdperk van toenemende klimatologische en antropogene druk. Individuele reacties, zoals gedragsaanpassingen, zullen variëren afhankelijk van de veerkracht van verschillende soorten en de levensstadia. Deze reacties zullen de populatietrajecten en de samenstelling van intertidale benthische macrofauna beïnvloeden. Door de effecten van sedimentdynamiek op benthische macrofauna te onderzoeken, kunnen we de complexe interacties tussen dieren en sedimenten in intergetijdengebieden, die ten grondslag liggen aan hun ecosysteemdiensten, helpen verduidelijken. Ten slotte kunnen de bevindingen van dit proefschrift worden toegepast om het ontwerp van herstelinitiatieven voor habitats van benthische macrofauna te verbeteren en ons begrip van de veerkracht van benthische macrofauna onder klimaatverandering te vergroten.

Effecten van sediment bulkdichtheid op bentische macrofauna (Hoofdstuk 2)

Benthische macrofauna gemeenschappen veranderen van samenstelling afhankelijk van fysieke eigenschappen van hun lokale omgeving, zoals de korrelgrootte van het sediment of de sterkte van de hydrodynamica. Bulkdichtheid van sediment (droog sedimentgewicht per nat sedimentvolume) is een belangrijk kenmerk van intergetijdengeomorfologie, maar de effecten ervan op benthische macrofauna zijn nauwelijks bestudeerd. In **Hoofdstuk 2** hebben we een mesocosm experiment uitgevoerd waarbij we het effect van bulkdichtheid op de graafsnelheid, graafdiepte, bioturbatie activiteit en zuurstofverbruik van tweekleppigen (*Macoma balthica*, *Scrobicularia plana*, *Cerastoderma edule*) en polychaeten (*Hediste diversicolor*, en *Arenicola marina*) onderzocht. In het algemeen vonden we dat de bulkdichtheid een sterk effect had op het gedrag van benthische macrofauna. Benthische macrofauna groef sneller en bioturbeerde intensiever in zachte sedimenten met een lage bulkdichtheid, ongeacht de korrelgrootte.

Weerstand van tweekleppigen tegen stormerosie (Hoofdstukken 3 en 4)

De intensivering van extreme klimatologische verstoringen, zoals winterstormen, zal de erosiedynamiek van wadplaten veranderen. Langzaam bewegende tweekleppigen kunnen in het bijzonder getroffen worden door stormen omdat ze slechts in beperkte mate kunnen ontsnappen aan erosie door extreme stormen. In **Hoofdstukken 3 en 4** onderzoeken we hoe de bestendigheid tegen stormerosie van tweekleppigen afhankelijk is van soort en grootte. In beide hoofdstukken gebruiken we nieuwe stroomgoten om de erodeerbaarheid van tweekleppigen (*Cerastoderma edule*, *Ruditapes philippinarum* en *Macoma balthica*) in een experimentele omgeving te onderzoeken.

Hoofdstuk 3 betreft de aanpassing van inheems versus niet-inheems soorten aan door stormen veroorzaakte sedimenterosie. Invasieve soorten kunnen zich in hoge mate aanpassen aan een groot aantal abiotische kenmerken en dit aanpassingsvermogen maakt hen wellicht beter bestand tegen erosie. In dit hoofdstuk concludeerden we dat de inheemse *C. edule* en de niet-inheemse *R. philippinarum* verschillende strategieën hebben om sterfte door zware stormerosie te vermijden: *C. edule* vermeed aan de oppervlakte te komen liggen en *R. philippinarum* vermeed transport. In dit geval blijkt dat extreme stormen de specifieke aanpassingen van een inheemse soort bevoordelen boven het brede aanpassingsvermogen van een niet-inheemse soort. *C. edule* kan namelijk beter gematigd extreme stormen overleven dan *R. philippinarum*, hoewel de meest extreme stormen voor beide soorten even verwoestend zouden zijn.

In **Hoofdstuk 4** hebben we onderzocht hoe de kwetsbaarheid voor stormen, die afhankelijk is van de grootte van de tweekleppigen, het herstel van de populatie na dergelijke stormen kan beïnvloeden. We ontdekten in de stroomgoot dat de erosie van tweekleppigen afhankelijk is van grootte en pasten dit toe op een leeftijdsgestructureerd model van *M. balthica* populaties in de Schelde. Hieruit bleek dat de totale impact van één enkele extreme storm veel groter is in een populatie waar mortaliteit door stormen afhankelijk is van grootte dan in een populatie waar dit niet het geval is. Door stormerosie kan de diversiteit van samenstellingen in het slikveranderen door selectie van soorten die dergelijke verstoringen beter verdragen. Als gevolg van lokale extreme stormerosie en de grote verspreiding van larven, kan de veerkracht van tweekleppige populaties bij extreme stormerosie op landschapsschaal blijven bestaan. Op lokale schaal kunnen we echter een groter contrast verwachten in het populatietraject en de levensvatbaarheid van tweekleppigen tussen slikplaten die aan golven zijn blootgesteld en slikplaten die niet aan golven zijn blootgesteld.

Verbetering van de benthische macrofauna door menselijke ingrepen (Hoofdstuk 5)

Het aanbrengen van fysieke aanpassingen die gunstig zijn voor de ecologie van een intergetijdensysteem vereist veel inzicht in de relaties tussen de abiotische en biotische componenten van een bepaalde intergetijdenhabitat. In **Hoofdstuk 5** hebben we geëvalueerd hoe abiotische kenmerken de ontwikkeling van de bentische macrofaunagemeenschap beïnvloeden gedurende de eerste vijf jaar na de uitvoering van technische maatregelen ter verbetering van de biomassa en diversiteit van benthische macrofauna in drie case studies in de Westerschelde, Nederland, vanaf de start van het project in 2015 of 2016 tot 2020. We onderzochten de gelijktijdige ontwikkeling van de hydrogeomorfologie en de benthische macrofaunagemeenschap met behulp van multivariate statistiek. We concluderen dat een laagdynamische habitat weliswaar een meer diverse samenstelling van benthische macrofauna kan herbergen dan een hoogdynamische, maar dat een extreem hoog slibgehalte, dat typisch is voor laagdynamische habitats, de ontwikkeling van de benthische gemeenschap kan vertragen.

Belangrijke gevolgen voor het beheer

Onze studies ondersteunen de waarde van laagdynamische (rustige, beschutte) habitats voor bentische macrofauna samenstellingen. Laagdynamische habitats kunnen de biomassa en de diversiteit van benthische macrofauna verhogen die wenselijke ecosysteemfuncties vervullen, zoals het voeden van trekvogels (**Hoofdstuk 5**). Hoewel het verschil tussen laagdynamische en hoogdynamische habitats doorgaans wordt bepaald door de hydrodynamische omstandigheden (bv. stroomsnelheid meer of minder dan 0,6 m/s), blijkt uit onze studies dat stormerosie een belangrijke rol spelen bij de verschillen tussen de samenstellingen van benthische macrofauna in deze habitats (**Hoofdstukken 3 en 4**). Bovendien kunnen laagdynamische habitats langzaam bewegende benthische macrofaunasoorten beschutting bieden tegen plotselinge en ernstige sedimenterosie als gevolg van steeds intensere stormen (**Hoofdstukken 3 en 4**). Sedimenten in laagdynamische habitats neigen echter naar een extreem hoog slibgehalte dat de ontwikkeling van de bentische macrofauna biomassa kan vertragen (**Hoofdstuk 5**), wellicht als gevolg van stress door de extreem bulkdichtheid van het sediment (**Hoofdstuk 2**). Hoewel een laagdynamische habitat voordelen oplevert voor bepaalde gemeenschappen van benthische macrofauna, moeten herstelinspanningen niet alleen gericht zijn op één reeks omstandigheden, omdat homogeniteit van de habitat de diversiteit, en dus de veerkracht, van de gemeenschappen, in intergetijdensystemen vermindert (**Hoofdstuk 5 en discussie in Hoofdstuk 6**).

Chapter 1

General introduction

Lauren E. Wiesebron

The marine intertidal environment: a challenging home

It's difficult to live in the intertidal. Intertidal inhabitants must withstand daily switches from dry land to ocean, and the seesawing food availability, shelter, and predators that tides entail. Not only that, but estuaries are very dynamic environments, where factors like salinity and nutrient import are constantly changing. So the animals that live in the intertidal, and in estuarine areas in particular, must be well-adapted to these conditions, which means that they are extremely resilient creatures and tolerant of large environmental changes (Gray and Elliott 2009). Despite the challenges of living in the intertidal, many creatures call it their home and are well-suited to the harsh and constantly changing conditions. One group of highly successful inhabitants of the intertidal are called benthic, or bottom-dwelling, macrofauna.

The many ecosystem services of benthic macrofauna depend on their assemblages and behavior

Benthic macrofauna are invertebrates that are larger than 5 mm and live in marine sediments. In the intertidal, these animals perform many functions (Aller 1994, Gray & Elliott 2009). They provide food for birds and fish (Piersma et al. 1993, Bocher et al. 2014) and drive many biogeochemical processes on tidal flats such as nutrient cycling (Kristensen 1988), organic matter decomposition (Levin et al. 2001), and pollutant removal. They also engineer their environment (Jones et al. 1997) by, for example, trapping and eroding sediment. Not only does this environmental engineering, or bioturbation, change the geomorphology of the tidal flat, but it can improve the surrounding habitat for other organisms (Mermillod-Blondin et al. 2004, Sturdivant & Shimizu 2017). Thus, benthic macrofauna are integral to the functioning of intertidal ecosystems and provide many ecosystem services.

The type of ecosystem services the benthic macrofauna provide depends largely on the species that makeup the assemblages and their behaviors. Different species perform different kinds of functions, such as distinct manners of bioturbation. For example, certain species, like *Cerastoderma edule* mix the top layer of sediment with their shallow burrowing (Li et al. 2017), while others, like the polychaete *Hediste diversicolor*, create burrows that oxygenate the sediment and stimulate the microbial community (Mermillod-Blondin et al. 2004). A benthic community that is dominated by bivalves will feed different predators than one that is dominated by polychaetes. Furthermore, the behavior of certain species can also drive macrobenthic invertebrate community composition. For example, because the depth to which an animal burrows in the marine sediment determines the depth of the layer which it oxygenates (Sturdivant and Shimizu 2017), burrowing deeper or shallower will impact the extent of the habitable zone that animal creates for other organisms. Because the assemblages and behavior of benthic macrofauna underpin many ecosystem services, it is vital to know what processes affect them.

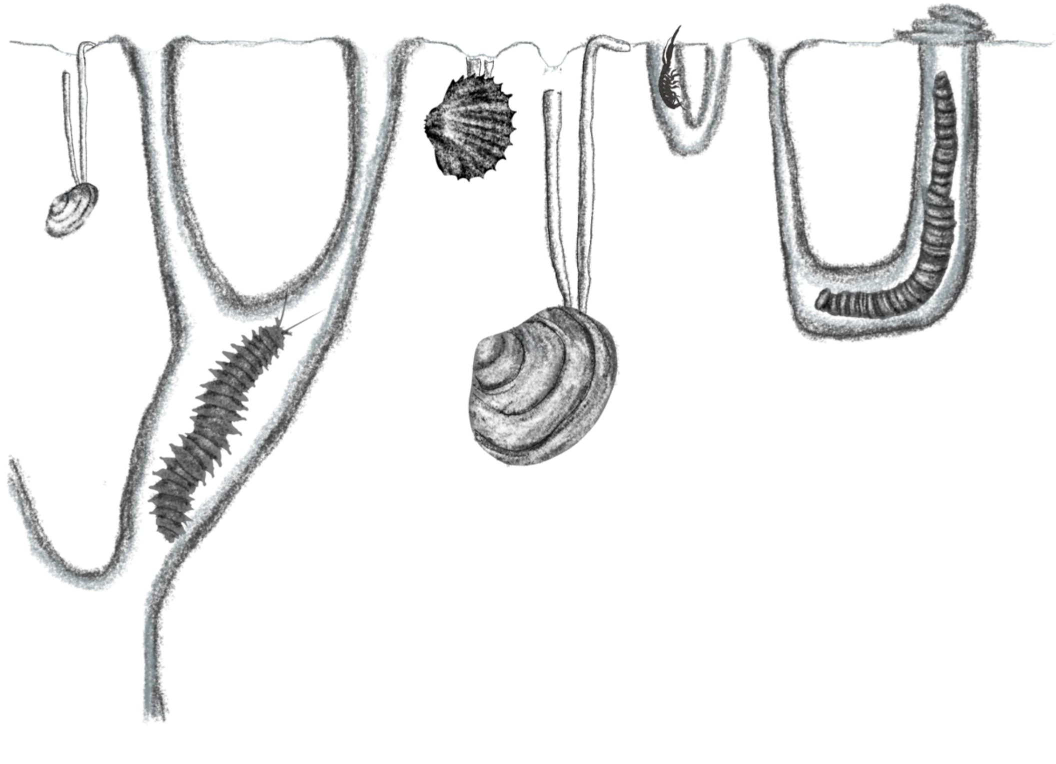

Figure 1: Cross-section of sediment showing common benthic macrofauna in low-dynamic habitat in the Scheldt estuary. From left to right: *Macoma balthica, Hediste diversicolor, Cerastoderma edule, Scrobicularia plana, Corophium volutator, Arenicola marina*. These modify their environment through bioturbation. *M. balthica, C. edule*, and *S. plana* are slow moving bivalves, and mix the sediment at different depths through by moving their siphons and pumping water during feeding. *H. diversicolor* is an omnivorous polychaete and crawls through extensive gallery burrows. *A. marina* is a slow-moving, deposit-feeding polychaete which creates distinctive fecal mounds on the sediment surface. The amphipod *C. volutator* frequently occurs at high densities and its bioturbation activity can have a huge impact on the surface sediment structure. See Chapter 2 for more descriptions on these benthic macrofauna (except *C. volutator*).

Benthic macrofauna assemblages and behavior change depending on their environment

One of the most important factors that affects the behavior and assemblages of benthic macrofauna is their environment (Ysebaert & Herman 2002). While benthic macrofauna are very resilient creatures and are adapted to living in a highly variable environment (Ellis et al. 2000), they are better suited to certain environmental characteristics than others. The suite of environmental characteristics that they prefer to inhabit is called their niche. Niches vary between species and within species, depending on their life history. For example, juveniles of bivalve *M. balthica* prefer to live higher in the intertidal than adults to avoid predation by shrimp (Hiddink & Wolff 2002). If species have overlapping niches, then they can live in the same habitats. Besides environmental preferences, biotic interactions such as competitions and predator-prey relationships will also determine the species that make-up an assemblage, however, these biotic interactions also change depending on the environment in which they take place (Menge & Sutherland 1987). Because species are adapted to different niches, different assemblages of species will live in different habitats.

Furthermore, benthic macrofauna change their behavior depending on their environmental conditions (Fig. 2). Changing behavior is a way to adjust to the extremely variable environment of the intertidal. For example, depending on the food availability and the water flow, a bivalve like *Macoma balthica* may use its siphon to either filter overlying water or to vacuum food particles from the sediment surface (Olafsson 1986, Peterson & Skilleter 1994). Changes in the behavior of benthic macrofauna also results in changes to their ecosystem function. For example, the crab *Austrohelice crassa* extends the water-sediment interface seven times deeper in muddy sediment where it builds burrows, than in sandy sediment where it plows through the surface layer (Needham et al. 2010). In the end, not only do benthic macrofauna change their behavior under different environmental conditions, but their ecosystem functions change as well.

Sediment properties are an important environmental characteristic which affect benthic macrofauna

By definition, benthic (meaning bottom-dwelling) macrofauna live in sediment, and so it is unsurprising that sediment properties are key factors that determine the quality of their habitat. Different species will have niches along different portions of the spectrum of possible values for an environmental characteristic (Fig. 2, Ysebaert and Herman 2002; Cozzoli et al. 2013). In particular, benthic macrofauna assemblages have been long-known to change along the sediment grain size gradient (Ysebaert et al. 2002) and these assemblages are frequently classified as "muddy" or "sandy". Not only do assemblages change depending on sediment grain size, but so do behaviors. For example, the bivalve *Macomona liliana* moves its siphon less in muddy sediment than sandy sediment (McCartain et al. 2017). Other, less well-studied sediment characteristics may also impact the assemblages and behavior of macrofauna species.

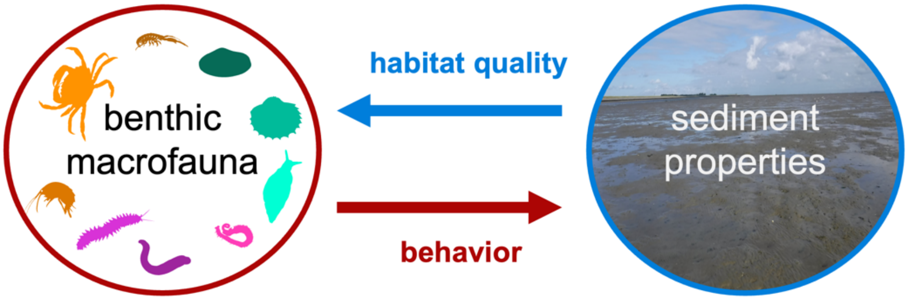

Figure 2: Schematic of benthic macrofauna— sediment interactions. Benthic macrofauna can change their behavior to better withstand their environment and their engineering behavior changes sediment properties. On the other hand, sediment properties determine the habitat quality for the benthic macrofauna, which affects the species composition. The benthic macrofauna (silhouettes from www.phylopic.org) depicted are three crustaceans, three mollusks, and three polychaetes that are common to the Scheldt.

Intertidal sediments are not static

In the dynamic estuarine environment, sediments are never in a stable state. These undergo cycles of erosion and deposition due to waves, tides (Hu et al. 2018), and seasons (Van Colen et al. 2014). The strength of the sediment dynamics is driven by the system's hydrodynamics. An intertidal area that is calm and sheltered and experiences low hydrodynamic forcing (low-dynamic habitat is loosely defined as having mean current velocity less than 0.5 m/s) will typically have fine-grained sediment and a less substantial erosion and deposition cycle, whereas a high-dynamic system tends to have coarser-grained sediment and a stronger sediment erosion and deposition cycle. Furthermore, biota can also contribute to sediment stabilization (De Backer et al. 2010) and destabilization (Montserrat et al. 2008). Sediment dynamics greatly impact benthic macrofauna behavior as many animals adjust their position in the sediment due to the constant erosion and deposition of their sedimentary habitat. In addition, sediment dynamics affect benthic macrofauna recruitment success (Bouma et al. 2001) and the dispersal of juveniles (Hunt 2004).

It is important not only to consider how the mean conditions of sediment dynamics affect benthic macrofauna, but also how they respond to extremes. Beyond the constant daily and seasonal cycles, intertidal systems also experience extreme sediment dynamics during storms, which can have devastating consequences for benthic macrofauna due to rapid erosion (Yeo & Risk 1979) or deposition (Lohrer et al. 2006). Environmental extremes, including the frequency and magnitude of storms, will only increase with climate change (Stocker et al. 2013). The ability to tolerate extremes in sediment dynamics may become more important for determining benthic macrofauna assemblages in the future.

Sediment conditions vary widely due to direct anthropogenic intervention

In addition to increasing extremes in sediment dynamics due to climate changes, environmental conditions also change due to direct anthropogenic intervention. Indeed, coastal areas are some of the most widely used and impacted areas in the world (Murray et al. 2019), and human activity from different land use, pollution, overfishing etc. greatly affects the sedimentary conditions that benthic macrofauna live in.

However, anthropogenic change can also be applied to try to improve conditions for benthic macrofauna. One of the goals for restoration initiatives can be to improve habitat quality for benthic macrofauna. Knowing which suite of sediment characteristics are suitable for which assemblages is crucial for engineering physical changes to a habitat that would benefit specific benthic communities. The goals of the restorations can often be to encourage benthic communities that would provide highly desired ecosystem services, such as feeding migratory birds.

Benthic macrofauna’s response to disturbances is governed by their adaptability

While environmental disturbances provide heterogeneity to habitat conditions which is essential for the establishment and permanence of many species (Sousa 1984), disturbances can also cause direct mortality in biota (Huston 2014) and alter environmental conditions to outside the range of species’ tolerances (Menge & Sutherland 1987, Smale & Wernberg 2013). In the context of the thesis, I include both the storm erosion, investigated in Chapters 3 & 4, and the restoration initiatives, the subject of Chapter 5, as disturbances (see Fig. 3). Disturbance can be defined as any biotic or abiotic, natural or man-made process that can destabilize the natural systems at any hierarchical level (Hobbs & Huenneke 1992), with natural physical causes being the most commonly associated, e.g. floods, fires, storms (Sousa 1984). Though restoration initiatives are perhaps not traditionally placed under the umbrella term “disturbance,” because of their intended beneficial outcomes, I believe that the measures employed for the restoration initiatives detailed in Chapter 5 (managed realignment and groins) are sufficiently disruptive to fall under the disturbance definition.

Faced with a dynamic environment, the biggest protection that benthic macrofauna have from the harsh changeability of their environment is their resilience. Resilience is a measure of how well a system can absorb changes when subject to disturbance (Holling 1973). It is determined by two mechanisms: the ability of an individual or species to withstand change (resistance) and the ability of a population to return to pre-disturbance levels (recovery) (Gladstone-Gallagher et al. 2019). Resistance is modulated by behavioral or species-specific sensitivity to a particular disturbance which may make an individual more or less successful at tolerating a disturbance. The resilience traits of an individual or species can often define how well it will survive a disturbance as well as contribute to population persistence in the intertidal.

Experiments are useful for better understand animal-sediment relations

Environmental characteristics are highly correlated and sediment characteristics are no exception. Because sediment characteristics are so highly correlated, but at the same time so variable in space and time, it is difficult to know which characteristic (if any) is the most important for driving benthic community assemblages. One approach to untangling the various effects of sediment characteristics on benthic macrofauna assemblages and behavior is to perform manipulative experiments. With experimental work, one can isolate the various factors that drive responses from the subjects, and this can help us get at a mechanistic understanding of the relationship between the driver and the response, rather than a correlation. Mechanistic understanding greatly improves our interpretation of observation-based studies like monitoring. However, it is important to supplement experiments with observation in the real world to ascertain if the relationships isolated in the lab also exist in the field. In addition, in the field it is easier to not only observe real-world condition, but also interactions between the various components in the system.

There's still a lot we don't know about sediment dynamics drivers of benthic macrofauna assemblages and behavior

While some effects of sediment dynamics on benthic macrofauna are already well-studied, other are less well-known. Certain sediment characteristics have already been well-investigated for correlations with species assemblages and behavior. For example, it is well known that species assemblages change with sediment grain size (Ysebaert and Herman 2002). However, other sediment characteristics, such as sediment bulk density which describes the compaction of a sediment (Grabowski et al. 2011), are less well-known, but could be important. In addition, extremes in sediment dynamics have been infrequently investigated for their effects on benthic macrofauna. Storms can cause extremes in sediment erosion or deposition (de Vet et al. 2020), and while extreme sediment deposition has been investigated for its effects on benthic macrofauna (Lohrer et al. 2006), extreme erosion has not. Finally, while research on the evolution of benthic macrofauna assemblages in restored areas has been done (e.g. Beauchard et al. 2013), the focus has more frequently been on the evolution of the community and fewer studies have examined the physical drivers of that change.

Research can help shrink the gap!

Research on poorly known effects of sediment dynamics on benthic macrofauna behavior and assemblages will help clarify the complex animal-sediment interactions that occur on tidal flats which underpin their ecosystem services. Furthermore, this research can increase our understanding of the resilience of benthic macrofauna communities to climate change, as well as their response to deliberate anthropogenic environmental change, such as restoration projects.

Outline of thesis

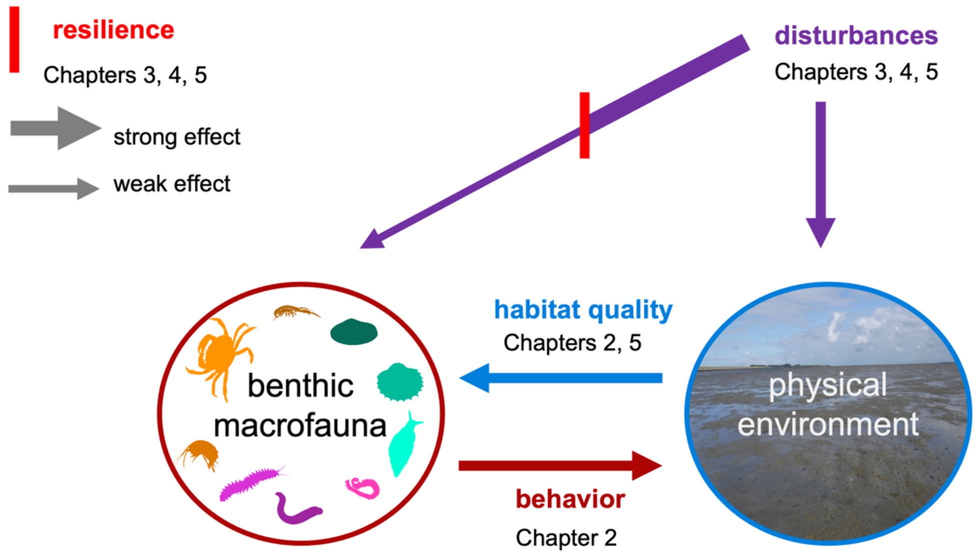

Figure 3: Schematic of thesis themes. Benthic macrofauna-environment interactions are born from habitat drivers (Chapters 2 and 5) of species assemblages and faunal behaviors (Chapter 2) that engineer the habitat. Disturbances (extreme storms in Chapters 3 and 4, and human interventions in Chapter 5) affect these

interactions, by directly impacting both the intertidal environment and benthic macrofauna assemblages. The severity of the benthic macrofauna response to disturbances or extreme environmental conditions will change depending upon the adaptability of benthic macrofauna on an individual level (Chapters 2 and 3) and on a population or assemblage level (Chapters 4 and 5). The benthic macrofauna depicted (silhouettes from www.phylopic.org) are three crustaceans, three mollusks, and three polychaetes that are common to the Scheldt.

In my thesis, I have examined the response of benthic macrofauna assemblages and behavior to dynamic sediment drivers. In particular, I focus on uncovering behaviors and traits that confer resilience in benthic macrofauna against disturbances and extremes in sediment dynamics (see Fig. 3). In Chapter 2, I use an experiment to better understand the effects of sediment bulk density, a little studied but important sediment characteristic, on benthic macrofauna burrowing and bioturbation behavior. In Chapters 3 and 4, I examine the effects of storm erosion in relation to benthic macrofauna in terms of species-specific and size-specific differences in responses. In these chapters I show how species-specific and size-specific traits modulate tolerances to extreme sediment dynamics, which has consequences for long-term success of species and population resilience in the intertidal. In Chapter 5, I take a multivariate approach to the effects of sediment dynamics on the benthic community by analyzing the concurrent development of hydrogeomorphology and benthic macrofauna community of three restoration projects in the Western Scheldt. In the text below, I briefly address the key question addressed in each chapter.

Sediment bulk density effects on benthic macrofauna burrowing and bioturbation behavior (Chapter 2)

Many physical drivers of benthic macrofauna behavior, such as sediment grain size, have been well-studied. However, little is known about how sediment bulk density (a measure of sediment compaction and water content) affects this behavior.

Research question: How does sediment bulk density of a muddy and sandy sediment effect the burrowing and bioturbation of five functionally different benthic macrofauna species?

We investigated the effect of bulk density on the burrowing rate, burrowing depth, bioturbation activity, and oxygen consumption of bivalves (*Macoma balthica, Scrobicularia plana, Cerastoderma edule*) and polychaetes (*Hediste diversicolor*, and *Arenicola marina*) during a 29-day mesocosm experiment. We compared four sediment treatments consisting of two sediments of differing grain size classes (sandy and muddy) with two bulk densities (compact and soft).

Contrasting strategies to cope with storm-induced erosion events: a flume study comparing a native vs. invasive bivalve (Chapter 3)

Storm-induced erosion events may alter the diversity of tidal flat communities by selecting for species that can better tolerate such disturbances. Invasive species are highly adaptable to a wide range of abiotic characteristics, and this adaptability may make them better able to withstand erosion events. It is not well-known how storm-induced erosion may affect native vs. invasive species.

Research question: Is there a difference between the erodibility of the native *Cerastoderma edule* and invasive *Ruditapes philippinarum*?

With a novel flume method, we compared the ability of two bivalve species to resist storm-induced erosion: *Cerastoderma edule*, a native species to the Scheldt estuary in the Netherlands, and *Ruditapes philippinarum*, an invasive species that is successful worldwide. We used three sediment erosion rates to simulate storms of increasing severity and observed the differences in their surfacing rates. We also examined whether there were differences in how readily the *C. edule* vs. *R. philippinarum* would be transported by currents and waves.

Size-dependent burrowing behavior determines bivalve population vulnerability to changes in storminess (Chapter 4)

Climate change may alter the future frequency and intensity of winter storms, and thereby altering the erosion dynamics of tidal flats. Extreme storm-induced sediment erosion may also have size-dependent effects due to differences physical attributes like size-dependent differences in particle entrainment velocity, but also biological factors, such as age-dependent living depth and burrowing speed. Better understanding size-dependent effects of storm-induced erosion on bivalve erodibility is needed to more realistically predict bivalve population trajectories in a future with greater incidence of extreme storms.

Research question: Does the size of the bivalves *M. balthica* and *C. edule* affect their vulnerability to storm-induced erosion?

To better understand how climate change will affect bivalve populations, we used a flume experiment to examine the dependence of bivalve erosion on shell length, initial burying depth, and active burial behavior for both juveniles and adults of two bivalve species that commonly co-occur on tidal flats in the Scheldt estuary: *M. balthica* and *C. edule*. We then applied the experimental results to an age-structured model of *M. balthica* to explore how size-dependence in bivalve erodibility may affect their populations.

Intertidal flat alterations can enhance their ecological value (Chapter 5)

In creating or enhancing intertidal areas through managed realignments and groins, environmental characteristics are modified to trigger a change in the ecosystem's ecology. However, these projects are not always successful. Creating physical modifications which are beneficial to an intertidal system's ecology necessitates a good understanding of the relationships between the abiotic and biotic components of a given intertidal habitat. This requires learning from large-scale restoration efforts.

Research question: Do we see concurrent change in the abiotic and biotic components of the intertidal ecosystem over these three case studies?

we evaluated how hydrodynamics and sediment characteristics drive the development of the benthic macrofauna community in three case studies in the Western Scheldt, The Netherlands, from project initiation in 2015 or 2016, until 2020. We examined the concurrent development of the hydrogeomorphology and benthic macrofauna community using multivariate methods and we use these results to speculate about the trajectory of the restored areas.

General Discussion (Chapter 6)

I summarize my main findings and give some ideas for future research themes which could build upon this thesis's results. Finally, I explore how we can increase the resilience of intertidal benthic macrofauna assemblages against climate change and anthropogenic pressure by improving habitat.

Chapter 2

Sediment bulk density effects on benthic macrofauna burrowing and bioturbation behavior

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Abstract

Benthic macrofauna are a key component of intertidal ecosystems. Their mobility and behavior determine processes like nutrient cycling and the biogeomorphic development of intertidal flats. Many physical drivers of benthic macrofauna behavior, such as sediment grain size, have been well-studied. However, little is known about how sediment bulk density (a measure of sediment compaction and water content) affects this behavior. We investigated the effect of bulk density on the burrowing rate, burrowing depth, bioturbation activity, and oxygen consumption of bivalves (*Macoma balthica*, *Scrobicularia plana*, *Cerastoderma edule*) and polychaetes (*Hediste diversicolor*, and *Arenicola marina*) during a 29-day mesocosm experiment. We compared four sediment treatments consisting of two sediments of differing grain size classes (sandy and muddy) with two bulk densities (compact and soft).

Overall, bulk density had a strong effect on benthic macrofauna behavior. Benthic macrofauna burrowed faster and bioturbated more intensely in soft sediments with low bulk density, regardless of grain size. In addition, *M. balthica* burrowed deeper in low bulk density sediment. Finally, we found that larger bivalves (for both *C. edule* and *S. plana*) burrowed slower in compact sediment

than smaller ones. This study shows that benthic macrofauna change their behavior in subtle but important ways under different sediment bulk densities which could affect animal-sediment interactions and tidal flat biogeomorphology. We conclude that lower bulk density conditions lead to more active macrofaunal movement and sediment reworking.

Introduction

Estuarine intertidal systems are among the most productive ecosystems globally and are responsible for important ecosystem services such as providing coastal protection, carbon sequestration, food production, recreation areas, as well as habitat and nursery grounds for fish and birds (Meynecke et al. 2008, Koch et al. 2009, Barbier et al. 2011, Seitz et al. 2014). At the margins of the land and sea, many factors, both biotic and abiotic, drive the development of these ecosystems (Gray & Elliott 2009). Benthic macrofauna are a key component of intertidal systems: not only are these animals important prey for birds and fish (Piersma et al. 1993, Zwarts & Wanink 1993, Bocher et al. 2014), as ecosystem engineers they modify their sedimentary environment (Bouma et al. 2009). Benthic macrofauna–sediment interactions vary considerably in space and time. They depend on species distribution and behavior as well as local environmental conditions such as sediment composition. The strength of these interactions, in turn, underpins the supply of ecosystem services delivered by intertidal ecosystems. Some sediment characteristics, such as grain size and mud content, have been highly investigated for correlation with species occurrence (Thrush et al. 2003, Pratt et al. 2014) and effects on benthic macrofauna behavior (Dorgan 2015, McCartain et al. 2017). One sediment characteristic that does not have a well-known effect on benthic macrofauna and their behavior is sediment bulk density, an indicator of both sediment compaction and water content (Grabowski et al. 2011), which is the focus of this paper.

By being inversely related to sediment porosity, or the amount of water retained in a waterlogged sediment, bulk density influences the sediment oxygen content, chemistry, and organic matter (Gray & Elliott 2009, Dowd et al. 2014). Thus sediment bulk density (dry sediment weight per sediment wet volume) is an important characteristic of intertidal geomorphology and describes a measure of sediment compaction which is missing from grain size gradients. The range of bulk density values vary on a regional and local scale. Bulk density tends to increase with grain size (Ysebaert et al. 2005) and sediment strength (Lucking et al. 2017), while it tends to decrease with silt content, erodibility, and organic matter content (Grabowski et al. 2011, Stringer et al. 2016, Joensuu et al. 2018). More compact sandy sediments typically have a bulk density of around 1-2 g cm^{-3} and softer, muddier sediments typically have a bulk density of around 0.2-1.5 g cm^{-3} (Andersen et al. 2005, Grabowski et al. 2011, Stringer et al. 2016). However, sediments with similar grain size composition can have a range of bulk densities due to different water contents (e.g. Widdows et al. 2007; Soares and Sobral 2009). At very low bulk densities, the sediment is viscous and more akin to a fluid (Grabowski et al. 2011). These conditions are found in many systems worldwide, in particular mangroves (Stringer et al. 2016) and intertidal mud flats (Walles et al. 2017). Furthermore, sediment bulk density tends to increase with erosion and decrease with sediment deposition (Dyer et al. 2000). Besides long-term erosion and sedimentation trends, intertidal flats experience short-term bed-level variation which differs between sites of contrasting wave exposure (Hu et al. 2017). These bed-level trends may contribute to the variation of sediment bulk density over several temporal and spatial scales in estuarine areas. Though bulk density is an important biogeomorphological characteristic of intertidal sediments, we still do not understand how significant this characteristic is for determining benthic macrofauna organism-sediment interactions.

Macrofauna's mixing of sediment, or bioturbation, typically affects parameters like sediment permeability, grain size, and erodibility (Volkenborn et al. 2009, Kristensen et al. 2013, Harris et al. 2016), and also drives many biogeochemical processes of tidal flats (Kristensen 1988, Gray & Elliott 2009). Sediment mixing by benthic macrofauna increases sediment permeability, which plays a vital role in nutrient cycling by driving the circulation of oxygen and nutrients below the sediment surface (Aller 1994, Thrush et al. 2006). Though benthic macrofauna can move laterally by crawling through the sediment (e.g. *H. diversicolor* (Aberson et al. 2011) and *C. edule* (Richardson et al. 1993) animals usually avoid crawling at the sediment surface since it exposes them to predation (Ens et al. 1997). In this study we focus on vertical sediment mixing which is produced mainly by burrowing and deposit feeding (Kristensen et al. 2012). The mode of mixing is important for determining what kind of ecosystem services the organisms provide. Local mixing, or biodiffusion (Boudreau 1986a), such as by *C. edule*, can discourage the build-up of fine mud (Montserrat et al. 2008) and oxygenate the top sediment layers (Mermillod-Blondin et al. 2004). Non-local mixing, where surface particles are transported from depth to the surface and vice versa (Boudreau 1986b), such as by the polychaete *H. diversicolor*, transports particles faster and deeper in the sediment, which creates new habitat for deeper living organisms (Gray & Elliott 2009), thus increasing biodiversity (Sturdivant & Shimizu 2017). Moreover, non-local mixing also facilitates biogeochemical processes such as denitrification and permanent burial of pollutants (Mermillod-Blondin et al. 2004).

While macrofauna drive tidal flat biogeomorphology and biogeochemistry through their movement behavior, they also change their behavior under different sediment conditions. Many studies have shown that sediment properties determine macrofauna behavior, for example, *Macomona liliana* decreases its siphon movement in cohesive muddy sediment compared to sandier sediment (McCartain et al. 2017), which could have consequences for sediment permeability and oxygen flow. While the effects of some sediment characteristics, like sediment grain size, on behavior have been well-studied, bulk density effects have not. Studying how macrofauna change their behavior under different bulk densities will help better understand how sediment conditions affect the ecosystem functioning of benthic macrofauna and thus the biogeochemistry and biogeomorphology of tidal flats.

The objective of this study was to investigate how five dominant and functionally different bivalve and polychaete species modify their burrowing and bioturbation behavior under different bulk densities. We hypothesized (1) that both bivalves and polychaetes would have lower mobility (slower burrowing speed, shallower burrowing depth, less active bioturbation) in more compact sediments, (2) that bulk density would have a similar effect on benthic macrofauna behavior in both sandy and muddy sediment, and (3) that larger bivalves would be slower and less active in higher bulk density sediments than the smaller and younger ones, due to greater biomass hampering their mobility. To test our hypotheses, we performed a mesocosm experiment where we subjected three bivalve species (*Macoma balthica*, *Scrobicularia plana*, and *C. edule*) and two polychaete species (*Hediste diversicolor* and *Arenicola marina*) to four sediment treatments of varying bulk density and mud content. We measured the following indicators of movement behavior: burrowing speed, burrowing depth, bioturbation activity and respiration rates. We selected the species based on their dominant prevalence in the Scheldt intertidal (Cozzoli et al. 2013) as well as their functional differences. In particular, the five species covered the different bioturbator types (Table 1).

Methods

Experimental design

We designed a mesocosm experiment in which three bivalve species (*Macoma balthica*, *Scrobicularia plana*, and *Cerastoderma edule*) and two polychaete species (*Hediste diversicolor* and *Arenicola marina*) were subjected to two crossed bulk density (dry sediment weight per sediment wet volume) and sediment grain size treatments (Fig. 1b). Our four treatments were: compact-sandy (CS), soft-sandy (SS), compact-muddy (CM), and soft-muddy (SM) (see Table 2 for sediment characteristics). We used two sediment grain sizes to cover a larger part of the range of bulk densities observed in the Scheldt intertidal, as well as to test the interaction between sediment bulk density and grain size on animal behavior. We prepared the treatments from two sediments collected from intertidal flats in the Eastern Scheldt estuary (Fig. 1a). The sandier sediment was collected at the Oesterdam (51.466700, 4.221389) and the muddier sediment was collected from Prosperhaven (51.490305, 4.259167) nearby. Both were collected several months before the start of the experiment and were stored in outdoor closed bins. The sandier sediment was drained and passed through a large (5 mm) sieve before use. The sticky consistency of the muddy sediment did not allow it to be passed through a sieve, therefore we removed the larger fragments, such as shells, by hand. We incorporated seawater (amount equaling 7% of the sediment weight for compact high bulk density treatments and 15% for soft low bulk density treatments) into the sifted sediments with a standing industrial mixer the day before we added the animals (See Table 2 for resulting sediment characteristics). The sediment was mixed in batches of 5 kg for at least five minutes to ensure the mixture was homogenous. The sediment was placed in pots made from a sawed-off PVC pipe (height 12 cm, diameter 11.5 cm). Each PVC pipe was capped off on the bottom with a removable plastic cap and lined with a plastic bag to prevent water loss. We encircled the brims of the pots with mesh (1 mm mesh size) that extended 2 cm above the high tide height to keep the animals contained to their unit. The pots were filled to 0.5 cm below the brim and placed in the mesocosm tanks.

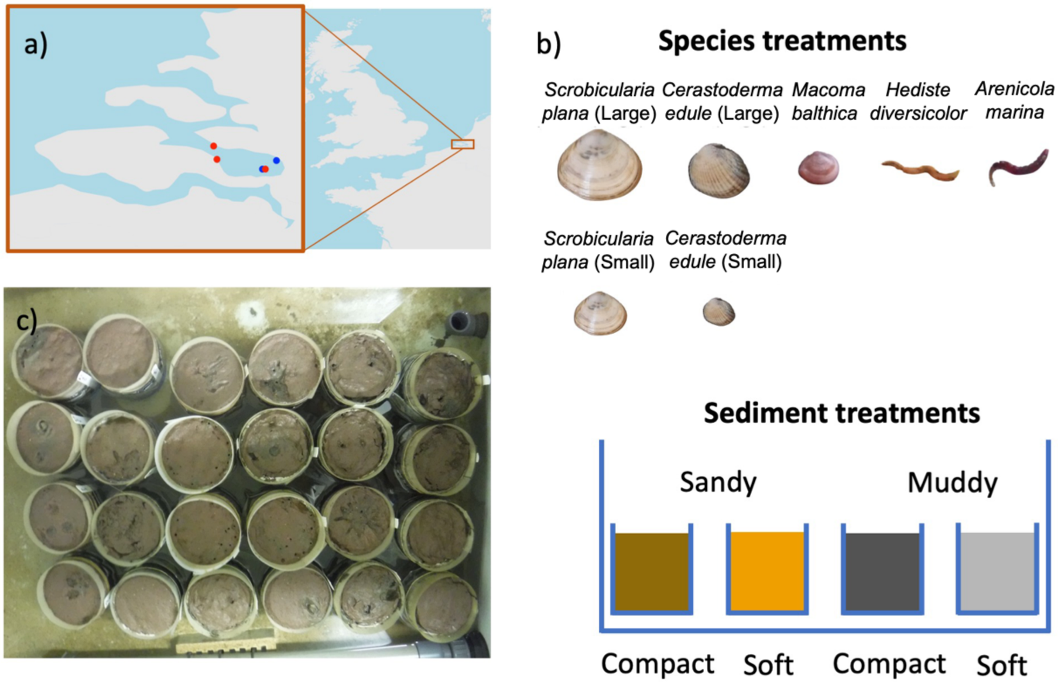

Figure 1: Map of our study area in the Scheldt (a) with points of sediment collection (blue) and macrofauna collection (red). Experimental design (b) with (upper panel) seven species treatments, four of which were *C. edule* and *S. plana* size classes, and (lower panel) four sediment treatments. We had six replicates for each sediment – species combinations. A picture of the sediment cores in a tidal tank halfway through the experiment is shown in (c) with visible surface rugosity from bioturbation and animal movement.

The experiment was conducted in ten tidal tanks in a climate-controlled room where the water was kept at 18 ºC, the same temperature as the Eastern Scheldt in July 2018 when the experiment was carried out. Each tidal tank was composed of two 1.2 m by 0.8 m tanks stacked on top of each other. Unfiltered water from the Eastern Scheldt estuary was pumped from the bottom tank up to the top tank to simulate tidal conditions. High tide conditions (5 cm water above experimental units) lasted six hours and occurred twice a day. We changed the water once a week, and in addition to the nutrients contained in the raw Eastern Scheldt water, we fed the animals with an algal concentrate (Shellfish Diet from Reed Mariculture) 5 mL per tank twice per week.

Table 1: Overview of all 'species-types' and their traits per experimental block, including two size classes for *C. edule* and *S. plana*, plus a control treatment. The main ecological traits for all species used in the experiment are listed. Species traits from literature: feeding and mobility trait (Van Colen et al. 2012[1]; Riisgard and Banta 1998[2]; Olafsson 1986[3]; Orvain 2005[4]), sediment reworking (Morys et al. 2017[5]; Queirós et al. 2013[6]; this study[7]; Gérino et al. 2003[8]), sediment preference (Ysebaert et al. 2002[9]; Van Colen et al. 2014[10]).

Species	Feeding trait	Mobility	Sediment reworking	Sediment preference	Size class (mm)	Animals per pot
Cerastoderma edule	Suspension feeder[1]	Slow movement through sediment[1]	Surficial biodiffusor[6]	Sandy (median grain size 125 um)[9]	small: 8-13; large: 14-25	2
Macoma balthica	Surface deposit feeder[1]/Suspension feeder[3]	Limited movement[1]	Surficial biodiffusor[6]/ Conveyor[5]	Mixed sandy/muddy (median grain size 100 um)[10]	10-14	5
Scrobicularia plana	Surface deposit feeder[1]/Suspension feeder[4]	Limited movement[1]	Surficial biodiffusor[6]/ Conveyor[7]	Muddy (median grain size 75 um)[10]	small: 28-34; large: 38-43	1
Hediste diversicolor	Omnivore[1]	free movement via burrow system[1]	Gallery biodiffuser[6]	Very muddy (median grain size 25 um)[10]	40-100	3
Arenicola marina	Sub-surface deposit feeder[2]	limited movement via burrow system[2]	Up/downward conveyor[8]	Sandy (median grain size 175)[8]	25- 55	5
Controls						0

We had eight experimental blocks composed of two polychaete species, three bivalve species with two size classes for *S. plana* and *C. edule*, and controls without animals (Table 1). We collected the animals at three sites in the Eastern Scheldt: *A. marina* were collected at the Oesterdam (51.46670, 4.22139), *C. edule* and *M. balthica* were collected at Dortsman (51.543678, 4.055841), and *S. plana* and *H. diversicolor* were collected in Yerseke (51.489245, 4.057288), three days to 24 hours before the start of the experiment and stored in a tidal tank in the mesocosm (Fig. 1a). Each block was replicated six times for each sediment treatment. Thus, we had 24 units for each species/size block, resulting in a total experiment of 8 x 24 = 192 units (see details in Table 1).

All the animals used occurred naturally in the two sediments we used for the experiment (see Cozzoli et al 2013 for biomass probability distribution in the Scheldt depending on grain size for *C. edule*, *M. balthica*, *H. diversicolor*, and *A. marina*; see probability distribution for *S. plana* depending on grain size in Van Colen et al., 2014). *A. marina* was the only species placed in unnatural conditions (muddy sediment) not found in the field. Not unexpectedly, *A marina* had low survival in the muddy sediment treatment, especially the compact-muddy treatment. There was some low mortality for *H. diversicolor* (See Results 3.1), but this was not linked to any sediment treatment. We recorded no mortality in the bivalves.

Table 2: Median values for sediment characteristics (median grain size, grain size composition, water content, bulk density, penetration resistance as measured by a universal testing machine (Instron, Maryland, USA) for the four sediment treatments.

Sediment characteristic	compact-sandy	soft-sandy	compact-muddy	soft-muddy
Median grain size (μm)	108	106	44	43
Coarse sand (0.5-1mm) (%)	2.23	3.49	0.26	0.21
medium sand (0.25-0.5 mm) (%)	17.35	17.31	2.22	2.79
fine sand (0.125-0.25 mm) (%)	25.88	24.4	10.78	11.07
very fine sand (0.062- 0.125 mm) (%)	16.66	15.74	24.09	22.85
Silt (0.004-0.062 mm) (%)	38.02	39.18	62.94	63.36
Water content (%)	17.87	21.94	47.39	53.14
Bulk density (g cm^{-3})	1.32	1.25	0.67	0.59
penetration resistance (N)	25053	1058	799	264

The units were divided randomly into the ten tidal tanks (24 per tank) to minimize a tank effect. We used realistic but low animal densities to avoid competition for space and food resources. The realistic densities also allowed us to obtain realistic behavioral responses from the animals. Thud, the number of animals per core varied between species, which means that responses and animal abundances were colinear. The number of animals per pot were one *S. plana*, two *C. edule*, five *M. balthica*, five *A. marina*, and three *H. diversicolor*. We only compared the magnitude of the species effect between size class treatments (i.e. small and large *C. edule* and *S. plana*). Though the abundances varied per species, the biomass per pot was roughly similar.

Sediment characterization

We prepared 24 extra cores to take bulk density and sediment penetration resistance measurements to determine whether the sediment treatments changed over the course of the experiment. The cores were placed in a separate tidal tank in the same climate room as the experiment. We used a universal testing machine (Instron, Maryland, USA) to measure sediment penetration resistance, or the amount of pressure necessary to compress the sediment. The universal testing machine measures the load as a crosshead penetrates the sediment and extends to the bottom of the sediment core at a constant speed (Bokuniewicz et al. 1975). To measure bulk density (dry sediment weight per sediment wet volume), we determined the water content of a fixed volume of sediment which was collected using a cut-off syringe and weighed before and after freeze-drying for 48 hours. We took penetration resistance and bulk density measurements of the different sediment treatments after twelve hours, one week, two weeks, and at the end of the experiment. The four sets of cores were only used for each set of measurements once because the sampling for bulk density destroys the core.

While the penetration resistance changed over time, there was no overlap in penetration resistance profiles between the four treatments by the end of the experiment (Fig. 2). The bulk densities of the four treatments remained significantly distinct from each other over the course of the experiment, $F(3,80) = 649$, $p < 0.001$, and post hoc Tukey test $p < 0.008$ for all treatment comparisons. In addition, the inclusion of the measurement date in the linear model evaluating treatment effects on sediment bulk density did not improve the model fit, $F(1,79) = 0.001$, $p = 0.97$, indicating that the sediment bulk densities did not change between the beginning and end of the experiment.

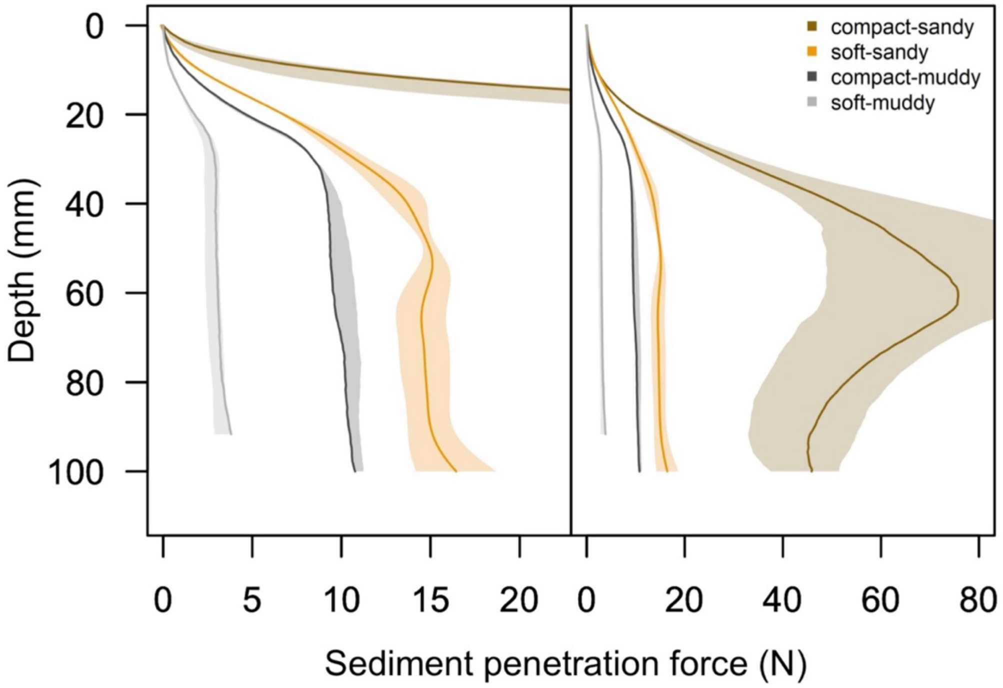

Figure 2: Mean sediment penetration force profiles and 95% confidence intervals as measured by the universal testing machine for the four sediment treatments, with 95% confidence intervals encompassing the beginning and end of the experiment. We present a panel with a reduced x-axis scale on the left to show the details of the soft-sandy, compact muddy, and soft-muddy sediment treatments, and we present a panel with a full x-axis scale on the right to show the extent of the compact-sandy sediment profile. Note that the resistance of the compact-sandy treatment is an order of magnitude greater than the other three treatments and that in the right plot the profile for the compact-sandy sediment is scaled to 1/5 of the original sediment penetration force to fit into the plotting area.

Process measurements: burrowing rates

Burrowing rates of bivalves were monitored by counting the animals still present at the sediment surface shortly after the start of the experiment and then every twelve hours until they were all buried, after two days. This method worked well for the bivalves, but not for the fast-burrowing polychaetes as they burrowed almost immediately. Hence, we performed an additional short experiment to investigate how bulk density impacted the burrowing ability of polychaetes. We prepared four sediment treatments with different bulk densities from the sandy sediment by adding in seawater at 2%, 10%, 15%, and 25% of the sediment weight and homogenizing with the standing cement mixer. The four sediment treatments had average bulk densities of: 1.35, 1.31, 1.26, 1.22 g cm^{-3}. We then added the sediment to empty pots in the same way as we did for the cores in the mesocosm. We placed six *A. marina* or six *H. diversicolor* on the sediment surface and recorded how many animals were still visible at thirty second intervals. We repeated the experiment twice for each species/sediment combination.

Process measurements: metabolic activity

We performed oxygen incubation experiments to test whether different sediment characteristics affected macrofaunal metabolic activity. The incubation experiments were run 24 days after the experiment had begun so that the animals had acclimated to the different sediment conditions. We performed the oxygen consumption experiments with three replicates each for: the controls, *H. diversicolor*, *M. balthica*, both size classes of *S. plana*, and the large *C. edule*. We could not perform the oxygen consumption experiments on all species blocks because of equipment limitations. The experiment consisted of a water bath containing capped PVC tubes filled with Eastern Scheldt water. We placed each core into the larger PVC tube. The cores descended into the tube slowly and the surfaces of the sediment were not disturbed. We oxygenated the water to raise the oxygen content until it was near saturation and sealed the cores with a custom cap. The cap included a stirrer to homogenize the entire water column's oxygen content. We then measured the amount of oxygen in the water over time using a firesting sensor (see Braeckman et al. (2014) for oxygen incubation method). The experiments ran for at least 5 hours and we did not allow the oxygen level to descend below 60%. There was a possibility that differences in respiration rates between cores could have been due to animal death, however, all the bivalves used in the oxygen incubation experiments were alive at the end of the 29 days. *H. diversicolor* experienced low mortality, but without a sediment treatment effect.

Process measurements: sediment mixing

To better understand how the sediment treatments would affect animal bioturbation activity and the resulting sediment mixing, we added luminophores (Environmental Tracing Systems, UK) to the sediment cores, which are inert natural sediment particles dyed with luminescent paint used to track bioturbation (Gérino et al. 2003, Solan et al. 2004). Luminophores are widely used as a non-toxic tracer to study sediment mixing by benthic animals as small amounts do not affect the animal behavior and do not harm the animals (Maire et al. 2008). We made frozen sediment disks following our standard procedure for mixing the sediment treatments but replaced ten percent of the sifted sediment with luminophores. We added one 0.5 cm thick disk to the top of all cores after the animal had burrowed in to avoid recording the initial burrowing movement as bioturbation activity. Some of the large *S. plana* never burrowed and so we added the luminophores on top of them.

After 29 days, we processed the experiment. We sliced the cores once lengthwise to obtain a vertical profile of luminophore incorporation into the sediment. These profiles show the total amount of mixing that was done by the animal over the course of the experiment, thus representing the time-integrated outcome. As we were not using the luminophores to model bioturbation intensity, a single lengthwise slice was sufficient for our purposes of investigating the sediment treatment effect on bioturbation activity and mixing mode. In addition, the lengthwise slicing allowed us to recover the animals intact for subsequent physiological measurements. Because of the vertical slicing, we may in some cases have underestimated bioturbation activity if a burrow did not traverse our slice. However, we compensated for possible underestimation by averaging the profiles over six cores for each species-sediment combination. This allowed us to obtain a general estimate of the bioturbation patterns.

To count the luminophores as a function of depth we photographed the two halves of the core under a blacklight using a digital mirror-reflex camera (Canon EOS 1100d) attached to a tripod. The pictures (2848x4247 pixels) were analyzed using a custom ImageJ (Fiji) script. In this process, the red layer of an RGB filter was used to highlight the magenta colored luminophores. The brightness value (125-255) was used to select luminophores from other pixels. We estimated bioturbation activity by counting the luminophore pixels in the pictures of the halved cores by 0.5 cm layer, or "bin". The bins had an area of 10.5 × 0.5 cm, which corresponded to 1722 × 82 pixels. Because one luminophore pixel does not necessarily correspond to a single luminophore grain, we use "luminophore pixels" instead of "luminophore count" as the unit for luminophore quantity throughout the text. The edges of the cores (0.5 cm from the sides and the bottom 1.5 cm) were excluded to avoid skewing our estimates because the plastic lining caused luminophores to accumulate at the sides and bottom of the cores. We used a pixel count value averaged between the two halves of the cores for each bin to get a more robust measure of the luminophore distribution through the sediment. We smoothed the average profiles by species and sediment treatment using local polynomials with R package KernSmooth (Wand 2021) to better show general patterns in mixing.

When examining the luminophore profiles we looked for subsurface peaks to differentiate between local (biodiffusion) and non-local (advective transport) mixing. Local mixing causes the number of luminophores to decrease exponentially with depth, whereas non-local mixing causes a peak in luminophores at depth. We determined whether there was non-local mixing by examining the depth of maximum values of luminophore pixel counts over a moving depth window. We were interested in how mixing activity might differ close to the surface and at depth, so we isolated the peaks in the diffusion layer (0-4 or 0-6 cm depending on species/sediment treatment) and in the lower part of the core. We compared the depth and intensity of peaks between species and sediment treatments.

Process measurements: burying depth and survival

To measure animal burrowing depth for the bivalves, we recorded the lowest point of the bivalve's position. For the polychaetes, we separated the cores containing polychaetes into 0 to 2 cm, 2 to 5 cm, and 5 to 12 cm layers and sieved each layer and recorded which contained animals. We considered all unrecovered animals as dead.

Statistical analysis

We wished to determine the effect of sediment bulk density on the behavioral response of our species. Because we wished to know whether the response to bulk density would be different depending on grain size, we evaluated models with only main effects of the sediment treatment (Response ~ Species + grain size + bulk density) and models that included an interaction between sediment grain size and bulk density (Response ~ Species + grain size × bulk density). Because we wanted to compare the direction of the response between species, we also tested for an interaction between the species and sediment treatments (Response ~ Species × grain size × bulk density). We selected the best models based on Akaike Information Criterion (AIC). We mainly used ANOVAs and logistic regression to evaluate the animal behavioral responses to sediment bulk density. See Table S2 for a summary of the logistic regression model and Table S3 for a summary of the best ANOVA models.

The model fit for all linear regressions and ANOVAs were evaluated using residual plots and qqplots. The logarithm of the dependent variable (i.e. depth and luminophore pixel count) was used when appropriate. For all models, the species treatments included separate categories for the two bivalve size classes. After performing ANOVAs, we used post hoc Tukey tests to compare relevant sediment treatment effects, as well as differences in responses between size classes for *C. edule* and *S. plana*.

We modeled the initial burrowing time of the bivalves using logistic regression. The response variable was the presence of animals at the surface in each unit at each time step. Our model was of the form of: Response ~ Species + grain size + bulk density + hour, with interactions tested as detailed above. We used Wald tests to compare sediment treatment effects and investigate the effect of bivalve size on burrowing speed. We also used logistic regression to examine whether sediment treatment had an effect on polychaete survival and burrowing time.

The oxygen data were analyzed in R using R package turbo (Soetaert & Provoost 2017). We corrected for the respiration of the microbial community by subtracting the mean control value for each sediment treatment from the values for cores containing animals. We evaluated whether oxygen consumption significantly varied among species, bulk density, and grain size using a three-way ANOVA.

We performed a three-way ANOVA to test whether there were differences in burial depth among bivalve species and sediment bulk density, and grain size. To satisfy the condition of normality, we excluded zeros (non-buried *S. plana*). To compare polychaete depth strata, we performed a multinomial logistic regression using functions from R package nnet (Venables & Ripley 2002).

Luminophore dispersal was calculated as an indicator for bioturbation intensity by summing the number of luminophore pixels counted in each 0.5 cm depth bin for each luminophore profile. The values of the luminophore dispersal increased when more luminophores were transported into the sediment. The final dispersal values were corrected for the average dispersal values of the controls. This correction allowed us to account for the greater permeability of the sandy sediments. We performed a three-way ANOVA to evaluate whether there were differences in luminophore dispersal among species, sediment bulk density, and grain size.

We also compared the depth and luminophore pixel counts of non-local mixing peaks for species that showed non-local mixing in the luminophore profiles (Fig. 8): *M. balthica*, and *H. diversicolor*, and both size classes of *S. plana*. The peaks at depth for *M. balthica* were not as prominent in the profiles as for the other two species however there is evidence from literature that *M. balthica* induces non-local mixing (Morys et al. 2017). We evaluated whether there were differences in the depth and the value of the peak luminophore pixel counts between 4.5 cm and 10.5 cm among species and sediment treatments using a three-way ANOVA.

Results

Survival rate and growth

Survival was very high for the bivalves (99% +/- 7%). We recovered the polychaetes at a lower rate (71% +/- 33% of *H. diversicolor* and 20% +/- 31% for *A. marina*), but it's unclear to what extent this was due to mortality or due to the polychaetes escaping the cores. If we assume that the treatment effect was due to mortality, then *A. marina* survived at a higher rate in the soft sediments vs. the compact sediments (30% +/- 39% vs. 10% +/- 13% survival), Wald's χ^2 (1) = 7, p = 0.008. There was no sediment treatment effect on *H. diversicolor* survival.

Burrowing rates of bivalves

The burrowing rate was significantly slower for the compact, high bulk density treatments than for the soft, low bulk density treatments, Wald's χ^2 (1) $p < 0.001$ (Fig. 3, Table S2). Burrowing was around 200 times slower in the compact-sandy treatment and 80 times slower in the compact-muddy treatment than the corresponding soft treatments.

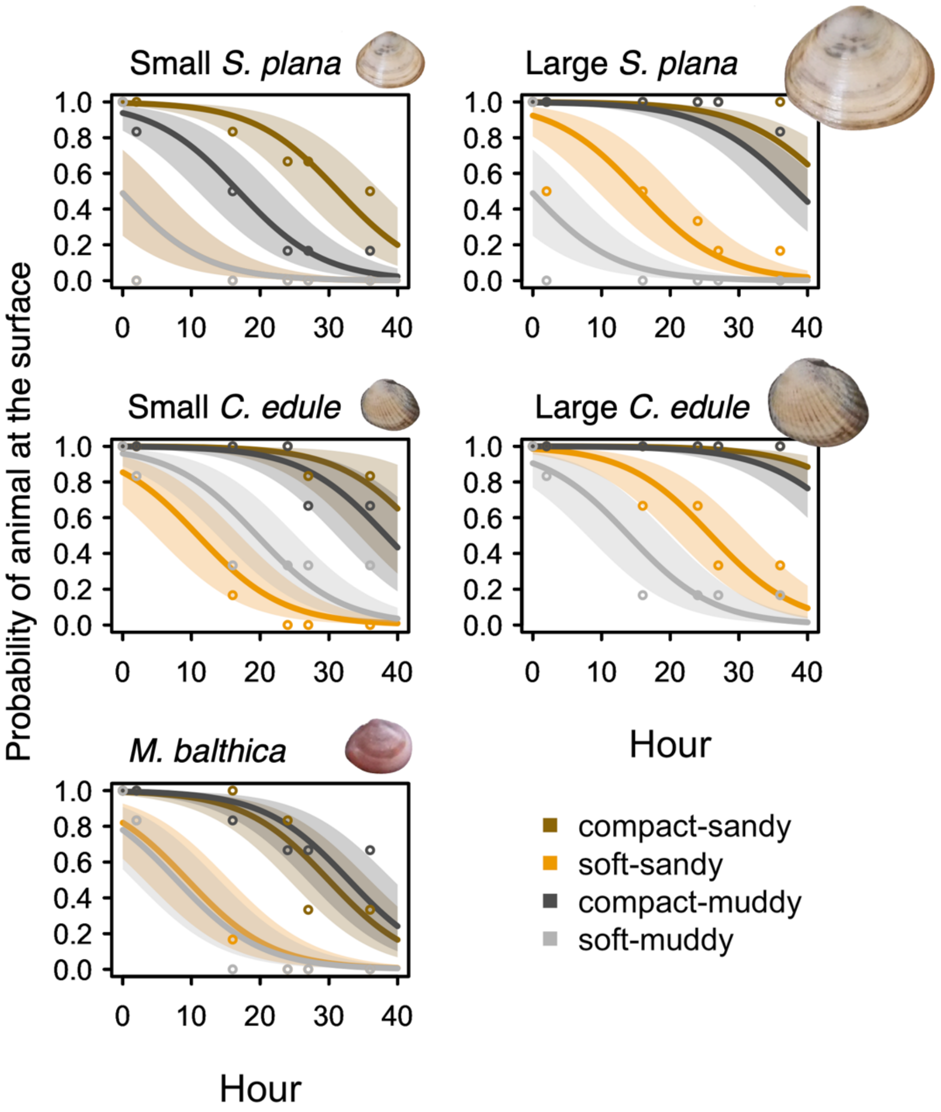

Figure 3: Logistic regression models of bivalve burrowing showing the probability of a bivalve's presence at the sediment surface over the first 40 hours of the experiment. The results are shown by species and sediment treatment, with best fit line and 95% confidence intervals. Mean observed values per time-step are depicted by open circles.

The small *S. plana* had significantly faster burrowing rates than the larger *S. plana*, Wald's χ^2 (1) = 11.7, p = 0.001, but the effect was sediment dependent. The small *S. plana* burrowed 2 times faster than the large ones in the soft-sandy treatment and they burrowed 5 times faster than the large ones in the muddy-compact treatment, Wald's χ^2 (1) = 9.9, p = 0.002. The small *C. edule* burrowed 0.7 times faster than the large *C. edule* in the soft-sandy treatment, Wald's χ^2 (1) = 5.7, p = 0.017. Size had no effect on burrowing rate in the soft-muddy treatment (fastest burrowing rate overall) and compact-sandy treatment (slowest burrowing rate overall) for both species. And while all the small *S. plana* successfully burrowed, 60% of the large *S. plana* in the compact-sandy treatment and 30% of the large *S. plana* in the compact-muddy treatment failed to burrow at all.

Burrowing rates of polychaetes

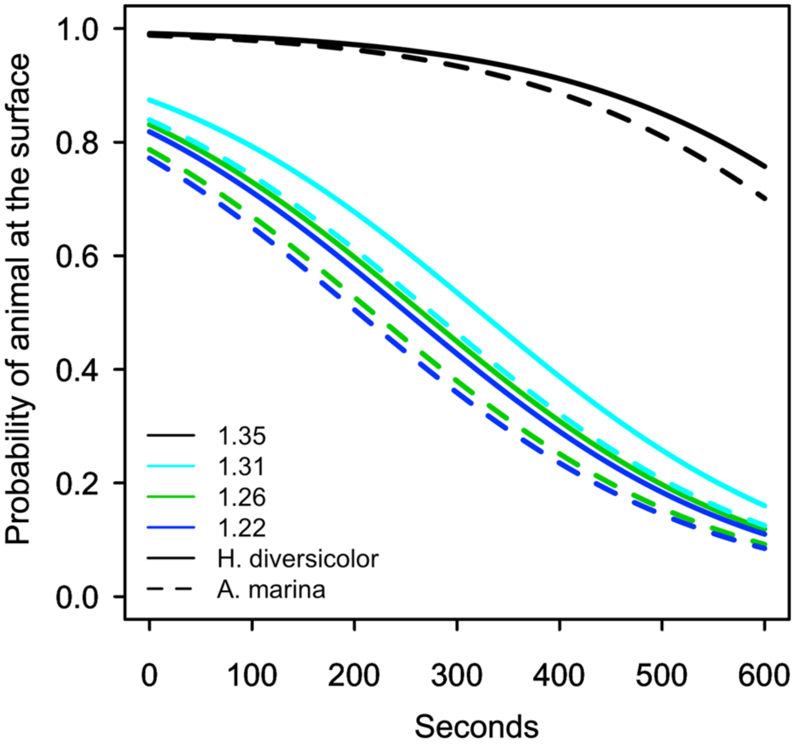

Figure 4: Logistic regression models of polychaete burrowing, showing the probability of the polychaete's presence at the sediment surface for the first 600 seconds. The dotted lines are *A. marina* models and the solid lines are *H. diversicolor*. Results are shown for the sandy sediment with a bulk density (g cm-3) of 1.35, 1.31, 1.26, 1.22. The experiment was not performed with muddy sediment (see Methods section 2.3).

The effect of bulk density on the burrowing of polychaetes followed a similar pattern to the bivalves, though at a different scale (i.e., note difference in the x-axis in Fig. 3 - hours versus Fig. 4 - seconds). The polychaete burrowing rate significantly increased with the softness of the treatments (Fig. 4), Wald's χ^2 (4) = 357.6, $p < 0.001$. The biggest difference in burrowing rates was between the two sediment treatments with the highest bulk densities: burrowing rate was 150 times slower in the 1.35 g cm^{-3} treatment compared to the 1.31 g cm^{-3} treatment, Wald's χ^2 (1) = 18.4, $p < 0.001$, suggesting that there might be an absolute threshold that prevents burrowing. Burrowing rates did not significantly differ between 1.26 g cm^{-3} and the 1.22 g. cm^{-3} treatments, Wald's χ^2 (1) = 0.31, p = 0.58. *H. diversicolor* burrowing four times slower than *A. marina*, Wald's χ^2 (1) = 5.7, p = 0.017.

Oxygen consumption as an indicator of metabolic activity

Overall, oxygen consumption significantly differed between species, F (3, 53) = 32.480, $p < 0.001$, but not sediment treatments (Fig. 5). The mean oxygen consumption in the control muddy sediments was 1.6 times greater than the oxygen consumption in the control sandy sediments. That is, the average muddy sediment oxygen consumption was 20.7 + 2.6 SE mmol O2 m^{-2} d^{-1} versus an average oxygen consumption of 13.3 + 2.3 mmol O2 m^{-2} d^{-1} for sandy sediment, which might be explained by the greater amount of organic material available for microbial consumption in muddy sediment. There was no significant difference between the oxygen consumption of the large and small *S. plana*.

All the animals tended to be most active in the sediments that were closest to their natural habitat (See Table 1 for sediment preferences). *C. edule* and *M. balthica* tended to have the greatest oxygen consumption in the soft-sandy sediments whereas the *H. diversicolor* and *S. plana* tended to have the greatest oxygen consumption in the compact-muddy sediment (Fig. 5). While the sediment treatment effect on the species' oxygen consumption was not significant, the higher oxygen consumption in these sediments could indicate greater activity.

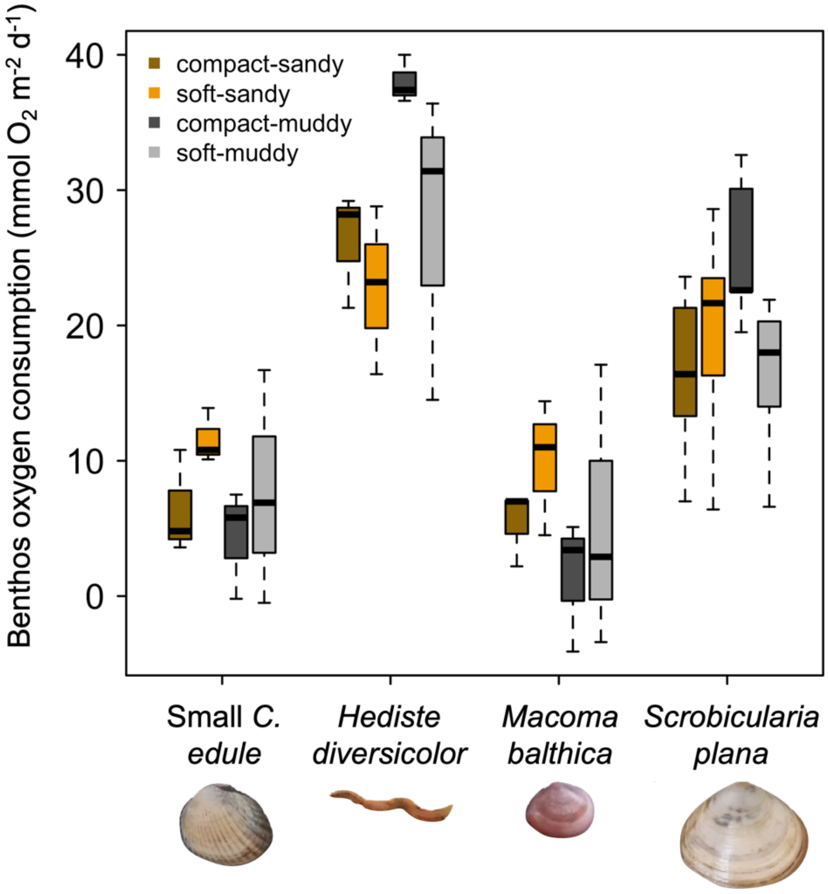

Figure 5: Oxygen consumption rate for species by sediment treatment represented by boxplots where the box (25-75% of the data) contains a black line (median) and has whiskers extending to the minimum and maximum data values. Large *C. edule* and *A. marina* were not included in the experiment due to equipment limitations. We pooled the results for the large and small *S. plana* because they were so similar. Since the microbial respiration was different in the sandy vs. muddy sediment, we corrected the values of animal respiration obtained from the sediment cores by subtracting the mean respiration value of controls which represent the microbial respiration. 13.3 mmol O2 m^{-2} d^{-1} were subtracted from sandy treatments, 20.7 mmol O2 m^{-2} d^{-1} were subtracted from muddy sediments. There were no significant sediment treatment effects.

Macrofauna burrowing depth

Bivalve burrowing depth was significantly different between sediment bulk densities, grain size, and species, with interactions between the sediment characteristics and species. (Fig. 6; Table S1 & Table S3). A post hoc Tukey test showed that the sediment treatments affected the burrowing depth of two out of the five bivalve species: the *M. balthica* and small *C. edule*. The *M. balthica* burrowed deeper in the soft sediments and the small *C. edule* burrowed deeper in the muddy sediments (Fig. 6). The lack of a visible treatment effect on depth for *S. plana* could be due to the short length (12 cm) of the cores. Many of the *S. plana* were found near the bottom of the cores and perhaps would have burrowed deeper had they been given more space. While there was a statistically significant difference in the burrowing depth for the two size classes of *C. edule*, this was not the case for *S. plana* (Tukey post hoc p = 0.0001 and 0.16 respectively). The best multinomial model of polychaete depth distribution included sediment treatment. Including species did not improve the model, X2 (2) = 2.76, p = 0.25. There is small evidence that polychaetes burrowed deeper in compact muddy treatment than the soft-muddy treatment (p = 0.057).

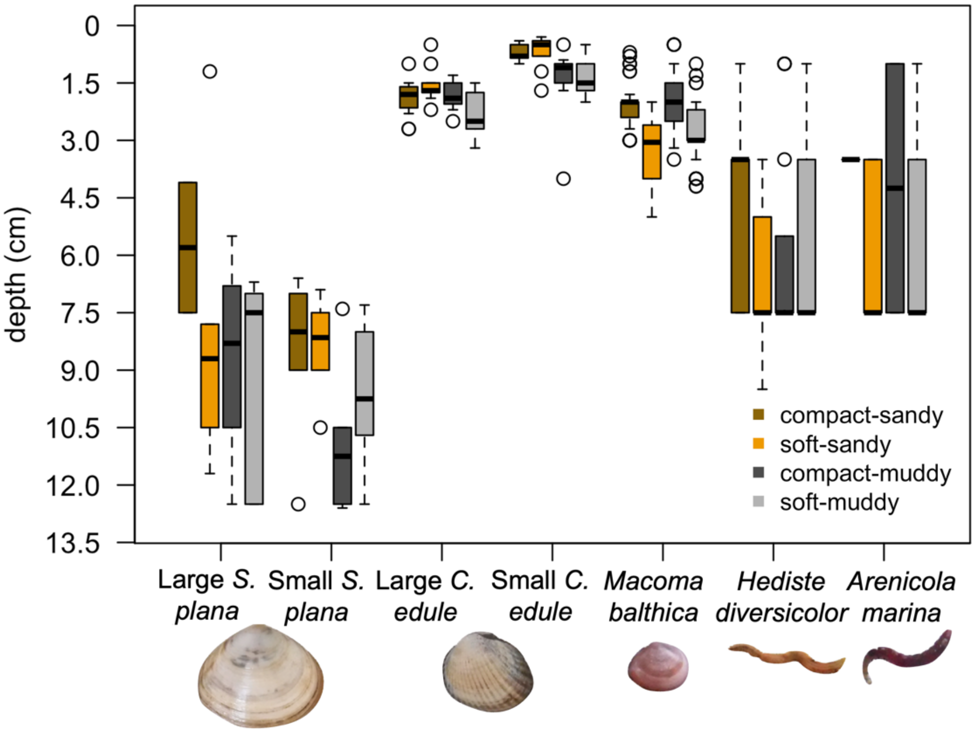

Figure 6: Boxplots of burrowing depth by species and sediment treatment, where the box (25-75% of the data) contains a black line (median) and has whiskers extending to the minimum and maximum data values, with outliers as open circles. Bivalve burrowing depth was measured precisely (lowest point animal). Polychaete burrowing depth was measured by strata (0-2 cm, 2-5 cm, 5-12 cm) and extrapolated to the mean value of each stratum. For some *H. diversicolor*, a burrow point was visible and was used instead of the strata. Note that the bottom of the pots was at 12.5 cm which is close to many of the *S. plana's* position. The sediment treatments only had a significant effect on the burrowing depth of *M. balthica* and the small *C. edule*.

Sediment mixing as measured by luminophores

Overall, the benthic macrofauna induced significantly greater luminophore dispersal in the soft sediments than in the compact sediments (Fig. 7; F (1,154) = 32.7, $p < 0.001$). The greatest luminophore dispersal occurred in the soft-muddy sediment (average = 4.02 × 105 luminophore pixels +/- 0.78 × 105 luminophore pixels). The luminophore dispersal was greater in soft-sandy sediment (average 3.68 × 105 luminophore pixels +/- 1.75 × 105 luminophore pixels) than in the compact sandy-sediment (average 2.97 × 105 luminophore pixels +/- 1.10 × 105 luminophore pixels).

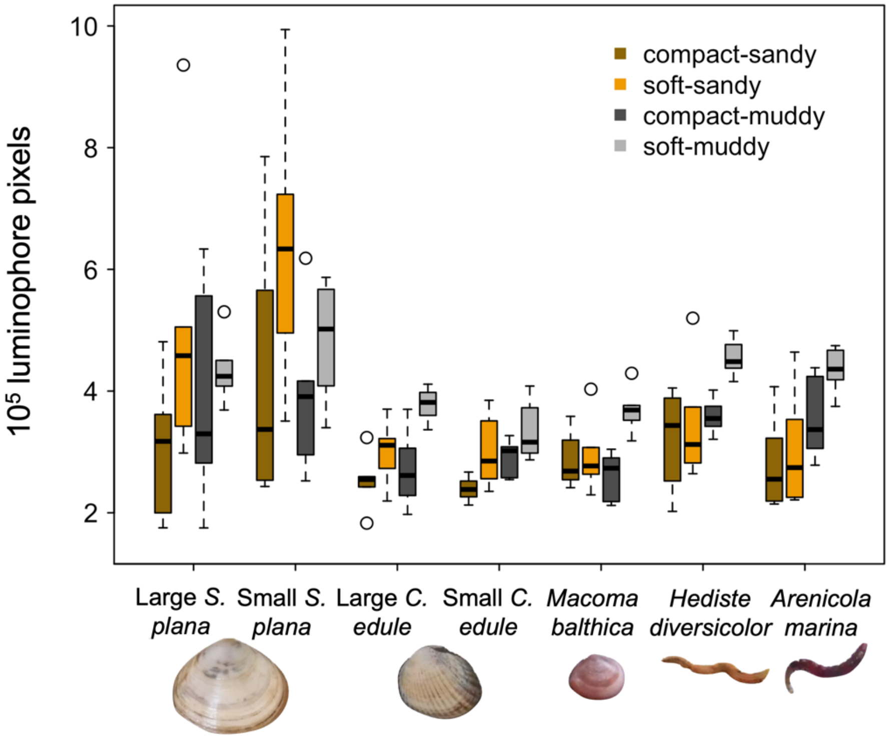

Figure 7: Boxplots showing luminophore dispersal, i.e. the integral of luminophore profiles over depth (see Fig. 8 for average profiles), by species and sediment treatment, where the box (25-75% of the data) contains a black line (median) and has whiskers extending to the minimum and maximum data values, with outliers as open circles. All species transported more luminophores in soft vs. compact sediment and polychaetes also transported more luminophores in muddy vs. sandy sediment. The area has been corrected for the average control values (compact-sandy: - 0.31 × 105 luminophore pixels, soft-sandy: - 0.44 × 105 luminophore pixels, compact-muddy: + 0.23 × 105 luminophore pixels, soft-muddy: + 0.39 × 105 luminophore pixels).

Species induced different amounts of sediment mixing, F (6,154) = 9.4, $p < 0.001$ (Fig. 7). Both size classes of the *S. plana* and the polychaetes mixed greater amounts of luminophores into the sediment than the *M. balthica* and *C. edule* (Fig. 7). There was no significant difference between the luminophore dispersal of either *C. edule* or *S. plana* size classes, though the small *S. plana* tended to induce greater sediment mixing than large *S. plana* (Fig. 7 and 8).

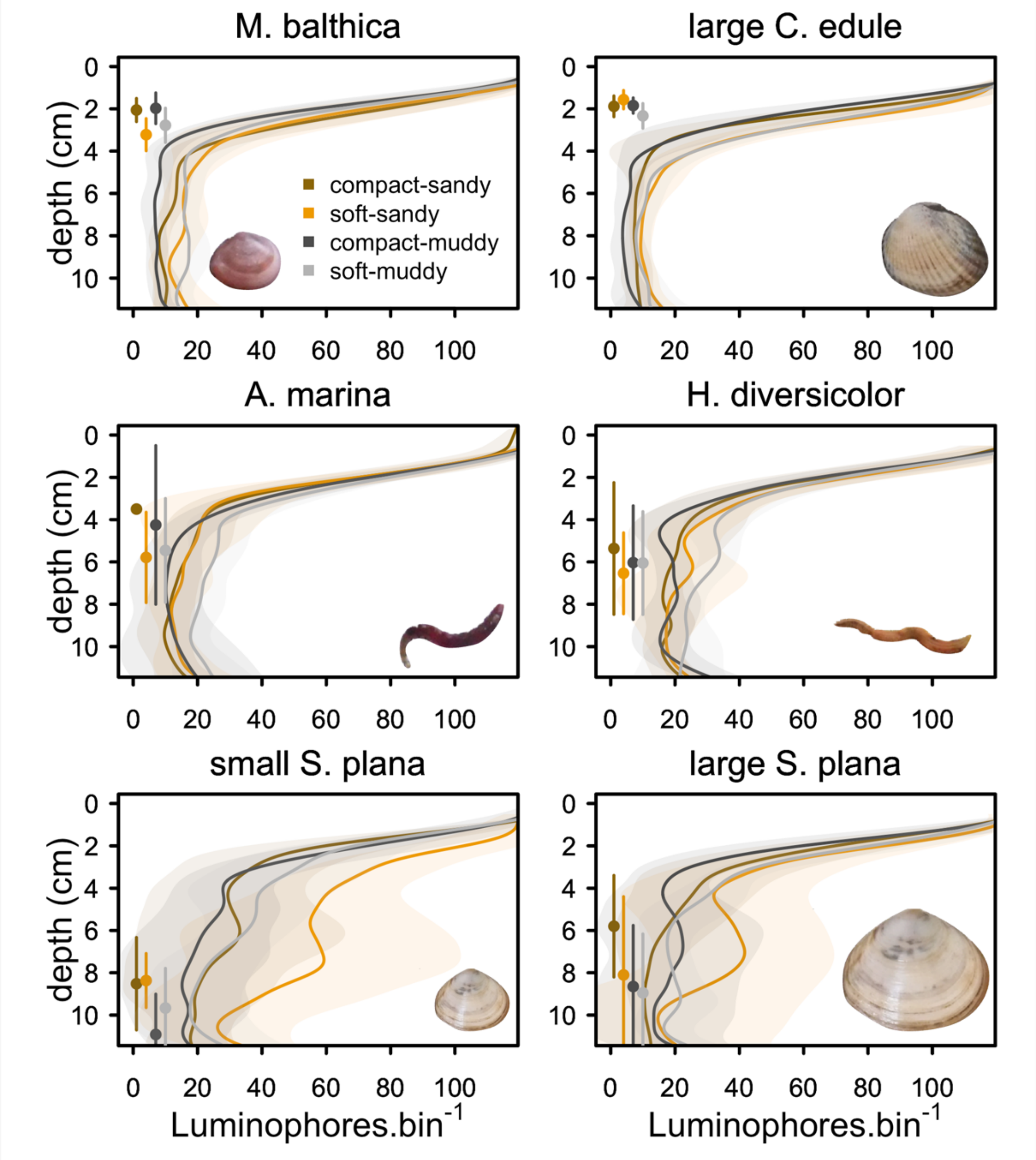

Figure 8: Smoothed average luminophore profiles for *M. balthica*, *C. edule*, *H. diversicolor*, *A. marina*, and *S. plana* with standard deviation intervals, showing the incorporation of the luminophores into the sediment. We only show the profiles for the large *C. edule* because the two size classes produced very similar ones. The luminophores were counted in 0.5 cm bins. Luminophores are added to the sediment surface and permeate through the sediment. Local mixing

causes the number of luminophores to decrease exponentially with depth whereas non-local mixing results in an increase of luminophores below the sediment surface. Depths where non-local mixing are dominant typically become visible as (small) bumps in the curve where the luminophore value reaches a local maximum. For example, the *S. plana* displays non-local mixing at 6-8 cm depth in the soft-sandy sediment. The points to the left of the profiles represent average depth for the species by sediment treatment (as in Fig. 6), with standard deviations (vertical lines).

We further compared the bioturbation mode of the macrofauna by examining the shapes of the luminophore profiles, especially by looking at the presence and depth of non-local mixing (Fig. 8, Fig. 9). *C. edule* performed local mixing in the top three centimeters, with the greatest activity occurring in the low bulk density sediment which is visible by the greater quantity of luminophores mixed into the low bulk density sediments than the high bulk density sediments at the same depth (Fig. 8). The luminophore profiles for *S. plana*, *M. balthica*, and *H. diversicolor*, showed non-local mixing peaks at depth (Fig. 8, Fig. 9 white depth interval). The *M. balthica* and *H. diversicolor* peaks seemed most prominent in the soft sediments, whereas the *S. plana* appeared to produce greater peaks in the soft-sandy sediment (Fig. 8).

For the species that showed the clearest non-local mixing (*S. plana* and *H. diversicolor*), the maximum luminophore pixel counts at depth were greater in soft sediment than in compact sediment, F (1, 64) = 8.7, p = 0.004 (Table S3). Across all species that exhibited non-local mixing, the peaks were greatest in the soft-sandy sediment (average = 0.57 × 105 luminophore pixels +/- 0.31 × 105 luminophore pixels).

For all species, greater mixing occurred in the soft treatments vs. the compact treatments. The polychaetes transported more luminophore in the muddy treatments than the sandy ones. Of all the species, *S. plana* mixed the greatest amount of luminophores into the sediment and was the only species that tended to transport more luminophores in the soft-sandy treatment than the soft-muddy treatment. *H. diversicolor* and *S. plana* had greater non-local mixing peak values at depth in the soft treatments than the compact treatments

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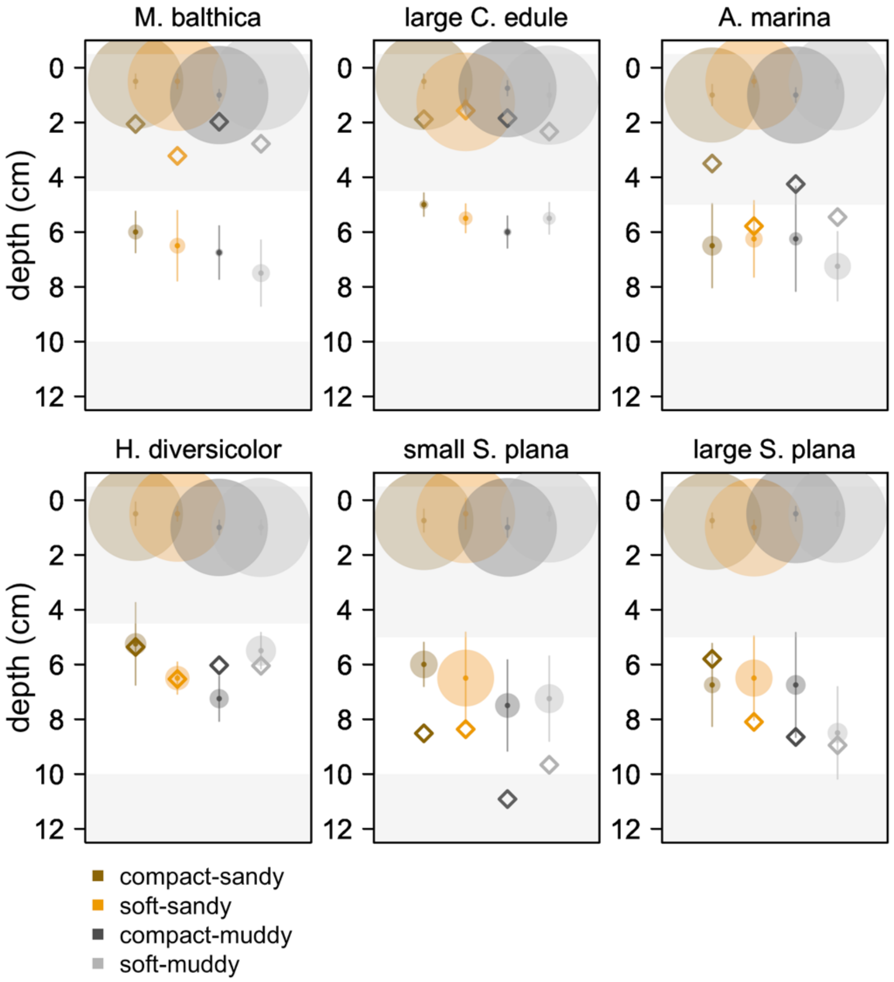

Figure 9: Median locations (with standard deviation in vertical lines) of peak luminophore pixel counts (center of the circle circle) for the 0-4 cm diffusion layer interval and for the non-local mixing interval, represented by a white layer in the plot. white depth interval. We wanted to show peaks in luminophores in the top diffusion layer and at depth. The white depth interval excludes the diffusion layer (0-4.5 cm for *M. balthica*, *C. edule* and *H. diversicolor*, 0-5 cm for *S. plana* and *A. marina*) and the bottom of the core (10-12 cm) where excess luminophores pooled. The limit of the diffusion layer was determined as the depth of first inflection point in the luminophore profile curves of the previous figure, rounded to the closest 0.5 cm. The 10 cm lower limit was a conservative estimate to exclude edge effects. The size of the circle is scaled to the median luminophore pixel count at the peak luminophore pixel location. The diamonds indicate the mean depth of the species/sediment block.

Discussion

The aim of our study was to investigate how bulk density affects benthic macrofauna behavior, as a step towards understanding how biogeomorphological and biogeochemical processes on intertidal flats might change under different bulk density conditions. We found clear effects of bulk density on benthic macrofauna burrowing behavior and bioturbation activity, which are summarized in Fig. 10. In line with our first hypothesis that the mobility of the benthic macrofauna would be lower in compact (i.e. high bulk density) vs. soft (i.e. low bulk density) sediment, we found that in compact (vs. soft) sediment all animals burrowed slower, all animals transported fewer luminophores, and *M. balthica* burrowed shallower. Our second hypothesis was that bulk density would have similar effects on the behavior of benthic macrofauna in both sandy and muddy sediment. We did not detect any significant interactions between sediment grain size and sediment bulk density, indicating that animal responses had similar directions in both muddy and sandy sediments. We also did not detect a sediment treatment effect on respiration rate, however the animals tended to have the greatest respiration in the sediment that were closer to their natural habitat. In line with our third hypothesis that larger bivalves would be more sensitive to differences in bulk density than smaller bivalves of the same species, we found that smaller *C. edule* and *S. plana* burrowed significantly faster than the larger ones in the compact muddy treatment (*S. plana*) and soft sandy treatment (*C. edule*). In addition, the small *S. plana* tended to transport more luminophores than the larger ones, but this appeared to be independent of sediment treatment.

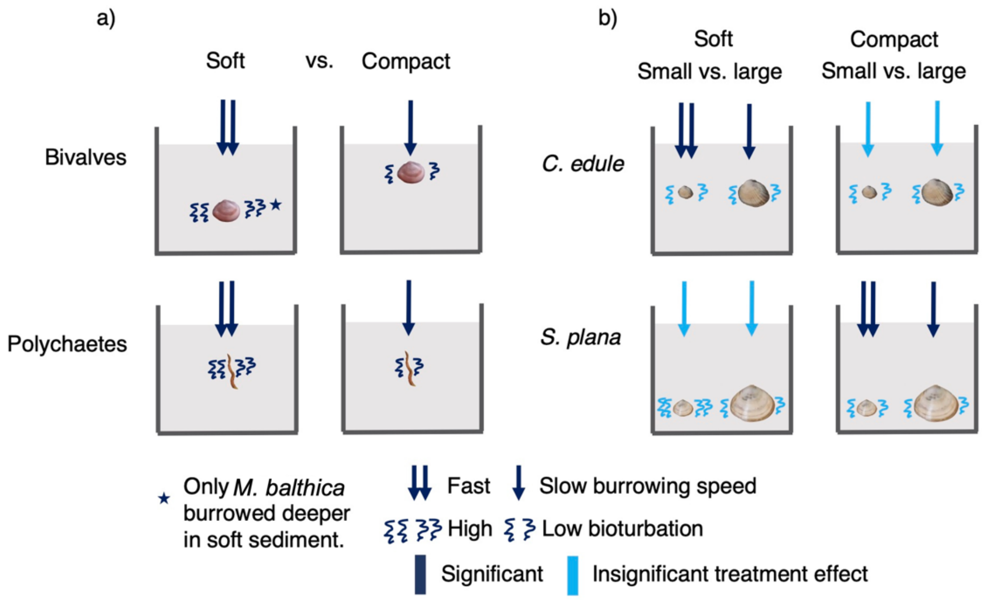

Figure 10: Summary of sediment bulk density treatment main effects on burrowing speed, depth, and bioturbation amount. Because there were no significant interactions between sediment bulk

density and grain size, we show a single figure to summarize bulk density effects under the different sediment grain sizes. We did not present respiration effects as there were no significant sediment bulk density effects on respiration. The left panel (a) shows bulk density treatment main effects on bivalves and polychaetes. The effect pertains to all bivalves or polychaetes unless indicated with a star. The right panel (b) shows comparisons between *C. edule* and *S. plana* size class responses under soft and compact sediments.

Importance of sediment grain size vs. bulk density effects on burrowing

We found it surprising that the burrowing rates of bivalves were significantly faster in the soft treatments compared to the compact treatments, rather than being largely driven by sediment grain size. Indeed, we expected the burrowing rates to be driven by penetration resistance and the muddy treatments had much lower penetration resistance than the sandy treatments (Fig. 2, Table 2). The observed burrowing patterns might be explained through the difference in sediment cohesiveness between the sandy and muddy treatments. Cohesiveness is largely governed by clay content (Joensuu et al. 2018). At high water contents, muddy sediment becomes akin to a viscous liquid and easy to entrain, whereas at low water contents, muddy sediments have much greater cohesion and a higher erosion threshold (Grabowski et al. 2011). In our study, although the compact-muddy sediment was more penetrable and had a lower absolute bulk density than the soft-sandy sediment (see Table 2), it was noticeably more cohesive and stickier than any of the other sediment treatments. The biomechanics of burrowing are different depending on the sediment type (Crane & Merz 2017): in cohesive mud, animals burrow through crack propagation, whereas in coarse sand they may burrow through local fluidization or excavation (Dorgan 2015). The cohesiveness of the compact-muddy sediment could have presented an obstacle to the bivalves' burrowing of similar magnitude to the high penetration resistance of the compact-sandy sediment, and probably affected the biomechanics of the burrowing animals.

Though we found that within our experiment behavioral differences between the treatments were mainly driven by sediment bulk density rather than grain size, in nature the sediment grain size provides important constraints for species habitat. Many studies have described species assemblages to vary along a sediment grain size gradient (Ysebaert et al. 2002, Thrush et al. 2003, Compton et al. 2013, Pratt et al. 2014). However, most of these studies are correlative and the mechanics that underpin the habitat-animal associations prove to be elusive (Snelgrove & Butman 1994). Other factors, like hydrodynamics, may be equally important. For example, the sandy areas in the Western Scheldt have a high degree of hydrodynamic stress and have impoverished benthos communities compared with the species-rich sandy areas in the Eastern Scheldt which have low hydrodynamic stress (Cozzoli et al. 2013). Bulk density effects are generally not included in these kind of field studies. Our study highlights that including bulk density measurements may add an extra level of understanding to benthic macrofauna distribution and especially macrofauna activity in terms of sediment mixing.

High burrowing ability is essential for bivalves to survive in unstable sediments (Alexander et al. 1993, Takeuchi et al. 2015). All animals in our study burrowed faster in the soft sediments, and the small *C. edule* and *S. plana* burrowed faster than the larger adult ones in certain treatments. However soft sediment is more easily eroded than compact sediment (Grabowski et al. 2011). In most bivalve species, like *C. edule* and *M. balthica*, juveniles live closer to the surface than adults and may hence be more easily dislodged by erosion during storms (Tallqvist 2001, St-Onge & Miron 2007). Yet, smaller and younger bivalves may compensate for their shallower living depth during erosion events by being able to burrow faster than adults in high bulk density conditions. It would be interesting to further investigate whether there is a tradeoff between sediment compaction effects on the erodibility and burrowing rate, and how this might impact the overwintering survival of juvenile versus adult bivalves.

Sediment bulk density effects on benthic macrofauna survival and predation

Extreme bulk density sediments may present difficult living conditions for benthic macrofauna and affect their survival due to physiological constraints. At very low bulk densities, sediments might become so soft that animals have to expend a great amount of energy to keep their position in the sediment or unclog their feeding apparatus of small mud particles (Lohrer et al. 2006, Mestdagh et al. 2018). High bulk densities would present different challenges. For example, our high bulk density treatments most likely inhibited *A. marina*'s ability to ventilate their burrows which is energetically costly in low sediment permeability (Meysman et al. 2005), thus greatly reducing their survival.

Other ecological mechanisms, like predation risk and growth efficiency, might be affected by sediment bulk density as well. At shallower depths, the feeding area of deposit-feeding bivalves is increased as the siphon can be extended onto a larger surface area (Zwarts et al. 1994), whereas bivalves respond to predator presence by burrowing deeper (Griffiths & Richardson 2006, Flynn & Smee 2010). In high bulk density sediment, *M. balthica* may have increased energy expenditure during burrowing or feeding, which would reduce *M. balthica*'s growth efficiency. In addition, *M. balthica* would also stay closer to the surface in high bulk density sediment, thereby increasing its vulnerability to predation. Similarly, when *H. diversicolor* feeds at the surface, it is vulnerable to predation and its escape depends on speed (Ens et al. 1997). Considering that *H. diversicolor* burrowed significantly faster in softer low bulk density sediments, we can conclude that *H. diversicolor* and other surface deposit feeding polychaetes might also be more vulnerable to predators in high bulk density sediments because of decreased possibility of escape. Thus benthic animals may have lower survival in high bulk density conditions due to increased risk of predation.

Implications for animal-sediment interactions and ecosystem-scale impacts

Benthic macrofauna change their behavior under different bulk densities which can have consequences for the biogeomorphology and biogeochemistry of tidal flats. Under higher bulk densities, a reduction in the depth at which infauna burrow, which we observed in particular for *M. balthica* (Fig. 3), may lead to a shallower apparent redox potential discontinuity (Gerwing et al. 2017), which could decrease the depth of the biologically active zone depth (Sturdivant and Shimizu 2017). Furthermore, a decrease in bioturbation and especially non-local mixing activity in high bulk density sediment, which we observed for important gallery diffusor *H. diversicolor* (Fig. 7), could lead to reduced sediment permeability and oxygen penetration of the sediment (Aller & Aller 1998, Michaud et al. 2006) as well as a build-up of a mud layer due to decreased resuspension or incorporation of mud into the sediment matrix (Montserrat et al. 2008; McCartain et al. 2017). In addition, a reduction in non-local mixing of *H. diversicolor* would decrease microbial processing of organic material which would reduce nutrient release into the porewater (Mermillod-Blondin et al. 2004). Changes in bivalve behavior may also affect tidal flat biogeochemistry, for example, reduced siphon movement and pumping rate due to more compact high bulk density sediment would increase the time between bouts of oxygenation of the sediment which might lead to short-term anoxic conditions and decreased denitrification (Volkenborn et al. 2012). Thus higher sediment bulk densities may have negative consequences for the ecosystem function of benthic macrofauna. Indeed, a reduction in their burrowing depth and bioturbation activity could lead to a shallower and less well-oxygenated surface sediment layer which would impact microorganisms and eventually nutrient cycling. Low bulk density sediments may have the opposite effect and stimulate nutrient cycling due to increased bioturbation.

Because sediment bulk density tends to increase with sediment erosion and decrease with sediment deposition (Dyer et al. 2000), we speculate that the macrofauna in an eroding tidal flat are typically less mobile than macrofauna in a depositing tidal flat of a similar sediment grain size. Animal-sediment interactions between bioturbation and bulk density are likely to create positive feedback loops for tidal flat biogeomorphology. Bioturbation destabilizes sediment (Widdows et al. 2000) which decreases sediment bulk density and, as we found in our study, a soft sediment encourages animal movement. These interactions could create a positive feedback loop between low sediment bulk density conditions and elevated benthic macrofauna movement. The opposite feedback loop would occur under high bulk density sediment where sediment conditions discourage animal movement which in turn may lead to further sediment compaction. However, non-cohesive soft sediments are generally more vulnerable to erosion than compact sediments (Grabowski et al., 2011), and greater animal activity may cause these sediments to be even more easily eroded. More investigation on animal-sediment interactions, particularly on whether animal activity under different bulk densities affects tidal flat biogeochemistry and generates positive biogeomorphology feedback loops, would be necessary to tease out the importance of sediment bulk densities for tidal flat functioning and evolution.

Acknowledgements

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Supplementary tables

Table S1: Mean and standard deviations for measured variables burrowing depth, luminophore dispersal, and oxygen consumption. Each experimental block (species-sediment combination) has an N=6, except for the oxygen consumption blocks which have an N=3. CS = compact-sand, SS = soft-sandy, CM = compact-muddy, SM = soft-muddy; (S) = Small, (L) = Large.

		Burrowing Depth (mm)		Luminophore Dispersal (10^5 luminophore counts)		Oxygen Consumption (mmol O_2 m^{-2} d^{-1})	
Sediment	Species	Mean	Std. Deviation	Mean	Std. Deviation	Mean	Std. Deviation
CS	*C. edule* (S)	7.1	2.2	2.376	0.197		
SS	*C. edule* (S)	6.9	4.3	2.982	0.596		
CM	*C. edule* (S)	13.7	8.9	2.863	0.290		
SM	*C. edule* (S)	13.2	5.3	3.321	0.505		
CS	*C. edule* (L)	18.8	4.9	2.519	0.454	6.4	3.9
SS	*C. edule* (L)	15.7	4.4	3.004	0.527	11.6	2.0
CM	*C. edule* (L)	18.5	3.6	2.668	0.621	4.4	4.1
SM	*C. edule* (L)	23.3	5.9	3.762	0.308	7.7	8.6
CS	*M. balthica*	20.6	5.5	2.828	0.472	5.4	2.8
SS	*M. balthica*	32.2	7.6	2.878	0.581	10.0	5.0
CM	*M. balthica*	19.8	7.3	2.560	0.416	1.5	4.9
SM	*M. balthica*	27.8	8.1	3.663	0.366	5.5	10.5
CS	*S. plana* (S)	85.2	21.9	4.189	2.170	13.9	7.2
SS	*S. plana* (S)	83.7	12.8	6.381	2.492	20.5	3.7
CM	*S. plana* (S)	109.2	19.1	3.898	1.43.4	24.1	5.5
SM	*S. plana* (S)	96.7	18.8	4.802	0.964	14.9	7.3
CS	*S. plana* (L)	58	24	3.065	1.147	18.8	4.2
SS	*S. plana* (L)	81	37	5.005	2.284	18.9	11.4
CM	*S. plana* (L)	86.5	28.9	3.785	1.754	25.9	5.8
SM	*S. plana* (L)	89.5	27.8	4.328	0.632	18.1	4.0
CS	*A. marina*	35	0	2.770	0.764		
SS	*A. marina*	57.9	21.4	2.984	0.934		
CM	*A. marina*	42.5	37.5	3.482	0.649		
SM	*A. marina*	54.5	24.5	4.313	0.374		
CS	*H. diversicolor*	53.6	31.2	3.196	0.790	26.2	4.3
SS	*H. diversicolor*	65.4	19.2	3.394	0.962	22.8	6.2
CM	*H. diversicolor*	60.3	26.9	3.520	0.294	38.0	1.8
SM	*H. diversicolor*	60.5	24.3	4.490	0.295	27.4	11.5

Table S2: Model estimates and Wald test results for the logistic regression model of bivalve burrowing. The best model was of the form: Burial ~ bulk density × grain size × species + hour. Because there was an interaction between the sediment characteristics, we present the model results for the sediment treatment combination (CS = compact-sand, SS = soft-sandy, CM = compact-muddy, SM = soft-muddy; (S) = Small, (L) = Large.) We presented relevant interaction with species only. The intercept for the estimates corresponds to the soft-sandy/small *C. edule* experimental block. We used Wald tests to estimate the significance of sediment and species treatments, as well as relevant comparisons, indicated by dashes (-) between treatments and blocks.

model estimate						Wald tests			
	B	Std. Error	e^B	2.50%	97.50%	source	χ^2	df	$p>\chi^2$
Intercept	7.1	0.89	1181.9	2.16	17.58	sediment			
Muddy (grain size)	-0.89	0.97	0.41	37.46	1812.77	Grain size	0.85	1	0.36
Compact (bulk density)	-5.31	0.95	0.0049	18.73	477.63	Bulk density	30.6	1	0
Compact - muddy	-2.24	0.91	0.11	1.06	16.2	Grain size - Bulk density	3.6	1	0.057
M. balthica	-0.25	0.71	0.78	0.19	3.14	species	33.0	4	0.000
S. plana (L)	0.73	0.70	2.08	0.53	8.30	*C. edule* (L) - *C. edule* (S)	12.0	1	0.001
C. edule (S)	2.45	0.70	11.57	3.02	47.55	*S. plana* (L) - *S. plana* (S)	11.7	1	0.001
S. plana (S)	-1.83	0.74	0.16	0.04	0.67				
Hour	-0.16	0.02	0.85	0.82	0.87				
CS:*M. balthica*	-2.00	1.16	0.14	0.01	1.19	SS:*C. edule* (S) - SS:*C. edule* (L)	1.0	5.7	0.020
CM:*M. balthica*	-0.63	1.06	0.53	0.06	4.17	CM:*S. plana* (S) - CM:*S. plana* (L)	1.0	9.9	0.000
SM:*M. balthica*	-1.66	1.00	0.19	0.03	1.33				
CS:*S. plana* (L)	0.06	1.48	1.06	0.06	31.15				
CM:*S. plana* (L)	0.95	1.39	2.59	0.20	69.54				
SM:*S. plana* (L)	-3.97	1.04	0.02	0.00	0.14				
CS:*C. edule* (L)	-1.66	1.48	0.19	0.01	5.57				
CM:*C. edule* (L)	-0.76	1.39	0.47	0.04	12.42				
SM:*C. edule* (L)	-3.36	0.99	0.03	0.00	0.23				
CS:*S. plana* (S)	-0.19	1.17	0.83	0.07	7.75				
CM:*S. plana* (S)	-1.66	1.06	0.19	0.02	1.47				
SM:*S. plana* (S)	-1.40	1.02	0.25	0.03	1.83				

Table S3: Analysis of Variance for burrowing depth, oxygen consumption, luminophore dispersal, and luminophore peak value according to sediment bulk density, grain size, and species. The best model form as selected by AIC is shown in parentheses next to the source variable (BD = bulk density, GS = grain size).

Source	df 1	df 2	F value	p value
Burrowing depth (BD x GS x Species)				
bulk density	1	278	46.3	0
grain size	1	278	8.5	0.004
species	4	278	206.4	0
bulk density x grain size	1	278	0.04	0.83
bulk density x species	4	278	7.2	0
grain size x species	4	278	10.4	0
bulk density x grain size x species	4	278	1.3	0.28
Oxygen consumption (BD x GS + Species)				
bulk density	1	53	0.17	0.67
grain size	1	53	0.56	0.45
species	3	53	32.47	0
bulk density x grain size	1	53	3.7	0.06
Luminophore dispersal (BD + GS + Species)				
bulk density	1	154	9.6	0
grain size	1	154	32.7	0
species	6	154	9.4	0.0026
Luminophore peak value (BD + GS + Species)				
bulk density	1	64	1.2	0.27
grain size	1	64	8.7	0.004
species	2	64	2.3	0.1


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Chapter 3

Contrasting strategies to cope with storm-induced erosion events: a flume study comparing a native vs. introduced bivalve

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Abstract

Storm-induced erosion events may alter the diversity of tidal flat communities by selecting for species that can better tolerate such disturbances. Introduced and invasive species are highly adaptable to a wide range of abiotic characteristics, and this adaptability may make them better able to withstand erosion events. With a novel flume method, we compared the ability of two bivalve species to resist storm-induced erosion: *Cerastoderma edule*, a native species to the Scheldt estuary in the Netherlands, and *Ruditapes philippinarum*, an introduced species that is successful in the Netherlands and worldwide. We used three sediment erosion rates to simulate storms of increasing severity. At the 10.6 cm/h and 15.9 cm/h sediment erosion rates, all *R. philippinarum* were surfaced whereas only half *C. edule* were surfaced. However, after being brought to the sediment surface, *C. edule* were more readily transported by currents and waves than *R. philippinarum* due to differences in their shell shape. We concluded that the two bivalve species have different strategies to avoid mortality by severe storm erosion: *C. edule* avoided being surfaced and *R. philippinarum* avoided being transported. In this case, it appears that extreme storms favor the specific adaptations of a native species over the broad adaptability of a non-

indigenous one. Indeed, *C. edule* may be more likely to survive moderately extreme storms than *R. philippinarum*, though the most extreme storms would be equally devastating to both species.

Introduction

Bivalves are key components of intertidal marine ecosystems: not only do they serve as food for many birds and fish (Hiddink et al. 2002, Bocher et al. 2014), but they also perform vital ecosystem services such as oxygenating the sediment and creating habitat for deeper living organisms (Kristensen 1988, Thrush et al. 2006, Gray & Elliott 2009). Under daily hydrodynamic forcing, slow-moving adult bivalves are safe from erosion due to their size and burrowing depth (Yeo & Risk 1979, Hunt 2004). However, extreme storms can erode 10-15 cm of sediment on intertidal flats in a single event (see (Yeo & Risk 1979, Hu et al. 2017, Zhu et al. 2019, de Vet et al. 2020), thereby not only threatening shallow-buried juvenile bivalves, but also adults. Severe storm-induced erosion can decrease macrofaunal abundances (de Vet et al. 2020), cause long-term community structural change (Ong & Krishnan 1995), and large bivalve mortality events (Rees et al. 1977, Yeo & Risk 1979, Cadée 2016, Shi et al. 2021). Indeed, exposure of bivalves to the sediment surface can increase the risk of mortality by predation (Hiddink & Wolff 2002), desiccation (Kurihara 2003), and transport to unfavorable habitat (Cadée 2016). In addition, the majority of storms in temperate regions occur in the autumn and winter which coincides with low temperatures and food scarcity that can send bivalve into a dormant, or quasi-hibernating, state (Newell & Bayne 1980). Bivalves in a dormant state have reduced mobility (Haider et al. 2020) which makes them even more vulnerable to storm-induced erosion than if they were actively able to burrow further down into the sediment. As the frequency and intensity of storms may increase with climate change (Stocker et al. 2013), they could shape tidal flat communities by selecting for species that are less vulnerable to disturbances from storms.

Invasive and introduced bivalve species are in general highly adaptable (Bates et al. 2013), which may make them more resilient to severe storm-induced sediment erosion events than native species. Many studies (Schneider 2008, Bielen et al. 2016, Vázquez et al. 2021, Domínguez et al. 2021) have shown that invasive and introduced bivalves have lower mortality and lower indicators of physiological stress under extreme temperatures and salinities compared to their native counterparts. It remains however unknown whether invasive and introduced species show a similar tolerance towards extreme physical disturbances like storm-induced erosion. Because burrowing faster than the sediment erosion rate would allow a bivalve to escape storm-induced erosion, the ability to burrow quickly may be a trait that facilitates invasions of shallow-burying bivalves in tidal flats that face increasingly frequent and severe storms.

The manila clam *Ruditapes philippinarum* (Adams and Reeve 1850), a native of the subtropical Pacific, is a successful introduced species worldwide to the extent that it has replaced the native *Ruditapes decussatus* (Linnaeus, 1758) in several disturbed estuaries in Europe like Arcachon Bay in France and the Venice lagoons in Italy (Bidegain & Juanes 2013). Since 2008, it has been found in the Scheldt estuary on the border of Belgium and the Netherlands (Foekema et al. 2014), living in the same sediment as the native cockle, *Cerastoderma edule* (Linnaeus 1758). *C. edule* and *R. philippinarum* are filter feeders and live close to the sediment's surface (generally 1-3 cm depth for *C. edule* (Zwarts & Wanink 1989) and 1- 4 cm depth for *R. philippinarum* (Lee 1996)). While *R. philippinarum* is not assessed to be an invasive species in the Scheldt, it is a species on the Watch list risk category because of its high fecundity, pelagic larvae, and high colonization potential (Foekema et al. 2014). Because the two species are found in the same sediments and occupy a similar function, there is concern that the two may compete for habitat. Indeed, the presence of *R. philippinarum* has increased in the Scheldt estuary over the past few years, as has its habitat overlap with *C. edule*. In 2014, Wageningen Marine Research's monitoring campaign conducted in the Scheldt estuary found that 8% of samples with either species contained both, whereas in 2019 and 2020, 29% of samples with either species contained both (Troost et al. 2021).

While the spatial overlap between the two species is increasing in the Scheldt, studies have shown that *R. philippinarum* prefers habitat with less hydrodynamic forcing than *C. edule* (Bouma et al. 2001, Bidegain & Juanes 2013, Cozzoli et al. 2014). However, a habitat preference for lower hydrodynamic forcing does not necessarily translate to a lower tolerance towards rare extreme events of high hydrodynamic forcing, like storms. Indeed, invasive and introduced species can frequently tolerate a wide range of abiotic conditions (Lenz et al. 2011), and *R. philippinarum* has demonstrated high physical tolerance to extreme temperature and salinity (Brusà et al. 2013) which can translate to lower mortality risk from non-environmental factors like predation (Domínguez et al. 2021). The flexibility shown by *R. philippinarum* to other abiotic stressors may manifest in greater resilience to storm-induced erosion events than *C. edule*, despite its preference for a habitat with calmer hydrodynamics.

Although storm events can have a large impact on benthic macrofauna, their effects are difficult to study *in situ*, as their unpredictable nature can make fieldwork hard to plan and unsafe. Laboratory flume experiments simulating stormy conditions provide an alternative that allows for direct observation during storm-like conditions. Thus, we firstly studied the erodibility of *R. philippinarum* and *C. edule* in a custom-designed flume that allowed us to simulate rapid sediment erosion at precise rates. To our knowledge, the vulnerability of adult bivalves to storm-induced erosion events has not explicitly been studied before in an experimental context. Secondly, we examined whether the two species had different dormancy incidences over a late fall-early winter season, as this may strongly affect a species ability to escape surfacing during erosion events. Thirdly and finally, we tested if the differences in shape between the two bivalves would affect their transport speed, once brought to the surface. Although the two species have similar functions and habitat, they are morphologically different with *C. edule* having a round shell and *R. philippinarum* having a flatter shape. We expected their difference in shape to translate to a difference in transportability because the initiation of particle movement is known to mainly depend on shape (Paphitis et al. 2002). Our overarching hypotheses for the experiments were: 1) *R. philippinarum* would have a higher surfacing rate than *C. edule* due to its preference for habitat with lower hydrodynamic forcing; 2) *R. philippinarum* would have a higher rate of dormancy than *C. edule* due to its subtropical origins, and 3) once surfaced, the transport speed of *C. edule* would be faster than that of *R. philippinarum* due to its rounder shape.

Methods

Mimicking storm-induced rapid erosion events: the concept and flume design

Manipulating sediment erosion rates is important to better understand bivalve vulnerability to storm-induced erosion, because storms do not all have the same intensity. As storms of higher intensity can induce larger volumes of sediment erosion than storms of a lower intensity (Hu et al. 2017, de Vet et al. 2020), the proportion of surfaced bivalves in a population is likely to increase with the intensity of a storm. We may also observe threshold effects, where once a certain sediment erosion rate is reached, all the individuals of a population are surfaced. Racetrack flumes have been used to study the erodibility of newly settled bivalves to great success (Lundquist et al. 2004, Hunt 2004, St-Onge & Miron 2007), however, it is difficult to mimic extreme sediment erosion rates in a racetrack flume with a controlled intensity. For example, Hunt (2004) caused only 0.5 to 1 cm of erosion using a racetrack flume, whereas we wished to be able to mimic intense storms where much larger volumes of sediment can be quickly eroded (5-15 cm, cf. de Vet et al., 2020; Hu et al. 2017). In our experiment, we used a custom-made flume (Fig. 1a & b) where we could control the sediment erosion rate precisely, which was ideal for examining the effects of varying intensity of storm-induced erosion on adult bivalve erodibility.

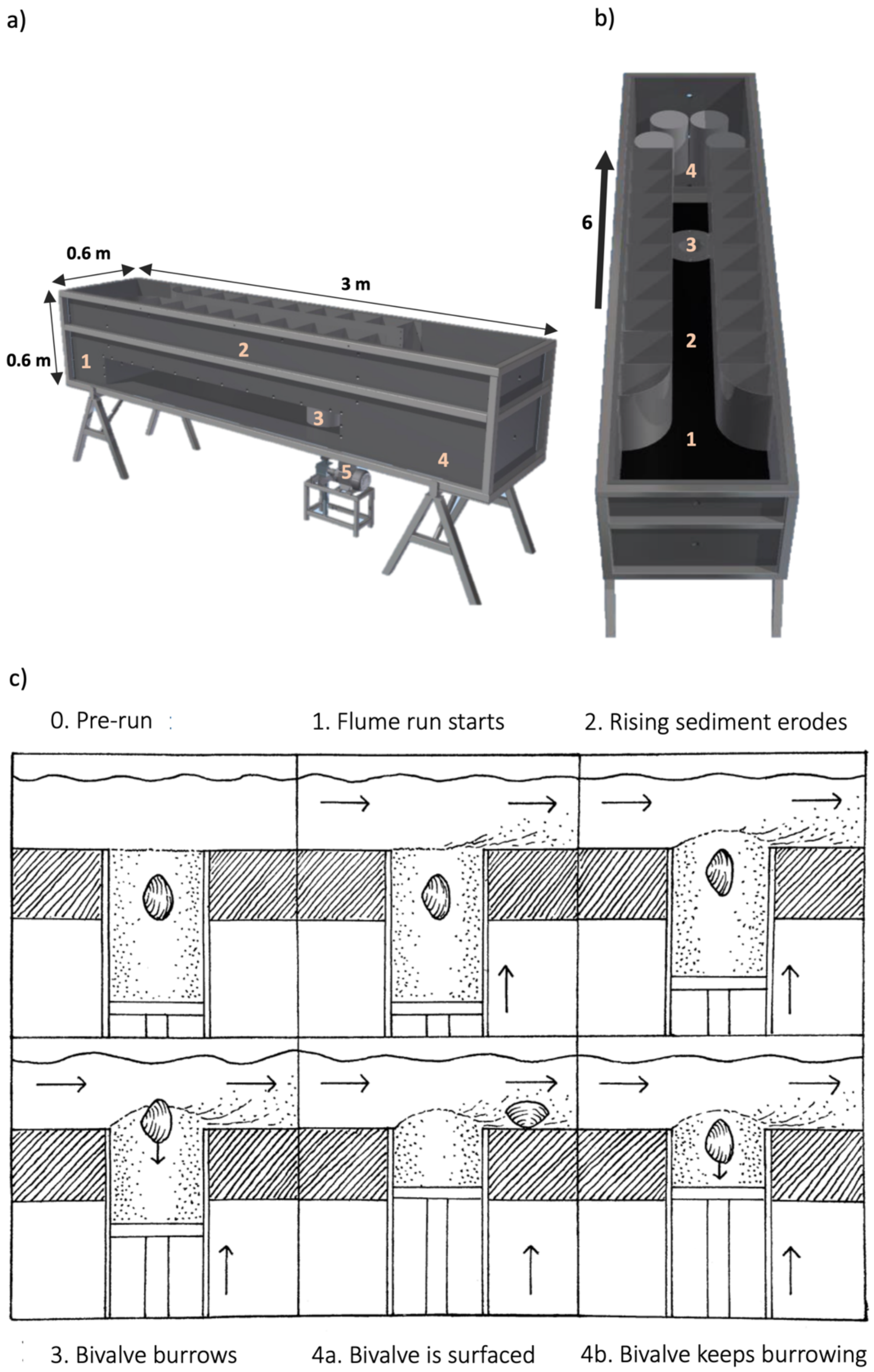

Figure 1: Schematic of the storm erosion flume showing a) the exterior, b) top view with: (1) Front basin and cooling system (2) Flume channel (3) Sediment core (4) Back basin, pumps, and circulation tubes (5) Cart with pneumatic piston to raise the sediment core (6) Direction of water through flume channel. The water flows through the main channel (2) of the flume, over the sediment core (3), and is then circulated

back with tubes running beneath the main channel. A constant water flow of 40 cm/s was generated by three pumps at the end back basin of the flume (4). A Lauda WKL 3200 Recirculating Chiller with a stainless-steel cooling spiral was used to counteract the heating of the water by the pumps (1). c) A schematic drawing showing the functioning of the flume during a run to test the erodibility of a bivalve. The sediment core is pushed upwards into the 40 cm/s water flow (panels 1,2,3). As the sediment overlying the bivalve is eroded (panel 2), the bivalve needs to burrow down into the sediment to escape being surfaced (panel 3). The speed of sediment erosion is determined by the upwards movement of the sediment. If the bivalve's burrowing speed is slower than the upwards movement of the sediment core the bivalve is surfaced (panel 4a). If the bivalve is faster, it remains burrowed (panel 4b). The run ends when the bivalve is surfaced or after 60 minutes.

To study the effect of rapid storm-induced erosion during winter, when benthic animals are least active and storms are most prevalent, we conducted a flume experiment from November 12, 2019 to January 15, 2020. All experiments were conducted in the previously described custom-made flume (Fig. 1a), containing a sediment core that could be pushed up with a pneumatic pump through a 16 cm diameter hole in the bottom of the flume. Given that the sediment core directly erodes as soon as the sediment enters the 40 cm/s flow in the flume, the erosion rate that animals in the sediment core experiences is equal to the rate by which the core was pushed into the flume. The water flow of 40 cm/s does not affect the erosion rate. Rather, the 40 cm/s flow was chosen to be fast enough to erode the gradually surfacing part of the sediment core and immediately transport the sediment to the back of the flume. For animals to withstand erosion, they thus must actively burrow down into the sediment with at least the same speed as the core is being pushed into the flume (Fig. 1c).

We used three sediment erosion rates to simulate different levels of storm intensity: 5.3 cm/h, 10.6 cm/h, 15.9 cm/h. The final erosion rate represents the upper limit of storms that we have observed in the Scheldt estuary in the past 30 years (Hu et al. 2017, de Vet et al. 2020). By using three different sediment erosion rates, we could test whether there was an interaction between erosion rate and species on bivalve erodibility.

Bivalve collection and experimental set-up

We collected at least fifty adults per species between 25 and 35 mm in length at Oesterdam, a sandy site in the Eastern Scheldt (51.46670, 4.22139), on a biweekly basis. Because their shell morphologies were different, we selected *Ruditapes philippinarum* and *Cerastoderma edule* that had the same dry weight (shell and flesh mean: 5.2 g and SD: 1.2 g) instead of the same shell length. *R. philippinarum* had a greater shell length than *C. edule* (mean: 30.9 mm and SD: 2.4 mm vs mean: 28.1 mm and SD: 2.1 mm), but *C. edule* had a greater shell width and height than *R. philippinarum* (*C. edule* shell width mean: 25.5 mm and SD: 1.4 mm vs. *R. philippinarum* mean:

23.2 mm and SD: 1.9 mm, and *C. edule* shell height mean: 21.1 mm and SD: 1.5 mm vs. *R. philippinarum* mean: 17.0 mm and SD: 1.7 mm). The narrow size range ensured that there was no size effect on erodibility. The bivalves were stored in baskets in tidal tanks in a climate-controlled room with an air temperature of 9 °C, for at least a week to ensure acclimatization to laboratory conditions before being used in the experiments. This temperature was chosen to mimic the mean November and December air temperature. Each tidal tank system was composed of two 1.2 m by 0.8 m tanks stacked on top of each other (Cao et al. 2018). Unfiltered water from the Eastern Scheldt estuary, which has a salinity of 31 ppt, was pumped from the bottom tank up to the top tank to simulate tidal conditions. High tide conditions (5 cm water above experimental units) lasted six hours and occurred twice a day. High tide was imposed by pumping water to the higher basin, using a free-fall overflow system for the return flow. The latter kept the water well-oxygenated. The water temperature in the tidal tanks was around 9 °C in November 2019 and around 7.5 °C in January 2020 when the experiment ended, which was 1-2 degrees warmer than the water in the Scheldt. There was no sand in the tidal tanks and the bivalves were kept in baskets, with around 30 individuals per basket. We changed the water once a week. Since the bivalves are filter feeders, we fed them with an algal concentrate (Shellfish Diet from Reed Mariculture) 5 mL per tank twice per week to supplement the food contained in the raw Eastern Scheldt water.

The day before the experiment, we selected twelve individuals randomly from the two species (six per species). The twelve individuals were placed on top of twelve cores to burrow. Each core was made from a sawed-off PVC pipe (30 cm length, 11.5 cm width) with a removable bottom cap, and was filled to 10 cm below the rim. We filled the experimental cores with a single sediment which had a comparable grain size distribution to the sediments from the collection location at the Oesterdam. The Oesterdam sediment had an average grainsize ranging between 250 and 270 µm and the sediment used in the experiments had an average grain size of 246 µm. The field and experimental sediments mainly consisted of medium (250-500 µm; 40-45%) and fine (125-500 µm; 40-60%) sand. The twelve cores were kept in a tidal tank in the same mesocosm room that the bivalves were stored and set to the same tidal cycle as the other tanks. The morning after placing the twelve bivalves (six per species) on top of the twelve cores, we checked the dormancy of the bivalves by noting if any had remained lying on the sediment surface. We then selected one core that had a burrowed (i.e. active) individual for each flume run (maximum three flume runs a day).

Estimating species-specific dormancy rates

We monitored the proportion of dormant individuals in our collected bivalve populations from November 2019 to January 2020 because we were interested in whether winter-induced dormancy would impact the erodibility of the bivalves. We considered “dormancy” the hibernation state that bivalves can enter in cold winter conditions (Newell & Bayne 1980) when it may experience food scarcity and even starvation (Haider et al. 2020). The state that we call dormancy throughout the paper can also be caused by environmental stressors, like hypoxia (Storey & Storey 1990). It is characterized by low metabolic activity (Haider et al. 2020), thus dormant bivalves stayed on top of the sediment and did not burrow. *C. edule* are also known to have their burrowing capacity inhibited by parasites, but as infected *C. edule* are usually found on top of the sediment in the field (Thieltges 2006), we hopefully avoided infected cockles by only collecting burrowed individuals. It is also possible that the dormant state was partly a response to the stress of acclimation to the mesocosm environment. Whatever the cause, we kept track of the number of *C. edule* and *R. philippinarum* that were dormant over the season. As we only used burrowed individuals for our flume experiments, dormancy did not impact our experiments. However, dormancy could impact the erodibility of bivalve populations in the field, as dormant bivalves may be passively surfaced by a storm by being unable to escape erosion by digging.

To track the proportion of dormant individuals, we counted the number of unburrowed individuals on the mornings of days that we conducted flume experiments out of the twelve individuals (six per species) that were laid out on cores 24 hours prior. Because we collected new bivalves every two weeks, this allowed us to better understand if dormancy changed over the course of the late fall-early winter season (November 12, 2019 to January 15, 2020). Please see Table S1 for the dates that we checked bivalves for dormancy.

Storm erosion flume runs with increasing intensity of sediment erosion

Experiments were conducted in the custom-made flume (Fig. 1a & b). The flume was filled with sea water to a height of 15 cm, which minimized turbulence within the flume, and during each run the current velocity was 0.40 m/s. In addition, the water used in the flume was chilled overnight in 1000 L tank to a temperature of 3-5 °C before being used to simulate winter water temperatures. While we acclimated the bivalves to the flume conditions for thirty minutes before each run, the bivalves may have experienced some shock due to the water temperature difference between the tidal tanks (7.5-9 °C) and the flume environment (3- 5 °C), which may have affected their ability to burrow into the sediment.

We performed 50 flume runs (25 *C. edule* and 25 *R. philippinarum*) over the course of 6 weeks. During each run, a sediment core containing a single bivalve was used. We conducted three trial types with three sediment erosion rates: 5.3 cm/h (10 single-individual runs per species), 10.6 cm/h (8 single-individual runs per species), and 15.9 cm/h (7 single-individual runs per species). We could perform a maximum of three runs per day because we needed to drain and refill the flume chamber from the chilled water storage tank after every run to minimize warming of the water due to pump friction. The run ended after 60 minutes had elapsed or when a bivalve was transported outside of the core. A bivalve was considered to be surfaced when it was completely exposed on top of the sediment. The flume runs were recorded with a camera to assess bivalve behavior within the flume and confirm the time of erosion. We retrieved the bivalve after the run was complete for morphological measurements.

Racetrack flume to measure bivalve transport speed once surfaced

To gain a better understanding of whether the fate of the bivalves may be different once surfaced, we measured the transport speed for both species under currents and waves. We used the NIOZ racetrack flume, a large flow channel (17.5 m length, 3.25 m width) where waves and a constant unidirectional flow of up to 0.60 m/s can be generated. We inserted a 30 cm wide × 40 cm long × 10 cm deep bed of sand in the test section, which we flattened in between runs. Before each run, we deposited six bivalves (three of each species) in a line perpendicular to the current on top of the sand. We performed separate trials to test the effects of current speed and increasing wave height on bivalve transport. We used four levels of current velocity (i.e. 0.089 m/s, 0.114 m/s, 0.135 m/s, and 0.168 m/s) and four levels of wave height with a constant underlying current velocity of 0.089 m/s (i.e. 3.6 cm, 5 cm, 5.6 cm, and 6.4 cm). We used six new bivalves (three per species) for each run and performed two runs per current speed or wave height setting. During each flume run, we measured the speed at which the bivalves were transported across the sand.

Statistical analysis

We used logistic regression to determine whether there was a difference between the surfacing probability of the two species and whether the surfacing probability increased with increasing erosion rate. Logistic regression is a generalized linear model with a logit-link function to a binomial distribution, where the response variable is modeled as a binary outcome (Equation 1). We fit the bivalve surfacing (0 = burrowed, 1= surfaced) to erosion rate (continuous), species (two-level categorical), water temperature in the flume (continuous) and date (continuous). It is appropriate to treat erosion rate in the surfacing model (Equation 1) as a continuous variable because the differences between our measurement points are meaningful quantitative measures (Quinn and Keough, 2002, page 136). Surfacing probabilities in between our three measured points can be interpolated from the logistic regression model (see Fig. 3 for model fits). Because we wanted to know whether there was a difference in the direction of responses to accelerating sediment erosion depending on the species, we tested an interaction between erosion rate and species.

Our model was as follows:

$$Surfacing_i \sim Binomial\ (p_i)$$
$$p_i = \frac{e^{\beta_0 + ErosionRate_i \times Species_i + Date_i + WaterTemperature_i}}{1 + e^{\beta_0 + ErosionRate_i \times Species_i + Date_i + WaterTemperature_i}}$$

(Equation 1)

Where $Surfacing_i$ is ith observation of surfacing, p_i is the probability of surfacing occurring, and β_0 is the model intercept.

We also used a logistic regression model to examine whether there was a difference in dormancy probability (0 = active, 1 = dormant) between species as well as whether there was a seasonal trend to dormancy probability. The model for dormancy probability was similar to the one depicted in Equation 1, with dormancy probability as the response variable, and species (categorical) and date (continuous) as covariates. We included an interaction between species and date to test whether a seasonal trend differed by species. We tested the significance of the logistic regression coefficients using a Wald test, which is similar to a t-test but uses ratios which is appropriate for logistic regression (Quinn and Keough, 2002, page 363).

The bivalve transport speed was modeled using a lognormal two-part, or hurdle, model with current speed (continuous) or wave height (continuous) and species (two-level categorical) as covariates. A hurdle model is used to model a process where the response variable must overcome a "hurdle" to be measured. In this case, the bivalves must first be transported to have a measured transport speed. The hurdle model has two parts (Equation 2). In the first step, a binomial model is used to model the probability (p_i) that a zero is observed, which in our case is whether a bivalve remains untransported and stationary. In the second step, a lognormal model is used to model non-zero response data, which is the speed of the transported bivalves (μ_i). The lognormal distribution for the non-zero transport speed was appropriate because these data were positive, continuous, and lognormally distributed.

$$Transport\ (y = 0)_i \sim Binomial\ (p_i)$$
$$p_i = \frac{e^{\beta_0 + CurrentOrWaves_i + Species_i}}{1 + e^{\beta_0 + CurrentOrWaves_i + Species_i}}$$

$$Transport\ (y > 0)_i \sim Lognormal\ (\mu_i)$$
$$\mu_i = e^{\beta_0 + CurrentOrWaves_i + Species_i}$$

$$E(Transport_i) = (1 - p_i) \times \mu_i$$

(Equation 2)

Where $Transport\ (y = 0)_i$ is the ith observation of untransported bivalves and $Transport\ (y > 0)_i$ is the ith observation of transported bivalves, and $E(Transport_i)$ is the expected mean of the lognormal hurdle model of bivalve transport speed. CurrentOrWaves was the current speed in the model for experiments where the flow rate in the flume increased without waves, and CurrentOrWaves was wave height in the model for experiments where the wave increased and the flow was fixed at 0.089 m/s.

We checked hurdle model fit by ensuring that there was no statistically significant difference between the model's null and residual deviances with a Chi-square test, and by examining the residual and Q-Q plots for abnormalities. All models that we report had a good fit according to the Chi-square test. As in the logistic regression, we considered the independent variables current speed (4 levels) and wave height (4 levels) as continuous variables.

Finally, we used linear regression to model the time it took for a bivalve to be surfaced as a function of species (categorical), sediment erosion rate (continuous), date (continuous), and flume water temperature (continuous). T-tests were used to determine the significance of the model intercept and coefficients. Statistical analyses were performed with the "stats" package in R (R Core Team 2020) and we used additional functions from packages "aod" (Lesnoff & Lancelot 2012) and "binom" (Dorai-Raj 2014). See Table 1 for details on model fits.

Results

Species and seasonal effects on dormancy

R. philippinarum had a higher dormancy rate (on average 20%) than *C. edule* (on average 7%, Wald's χ^2 (1) = 13.5, p = 0.0). The probability of *C. edule* being dormant increased over the course of the experiment with small statistical significance (Wald's χ^2 (1) = 3.8, p = 0.04), while the dormancy probability of *R. philippinarum* stayed constantly high (Fig. 2).

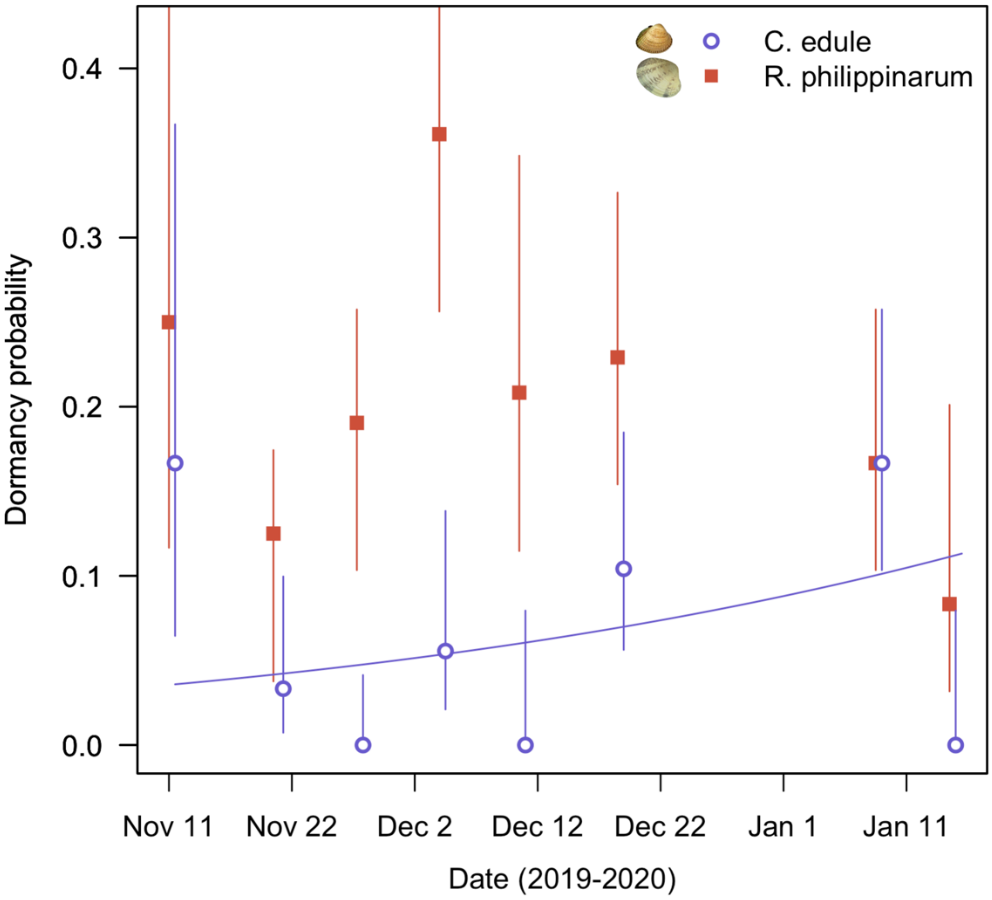

Figure 2: The probability of dormancy for *C. edule* (circles) and *R. philippinarum* (squares) as a function of days since the beginning of the experiment (November 12, 2019) until the end of the experiment (January 15, 2020). We observed the dormancy of 12 individuals (six per species) each day that we performed flume runs (see Table S1 for dates). The symbols (circles and squares) represent the observed probability of dormancy per week and the vertical lines represent the 90% confidence intervals for these observations. We include the model fit for probability of dormancy as a function of days for *C. edule*, but not for *R. philippinarum* as the model fit was insignificant. See Table 1 for model equation and covariate significance.

Table 1: Model formula (Model), coefficients (Coef.), standard errors (Std. Error), confidence intervals for the coefficient (2.5% & 97.5%), test statistics (Test stat.) and p-values (p) for the intercept and covariates. We present models of bivalve surfacing, dormancy, surfacing time, and transport in current and waves. The transport models have two parts: the first part is a logistic regression describing the probability that a bivalve remain untransported (Transport, y=0) and the second part describes the speed of the transported bivalve (Transport, y>0). For all models, we indicate in the model formula if the generalized linear model required a link (either "logit" or "log") function. The test statistic for the logistic regressions was a Wald's Chi-square statistic and for the lognormal and normal regressions was a t-statistic. We present the test statistic along with its associated degrees of freedom (df). In all models, "Species" is a categorical variable and modifies the model intercept when significant. The reference level for the "Species" covariate

is *R. philippinarum*, which means that model predictions for *R. philippinarum* include the model intercept without modification from the "Species" coefficient. The intercept for model predictions for *C. edule* are modified with the "Species" coefficient.

Model	Response	Covariate	Est.	Std.	2.50%	97.50%	Test stat.	p
Logit (Surfacing) ~ Intercept + Sediment erosion rate × Species + Water temperature + Date								
	Surfacing	Intercept	4.01	3.37	-2.61	11.00	1.40 (df=1)	0.75
		Sediment erosion rate	0.63	0.22	0.28	1.20	8.00 (df=1)	0.005
		Species	-6.00	1.95	-10.95	-3.02	9.40 (df=1)	0.002
		Water temperature	-1.58	0.86	-3.48	-0.02	3.40 (df=1)	0.06
		Date	-0.02	0.06	-0.13	0.09	0.081 (df=1)	0.78
Logit (Dormancy) ~ Intercept + Sediment erosion rate + Species × Date								
	Dormancy	Intercept	-1.00	0.30	-1.63	-0.49	13.1 (df=1)	<0.001
		Species	-2.20	0.60	3.52	-1.1	13.5 (df=1)	<0.001
		Date	0	0	0	0.006	1.40 (df=1)	0.23
		Species × Date	0.03	0.02	0	0.05	3.80 (df=1)	0.04
(Surfacing time) ~ Intercept + Sediment erosion rate + Species + Water temperature + Date								
	Surfacing	Intercept	37.81	14.98	-2.61	11.00	2.52 (df=19)	0.02
		Sediment erosion rate	-1.07	0.47	0.28	1.20	-2.28 (df=19)	0.03
		Species	1.53	4.69	-10.95	-3.02	0.37 (df=19)	0.74
		Water temperature	-2.13	3.19	-3.48	-0.02	-0.66 (df=19)	0.51
		Date	-0.03	0.22			-0.13 (df=19)	0.89
Logit (Transport, y=0) ~ Intercept + Current speed + Species								
	Transport,	Intercept	-15.79	4.29	-26.19	-8.93	10.60 (df=1)	0.001
		Current speed	97.07	27.05	53.38	162.02	10.30 (df=1)	0.001
		Species	3.78	1.18	1.81	6.59	6.60 (df=1)	0.01
Log (Transport, y>0) ~Intercept + Current speed + Species								
	Transport,	Intercept	-8.61	3.01	-11.75	-5.59	-5.52 (df=15)	<0.001
		Current speed	58.49	19.77	38.62	78.46	5.76 (df=15)	<0.001
		Species	2.39	0.73	2.11	3.35	8.62 (df=15)	<0.001
Logit (Transport, y=0) ~ Intercept + Wave height + Species								
	Transport,	Intercept	-13.41	4.62	-24.97	-6.19	8.4 (df=1)	0.004
		Wave height	2.39	0.82	1.10	4.42	8.6 (df=1)	0.003
		Species	5.37	1.78	2.65	9.86	9.1 (df=1)	0.002
Log (Transport, y>0) ~Intercept + Wave height + Species								
	Transport,	Intercept	-7.04	1.35	-9.78	-4.29	-5.21 (df=28)	<0.001
		Wave height	1.19	0.22	0.75	1.64	5.43 (df=28)	<0.001
		Species	1.61	0.38	0.83	2.38	4.2 (df=28)	<0.001

Species and sediment erosion rate effects on bivalve surfacing

R. philippinarum (84% surfaced on average) were more easily surfaced than *C. edule* (28% surfaced on average) (Fig. 3). For both species, the surfacing probability of the individuals increased with the sediment erosion rate (Wald χ^2 (1) = 8, p = 0.005). In fact, all *R. philippinarum* were surfaced at the two highest erosion rates and 60% were surfaced at the slowest one (5.3 cm/h). On the other hand, no *C. edule* were surfaced at the 5.3 cm/h speed, but 25% were surfaced at the 10.6 cm/h erosion rate and 71% were surfaced at the 15.9 cm/h erosion rate. We observed active burrowing behavior in all bivalves used in the flume.

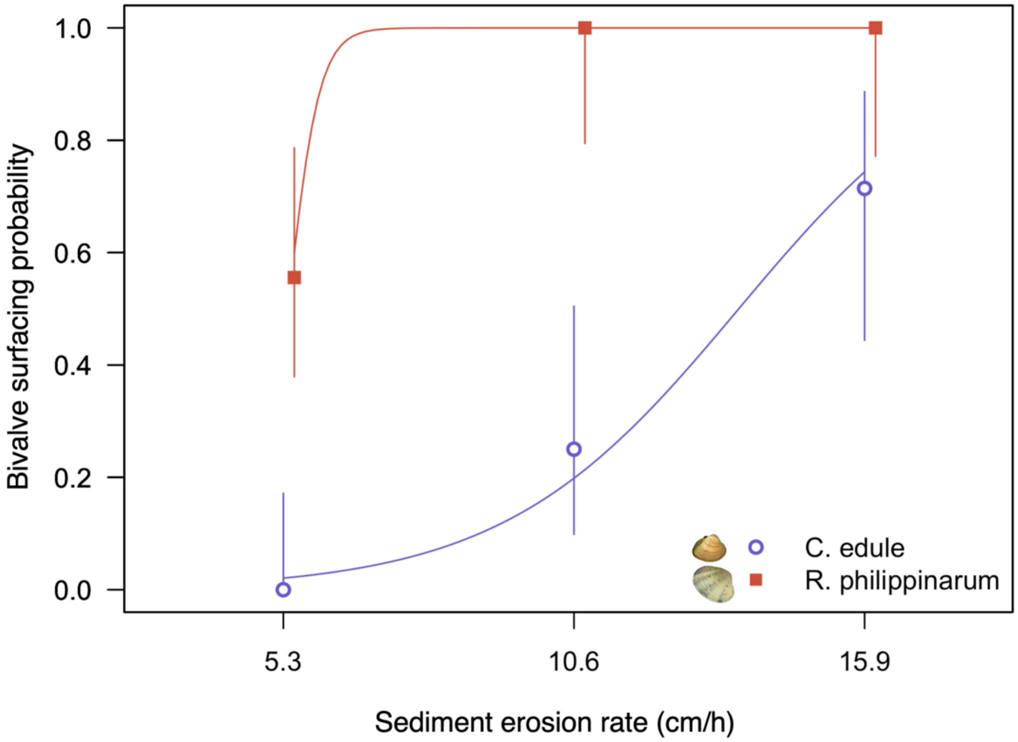

Figure 3: The surfacing probability (fitted lines) of *C. edule* (circles) and *R. philippinarum* (squares) as a function of sediment erosion rate, with 0 = no individuals surfaced and 1 = all individuals surfaced. We tested bivalve erodibility at three different sediment erosion rates: 5.3 cm/h, 10.6 cm/h, and 15.9 cm/h. The symbols represent the observed fraction of surfaced bivalves out of the total number of bivalves tested at an erosion rate-species combination. The vertical lines represent 90% confidence intervals, given a binomial distribution. See Table 1 for the model fit.

The bivalves appeared to more likely to be surfaced at colder water temperatures in the flume (Wald's χ^2 (1) = 3.4, p = 0.06). However, it should be noted that we kept the flume temperature within a narrow range (3-5 ºC) and so the lack of a strong temperature effect may be due to small variability of the covariate. Finally, the bivalves were surfaced faster with an increasing erosion rate (t(19) = -2.28, p = 0.03). This effect was likely driven by *R. philippinarum.* We did not detect a species difference in surfacing time, probably because few *C. edule* were surfaced in comparison to *R. philippinarum* (0 at 5.3 cm/h erosion rate, 2 at 10.6 cm/h erosion rate, Fig. 4). The time to surfacing was not affected by date or water temperature in the flume.

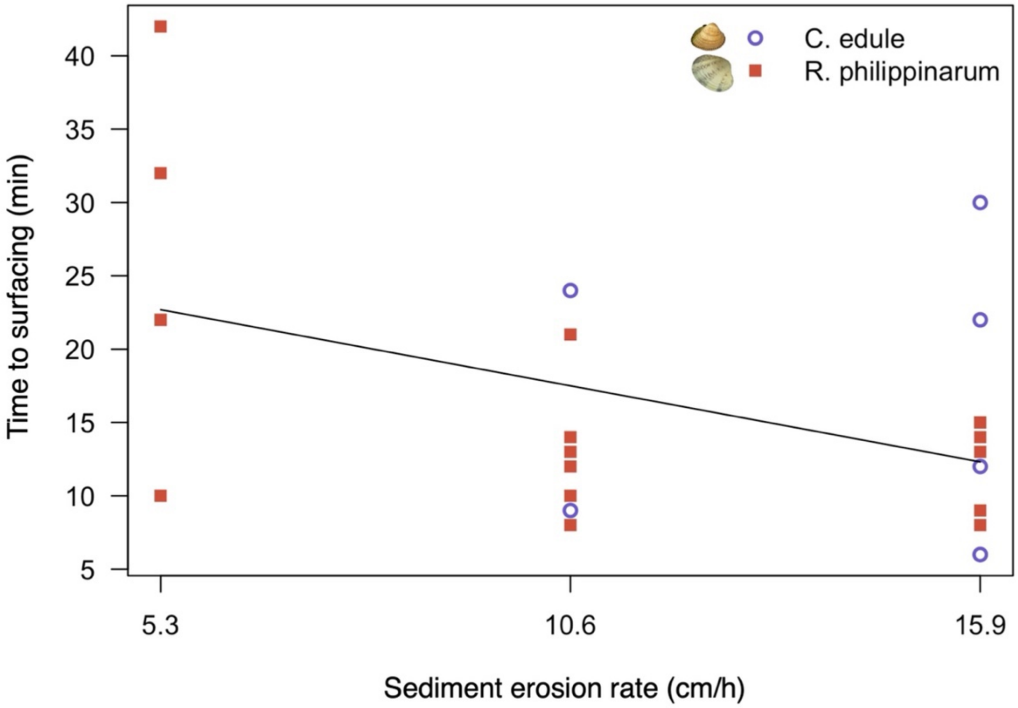

Figure 4: Time (minutes) elapsed in the flume until bivalve surfacing as a function of sediment erosion rate (cm/h) and species: *C. edule* (circles) and *R. philippinarum* (squares). We tested bivalve erodibility in the flume at three different sediment erosion rates: 5.3 cm/h, 10.6 cm/h, and 15.9 cm/h. In this linear regression, we treated erosion rate as a continuous variable. The line represents the model fit (y = 27.9 – 0.9 x, R2 = 0.21). Please note that there were no *C. edule* that were surfaced at an erosion rate of 5.3 cm/h and that the total number of *C. edule* that were surfaced was low, especially at an erosion rate of 10.6 cm/h (n = 2). As these non-surfacing animals could obviously not be included in these analyses, our statistical power for detecting a species effect on the surfacing time was low.

Bivalve transport speed

Once at the sediment surface, *C. edule* were transported faster than *R. philippinarum* (~11 × faster transport as a function of currents t(15) = 8.62, p<0.001 and ~5 × faster transport as a function of wave height with an underlying current speed of 0.089 m/s, $t(28) = 4.23$, $p<0.001$) and had lower entrainment velocity (fluid velocity that causes initiation of bivalve movement) than *R. philippinarum* (Fig. 5). For example, at a current velocity of 0.168 m/s, transported *C. edule* had a speed of 3.7×10^{-2} m/s whereas transported *R. philippinarum* had a speed of 3.3×10^{-3} m/s. Furthermore, *C. edule* initiated movement at a current speed of 0.135 m/s (no waves) and a wave height of 3.6 cm with an underlying current speed of 0.089 m/s, whereas *R. philippinarum* initiated movement at a greater current speed (0.168 m/s with no waves) wave height of 5.6 cm, again with an underlying current speed of 0.089 m/s (Fig. 5). In addition, a greater proportion of *C. edule* were transported than *R. philippinarum* at a same wave height or current speed (Wald's χ^2 (1) = 6.6 for current and 9.1 for waves, $p \leq 0.01$ for both). For example, at a wave height of 5.6 cm, 100 % of *C. edule* were transported, whereas 50 % of *R. philippinarum* were transported. We observed *R. philippinarum* sliding across the sand, whereas *C. edule* rolled.

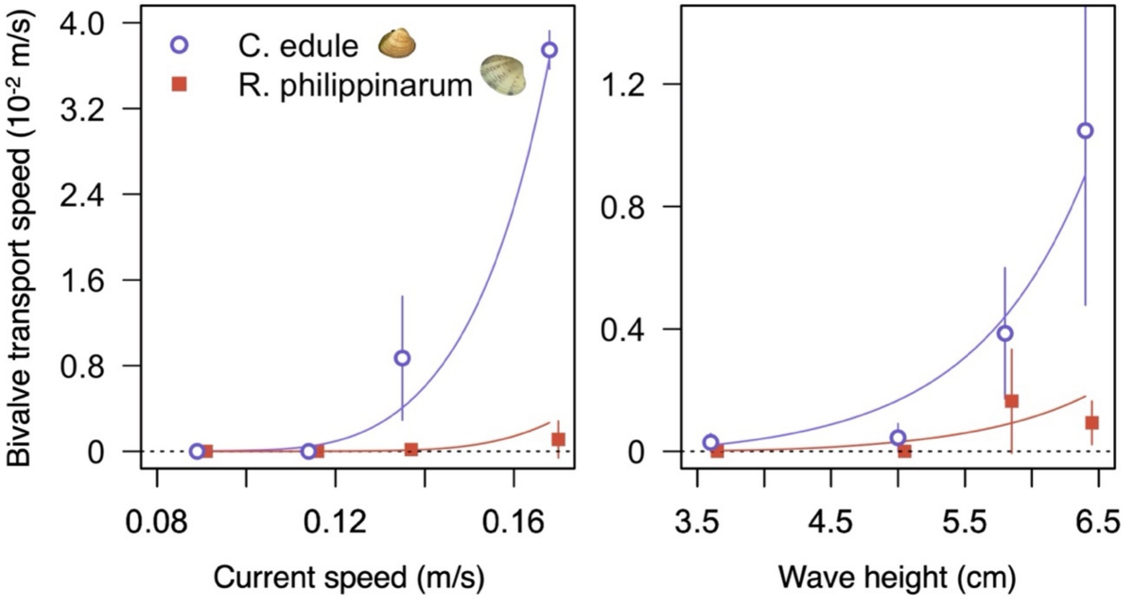

Figure 5: The transport speed of bivalves *C. edule* (circles) and *R. philippinarum* (squares) in the racetrack flume with (left) increasing current speed and no waves and (right) increasing wave height at a current speed of 0.089 m/s. The line represents the model fit and the circles represent the mean transport speed for each set of bivalves tested at that wave height or current speed (n=3 per species per run, we performed 2 runs at each wave height or current speed). The vertical lines represent the standard deviation around the mean. The dotted 0 line is shown to facilitate the identification of entrainment velocity, which occurs when the transport speed > 0. See Table 1 for model equations and covariate significance.

Discussion

Comparing the erodibility of a native (*C. edule*) and a non-indigenous (*R. philippinarum*) bivalve revealed that individuals from both species surfaced in greater proportion as the sediment erosion rate increased. In line with our first hypothesis, there were large differences in species erodibility: *R. philippinarum* surfaced quicker and at higher rates than *C. edule*. In line with our second hypothesis, we found a higher overall dormancy of *R. philippinarum* than *C. edule*, even though the incidence of dormancy for *C. edule* marginally increased over the autumn and winter. Although *R. philippinarum* were more likely to be surfaced by storm-induced erosion, this species had a higher entrainment velocity and lower transport speed than *C. edule* (in line with our third hypothesis). The latter implies that *R. philippinarum* would be less vulnerable to being transported to an unfavorable habitat once surfaced than *C. edule*.

Contextualizing the experiments in the natural setting

While our experiments offer insight into the response of bivalves to extreme sediment erosion, it is very challenging to predict when and where these events occur in a natural setting. This is because the occurrence of extreme erosion events is the result of the combination of different time- and space-varying processes (e.g., waves, tidal flow, wind-driven flow and sediment strength) that determine the potential for sudden bed-level changes (Fan et al. 2006, Zhu et al. 2019, de Vet et al. 2020). In addition, the storm's timing in relation to the tidal cycle, and thus the depth of the water column (Shi et al. 2017), is very important for determining a storm's impact (de Vet et al. 2020). And so, the return time of an extreme erosion event is difficult to determine. In addition, the largest bed-level changes occur during a short fraction of the tidal period. For example, a 2014 storm in the Western Scheldt caused 12 cm of erosion, but only when the water was shallow which was 20% of the tidal cycle, with no erosion occurring during the other 80% (Zhu et al. 2019). This means that though a storm may last several days, the sudden erosion of the tidal flat and transport of benthic macrofauna may occur in short bursts spread over a single or several tidal cycles. Furthermore, storm impacts are extremely spatially heterogenous. During a 2016 storm in the Western Scheldt, points that experienced ~20 cm and ~0.5 cm of sudden erosion were separated by only 300 m (de Vet et al. 2020). Typically, the lowest parts of tidal flats have a higher occurrence of extreme erosion than the highest parts of tidal flats. For example, the 2014 storm described by Zhu et al 2019 provoked ~12 cm of erosion at a tidal flat in the Western Scheldt at -1.25 m NAP but produced only ~ 1 cm of erosion at -0.25 m NAP, due to differences in the water depth during the storm. In summary, it is very difficult to predict when and where extreme erosion events with similar magnitudes as those we used in the flume would occur in the field. Nevertheless, given the upcoming increase in the frequency and magnitude of these storm events due to climate change (Stocker et al. 2013), insight into bivalves' capacity to cope with extreme sediment erosion will help us better predict the impacts of increasingly frequent storms on the benthic community.

It is important to note that our experiments approximated extreme events where erosion occurs relatively gradually, over hours. For example, our experimental set-up is comparable to the hydrodynamic conditions during an extreme erosion event described in (de Vet et al. 2020): 20 cm of erosion at an intertidal flat at the Western Scheldt occurred during a severe storm within a 3 hour window, indicating that the average erosion rate should be around 6.7 cm/h. This falls exactly between the lowest and middle erosion rates that we mimicked in the flume, but is a factor 2.4 lower than the most severe erosion rate we mimicked 15.9 cm/h. However, the comparison holds only if we assume relatively gradual and constant erosion during the storm. In reality, the peak erosion rate may occur within an hour or less. Unfortunately, there is a lack of detailed field data about the precise window in which extreme erosion occurs, due to data collection challenges from shallow water and extreme turbidity which can interfere with instrument recording during extreme conditions. The shorter the timeslot during which extreme erosion happens, the higher the chance that macrofauna may not be able to escape being surfaced and transported.

Lastly, our experiment did not take into account the habitat characteristics and density dependent factors that may influence the bivalve's erodibility. Both the erodibility of the sediment as well as the bivalve's burrowing speed will change based on sediment properties like grain size and bulk density. For example, a sediment with greater bulk density, or compaction, would have a lower shear stress, leading to lower erodibility (Xie et al. 2021), but also would be harder to burrow into (Wiesebron et al. 2021) which may affect a bivalve's ability to escape being surfaced. Furthermore, biofilms also reduce the sediment shear stress at the sediment-water interface (Le Hir et al. 2007), which can delay or reduce the amount of sediment erosion that may occur during a storm event. Finally, a high density of benthic macrofauna may increase the surrounding sediment's erodibility through destabilization (Le Hir et al. 2007, Cozzoli et al. 2018) or decrease its erodibility by armoring the sediment (Schönke et al. 2017). A high density of macrofauna may also reduce the transport rate of surfaced individuals (Anta et al. 2013). The processes underpinning density dependent effects on sediment and macrofauna erodibility are complex and may change depending on the sediment properties (Li et al. 2017), community composition (de Smit et al. 2021), and season (De Backer et al. 2010), which would certainly affect the surfacing and transport rate of macrofauna during an extreme storm. Furthermore, we can imagine that if the frequency of extreme storms increases, then surface sedimentary conditions and macrofaunal densities of animals may change between storms, thus affecting the vulnerability of remaining animals.

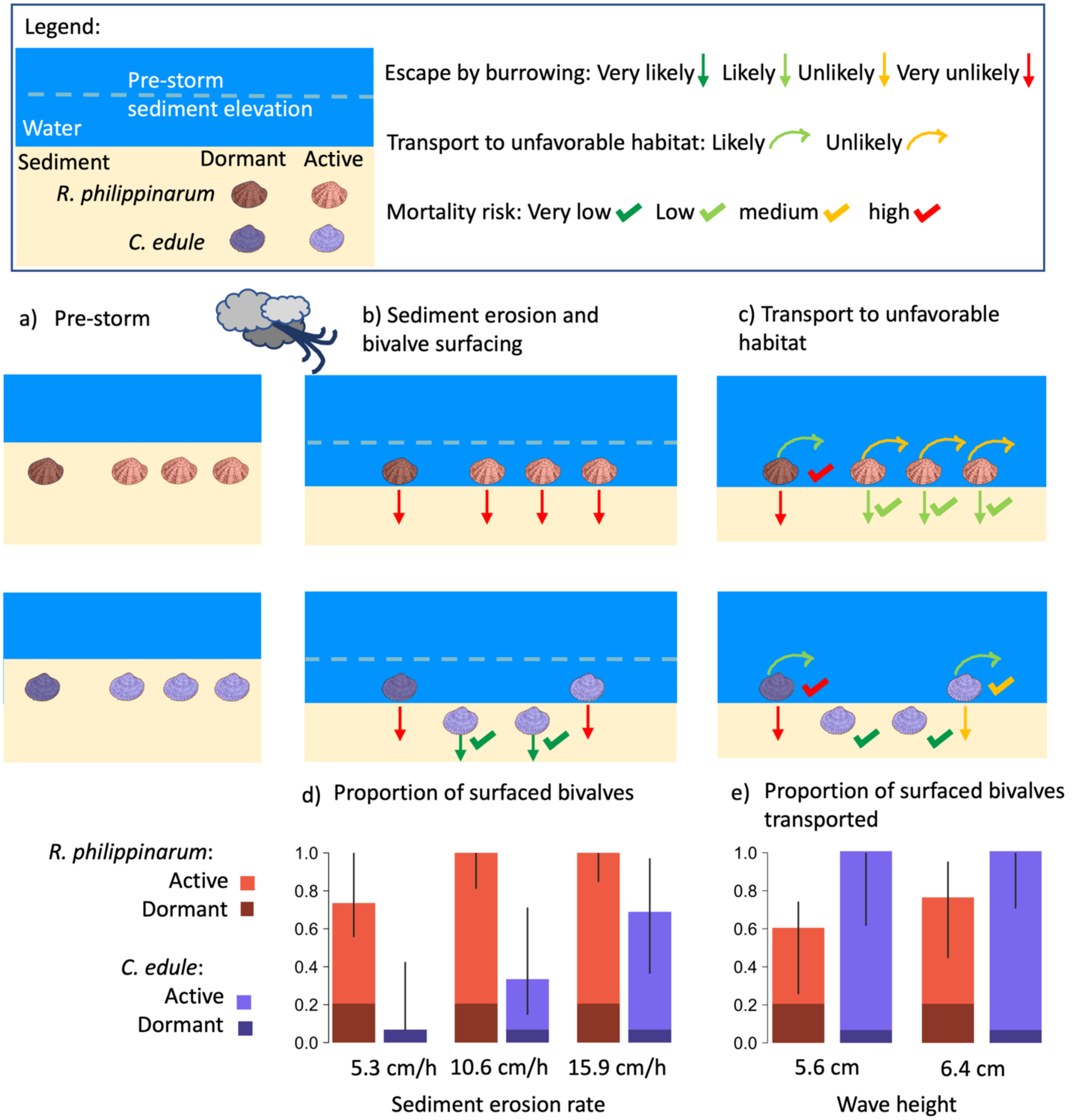

Figure 6: Schematic overview figure showing the mortality risk vectors for (a) active and dormant *C. edule* and *R. philippinarum* during a severe storm by (b) avoiding surfacing due to sediment erosion and (c) escaping transport to unfavorable habitat due to waves, as well as the associated proportions of the experimental population that were surfaced by (d) different sediment erosion rates (5.3 cm/h, 10.6 cm/h, and 15.9 cm/h) and were transported by (e) different wave heights (5.6 and 6.4 cm). Please note that in (d & e) the experiments were performed using active bivalves; we assume that all dormant bivalves (percentages shown in (d & e) are derived from our observations during experiments) would be surfaced and transported as they have a reduced capacity to reburrow into the sediment. In (d & e), the whiskers depict the 95% confidence intervals. This figure is a schematized conceptualization of the species-specific

mortality risk vectors based solely on our experiments and more research is necessary to improve our understanding of the bivalves' response to extreme sediment erosion.

Implications of the contrasting strategies to cope with storm-induced erosion events

Our results revealed that the two studied species have different strategies for surviving extreme sediment erosion due to severe storm events: *C. edule* avoided surfacing and *R. philippinarum* avoided transport. Because *R. philippinarum* was far more easily surfaced than *C. edule* (Fig. 3), one may conclude that an *R. philippinarum* population would experience greater mortality from extreme storm events than a *C. edule* population. However, this is not necessarily the case. Mortality due to storm-induced erosion is not caused by the erosion itself, but is indirectly caused by predation (Hiddink & Wolff 2002), desiccation (Kurihara 2003), and transport to unfavorable habitat (Cadée 2016). For any of these three vectors of mortality to occur, the animal must first be brought to the sediment surface (Fig. 6b & c). But, once the bivalve is brought to the surface, mortality is not an automatic outcome: a bivalve will survive provided it can avoid being transported to unfavorable habitat and can reburrow fast enough to prevent predation and desiccation.

By using our experimental results, we inferred that *C. edule* would have lower mortality due to storm induced erosion events in the Scheldt estuary than *R. philippinarum* during storms with conditions like those we simulated in the 5.3 and 10.6 cm/h erosion rates, but the gap in mortality between the two species narrows in more extreme conditions, like under the 15.9 cm/h erosion rate (Figure 6). We present our reasoning as follows: during extremes storms of a relatively moderate magnitude (5.3 cm/h of sediment erosion), no active *C. edule* will be surfaced while many active *R. philippinarum* (60% on average) will be surfaced (Fig. 6a & b). A portion of the active and surfaced *R. philippinarum* would be at risk of mortality (if 50% transported, as with a wave height of 5.6 cm (Fig. 6e), then 60% active *R. philippinarum* surfaced × ~50% transported = ~30% total active *R. philippinarum* at risk of mortality), whereas no active *C. edule* would be at risk for mortality because they are safely burrowed. In addition, the populations will experience mortality from the dormant portion (in our experiments, we found ~20% for *R. philippinarum*, ~7% *C. edule*, however, this percentage may be different in the field as some of the dormancy we observed could be caused by mesocosm stress), whose reduced burrowing capacity would make escape from mortality due to predation, desiccation, or transport unlikely (Fig. 6b & c). Because a much greater proportion of active *R. philippinarum* would be surfaced and experience a higher incidence of dormancy than *C. edule*, we can estimate that *R. philippinarum*'s mortality risk would be greater than *C. edule*'s due under these conditions.

On the other hand, in even more extreme conditions with a 15.9 cm/h sediment erosion rate, active *C. edule* would be surfaced, though in a smaller proportion to *R. philippinarum* (71% vs. 100%, Fig. 6b). However, out of the surfaced fraction, a higher proportion of *C. edule* would be transported than *R. philippinarum* (estimated ~100% vs ~70% with a wave height of 6.4 cm, Fig. 6e), resulting in a more similar fraction of mortality risk for the two populations (71% active *C. edule* surfaced × ~100 % transported = ~71 % total active *C. edule* at risk for mortality, and 100% active *R. philippinarum* surfaced × ~70% transported = ~70% total active *R. philippinarum* at risk for mortality). These estimates would change with additional mortality from dormant bivalves, which would almost certainly die from being surfaced. In conclusion, storms causing a sediment erosion rate of 15.9 cm/h may be equally devastating to populations of both bivalve species, while storms of a lower erosion intensity, like 10.6 cm/h, may be more devastating for *R. philippinarum* populations than *C. edule* ones.

We must emphasize that the above estimates of mortality risk for *C. edule* and *R. philippinarum* are only inferred from our experimental results and that the true fate of surfaced and transported bivalves due to extreme storms is poorly known. While there are papers reporting evidence of mass mortalities from single storm events, these are usually based on post-hoc observations, like Cadée et al (2016). Other studies on storms which have before and after observations on macrofauna (Yeo & Risk 1979, de Vet et al. 2020) can report differences in biomass, but have difficulty commenting on the fate of the missing macrofauna. A good approach to studying the actual transport distance of bivalves by a storm would be to use mark-recapture methods, such as those used by Hunt et al. (2020) to examine the transport of bivalves over a single tidal cycle. Field methods could be supplemented by models simulating the complex hydrodynamics during an extreme storm and calculating the transport range of bivalves under different tidal conditions and storm magnitudes. In addition, more experiments on the reburrowing capacity of bivalves would help to better estimate their mortality risk after transport. While our study provides a mechanistic foundation on how species can cope with storm induced erosion events, more research is necessary to better understand species viability in a more climactically extreme future.

Interactions between changing abiotic conditions may increase or decrease species tolerance to severe storm effects. In particular, the mortality effects of an increase in the frequency and intensity of storms may be dampened by warming winter temperatures, especially when bivalve dormancy is taken into account. Indeed, the prevalence of cold winters in the Wadden Sea have decreased over the past 30 years (Beukema et al. 2017). Such a decrease in the occurrence of cold winters might mean that bivalves are less likely to be dormant during winter storm events, making them less vulnerable to rapid erosion events. In addition, as *C. edule* appeared to have a higher surfacing rate in colder water temperatures, rising water temperatures could increase the active *C. edule*'s capacity to burrow and escape storm-induced erosion. On the other hand, more frequent heat waves in the summer may reduce a bivalve's overall health, and thereby its ability to burrow and escape storm erosion events. *C. edule* exhibits a reduction in burrowing activity during heat waves (Verdelhos et al. 2014, Domínguez et al. 2021), whereas *R. philippinarum* is less impacted (Macho et al. 2016). This means that *C. edule* may have lower burrowing ability during an extreme summer storm occurring during a heat wave (e.g. 2018 storm Hector in Ireland, Calderó-Pascual et al., 2020), than during an extreme winter storm.

The relevance of specific adaptations versus broad adaptability: an outlook

The introduced species always outperforms the native species when the changing environment favors the adaptability of the invader. For example, in temperate areas, tropical species or those that have a wide tolerance for temperature, like *R. philippinarum* (Jensen et al. 2004), will have a higher survival than native species during heat waves (Diez et al. 2012, Domínguez et al. 2021). However, the native species can outperform the introduced one during extremes that fall within its specialized adaptations. For example, in areas where flash floods occur, native species survive as these have evolved to withstand torrential precipitation, whereas non-indigenous ones are wiped out (Meffe 1984, Ho et al. 2013). Similarly, extreme drought events that lead to low stream flows have been shown to promote the survival of native fish species over invasive ones (Lake 2003, Leprieur et al. 2006).

Perhaps storms are the kind of extreme events, like flash floods and droughts, that favor native species' specific adaptations over introduced species' broad adaptability. Indeed, our study suggests that *C. edule* may be better equipped to survive extreme winter storms than *R. philippinarum*, except in the most extreme cases. Adaptations to withstand strong wave forcing, which is also induced by storms, have been shown to favor native species. For example, a study by Zardi et al. (2006) showed that a native mussel species had a greater attachment strength to rocky substrate than an invasive species, which meant that extreme wave action would favor the native, not invasive species. However, other studies have shown that strong wave action favors the dispersal and recruitment of colonizing species (Barry 1989). The success of a native or introduced species faced with an extreme storm disturbance may have to do with an evolutionary trade-off: either favoring fast recruitment and growth which allows for rapid recovery and colonization and facilitates invasions or investing resources to build resilience to a narrower set of conditions.

Conclusion

In this study we have demonstrated that bivalves can have different coping strategies for extreme storm events: *C. edule* avoids being surfaced, and *R. philippinarum* avoids being transported after surfacing. Thus, *C. edule* may be better equipped to survive extreme winter storms than *R. philippinarum*, except in the most extreme cases. While we provide a mechanistic foundation on how species can cope with storm induced erosion events, more quantitative research would help us to better understand species viability in a more climactically extreme future. This study demonstrates how addressing these kinds of questions can be done in a laboratory setting which can help circumvent the practical problems of studying animals in extreme, i.e. unpredictable and rare, conditions.

Acknowledgements

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Supplemental tables

Table S1: Number of Stormy flume runs on a given date with the associated number of bivalves checked for dormancy. A core containing a single bivalve was used for each Stormy flume run. We planned to check twelve bivalves for dormancy every morning that flume runs were scheduled, however, some days are omitted due to protocol adjustments and observer error.

Date (2019-2020)	Stormy flume runs	Individuals checked for dormancy
Nov 12	3	12
Nov 13	1	0
Nov 14	1	0
Nov 19	3	0
Nov 20	3	12
Nov 21	3	12
Nov 26	2	12
Nov 27	2	12
Nov 28	3	12
Nov 29	1	6
Dec 3	2	12
Dec 4	3	12
Dec 5	1	12
Dec 6	2	0
Dec 10	2	12
Dec 11	1	12
Dec 17	3	12
Dec 18	2	12
Dec 19	0	12
Dec 20	3	12
Jan 7	3	12
Jan 8	3	12
Jan 9	2	12
Jan 10	0	12
Jan 14	1	12
Jan 15	0	12

Table S2: Number of individuals per species tested in the Stormy flume for surfacing probability as a function of sediment erosion rate and in the racetrack flume for transport speed as a function of current speed and wave height. Separate trials were performed to test the effects of current speed and wave height on transport speed.

Stormy flume covariate		*C. edule*	*R. philippinarum*
Sediment erosion rate (cm/h)	5.3	10	10
	10.6	8	8
	15.9	7	7
Racetrack flume covariate			
current speed (m/s)	0.089	6	6
	0.114	6	6
	0.135	6	6
	0.168	6	6
wave height (cm)	3.6	6	6
	5.0	6	6
	5.6	6	6
	6.4	6	6


FREE THE CLAMS!

Chapter 4

Size-dependent responses to disturbances drive ecosystem trajectories: a case study on bivalve population responses to changes in storminess

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Abstract

The intensification of extreme climactic disturbances makes predicting ecosystem trajectories increasingly challenging as they experience novel disturbance regimes. In addition, disturbances can have size-dependent effects which further complicate these predictions due to resulting changes in population structures. To study the size-dependent impacts of extreme events on population trajectories, we use slow-moving bivalves, which are vulnerable to storm-induced sediment erosion. We combined process-measurements in a flume with age-structured modeling to predict the size-dependent effects of increased storms on the resilience of bivalve populations. In the flume experiment, we examined the dependence of bivalve erosion on shell length, initial burying depth, and active burial behavior for juveniles and adults of two bivalve species that co-occur on tidal flats in the Scheldt estuary: *Cerastoderma edule* and *Macoma balthica*. Though the two species live at different depths and have different shell shapes, the most important determinator of bivalve erosion was shell length. Applying the observed size-dependent bivalve erosion relationship to an age-structured model of bivalve populations in the Scheldt revealed that the total impact of a single extreme storm event is much greater in a population with size-dependent

storm mortality than in one without. Thus, an overall increase in storminess may considerably weaken or wipe out a local bivalve population. Our results imply that extreme storm-induced sediment erosion may result in a larger contrast in bivalve population trajectories and viability between wave-exposed and unexposed tidal flats on a local scale. However, at the landscape scale, bivalve populations may remain resilient to extreme storm-induced sediment erosion in case of sufficiently high larval dispersal. The inclusion of size-dependent disturbance impacts, along with other important factors such as impact scale, organism life history, and species' landscape presence, are crucial to better predict population and ecosystem trajectories in a more climactically extreme future.

Introduction

Environmental disturbances provide heterogeneity to habitat conditions which is essential for the establishment and permanence of many species (Sousa 1984, van Belzen et al. 2022). However, disturbances can also have negative impacts on ecosystems by causing direct mortality in biota (Huston 2014) and altering environmental conditions to outside the range of species' tolerances (Menge and Sutherland 1987; Smale and Wernberg 2013). In this way, disturbances can lead to regime shifts in ecosystems (Paine et al. 1998) and reductions in biodiversity (Folke et al. 2004). Extreme weather events e.g. heat waves, storms, droughts, rainfall, are highly impactful disturbances that can change ecosystem trajectories, and these are becoming more intense due to climate change (Jentsch et al. 2007). This intensification of extreme weather events makes the predictions of ecosystem trajectories more challenging as ecosystems experience novel or altered disturbance regimes (Carnell & Keough 2020). To respond to these challenges through ecosystem management, we need to better understand species and ecosystem responses to increasingly severe disturbances from extreme weather events. We study this using intertidal ecosystems inhabited by benthic infauna as case study.

Intertidal ecosystems are subject to highly variable environmental conditions, including inundation, temperature, and sediment dynamics (Gray and Elliott 2009), with the latter being the focus of our study. Daily variations in sediment dynamics are caused by wave and tidal action on the order of millimeters (e.g. 1 to 13 mm at two sites in the Western Scheldt; Hu et al. 2017). Benthic infauna, like bivalves, can change their vertical position in the sediment to adjust to their constantly shifting sedimentary habitat (Takeuchi et al. 2015). Bivalves are key components of the intertidal ecosystem. They are play a vital role in the biogeomorphic functioning of tidal flats (Kristensen 1988; Volkenborn et al. 2009) and are important prey for a wide variety of wading birds and fish (Zwarts and Wanink 1993; Hiddink et al. 2002; Bocher et al. 2014). While bivalves can shift their vertical position to adjust to daily sediment dynamics, they are slow-moving which makes them vulnerable to sudden and extreme sediment erosion caused by storms.

Intense storms can compress weeks and months of bed-level dynamics into a span of hours or even minutes. For example, Hu et al. (2015) and (de Vet et al. 2020) describes storm events in 2013, 2014 and 2016 that caused between 10 to 15 cm of sediment erosion, which amounted to 4 months of bed-level evolution. Storm-induced sediment erosion can cause bivalve erosion (Shi et al. 2021), defined here as the passive surfacing of buried bivalves. Exposure of bivalves to the sediment surface can increase the risk of mortality by predation (Hiddink and Wolff 2002), desiccation (Kurihara 2003), and transport to unfavorable habitat (Cadée 2016). Indeed, field studies have shown that severe storm-induced erosion can decrease macrofaunal abundances (de Vet et al. 2020; Shi et al. 2021), cause large mortality events (Rees et al. 1977; Yeo and Risk 1979; Cadée 2016) as well as long-term community structural change (Ong and Krishnan 1995). If storms will become more frequent and intense in the future due to climate change (Stocker et al. 2014), their importance in structuring the macrofaunal community will increase. This makes it important to obtain an in-depth mechanistic understanding of the traits that make certain species and age classes vulnerable to storm-induced erosion events.

The manner in which extreme storm-induced erosion will impact the trajectory of a bivalve populations will most likely depend on whether the impacts are size-dependent. Many processes that structure populations, such as predation (De Roos & Persson 2002) and intraspecific competition for resources (Donahue 2004), depend on size. Disturbances have also been shown to have size-dependent effects. For example, larger corals experienced greater mortality than smaller ones during a 2019 heatwave in French Polynesia (Speare et al. 2022). Extreme storm-induced sediment erosion may also have size-dependent effects. Factors which could contribute to size-dependent effects of storm-induced sediment erosion include physical attributes like size-dependent differences in particle entrainment velocity (Paphitis et al. 2002), but also biological factors, such as age-dependent living depth and burrowing speed. Indeed, juvenile bivalves live at a shallower sediment depth than adults (Zwarts and Wanink 1989), but during storm-erosion events, this may be evened out by their fast burrowing ability (Tallqvist 2001). White et al. (2022) showed that an extreme disturbance which causes mortality only in juveniles may have a lower impact than one causing mortality equal mortality in juveniles and adults, but that the recovery time may be slower. That is, as mortality propagates up through a cohort, an extreme event which impacts juvenile bivalve more than adults could wipe out an entire cohort, which may destabilize and depress adult stocks in later years. Furthermore, bivalve recruitment can vary between several orders of magnitude between years, which complicates predictions of bivalve populations' ability to recover. Thus, better understanding size-dependent effects of storm-induced erosion on bivalve erodibility is needed to more realistically predict bivalve population trajectories in a future with greater incidence of extreme storms. We addressed this issue by combining erosion-survival measurements in a flume with age-structured modelling of bivalve populations in a stormier future.

We performed a flume experiment examining the erodibility of two co-occurring and common bivalves in the Scheldt estuary, *C. edule* and *M. balthica*. Past studies have documented mass mortalities for both *M. balthica* (Yeo and Risk 1979) and *C. edule* (Cadée 2016) after storm events. *M. balthica* has a medium living depth (between 2-6 cm on average) and is a deposit feeder while *C. edule* lives at a shallow depth (1-3 cm on average) and is a suspension feeder. In addition, *C. edule* can reach sizes twice as large as *M. balthica*: 40 mm vs 20 mm maximum size (Zwarts and Wanink 1989). The morphological and behavioral differences between the two bivalves allowed us to examine the interaction between burying rate and initial burying depth in determining size-dependent vulnerability in bivalves to extreme storm-induced erosion, and whether or not there are species-specific differences. We then applied the experimental results to an age-structured model of *M. balthica* to explore how size-dependence in bivalve erodibility may affect their populations. Because the experimental outcomes were the same for both species, only one modeled species was necessary to explore the effects of size-dependence on storm-induced mortality. We had access to the necessary time-series to set up the model.

Methods

Flume experiment mimicking storm-induced rapid erosion events: the concept

To study the effect of rapid storm-induced erosion during winter, when benthic animals are least active and storms are most prevalent, we conducted a flume experiment from November 3 to December 16, 2020. All experiments were conducted in a custom-made flume, containing a sediment core that could be pushed up with a pneumatic pump through a 16 cm diameter hole in the bottom of the flume. Given that the sediment core directly erodes as soon as the sediment enters the 40 cm/s flow in the flume, the erosion rate that animals in the sediment core experiences is equal to the rate by which the core was pushed into the flume (Wiesebron et al. 2022). For animals to withstand erosion, they must thus either have a very deep initial burying depth or actively burrow down into the sediment with the same speed as the core is being pushed into the flume: 10 cm/h. The erosion rate of at least 10 cm/h was chosen as a realistic high-end erosion rate, given that 10 to 15 cm of sediment erosion has been observed during a single storm-affected high-tide (Hu et al 2017, de Vet et al. 2020). See Wiesebron et al. (2022) for a more detailed description of the flume.

Bivalve collection

We used two bivalve species in the experiment, *Cerastoderma edule* and *Macoma balthica*, which are common to the European intertidal (Malham et al. 2012, Nazarova et al. 2015). Fresh bivalves were collected on a biweekly basis from two mixed sandy beaches, Oesterdam (51.46670, 4.22139) and Rattekaai (51.57077, 4.01629). These beaches are close together and we found both *M. balthica* and *C. edule* at Rattekaai and large *C. edule* at Oesterdam. At least 50 individuals of both species spanning their size range were collected during each trip (See Fig. 1 for length distributions used). The bivalves were stored in baskets in tidal tanks in a climate-controlled room with a temperature of 9 °C for at least a week to ensure acclimatization before being used in the experiments. The 9 °C temperature was chosen to mimic the mean November and December air temperature. Each tidal tank system was composed of two 1.2 m by 0.8 m tanks stacked on top of each other (Cao et al. 2018). Unfiltered water from the Eastern Scheldt estuary was pumped from the bottom tank up to the top tank to simulate tidal conditions. High tide conditions (5 cm water above experimental units) lasted six hours and occurred twice a day. We changed the water once a week, and in addition to the nutrients contained in the raw Eastern Scheldt water, we fed the animals with an algal concentrate (Shellfish Diet from Reed Mariculture) 5 mL per tank twice per week.

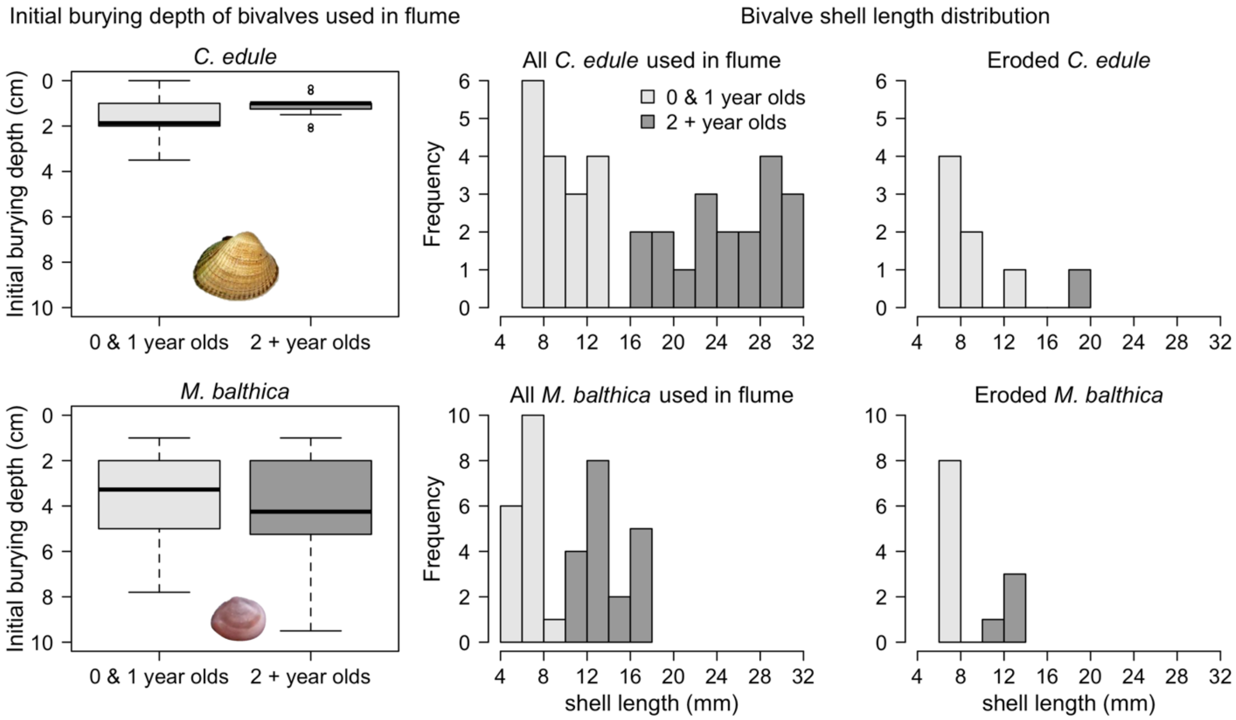

Figure 1: Initial burying depth (cm) (left column) and distribution of bivalve lengths (mm) for *C. edule* and *M. balthica* for all bivalves used in the flume studies (middle column), and the length distribution for

the eroded *C. edule* and *M. balthica* (right column). The groupings into age classes for this graph, with light grey being 0 and 1 year olds and dark grey being 2 years and older, were made using length cut-offs obtained from previously reported age-length distributions (Gilbert 1973, Rueda et al. 2005).

Determining initial bivalve burying depth

The day before the experiment, we selected the four individuals randomly from each of the two species. We glued a cotton thread to the corner of the bivalve's shell opposite the siphons to ensure that we captured the lowest position of the bivalve. The thread was marked in 0.5 cm increments. The bivalves were then allowed to burrow into a core of sediment in the mesocosm, with one core containing one bivalve. The core was made from a sawed-off PVC pipe (30 cm length, 11.5 cm width) with a removable bottom cap, and was filled to 10 cm below the rim. We filled the experimental cores with a single sediment which had a comparable grain size distribution to the sediments from the field sites. The sediment from field samples had an average grainsize ranging between 250 and 270 µm and the sediment used in the experiments had an average grain size of 246 µm. The field and experimental sediments mainly consisted of medium (250-500 µm; 40-45%) and fine (125- 500 µm; 40-60%) sand. The following day, the burying depth of the bivalve was determined using the marked increments before and after being placed in the flume. We waited 30 minutes between placing the core in the flume and starting the experiment to allow the bivalve to acclimatize to the flume conditions. In 16% of the experiments, the position of the bivalve shifted before the start of the flume run.

Flume runs: imposing controlled erosion rates and quantifying erosion vs. exposure of the bivalves

The experiments were conducted in a custom-made flume (see details in Wiesebron et al. 2022). The flume was filled with sea water to a height of 15 cm, which minimized turbulence within the flume, and during each run the current velocity was 0.40 m/s. To neutralize the heating of the pumps, a Lauda WKL 3200 Recirculating Chiller with a stainless steel cooling spiral was used to counteract the heating of the water by the pumps. We performed 72 flume runs over the course of 6 weeks.

Bedload transport of sediment and passive particles, like inactive bivalves, will be initiated when the fluid velocity crosses the critical erosion threshold of the particle. A water flow of 40 cm/s is well above the critical erosion threshold of our sediment as well as the critical erosion threshold of the bivalves. That is to say, if the bivalves acted like passive particle, they would be eroded from the sediment. We assumed that erosion of the bivalves would start when the sediment above and around them is entrained. They could avoid erosion by actively burrowing deeper into the sediment over the course of the experiment.

During each experiment, a sediment core containing a single bivalve was used. All runs were conducted with an upward core speed of 10 cm/h. This erosion effect has been observed during storms in the Scheldt estuary (Hu et al. 2020). The run ended after 60 minutes had elapse or when a bivalve was dislodged. We considered a bivalve to be eroded when it was completely exposed on top of the sediment or when it was transported away from the sediment. During the run, we checked every ten minutes whether the bivalve was partly visible on the sediment surface. We recorded visible bivalves as "surfacing" events. The flume runs were recorded with a camera to assess bivalve behavior within the flume and confirm the time of erosion. We retrieved the bivalve after the run was complete and measured its shell length, width, and height.

Statistical analysis of flume experiment results

We used logistic regression to test a set of biological and environmental covariates on erosion probability. The biological covariates we used were: species, shell length, and initial burial depth. We tested for a seasonal effect as well as a water temperature effect, but we found none so we did not discuss environmental effects in the results section. In addition to examining the factors for erosion, we tested covariates for the erosion time among eroded bivalves. The experiments were run until the bivalve was eroded or 10 cm of sediment was eroded. We wished to know if the factors affecting erodibility changed at shallower erosion depths so we tested models for bivalve erodibility at several erosion cut offs (5 cm, 2.5 cm, 1.67 cm, 0.75 cm). The covariates were examined for normalcy and log transformations were performed where necessary. We also examined how surfacing probability (using logistic regression) and surfacing frequency (using zero-inflated poisson regression) varied based on species, length, and burial depth. We defined surfacing probability as whether the bivalve was at all visible at the sediment surface when checked at ten minute intervals during the flume run, and surfacing frequency as the number of times that the bivalve was visible at the sediment's surface. Finally, we calculated the initial burrowing rates for surfaced bivalves (37% of total bivalves used in the experiments) by using their initial burrowing depth as a starting point and the depth at which it was first surfaced as an ending point. We assumed that the bivalves began burrowing when the overlying sediment was eroded. We compared initial burrowing rates between species, shell length, and burial depth. The best models were selected using AIC.

Age-structured model

We applied the size-dependent erodibility curve (i.e results Fig. 2) to an age-structured population model of *M. balthica* to better understand how the increase in the frequency and the magnitude of storms may affect bivalve populations. We do not present an additional model for *C. edule* because there was no species difference in the size-erodibility curve observed in the flume experiment.

In many models of marine populations, the population can be modeled as an "open" or "closed" system. In an open system, offspring come from an outside source, whereas in a closed system, the recruits depend on the reproduction within the population. In our model, the population can switch between an open and closed system, where the density of recruits is either is independent from adult densities when the local adult densities are high or the product of density dependence when the local adult densities are low. This switch between systems was observed for *M. balthica* in the Wadden Sea over a 44 year period (Beukema et al. 2017). In the first part of the period, adult densities were high (50 m^{-2} or higher) and recruitment was also generally high and varied over several orders of magnitude independently from the local adult densities. But in the second half of the period, Beukema et al. (2017) observed decreased adult survival and stocks, along with reduced and density-dependent recruitment. We wished to preserve this aspect of population dynamics within our model, as the "closed" or "open" attribute of a population can change how a population recovers from a size-dependent mortality effect (White et al. 2022).

To allow the population to switch between open and closed systems, we first defined adult density D_i for year *i* over ages *j* as:

$$D_i = \sum_{j>1} N_{i,j}$$

If D_i was high ($D_i > D_{lim}$) then the density for recruits $N_{i+1,0}$ was independent from D_i (i.e. in an open system) and $N_{i+1,0}$ was generated randomly from an exponential distribution with a rate λ. If D_i was low ($D_i < D_{lim}$), then $N_{i+1,0}$ exhibited density dependence on the adults (i.e. a closed system), so that:

$$N_{i+1,0} = 10^{1+D_i \times \theta}$$

In our model, survival depended on the instantaneous natural mortality rate M, a constant, so that survival to age *a* was:

$$S(a) = e^{-Ma}$$

Furthermore, if we define σ as the year-to-year survival, then σ = 1 - M, and the density of individuals in a year *i* and at an age *j* (j>0) is:

$$N_{i,j} = \sigma \times N_{i-1,j-1}$$

Beukema et al (2017) provide an estimate for D_{lim} and θ, but we fit these parameters in the model, in addition to the year-to-year survival σ, the recruitment rate λ, and the starting number of recruits in the first year $N_{0,0}$.

To fit the model, we used observations of adult *M. balthica* (ages= 2 years and 3+ years) in the Scheldt at the location Zuidgors (9 sampling points). We selected Zuidgors because the *M. balthica* population there has a high recruitment which is characteristic of an open population, and because sediment dynamics at Zuidgors has been well-documented (see de Vet et al 2020) with reports of extreme (10 cm or more) sediment erosion events in the past 20 years. We fit the model by minimizing the negative log-likelihood of the sums of squares using the "optim" function in R. The model fit was refined by fitting the model over a fixed range of the parameters one at a time, which allowed use to explore the entire parameter space and find the best fit which made biological sense. We compared our model parameters to those reported in (Van Der Meer et al. 2001) and Beukema et al. (2017) and found them to be within the similar range. See Table 1 for parameter estimates.

Table 1: Best fit parameter estimates for the *M. balthica* population models at Zuidgors. The parameters that we fit in the model were the year-to-year survival (σ), the recruitment rate (λ), and the starting number of recruits in the first year ($N_{0,0}$), low adult density limit (D_{lim}), low density recruitment rate θ, and the standard deviation for the model's predicted mean (sd).

parameter	estimate
σ	0.47
λ	0.002
$N_{0,0}$	71
D_{lim}	30
θ	0.042
sd	9.7

Once the age-structured model was fit to the Zuidgors population, we explored the effects of increased storminess at these locations with additional mortality to the populations during "storm-years." We specifically wished to test how important the size-dependent relationship quantified in the flume was to model outcomes. And so we included additional storm-year mortality rates with size-dependence and mortality rates without size-dependence. The size-dependent rates were derived from the length-erodibility relationship observed in the flume (see Table 2 for size-dependent and size-independent mortality values). The size-independent mortality was the average of rate of the erodibility curve (i.e 0.39, Table 2), This mortality rate was applied to all age classes during storm-years, so that the total initial impact of storm-induced mortality was equal in the populations with size-dependence and without size-dependence. Finally, we also aimed to determine the importance of the pattern of stormy years to the population's outcomes. All in all, we simulated populations for scenarios with 1) consecutive storm years 2) large interval between storm years and 3) small interval between storm years.

Table 2: Age-dependent and age-independent storm-induced erosion mortality *M. balthica* used in models. The size-dependent storm-induced erosion mortality is derived for the *M. balthica* age groups using the length-erosion curve observed in the flume. We assume that all eroded bivalves die. The size-independent storm mortality is the average of the size-dependent storm mortality.

Age group	Size-dependent storm mortality	Size-independent storm mortality
0	0.57	0.39
1	0.53	0.39
2	0.37	0.39
3+	0.09	0.39

Results

Effects of shell length and initial burying depth on bivalve erodibility

Out of the 72 bivalves used in flume experiments, 30% were eroded. We found that the most important factor for bivalve erodibility (i.e. probability of either complete exposure of the bivalve at the surface or transport) was the length of the individual (Wald's χ^2 (1) = 9.7, $p < 0.01$, Table 3, Fig. 2). Surprisingly, we found no species effect on erodibility (Wald's χ^2 (1) = 0.0023, $p = 0.96$). However, when examined separately, the model for *C. edule* erodibility had a greater intercept than the one for *M. balthica*, suggesting that at the smallest sizes (around 5 mm), the *C. edule* were more vulnerable to erosion than the *M. balthica*.

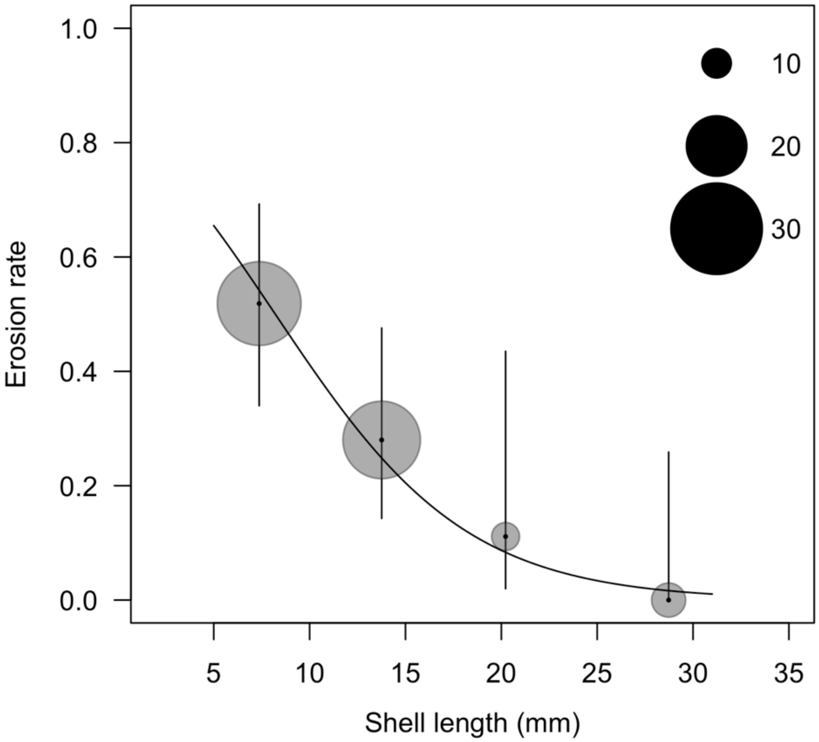

Figure 2: Erosion probability as a function of shell length for the bivalves (*C. edule* and *M. balthica*) used in the flume runs with observations (grey circles) and model fit (black line). Shell length was the best explanatory variable for erosion rate, and since there was no species effect, we present one model fit for the bivalves' erosion rate (black line). The circles represent the observed fraction of eroded bivalves out of total number of bivalves used in the flume for that size class. We used four size classes of equal length: 4-10 mm, 10-17 mm, 17-24 mm, 24-31 mm. The 17-24 mm bin was mostly composed of *C. edule* and the 25-31 mm bin was exclusively composed of *C. edule*. The size of the grey circles corresponds to the number of bivalves that were used in the flume experiments for that length bin. The vertical lines the 95% confidence intervals for the eroded fraction.

Table 3: Model estimates and test statistics for erosion rates and exposure rates/frequency. All models are logistic regression except the one for exposure frequency which was a zero-inflated poisson regression.

model estimate						Wald tests			
	B	Std. Error	exp (B)	2.50%	97.50%	source	χ^2	df	$p>\chi^2$
Erosion rate						Erosion rate			
Intercept	2.11	0.94	8.28	0.34	4.09	Intercept	5.0	1	0.03
Length	-0.20	0.07	0.82	-0.35	-0.09	Length	9.7	1	<0.01
Species	0.04	0.76	1.04	-1.48	1.52	Species	0.0023	1	0.96
Depth	-0.17	0.17	0.84	-0.54	0.15	Depth	1	1	0.31
Erosion rate (*C. edule*)						Erosion rate (*C. edule*)			
Intercept	3.31	1.66	27.3	0.52	7.19	Intercept	4	1	0.05
Length	-0.26	0.11	0.77	-0.54	-0.09	Length	5.8	1	0.02
Depth	-0.63	0.67	0.53	-2.38	0.56	Depth	0.89	1	0.35
Erosion rate (*M. balthica*)						Erosion rate (*M. balthica*)			
Intercept	1.5	1.24	4.48	-0.85	4.11	Intercept	1.5	1	0.22
Length	-0.15	0.10	0.86	-0.36	0.03	Length	3.2	1	0.07
Depth	-0.14	0.17	0.87	-0.50	0.19	Depth	0.65	1	0.42
Exposure rate						Exposure rate			
Intercept	0.73	0.81	2.07	-0.84	2.38	Intercept	3.6	1	0.06
Length	0.03	0.04	1.03	-0.05	0.11	Length	0.42	1	0.52
Species	-1.29	0.83	0.28	-3.02	0.31	Species	2.4	1	0.12
Depth	-0.56	0.29	0.57	-1.23	-0.05	Depth	3.8	1	0.05
Exposure frequency (*C. edule*)						Exposure frequency (*C. edule*)			
Intercept	-0.15	0.44	0.85	-1.01	0.7	Intercept	0.13	1	0.72
Depth	-0.12	0.20	0.88	-0.53	0.27	Depth	0.38	1	0.54
Length	0.06	0.02	1.06	0.01	0.1	Length	6.30	1	0.01

The relationship between shell length and erodibility was weaker at lower volumes of sediment erosion (Fig. 3). At erosion depths shallower than 2.5 cm, the erodibility did not depend on shell length. The average initial burying depth of the bivalves was 2.6 +/- 2.1 cm, which suggests that the relationship between erosion probability and shell length became significant once the overlying sediment was eroded and the bivalves actively burrowed. Though larger *C. edule* buried deeper than smaller ones, we did not find a significant relationship between erodibility and initial burying depth (Wald's χ^2 (1) = 1, p = 0.31). In addition, we did not observe a relationship between initial burrowing depth and shell size for *M. balthica*.

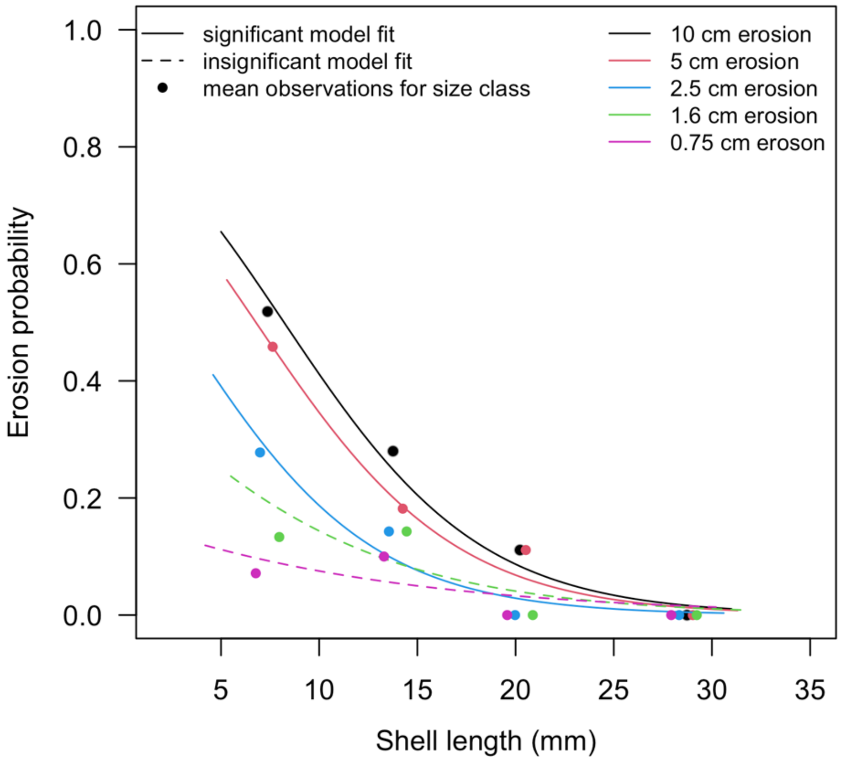

Figure 3: The erosion probability as a function of shell length for both *C. edule* and *M. balthica* at different sediment erosion depths with a constant sediment erosion rate of 10 cm/h. Only once 2.5 cm of sediment erosion was reached did the relationship between erosion probability and shell length become significant. The average initial burying depth was 2.6 +/- 2.1 cm, which means that the relationship between erosion probability and shell length became significant once the overlying sediment was eroded and the bivalves actively burrowed. Since there was no species effect, we present one model fit for the bivalves' erosion probability (lines) at each sediment erosion depth cut-off. The circles represent the observed fraction of eroded bivalves out of total number of bivalves used in the flume for that size class. The size classes were 4 equally spaced bins: 4-10 mm, 10-17 mm, 17-24 mm, 24-31 mm. The 17-24 mm bin was mostly composed of *C. edule* and the 24-30 mm bin was exclusively composed of *C. edule*. We do not show separate figures for the species as there was no significant difference between the two for any of the considered models.

While there was no species effect on erodibility, *C. edule* had a higher probability of being surfaced than *M. balthica*. Out of the 37% of bivalves that were surfaced, 80% were *C. edule*. While the probability of being surfaced did not depend on size for either species (Wald's χ^2 (1) = 0.007, p = 0.93), out of the surfaced *C. edule*, smaller ones had faster initial burrowing rates than larger ones (t = -2.75, df=1, p = 0.007). In addition, out of the surfaced *C. edule*, the larger ones were visible at the surface more frequently than the smaller ones (Wald's χ^2 (1) = 6.3, p = 0.012, Fig. 4). There was slight evidence that *M. balthica* with a shallower initial burrowing depth had a greater probability of being surface than more deeply buried ones (Wald's χ^2 (1) = 3.5, p = 0.062)

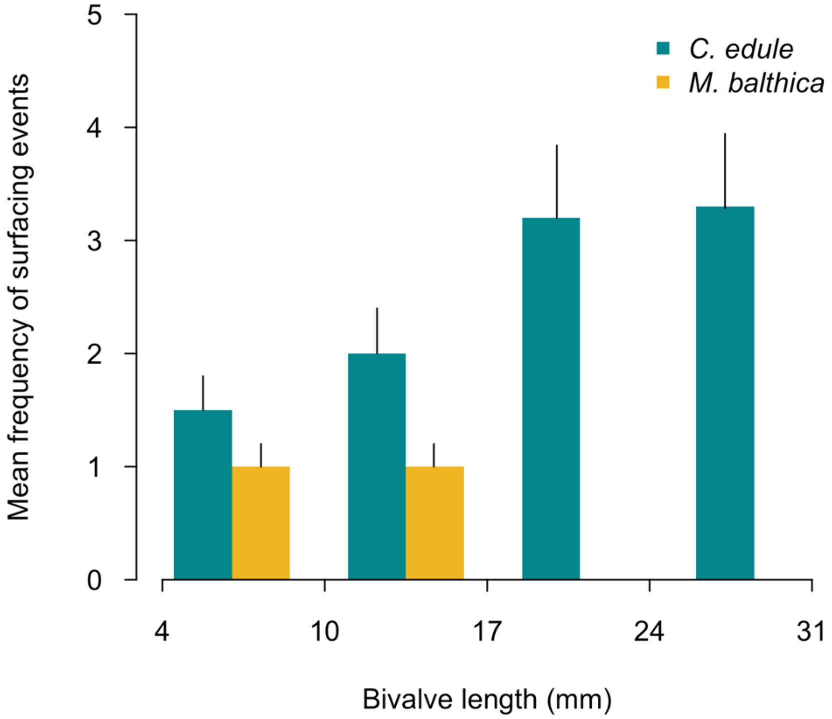

Figure 4: The mean frequency of surfacing events is the number of times (out of 5) that the bivalve was seen at the surface over at ten minute intervals during the flume run. The frequency of surfacing events increased with size for *C. edule*, and the relationship was significant when both including and excluding eroded individuals. About 60% of each *C. edule* size class of surfaced at least once over the course of the flume run. The size classes were 4 equally spaced bins: 4-10 mm, 11-17 mm, 18-24 mm, 25-31 mm, which are also the size classes used for the mean frequency of surfacing events for *M. balthica* (yellow) and *C. edule* (green) on the right panel.

All the bivalves that escaped erosion (70%) actively burrowed. Out of the bivalves that were eroded, we estimated that 50% were eroded passively, i.e. eroded with little to no burrowing once the overlying sediment was eroded (Fig. 5), with slight evidence that larger bivalves were more likely to be passively eroded (Wald's χ^2 (1) = 2.7, p = 0.098). The *M. balthica* were eroded on average 10 minutes later (t =0.74, df = 1, p = 0.07) than the *C. edule* (Fig. 5), which corresponds to 1.67 cm of erosion. The eroded *M. balthica* had burrowed deeper (initial burying depth = 4.0 +/- 2.9 cm), on average, than the eroded *C. edule* (initial burying depth = 1.1 +/- 0.4 cm) and we found slight evidence that the erosion time was explained by initial burying depth (t =1.79, df = 1, p = 0.09).

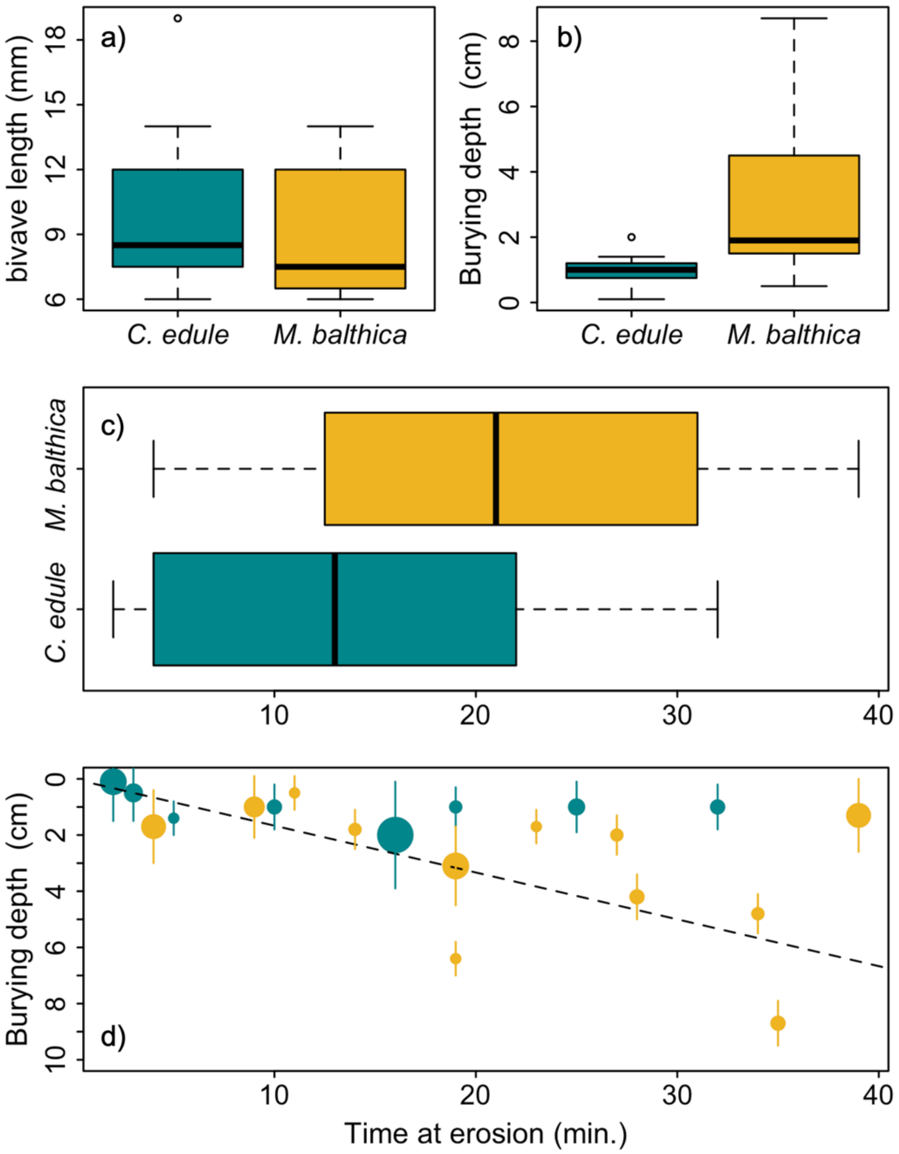

Figure 5: The length (a) and initial burying depth (b) of bivalves eroded in the flume. Time elapsed in the flume at erosion for *C. edule* (green) and *M. balthica* (yellow) in a boxplot (c), and time elapsed until erosion by the bivalve's initial burying depth (d). The dotted line represents the erosion of the sediment at the 10 cm/h erosion rate. The size of the dot represents the size of the bivalve, and we added a confidence interval of the animal's shell length around the initial burrowing depth. If the bivalves do not actively burrow to escape erosion, the time to erosion should fall on or near that line, which it does for 50% of the eroded bivalves. There are two *M. balthica* that fall well below the line (i.e., are eroded before the depth of

the eroded sediment exceeds the burying depth) which could be due to measuring error or upward movement of those *M. balthica* during the flume run.

Size-dependent storm-induced bivalve erosion

While it took populations with both size-dependent and size-independent storm mortality around seven years to recover from a single event, the recruit and adult stocks in the population with size-dependent mortality become much more depressed two year after the storm event (reduced to 55% and Fig. 6a) than those in the population without size-dependent mortality (reduced to 70% and Fig. 6b). In the population without size-dependent storm mortality, both the recruits and adults experience elevated mortality during the storm year (Fig. 6b & d). The adult stock was reduced to about 60% of its original abundance, but the adult mortality from the initial impact was not exceeded in the years following the event. On the other hand, in the population with size-dependent storm mortality, the recruits were reduced to 40% of their original abundances in the storm year, while adults were much less impacted (~20% reduction) as they were better able to escape storm-induced erosion (Fig. 6a). However, the adult stocks in the population with size-dependent mortality get reduced to 40% of their original abundances two years after the storm event due to the recruit mortality propagating up the cohort. Furthermore, the population with size-dependent storm mortality is more likely to experience lower recruitment in years following the storm event due to the depression in adult stocks, which switched the recruitment model from an open population with high recruitment to a closed one with low recruitment. Indeed, three years after the initial storm impact, the recruitment of the population with size-dependent mortality was on average 55% of the original level due to the lower adult stock, while the recruitment of the population without size-dependent mortality averaged 80% of the initial abundances three years after the storm event.

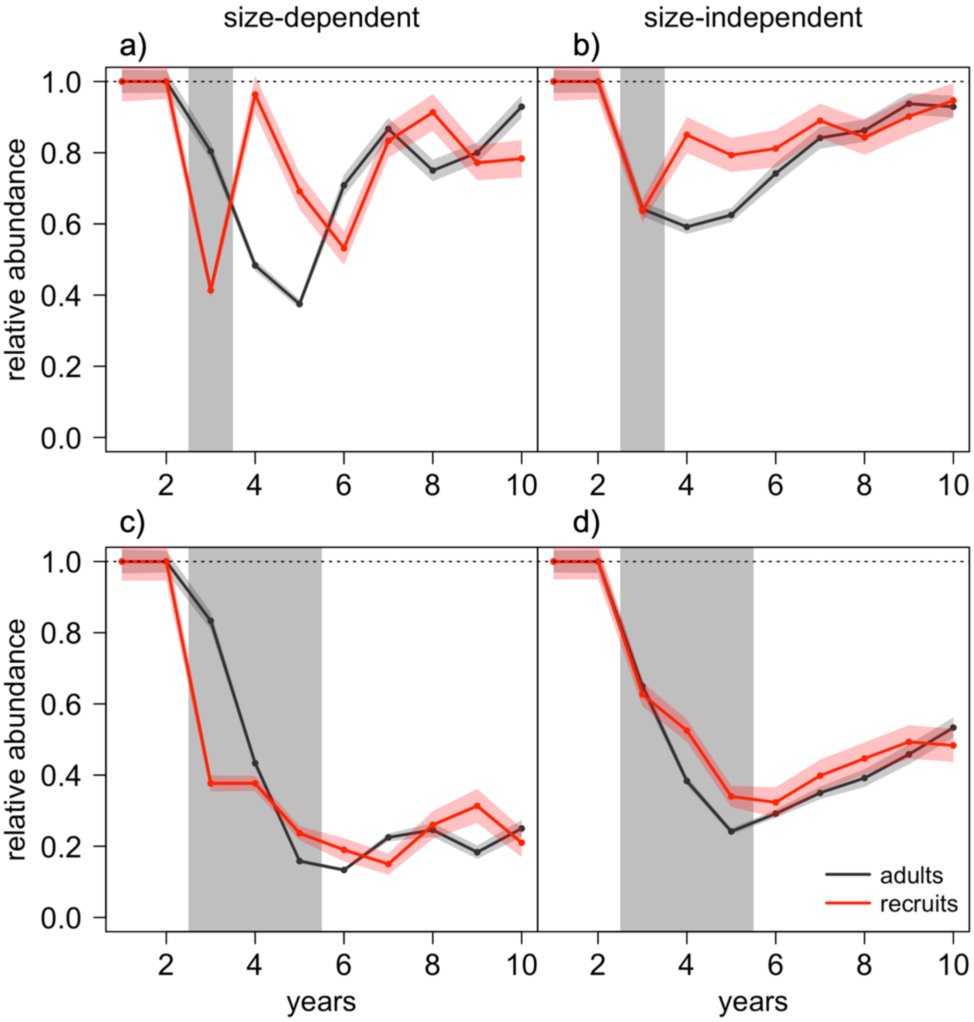

Figure 6: Modeled adult (black) and recruit (red) stock trajectories response to one year (a & b) and three consecutive (c & d) extreme storm events causing mortality with a size-dependent structure (a & c) and size-independent structure (b & d) as the relative abundance of the equilibrium levels. The vertical grey bands depict the extreme storm years. The points were averaged over a thousand simulations and the envelope around the points represent the standard errors.

The propagation of recruit mortality up the cohort became more dangerous to population recovery in scenarios with consecutive storm years. In the very extreme scenario with three consecutive storms, the adult population without size-dependent mortality recovered to 55% of their initial abundances in the 5 years following the storms, whereas the adults in populations with size-dependent mortality recovered to around 20% of their initial abundances (Fig. 6c & d). In addition, the recruit and adult abundances, on average, increased steadily in the population without size-dependent mortality after the initial storm impact, whereas the recruit and adult stocks fluctuated around low abundances in the populations that experienced size-dependent mortality.

A shorter interval length between storm years increased the cumulative severity of the storm mortality (Fig. 7). For the populations with size-dependent storm mortality, the recruits were reduced to about the same level after two storms separated by five years as they were in two storms separated by one year (i.e. about 30% original stock, t(1966) = 0.66, p =0.49). However, after three storms with a five year interval, the recruits were reduced to 27% their original stock, whereas with a one year interval, the recruits were reduced to 19% their original stock (t(1996) = -2.6821, p = 0.016). This was due to the reduced recovery between storm years when the interval was shortened. Recovery in populations without size-dependent storm mortality was faster than for population with size-dependent storm mortality. Ten years after the third storm event with five year intervals, the adult stock for the population without size-dependent storm-mortality increased on average to 86% of the original abundances, whereas in populations with size-dependent mortality, the adult stock only recovered to 76% of their original abundances.

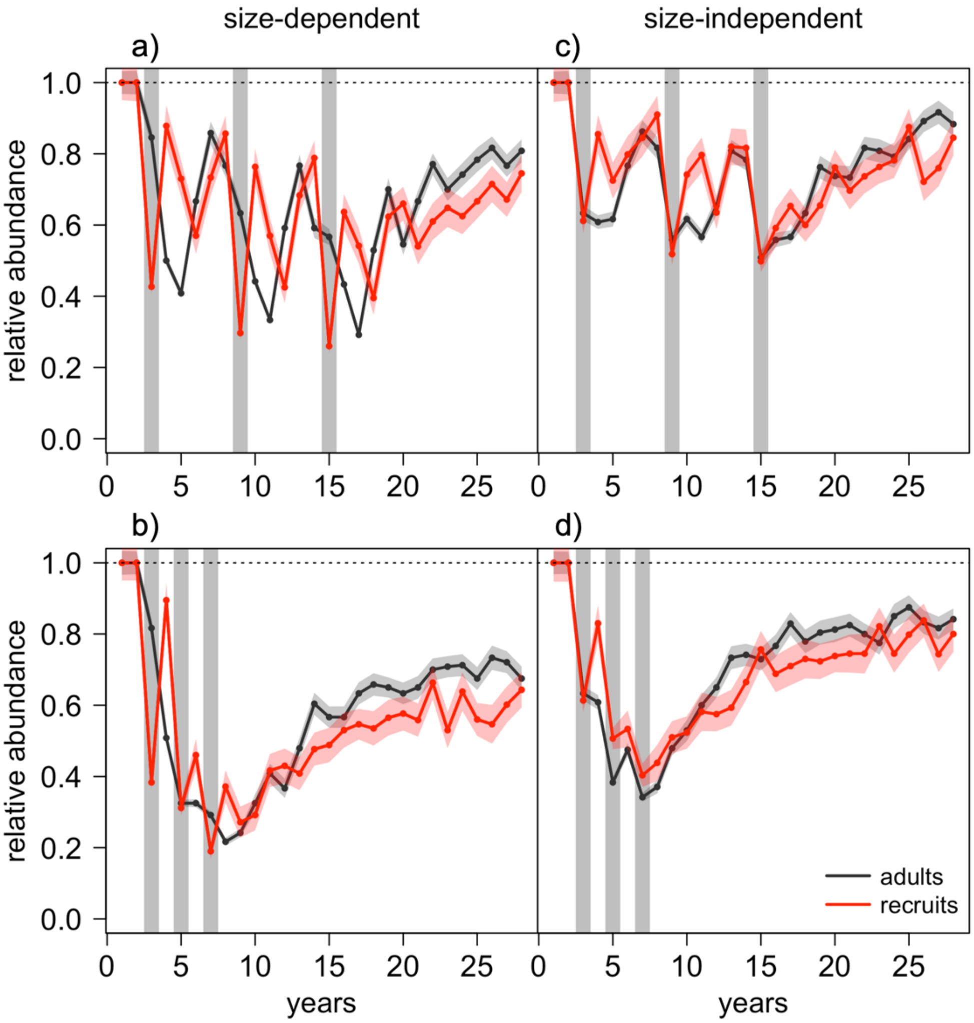

Figure 7: Modeled adult (black) and recruit (red) stock trajectories as the relative abundance of the equilibrium levels in response to three extreme storm events separated by six years (a & b) and one year (c & d) in populations with size-dependent storm mortality (a & c) and size-independent storm mortality (b & d). The vertical grey bands depict the extreme storm years. The points were averaged over a thousand simulations and the envelope around the points represent the standard errors.

Discussion

In this study, we explored the size-dependent impacts of extreme events on population's trajectory, using slow-moving bivalves that are vulnerable to storm-induced sediment erosion as model system. Over the course of flume experiments, we found that the most important factor governing bivalve erosion was shell length, with larger bivalves withstanding flume erosion better than smaller ones. To predict the size-dependent effects of storms on the resilience of bivalve populations in a stormier future, we applied the observed size-dependent bivalve erosion relationship to an age-structured model of *M. balthica*. The model revealed that the total impact of a single extreme storm event is much greater in a population with size-dependent mortality than in one without.

The role of population connectivity and species life history in disturbance-recovery potential

Life history factors and the species' presence in the landscape can change the recovery potential of a population, which can compound the vulnerabilities created by size-dependent extreme event impacts. A population with high connectivity and high species presence in a landscape is more likely to recover from a disturbance than one with low connectivity and low species presence. Many marine benthic species have high connectivity between populations due to a pelagic larval phase which ensures wide spat dispersal (Cowen and Sponaugle 2009). This increases the population's recovery potential as they do not have to rely on self-recruitment for population persistence. We included this feature in our model of *M. balthica* populations with the open recruitment system. Because recruits were supplied by outside areas, the population could more rapidly recover from extreme storm events, even when these occurred every few years (Fig. 7).

Even if a species usually has high connectivity between populations, recruits can only be supplied by outside areas if the species is ubiquitous in the landscape (as in Fig. 8a, iii & iv). If there is a low landscape presence of recruits, which could be a product of fragmented or unsuitable habitat (Fig. 8a, ii) or a disturbance with a large spatial impact (Fig. 8a, iii), then the recovery potential of the population is reduced because the impacted population must self-recruit instead of being supplied by abundant recruits outside of the area of impact (as in Fig. 8a, ii & iii). Low recovery potential can also be caused by low connectivity between a local population and the rest of the landscape (Fig. 8a, i). Barriers to connectivity for benthic marine species are usually traits which forces self-recruitment in a population (Fig. 8a, i), leading to slow recovery after a disturbance. For example, a sea star with a pelagic larval phase, *Pisaster ochraceus*, recolonized a disturbed 100 kilometer-wide area within a year, whereas *Leptasterias aequalis*, a sea star without a pelagic larval phase, failed to return to the area after three years (Schiebelhut et al. 2022). Thus, high connectivity and high species presence increases the recovery potential of a population. However, if the disturbance has landscape-scale impacts, then the high recovery potential at the local scale is reduced (Fig. 8a, iii vs Fig. 8a, iv).

Furthermore, life history will change how susceptible a species is to recruitment failure in a year-class. Shorter-lived species with high fecundity and low maturation times typically fluctuate greatly as their numbers depend on yearly recruitment (Hughes & Tanner 2000), and can be prone to local collapse if recruitment fails. However, shorter-lived species can recover quicker from disturbances than longer-lived species (White et al. 2022) due to low age at maturity and high fecundity, especially under open recruitment (Connell et al. 1997). Conversely, longer-lived species are buffered against fluctuations both in recruitment and in the environment (Botsford et al. 2014). For example, bivalve recruitment is highly variable, with year to year numbers of mean spat frequently spanning within three orders of magnitude (Beukema and Dekker 2014). Yet, because bivalve populations are composed of several age classes, the year to year variability in recruitment does not translate to year to year variability in biomass of the same magnitude (Beukema et al. 2001). This means that longer-lived species may be less sensitive to climactic extremes, as lower recruitment in one year is mitigated by the persistence of other year classes (Hughes & Tanner 2000, Pinsky & Byler 2015, see Morris et al. 2008 for terrestrial examples).

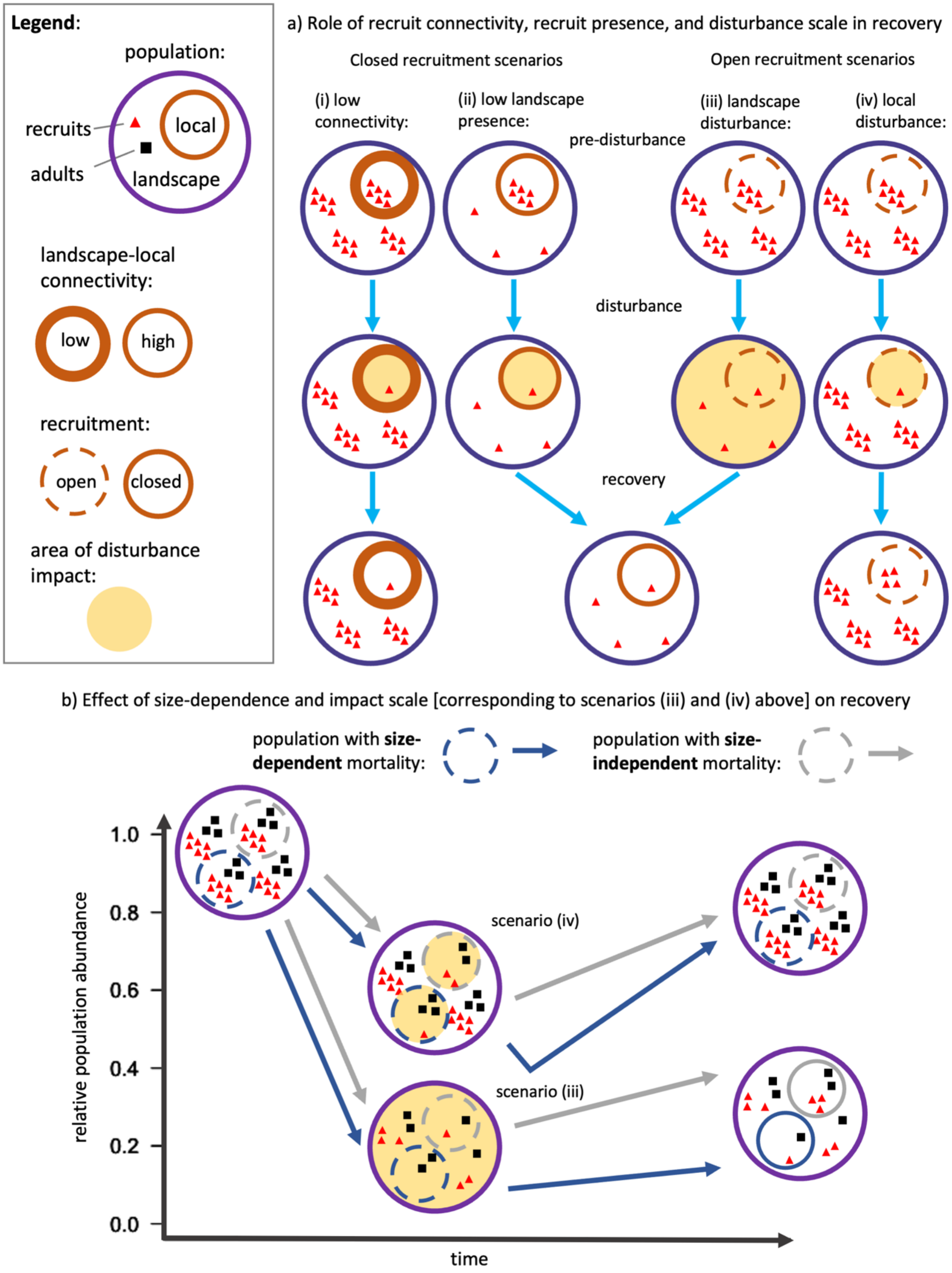

Figure 8: a) Four scenarios of recovery trajectories for populations depending on the whether the population self-recruits (closed recruitment system) or whether the recruits can be supplied to a population from the surrounding landscape (open recruitment system). We depict recruits only for

simplicity. A population with a closed recruitment system (scenarios i & ii) has a lower recovery potential than one with an open recruitment system (scenarios iii & iv). If a population does not have high local-landscape connectivity (scenario i) or high presence in the landscape (scenario ii), then a population cannot draw on recruits outside the local area and must self-recruit after a disturbance, which leads to a slow recovery. A population with high local-landscape connectivity and high presence in the landscape can be repopulated by recruits from outside the area of disturbance, leading to fast recovery (scenario iv). However, if the disturbance has a landscape impact (scenario iii), then the population cannot by supplied by recruits from the outside area, causing an open system to switch to a closed system as the population self-recruits and recovery is slowed.

b) Recovery trajectories for a population where a severe disturbance causes size-dependent mortality vs. the trajectory for a population with size-independent mortality. The population abundance depicted in the y-axis is relative to the pre-disturbance abundances. This figure is based off the results from the models of *M. balthica* (see Figures 6 & 7), with the assumption that the local population experiencing the disturbance has high recovery potential due to open recruitment. The two trajectories depict scenarios with a local disturbance vs. a landscape disturbance. A population is less resilient to disturbances when it experiences size-dependent mortality because a disturbance which disproportionately impacts recruits will cause adult stocks to depress in later years. This weakness is exacerbated if the disturbance has a landscape-scale impact, thereby forcing a population self-recruit (depicted here) or if a population experiences consecutive extreme events (see Fig. 6).

The role of size-dependent mortality in disturbance-recovery potential

Size-dependent mortality, by causing the collapse of specific year-classes, decreases a population's ability to recover from these extreme events. In our models of *M. balthica* populations with size-dependent storm mortality, highly reduced recruitment in one year weakened the capacity of the entire population to recover due to depletion of adult stocks in later years. In particular, when extreme storms were modeled in consecutive years, the reduction in cohort size traveled up the population's year classes for several cohorts. In our case, the storm disturbances disproportionately affected juveniles. An enhanced disturbance sensitivity of juveniles is quite common. For example, the Window of Opportunity establishment concept (Balke et al. 2011, Hu et al. 2015) is based on an enhanced disturbance sensitivity of juveniles over older and larger stages (Balke et al. 2011; van Belzen et al. 2022, Cao et al. 2018). We note, however, that other climactic extremes may specifically target larger individuals. For example, adult corals are more vulnerable to heat waves than juveniles (Speare et al. 2022). In addition, size-dependent vulnerability can change throughout an organism's life cycle: larger tree seedlings are less vulnerable to drought than smaller ones due to greater root reach (Holmgren et al. 2013), but larger adult trees experience higher mortality during drought than smaller trees due to greater vulnerability to hydraulic stress (Bennett et al. 2015, Ding et al. 2017).

The depletion of adult stocks in populations experiencing size-dependent mortality greatly slows down recovery (Fig. 8b) and could lead to population collapse. In comparison, a population which had experienced mortality independent of size would be better able to self-recruit due to mortality being spread between several year-classes. Furthermore, a closed recruitment system due to a storm with landscape-scale impacts would slow down recovery even further (Fig. 8b), because the impacted population would be forced to self-recruit from depleted adult stocks in the years following the extreme storm. The conclusion that size-dependent mortality has a more adverse effect on a population's recovery than size-independent mortality is supported by fisheries data and models, where fishing size limits have led to lower resilience (Law et al. 2016), lower ability to buffer against unfavorable environmental conditions (Planque et al. 2010), and fisheries collapse (Pinsky & Byler 2015). Not only would storm-induced size-dependent mortality weaken a population's ability to recover from such an event, it would also increase a population's sensitivity to climactic variability, especially in short-lived species (Morris et al. 2008). This means that storm-induced size-dependent mortality would weaken a population's ability to recover from subsequent events (as in Fig. 6b). Severe storms in consecutive years may considerably weaken or wipe out a local population depending on the severity of the storms and the numbers of cohorts affected, even under open recruitment.

The importance of size and burying depth in determining bivalve vulnerability to erosion and transport during storms.

The effect of bivalve size on erodibility could be due to size-related morphology (weight and drag) and size-related burrowing behavior (burrowing depth and rate). In our experimental set-up, all bivalves that succeeded in evading erosion burrowed at a speed greater than or equal to 10 cm/h when the overlying sediment was completely eroded. In addition, the relationship between bivalve size and erodibility manifested in our experiment at sediment erosion depths >2.5 cm, which was past the initial burying depth for many of the bivalves used in the experiment. Thus, the ability to withstand erosion had at least partly to do with size-dependent burrowing rate. However, burrowing rate is not the only important factor. Previous studies have found that there is a relationship between entrainment velocity and shell size in dead bivalves (Chattopadhyay et al. 2013), and in unburied *C. edule* (Anta et al. 2013). While juvenile bivalves may burrow faster than adults (e.g. *M. balthica* in Tallqvist 2001), larger and heavier bivalves can withstand a greater frontal area being uncovered in the water flow than the smaller ones because of their greater weight and drag coefficient (Peña et al. 2008). Indeed, we found that surfacing frequency increased with shell size for *C. edule* (Table 1), and we observed from flume run videos that larger *C. edule* allowed themselves to be partially uncovered by the water flow more frequently and to a greater extent than smaller ones before reburrowing. It is possible that larger bivalves can burrow at lower average rates than juveniles to escape erosion because these can allow themselves to be uncovered to a greater extent than juveniles without being dislodged.

Tidal flats in a stormier future

Storms are predicted to increase in frequency and intensity due to climate change (Harley et al. 2006), which will increase their importance in structuring macrobenthic communities in soft intertidal sediments, especially in wave-exposed sites (Hu et al. 2017). In addition to removing a portion of established populations, severe storms change the morphology of a tidal flat through extreme erosion and sedimentation (Hu et al. 2017; de Vet et al. 2020) which could present an added obstacle to recovery. While storms can have hundreds of kilometers of impact, the actual severe storm-induced erosion is likely to have a more localized effect (i.e. points that experience ~20 cm and ~0.5 cm of sudden erosion can be separated by only 300 m, (de Vet et al. 2020). This means, that storms may result in a patchier landscape, especially if, on a regional scale, a meta-population of a bivalve species remains healthy and ensuring a steady supply of spat to colonize depleted areas. However, if storms become so severe that their effects become as pronounced at the landscape as at patch scale (Fig. 8a, iii vs. Fig. 8a, iv), it's possible that storms may select for bivalve species with a higher resistance to storm-induced erosion.

It is also possible that bivalve species on certain impacted tidal flats may be replaced by other species altogether. While storm events do not necessarily have only negative effects as they can stimulate community diversity by facilitating recolonization opportunities (Corte et al. 2017) and increasing the dispersal of certain species (Dobbs & Vozarik 1983, Hunt et al. 2020), communities can take years to recover from severe storm events (Ong and Krishnan 1995). High-intensity disturbances select for species with better resistance traits or traits that increase recovery potential (Gladstone-Gallagher et al. 2019). In the case of storms, we can imagine that they might select for species with good resistance traits like high mobility (i.e. greater ability to burrow and escape sudden sediment erosion), or life history traits which ensure high recoverability, such as: high fecundity, low age at maturity, and pelagic larval dispersal. An increase in storm frequency and severity may lead some tidal flat communities to resemble an early succession stage (McCall 1977).

Conclusion

Predicting ecosystem trajectories will become more challenging as ecosystems experience novel or altered disturbance regimes due to the intensification of extreme climactic disturbances (Carnell and Keough 2020). In this study, we show how an extreme storm would disproportionately impact bivalve recruits and depress adult stocks in later years, which slows down a population's recovery.

Furthermore, this effect is intensified when a population self-recruits due to life history traits or because an extreme event has landscape-scale impacts (Fig. 8b). Because storms can have a huge impact on slow-moving benthic macrofauna and lead to local extinctions, an overall increase in storminess could lead to a larger contrast in community composition, as well as patchiness, between wave-exposed and unexposed tidal flats. While storms tend to have localized effects, other climactic disturbances, like heat waves or droughts, may have wider reaching impacts which would weaken a population's ability to recover even if the species has a high recovery potential (see Fig. 8a). For example, a marine heat wave triggered the decline of the macroalgae *fucus distichus* in the rocky intertidal over a 1200 km span of Alaskan coastline (Weitzman et al. 2021). In the end, the integration of the size-dependent impacts of climactic disturbances into predictions, as well as different life history and landscape scale presences of species and populations, will be crucial for understanding how ecosystem resilience and trajectories will be altered in a more disturbance heavy future.

Acknowledgements

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Supplementary table

Table S1: The observed eroded fraction of bivalves at increasing sediment erosion cut-offs (cm) with a constant sediment erosion rate of 10 cm/h (Top) and the corresponding models of bivalve erosion probability as a function of shell length. Only once 2.5 cm of sediment erosion was reached did the relationship between erosion probability and shell length become significant.

Fraction of eroded bivalves (observed)

Bivalve shell length	At 0.75 cm erosion	At 1.6 cm erosion	At 2.5 cm erosion	At 5 cm erosion	At 10 cm erosion
4-11 mm	0.07	0.13	0.27	0.45	0.52
11-17 mm	0.10	0.14	0.14	0.18	0.28
17-24 mm	0	0	0	0.11	0.11
24-31 mm	0	0	0	0	0

Models

Intercept	-1.56	-0.48	0.66	1.28	1.63
Length coefficient	-0.08	-0.13	-0.20	-0.19	-0.19
Length p-value	0.37	0.14	**0.03**	**<0.01**	**<0.01**

Chapter 5

How restoration engineering measures can enhance the ecological value of intertidal flats

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Abstract

Restoration engineering measures, such as managed realignments or the building of groins, modify the environmental characteristics of coastal ecosystems. Creating physical modifications which are beneficial to an intertidal system's ecology necessitates an in-depth understanding of the relationships between the abiotic and biotic components of a given intertidal habitat. In this study, we evaluate how hydrodynamics and sediment characteristics drive the development of the benthic macrofauna community during the first five years following engineering measures to enhance benthos diversity at three locations. The creation of low-dynamic habitats through groins (Knuitershoek and Baalhoek) and a managed realignment dike breach (Perkpolder) led to accumulation of fine sediments in all three target sites. Biomass of benthic macrofauna quickly increased between 2016 and 2020, with successional processes being more important in Perkpolder where the habitat was started completely from scratch due to a managed realignment, than at Knuitershoek or Baalhoek, where habitat conditions were improved by adding groins. In addition,

the density of benthos-eating birds, especially oystercatchers, increased at some of the modified sites. While a low-dynamic habitat may harbor more diverse assemblages of benthic macrofauna than a high-dynamic one, we also found that extremely high silt content, which is typical for low-dynamic habitats, may slow the benthic community development. The observed increase of biomass at our target sites highlights the value of the interventions, while the delays in the response of the benthic community emphasizes the need for extensive monitoring both in time and space and the identification of underlying abiotic-biotic mechanisms.

Introduction

Soft-sediment intertidal flats are some of the most productive systems in the world and provide a vast array of ecosystem services (Koch et al. 2009, Barbier et al. 2011, Seitz et al. 2014), many of which are driven by benthic macrofauna. Indeed, benthic macrofauna (invertebrates larger than 0.5 mm) provide food for birds and fish (Piersma et al. 1993, Bocher et al. 2014) and are ecosystem engineers (Kristensen et al. 2012) that drive both biogeomorphic (Cozzoli et al. 2021) and biogeochemical processes on tidal flats such as nutrient cycling (Kristensen 1988, Aller & Aller 1998), organic matter decomposition (Levin et al. 2001), and pollutant removal (Mermillod-Blondin et al. 2004). However, intertidal flats are some of the most degraded ecosystems in the world (Murray et al. 2019), prompting many restoration initiatives (Waltham et al. 2020). Among the many different forms of restoration, creating or enhancing intertidal areas through managed realignments and engineering measures such as building groins can contribute to coastal protection as well as increasing the ecologically valuable habitat for infaunal species (French 2006, Elliott et al. 2007), such as benthic macrofauna.

In creating or enhancing intertidal areas, environmental characteristics of tidal flats (such as sediment accretion) are modified to trigger a cascading change in the ecosystem's ecology and function (such as benthic macrofauna colonization) (Elliott et al. 2016). However, these projects do not always reach their ecological targets. For example, too little accretion of suitable sediment can severely delay the colonization of desired benthic macrofauna which can serve as food for (migratory) birds (Garbutt et al. 2006), whereas rapid sediment accretion can be detrimental to the desired benthic macrofauna as it encourages saltmarsh colonization (Mazik et al. 2010). Therefore, creating physical modifications that are beneficial to an intertidal system's ecology necessitates a good understanding of the relationships between the intertidal environment's abiotic and biotic components.

Understanding abiotic-biotic interactions is one of the longstanding goals of intertidal ecology (Pearson & Rosenberg 1978, Whitlatch 1981, Gray & Elliott 2009). Benthic macrofauna affect sediment characteristics such as erodibility, grain size, and permeability through their movements (Volkenborn et al. 2009, Kristensen et al. 2013, Harris et al. 2016), but at the same time they have distinct environmental associations (Thrush et al. 2003, Kraan et al. 2013) and are known to live along environmental gradients (Ysebaert & Herman 2002). Among the most important environmental variables for determining species assemblages are sediment grain size distribution, inundation time, and hydrodynamics (Ysebaert et al. 2002, Cozzoli et al. 2014, Lange et al. 2020). The relationships between environmental drivers and benthic assemblages are well-studied, but these are usually examined within ecosystems at an equilibrium (Ysebaert & Herman 2002, Thrush et al. 2003, Compton et al. 2013, Holzhauer et al. 2022). Studies examining the relationships between abiotic and biotic components in intertidal systems that are undergoing physical modification due to restoration are comparatively rarer (see e.g. Beauchard et al. 2013). Most intertidal restoration ecological studies focus on the benthic macrofauna colonization process (Marquiegui & Aguirrezabalaga 2009, Mazik et al. 2010, Valdemarsen et al. 2018), and less on concurrent abiotic (e.g. hydrodynamics, sediment properties) and biotic (e.g. benthos, birds) changes, which is the aim of this paper.

Since 2010, The Netherlands' province of Zeeland has implemented several projects in the Western Scheldt to create ecologically valuable intertidal estuarine habitat to develop benthic macrofauna biomass, which are an important food source for foraging birds. In 2016, groins were modified or built at Knuitershoek and Baalhoek to reduce water flow and encourage sediment accretion. In the nearby location of Perkpolder, a dike was breached in 2015 to inundate old farmland and create a new tidal flat. All these projects aimed to change the hydrogeomorphological conditions in such a way that the benthic macrofauna community and overall biomass thereof would be enriched over time, thereby providing food to the large numbers of migratory birds that visit the region to forage. To assess the effectiveness of these measures and to advise on future restoration designs, all study locations have been intensely monitored to follow the development of both their physical and biological characteristics.

In this paper, we evaluate how hydrodynamics and sediment characteristics drive the development of the benthic macrofauna community in our three case studies. In addition, because one of the goals in developing the benthos at these sites was to provide food for migratory birds, we include a brief examination of the bird density response to the interventions. Each of these projects represent different ecological engineering interventions (groin modification and sand nourishment at Knuitershoek, groin creation at Baalhoek, and depoldering at Perkpolder). All interventions were implemented nearby each other and at similar moments in time. This means that we can more easily partition differences among the site trajectories due to the interventions from natural spatiotemporal variability. We will 1) present key similarities and differences between the physical and biological trajectories of these sites, 2) identify the most important abiotic-biotic processes that drive the emerging ecosystems of each location, and 3) summarize the general lessons learned from these large-scale interventions on the development of intertidal mudflat ecosystems.

Methods

Description of study locations

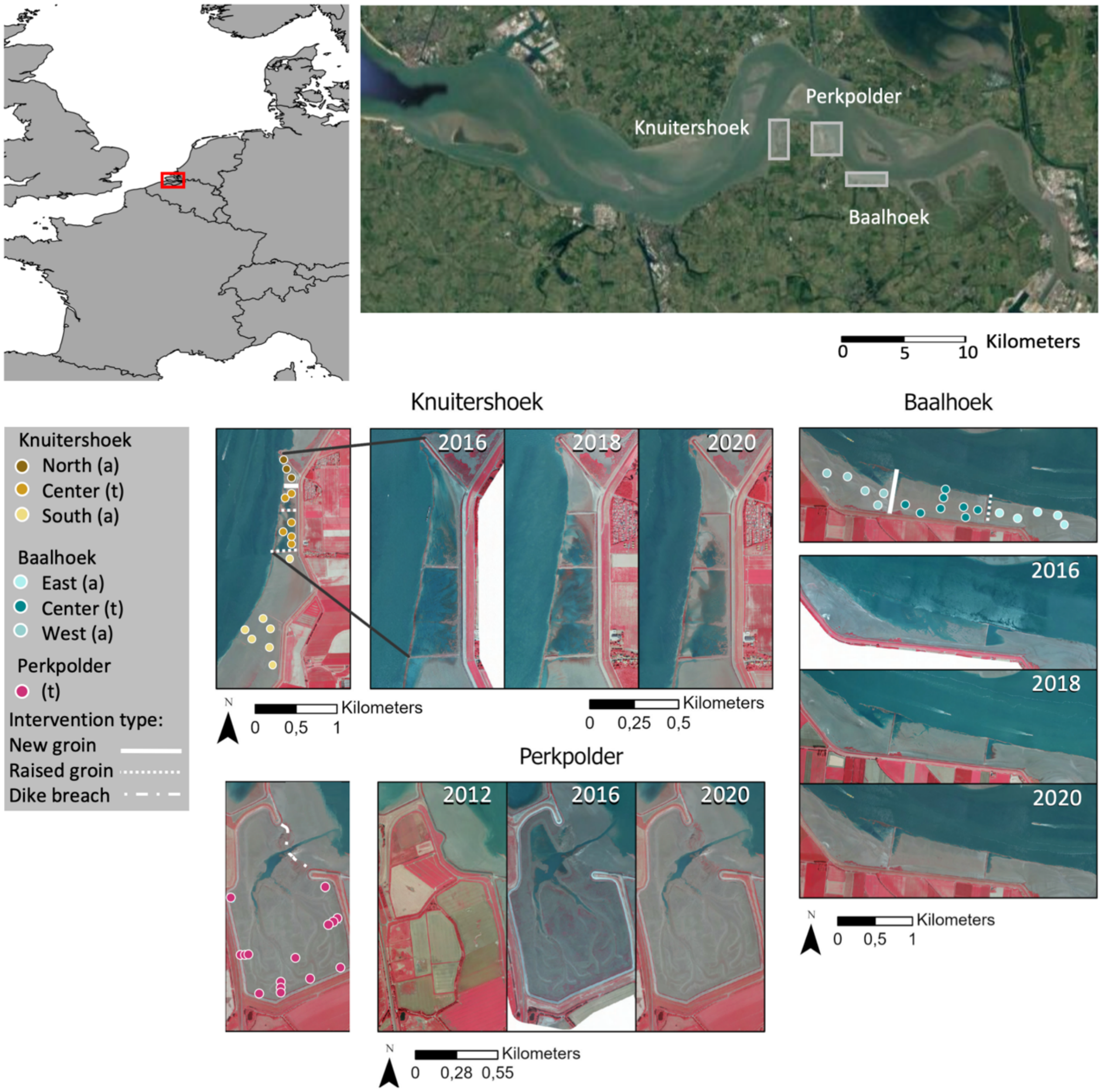

Figure 1: Top: Map of the Western Scheldt in the South of the Netherlands (source: Google Maps) showing the location of our three case studies. Bottom: Aerial photographs (source: Rijkswaterstaat) of Knuitershoek, Baalhoek, and Perkpolder showing the locations pre- and post-

intervention. In the first photograph of each series, we show benthos and sediment sampling stations by site, and intervention type. In the legend, (t) and (a) indicate whether the corresponding site is a target site (intended area of intervention impact) or an adjacent site (area next to target site). The northernmost groin at Knuitershoek is 3 m above mean sea level, while the other four groins at Knuitershoek and Baalhoek are elevated 0.5 m above mean sea level. Please note that the stations for Knuitershoek and Baalhoek are those sampled from 2017-2020 (5 additional station were added at Knuitershoek in 2017, while 2 were dropped; 3 additional stations were added in 2017 to Baalhoek).

As part of the 2010 Scheldt Estuary Development Outline, the province of Zeeland has implemented several projects to create 600 ha of estuarine habitat. Among these interventions are the construction or modification of groins in certain areas (Knuitershoek and Baalhoek), as well as the breaching of a formerly-enclosed polder (Perkpolder). These projects are large-scale interventions that would change the morphodynamic, sedimentary conditions, and ultimately, the area's ecological status over time.

Knuitershoek and Baalhoek: stimulating sediment accretion by groins

At both Knuitershoek and Baalhoek, several groins were either constructed or raised to create a low-dynamic area over time which would facilitate the development of the area's benthos. Within the project area of Knuitershoek (westernmost location of the three study sites; Fig. 1, top), the Northern groin was newly constructed between April and October 2016, while the other two existing ones were raised. The Northern groin is elevated three meter above mean sea level (i.e., above high water) and the two other groins are elevated half a meter above mean sea level (only the tips near the channel are locally elevated three meter above mean sea level), whereas the tidal flat's elevation is on average one meter below mean sea level. Like the Knuitershoek location, two groins were constructed at Baalhoek (easternmost location of the three study sites; Fig. 1, top). Both groins were constructed at half a meter above mean sea level, with the Western one being newly constructed in 2016 (See Fig. 1 bottom). The tidal flat's elevation is on average 0.3 m below mean sea level. At both Knuitershoek and Baalhoek, the changes in the sediment composition and the bottom morphology, as well as the benthic community composition, were determined through yearly sampling campaigns from 2016 through 2020.

Perkpolder: creating new tidal areas through managed realignment

Since June 2015, a dike-realignment pilot was carried out at Perkpolder (middle location of the three study sites; Fig. 1, top) to allow the former agricultural area to again come under the influence of tidal inundation and sediment dynamics (i.e., low-dynamic tidal nature). As a result of the breach, the 75 ha tidal basin is now flooded twice per day by water from the Western Scheldt.

While the sedimentary and hydrodynamic changes varied depending on the location within the basin, there was a net increase in sediment import of about 13 – 16 kT (5000 – 6000 m^3) over just a 5-month period of measurement. Additional estimates between 2016 and 2017 showed an influx of 16-48 kT per year (van de Lageweg et al. 2019). Annual monitoring work was carried out from 2015 to 2020 to determine how the benthic conditions changed over time.

Target and adjacent reference sites

At Knuitershoek and Baalhoek, monitoring was carried out at both the target sites and adjacent reference sites. Target sites are the areas between the groins (Knuitershoek Center and Baalhoek Center) which were expected to change the most rapidly due to the engineering measures. The adjacent reference sites (i.e, areas outside but next to the groins: Knuitershoek North, Knuitershoek South, Baalhoek East, Baalhoek West) were expected to not be significantly altered by the engineering measures. Monitoring both the target and adjacent sites allowed us to compare the evolution of the impacted ecosystem in between the groins with the less impacted system adjacent to the groins. While the adjacent sites act as reference locations for the target sites, we would like to note that sediment accumulation and scouring occurred on both sides of the groins and so the adjacent sites were impacted as well (See Fig. 1). We did not monitor adjacent sites in Perkpolder to use as a direct comparison, as the intervention affected the entire polder.

Data collection

Benthic macrofauna sampling

All locations were sampled in September or October within a few days of one another. A 10 cm diameter x 50 m long metal corer was used to collect the macrofauna in the field. At each sampling location, three separate replicates (down to 35 cm depth) were taken and pooled together as one sample. The sediment was sieved in the field over a 1-mm mesh and preserved in a 4% buffered solution of formalin dyed with Rose bengal. The macrofauna were analyzed to the lowest taxonomic rank possible. The individual specimens were first counted, then wet-weighed (blotted) to obtain biomass, which was later converted to ash free dry weight (AFDW). This allowed us to describe the community compositional patterns through the species richness, abundance and biomass.

Bird counts

Birds were counted and identified to species level every month within one low tidal cycle since August 2017 at the three locations, during the outgoing tide. To limit disturbance, countings were carried out from a car, moving slowly along the dike. Counts were performed for area blocks corresponding to the sites delineated in Fig. 1, with the exceptions that the Knuitershoek target site and the Baalhoek adjacent sites contained two bird counting blocks. In addition, Perkpolder was divided into six bird counting blocks. In our analyses, we used densities (counts/hectare) of birds that mainly forage on benthos (waders, shelducks, and gulls) from October to February, which are the months that birds would forage on benthic macrofauna stocks assessed from the autumn surveys.

Abiotic measurements

In addition to the benthic macrofauna samples, we also took sediment samples using a cut-off syringe to collect the top 3 cm of the sediment at the same exact locations as the benthic macrofauna. The samples were stored in small plastic vials and kept cool until they were transported back to the laboratory. They were subsequently wet-weighed and then frozen at –20 °C for several days before being placed into the freeze-dryer at –60 °C for at least 72 hours. The dry weight was recorded to calculate the bulk density of the sediment by subtracting the water content from the dried sediment. The samples were then analyzed for grain size composition using a Malvern Mastersizer 2000 particle size analyzer (McCave et al. 1986) through laser diffraction. This method measures the volume percentages of five different sediment fractions: silt (≤63 µm), very fine sand (62.5–125 µm), fine sand (125–250 µm), medium sand (250–500 µm) and coarse sand (500–1000 µm), which total 100% for every sample. From these values, the median grain size (D50) is also calculated.

At each station, we measured the elevation of the tidal flat using a dGPS which had a 1 cm error margin. In addition, we used a penetrollogger to measure the penetration resistance of the sediment up to 80 cm deep, and we measured the surface shear stress using a shear-vane. Five replicates were collected and averaged for both the penetration resistance and the surface shear stress measurements. During analysis, we cut the penetration resistance measurements off at 30 cm depth because many of the profiles did not reach past this depth and we wanted a more even profile length between stations for comparison.

Flow velocities from modeling

Tidal flow velocities were computed for all benthic macrofauna and sediment sampling locations. These velocities were derived from a depth-averaged Delft3D Flexible Mesh numerical model covering the Western Scheldt from Vlissingen to the Belgian border and was enforced with nested hydrodynamic boundary conditions (de Vet & Van de Werf 2022). The resolution of the computational mesh was 15 m in the project areas. The model was validated by flow velocity measurements. The bias and the root of the mean-squared-errors were less than 10 cm/s for most locations and less than 20 cm/s for all locations. From a model simulation covering two spring-neap cycles, the peak velocities of all tides were averaged such that for each sampling location an average peak velocity proxy resulted.

Statistical analysis

Abiotic characteristics

The seven hydrogeomorphological characteristics that we measured to assess the development of the tidal flat over time were: elevation in NAP (NAP, Normaal Amsterdams Peil, or Amsterdam Ordnance Datum, which is measured in reference to the mean water level for Amsterdam and is close to the mean sea level), bulk density (g/cm^3) shear stress (tkN/m^2), silt fraction (%), very fine sand fraction (%), penetration resistance (mPa), and peak current velocity (m/s). As the sediment was very silty, the D50 and the silt fraction were highly related and therefore we did not consider the D50 as an individual parameter in our analyses.

We evaluated the correlations between the different abiotic characteristics using Pearson correlation coefficients. We also used linear regression to examine whether relationships between abiotic characteristics were site-specific or universal across all sites (Fig. 2). In addition, we evaluated whether abiotic characteristics differed between the beginning and ending year of data collection. Because several different sampling stations were used in 2016 at Knuitershoek and Baalhoek than in other years at these locations, we used 2017 as the starting year instead of 2016 in the analyses comparing the beginning and ending year of data collection. This means that we may have underestimated the effect of the intervention as we did not take the beginning state into account for these temporal comparison analyses. For univariate and multivariate models, we excluded variables with a correlation coefficient above 0.6 from being in the same model to avoid redundancy. Lastly, we also used the Variance Inflation Factor (VIF) for models to verify that the variables within models were not overly correlated.

Benthos biomass

We summed the AFDW of all individuals in a sample to obtain the total biomass value for that sample. Subsequently, we evaluated the year and site effects on total biomass using linear regressions and analysis of variances (ANOVAs). In all models, biomass was log-transformed so that it would be normally distributed. We removed the following large species from the species counts and biomass estimates as these were too big to be reliably sampled with a 10 cm diameter corer: crab (*Hemigrapsus* sp.) and Pacific oyster (*Magallana gigas)*.

Multivariate analysis

We explored the community structure of benthic macrofauna across the different habitats in 2016, 2018, and 2020 through multivariate methods. Using functions from the "ade4" R package, we evaluated the biotic and abiotic components of the ecosystem separately with a Between Class Analysis (BCA; Thioulouse et al., 2018), to understand whether differences between the communities were better explained by spatial (between site) or temporal (between year) partitioning. We tested the effect of the habitat and year on the variation of community structure with a Monte Carlo permutation test using 999 random permutations. Prior to the BCA, we processed log-transformed individual densities of organisms by centered Principal Component Analysis (PCA). We used PCAs to determine which variables (environmental characteristics or species richness) best explained the ordination axes for the biotic and abiotic datasets.

To explore which abiotic variables best correlated with biotic community structure across both target and adjacent sites within the three years in more detail, we subsequently used a Canonical Correspondence Analysis (CCA, Ter Braak and Verdonschot, 1995) with functions from the "vegan" package in R. We applied single variable CCA models to assess how well an environmental variable explained the benthic macrofaunal community inertia, and we used full CCA models to determine the best combination of environmental variables explaining the benthic macrofaunal community inertia (Table 1). For the full models, we used forward selection to order the environmental variables according to the amount of inertia in the species dataset that they explained (Ter Braak & Verdonschot 1995, Ysebaert & Herman 2002). At each step, the statistical significance of the added variable was tested using a Monte Carlo permutation test with 999 random permutations.

Bird densities

We evaluated the year and site effects on total bird density and oystercatcher counts with a negative binomial regression using functions from the R package "MASS". We evaluated the model goodness-of-fit using a chi-square test and examining both model residuals and qqplots. We do not present a detailed analysis of the bird data, but rather discuss changes in benthos-eating bird assemblages in relation to the changes we observed in their prey base.

Results

Low current velocity led to an import of silty sediment in target sites

At Knuitershoek, the lowering of the current velocities between the groins led to substantial accretion and bed level change, whereas at Baalhoek and Perkpolder, the sediment did not accrete as dramatically at the measured locations (Fig. S1). Average peak velocity decreased the most at the Knuitershoek target site, from 0.51 m/s in 2016 to 0.34 in 2020, whereas the peak current velocity stayed relatively high at the Baalhoek target site (0.55 m/s). The average peak velocity at Perkpolder was relatively low after the dike breach (0.15 m/s) and has remained so as the tidal prism of the area is limited with an area of 75 ha.

The calmer hydrodynamic conditions allowed for sediment accretion and we observed bed-level changes at the benthic macrofauna sampling locations. Between 2017 and 2020 the target sites' bed-level increased on average 11 cm at Knuitershoek Center, 14 cm at Baalhoek Center, and 5 cm at Perkpolder. Additionally, in all cases, we observed an increase in the sediment silt content. The Knuitershoek and Baalhoek target sites experienced the greatest silt content increase between 2017 and 2020 (from 65% to 84% and 31% to 47% on average, respectively). Perkpolder also had increasingly high sediment silt content (58% in 2015 and 72% in 2020), like the Knuitershoek target site.

We found that the relationships between sediment properties (silt content, bulk density, shear stress, and penetration resistance) were universal across all sampling locations, while the relationships between sediment properties and geomorphology (elevation and peak current velocity) were more site specific. The most important universal correlations in geomorphological properties across sites was the relationship between sediment silt content and bulk density (Fig. 2). Siltier sediments were softer than sandier sediments at all of the monitored sites. However, the relationships between elevation and other geomorphological characteristics were not the same across locations. At both Knuitershoek and Baalhoek, higher elevation was associated with lower current velocities, and stiffer, sandier sediment (Fig. 2). Perkpolder, on the other hand, did not show the same relationships between elevation and the sediment characteristics as the other two locations. In contrast it had some of the highest sampled elevations, paired with very high silt content of imported sediment (Fig. 2). This is largely due to Perkpolder being a small tidal basin unlike the other two locations and is sheltered from waves and experiences no substantial alongshore flow.

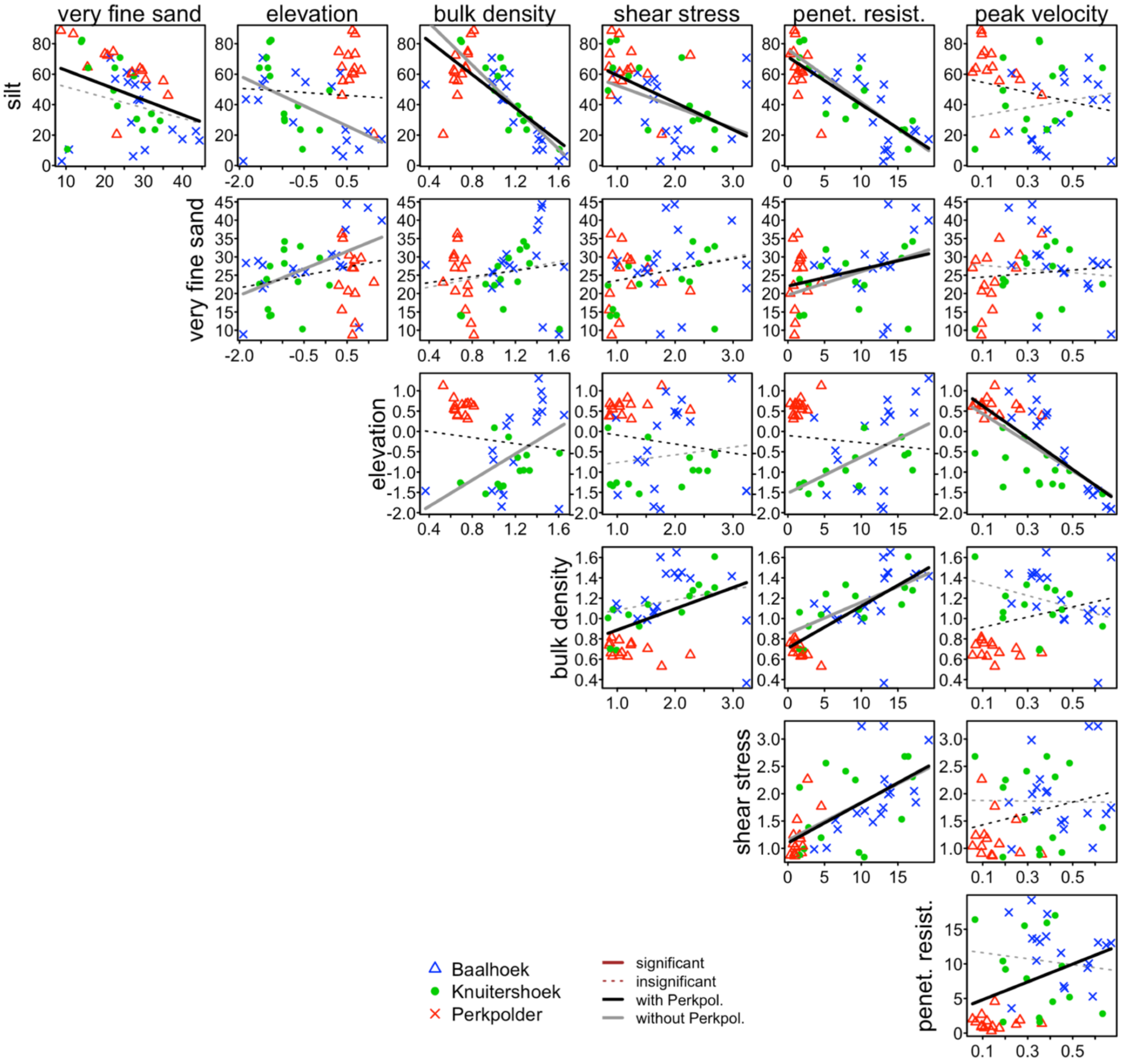

Figure 2: Correlations between abiotic variables in 2018 which were considered for inclusion in statistical models. The abiotic variables are elevation (NAP), bulk density (g/cm^3) shear stress (tkN/m^2), silt (%), very fine sand (%), penetration resistance (mPa), and peak velocity (m/s). Relationships for the full dataset are show in black lines, relationships for the dataset that excludes Perkpolder are shown in grey.

Biomass increased over time at most target sites, following the interventions

The project interventions succeeded at improving habitat quality for benthic macrofauna in terms of their biomass at the target sites. The most dramatic increase in biomass occurred at the Baalhoek target site: from an average of 1 g AFDW in 2016 to 56 g AFDW in 2020 [t(14) = 2.7, p = 0.02; (Fig. 3a)], largely due to the increase in bivalves. The adjacent sites at Baalhoek also experienced an increase in biomass from 2017-2020, although not as dramatic as the one in the target site (Fig. 3b). At Perkpolder, where the intertidal flat was started from scratch, there was also an increase in biomass over time: from an average of 3 g AFDW in 2015 to 18 g AFDW in 2020 [t(27) = 6.8, p < 0.01].

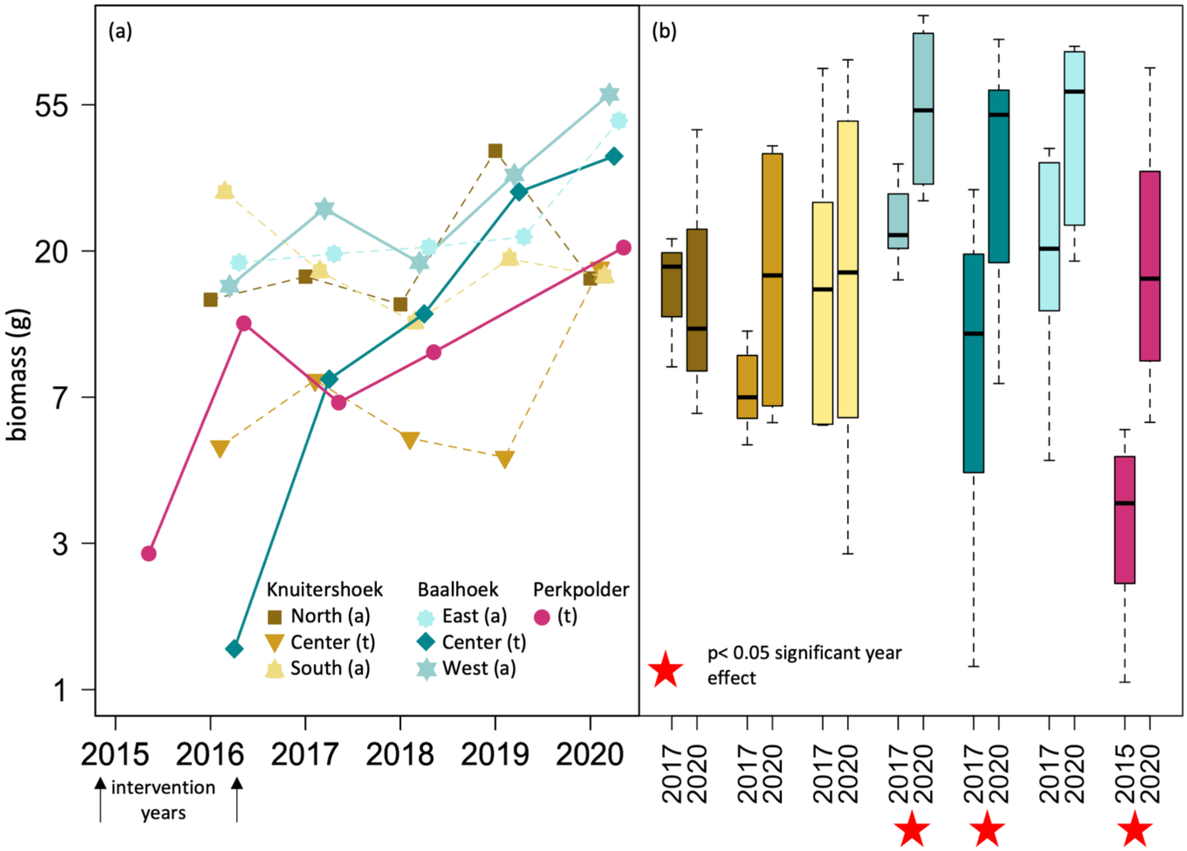

Figure 3: Left panel (a): Mean biomass (g AFDW) at the Knuitershoek, Baalhoek, and Perkpolder sites from 2015 to 2020. At Perkpolder and Baalhoek (center and west) the biomass had a linear increase over time (unbroken line). At the other sites, biomass did not increase linearly over time. Right panel (b): Comparison of biomass at the beginning of the project (in 2017 or 2015) and in 2020 at the different sites. The stars signify sites that had a statistically significant (p < 0.05) increase in biomass since the beginning of the project. The increase in biomass at Knuitershoek

Center had a significance of p = 0.1. In the legend, (t) and (a) indicate whether the corresponding site is a target site (intended area of intervention impact) or an adjacent site (area next to target site).

The increase in biomass at both Perkpolder and the Baalhoek target site had a linear trajectory (Fig. 3a). On the other hand, at the Knuitershoek target site' macrofaunal biomass increased from 2017-2020, but in a non-linear way [t(7) = 1.6, p = 0.1]. Indeed, the only significant increase in biomass occurred in the final year (Fig. 3a). In the first year of the project, all the target sites had a lower average biomass than the adjacent sites' average biomass (target site biomass was on average 1 to 3 g AFDW during the first year of the project vs. 15 to 30 g AFDW on average at adjacent sites). By 2020, the biomass in the Baalhoek and Knuitershoek target sites was at a similar level to their respective adjacent sites (Fig. 3a).

Macrofaunal communities were best distinguished by inundation time and silt content

Benthic macrofaunal communities differed the most in terms of elevation/immersion time. The silt content (first PCA axis) and the elevation or immersion time (2nd PCA axis) were the most important geomorphological variables for distinguishing between the sites in terms of environment. Indeed, when we examined the environmental variables that were most correlated with the structure of communities between sites in 2016, 2018, and 2020, we found that elevation and silt content were the most important in distinguishing between the benthic macrofauna communities (Table 1, Fig. 4 top). Interestingly, Perkpolder and the Knuitershoek target site were very similar in terms of sediment type. They both developed soft, very silty sediment. However, these two sites were the farthest apart in terms of elevation (Fig. 4 bottom), as well as community composition in 2018 and 2020 (Fig. 4 top).

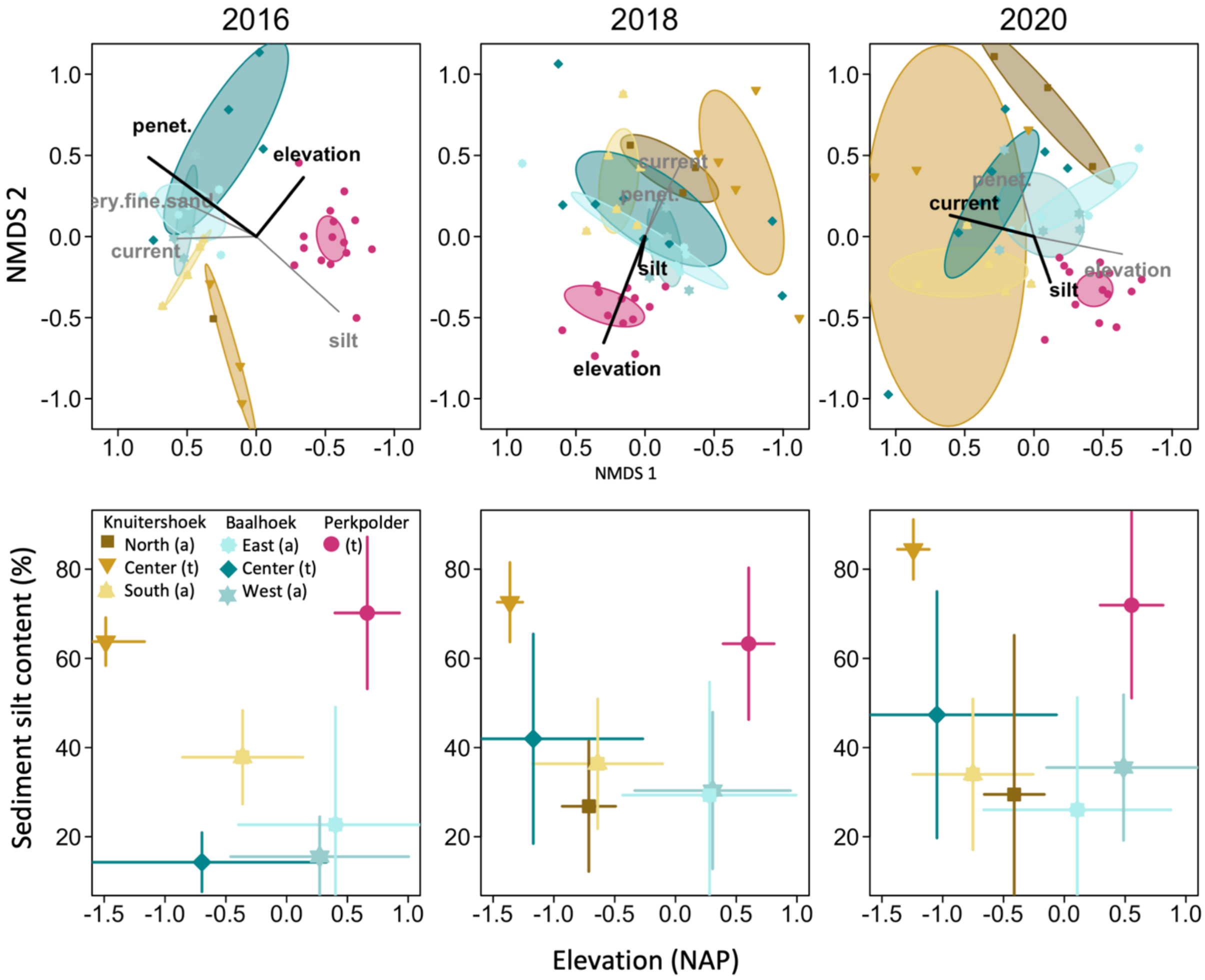

Figure 4: Top row: NMDS plot for benthos community abundances at sites in Baalhoek, Knuitershoek and Perkpolder in 2016, 2018, and 2020. The ellipses in the NMDS plots represent the standard error with 95% confidence around the centroid for the communities at the different sites. The vectors represent the abiotic variables (penet. = penetration resistance, current = peak current velocity) that best explain the sample ordination by CCA. Those in grey were statistically significant in single variable CCA models, but did not improve the full model where variables were added using stepwise forward selection (full model variables are the black vectors). The direction of the vector represents the steepest gradient, and the length represents the strength of the relationship. Highly correlated abiotic variables were not allowed in the same models.
Bottom row: Site averaged sediment silt content (%) as a function of elevation (NAP) for 2016, 2018, and 2020, with points scaled to the average biomass of the site-year combination. In the legend, (t) and (a) indicate whether the corresponding site is a target site (intended area of intervention impact) or an adjacent site (area next to target site). The lines around the points are the standard deviations for the elevation and sediment silt content. Knuitershoek Center and Perkpolder consistently have the highest silt content, but also have the largest difference in elevation.

Table 1: Effects of environmental variables on the benthic macrofauna community in 2016, 2018, and 2020. Explained inertia denotes the amount of explained multidimensional variance of community structure by the considered variable in CCA models. In the single variable model, only one variable was regressed against the benthic macrofauna community, in the full model, the variables were selected using stepwise forward selection. Highly correlated (correlation coefficient > 0.6) variables were not included in the same model. The best model was selected using the Akaike Information Criterion. Bolded values are statistically significant (p <0.05)

year	single variable model	% explained inertia	p-value
2016	elevation	20.1	<0.01
	silt	10.1	<0.01
	very fine sand	6.9	0.02
	bulk density	5.3	0.06
	penetration resistance	17.5	<0.01
	shear vane	4	0.15
	current velocity	18.4	<0.01
2018	elevation	15.3	<0.01
	silt	9.7	<0.01
	very fine sand	3.9	0.06
	bulk density	7.9	<0.01
	penetration resistance	9.5	<0.01
	shear vane	7.1	0.04
	current velocity	9.5	<0.01
2020	elevation	8.4	<0.01
	silt	8.8	<0.01
	very fine sand	4.1	0.04
	bulk density	8.1	<0.01
	penetration resistance	5.6	0.004
	shear vane	3.4	0.12
	current velocity	9.4	<0.01

year	variables in best full model	% inertia explained	p-value
2016	elevation + penetration resistance	36	<0.001
2018	elevation + silt	25	<0.001
2020	current velocity + silt	16	<0.001

An extremely silty and soft sediment may lead to lower biomass than a stiffer, sandier sediment in low-dynamic habitats. Overall, biomass decreased in softer, siltier sediment (Fig. S2). In particular, sediment penetrability had the clearest relationship with biomass, where biomass increased with bulk density [t(28) = 3.1, p= < 0.01] and penetration resistance [t(33) = 2.4, p = 0.02]. The siltiest target sites, Perkpolder and Knuitershoek Center, had the lowest total biomass across all the sites [F(6, 213) < 0.01, post hoc Tukey p-values <0.01 for comparisons between Knuitershoek Center and Perkpolder with the adjacent sites]. Furthermore, Perkpolder and Knuitershoek Center had consistently lower proportions of bivalves in their biomass compared to other target and adjacent sites (except adjacent site Knuitershoek North which had a consistently high proportion of polychaetes, Fig. 6). Finally, a softer, siltier sediment had a community with a lower diversity (Shannon index) than a sandier sediment, although this was only statistically significant in 2018.

Temporal biotic processes were loosely coupled to abiotic drivers in the short-term

We found that the macrofaunal assemblages had a greater temporal development than the abiotic characteristics. The BCA analysis showed that the environmental characteristics differed more between sites than between years (2% of inertia is explained by temporal differences, Monte-Carlo p = 0.3; whereas 43% can be explained by spatial differences, Monte-Carlo p < 0.001) which means that they did not change much over time compared with their between-site differences. The biotic communities, however, varied both over sites and years (12% of inertia is explained by temporal differences, Monte-Carlo p < 0.001; whereas 23% is explained by spatial differences, Monte-Carlo p< 0.001). This means that the biotic components evolved through time much faster than the abiotic ones.

The percent inertia of the benthic community explained by the abiotic variables across both target and adjacent sites decreased throughout time (36% in 2016, 25% in 2018, 16% in 2020, Table 1), indicating that the strongest correlation between the abiotic conditions and the benthic community composition occurred when the interventions began. This trend can be explained by the biological and environmental components of the sites becoming less distinct in later years due to the interventions, which likely caused the strength in the spatial correlation between the biotic and abiotic components to decrease. Indeed, in 2016, 53% of the benthic community inertia is explained by differences between sites, while in 2018, the inertia explained by spatial differences decreased to 42 % (33% when Perkpolder is excluded from the analysis), which shows that the benthic communities at all target and adjacent sites were growing more similar through time. This decrease in spatial heterogeneity over time was observed for the environmental characteristics, though to a lesser extent (56% inertia explained by spatial differences in 2016 and 47% in 2020). It is important to note that we did not include lag effects in our models correlating the abiotic and the biotic ecosystem components, and it is probable that the biota will adapt to the changes in the environment due to the interventions for years to come.

The composition of benthic assemblages in target sites changed post-intervention

Colonization processes also played a large role in determining the benthic community trajectories. When a completely new habitat is created (such as at Perkpolder), the colonization process starts from zero, leading to a highly evolving successional community (Fig. 5). We observed high abundances of smaller, shorter lived species such as *Corophium volutator* in the first years after the dike breach at Perkpolder, but these largely disappeared by 2018; by which point, longer-lived bivalves such as *Scrobicularia plana* gained a foothold (Fig. S3). Perkpolder also showed the clearest significant increase in sample diversity over time. The Shannon index was 0.74 in 2015 and 1.14 in 2020 [t(1) = 5.88, p = 0.04].

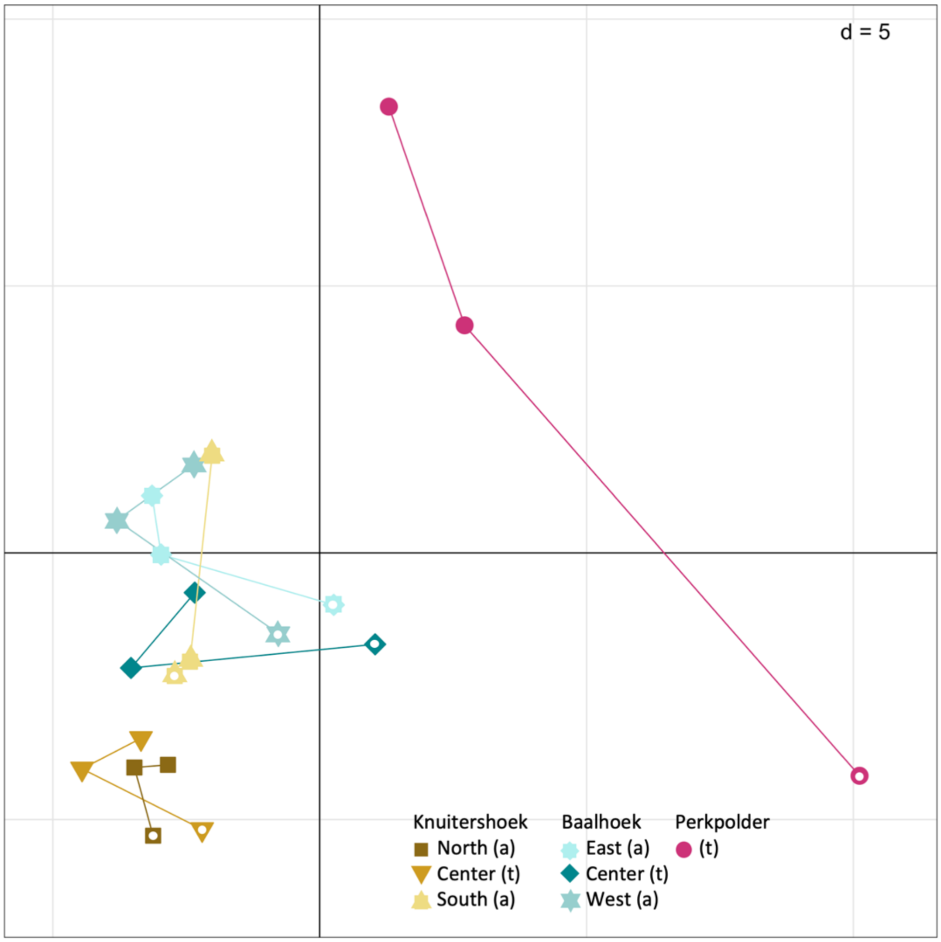

Figure 5: BCA trajectory for the benthic community densities at the different sites from 2016, 2018, to 2020. In the legend, (t) and (a) indicate whether the corresponding site is a target site

(intended area of intervention impact) or an adjacent site (area next to target site). The symbols represent the centroid for that year by site. The symbols with the white disk are the 2016 values. The Perkpolder community is the only one that changes significantly over time.

In the case of habitat modification (i.e. Baalhoek and Knuitershoek) where there was already biota at the target sites to start with, the community evolution through time was not so strong as at Perkpolder (Fig. 5). In 2016, polychaetes such as *Heteromastus filiformis* and *Aphelochaeta* were abundant in the Knuitershoek and Baalhoek target sites, but there were far fewer of the bivalve *Macoma balthica* in target sites compared to the adjacent sites [F(6,40)= 5.03, $p< 0.001$; post hoc Tukey $p <0.01$ for target-adjacent comparisons]. *S. plana,* the most massive species in 2019 and 2020, colonized both the target and adjacent sites in 2017 and 2018, and while *S. plana* were initially more massive in adjacent sites [F (6,40) = 5.02, $p< 0.001$; post hoc Tukey $p< 0.05$ for *S. plana* target-adjacent site comparisons, except with the Baalhoek target site], by 2020, the abundances and biomass of *S. plana* were similar between the target and adjacent sites [F (6,38) = 1.97, $p = 0.1$].

Overall, at all sites, the biomass of the assemblages shifted from polychaetes to bivalves over the monitored period (Fig. 6a). All the target sites had communities dominated by polychaetes (or. *C. volutator* in Perkpolder) in the first years (proportion of bivalve biomass < 50% in 2017 for all target sites, Fig. 6a), but the proportions of polychaetes to bivalves in target sites shifted closer to those of the adjacent sites very quickly. At Perkpolder and the Knuitershoek target site, which were the muddiest areas, the polychaete to bivalve ratios were slower to reach the same bivalve-heavy ratios of the Baalhoek and Knuitershoek South adjacent sites (Fig. 6a). The exception to this trend of polychaete to bivalve biomass shift was the sand-nourished adjacent site Knuitershoek North. Rather, the polychaetes *H. filiformis*, *Hediste diversicolor*, and *Arenicola marina* made the largest contributions to biomass in Knuitershoek North in 2020.

Benthos-eating birds may have responded to an increase in benthos biomass

The gradually changing composition of the benthic macrofauna community as well as the changing biomass may be expected to have had an effect on the benthos-eating birds that used the area (Fig. 6). Indeed, the number of oystercatchers increased in the Baalhoek target site from 0.9 to 7.7 oystercatchers/hectare between 2017 and 2020 (Fig. S4) [$X^2(1, N=10) = 24.9$, $p = < 0.001$]. The effect of the groins on the birds was less clear at the Knuitershoek target site, though the number of oystercatchers seemed to increase in 2020 (Fig. S4). In Perkpolder, the number of benthos-eating birds increased between 2017 and 2020 from 1.6 to 2.4 birds/hectare [$X^2(1, N=10) = 2.9$, $p = 0.08$]. In particular, the number of oystercatchers and dunlins appeared to have increased, but the numbers fluctuated spatially and temporally.

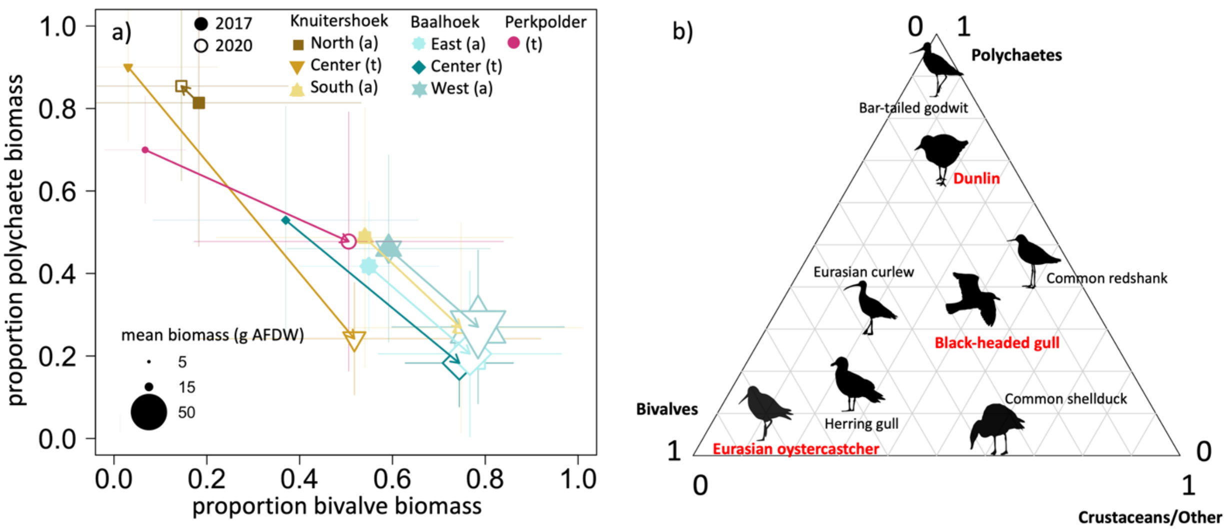

Figure 6: a) Proportion of polychaetes to proportion of bivalves in the biomass of target and adjacent sites in 2017 and 2020. In the legend, (t) and (a) indicate whether the corresponding site is a target site (intended area of intervention impact) or an adjacent site (area next to target site). b) Triangle plot showing the proportion of bivalves, polychaetes and crustaceans/other in the diets of the eight most common bird species at the sites. Birds close to the corners are specialized in one food category, birds close to the mid-sides target two food categories, and birds in the center of the triangle eat a mix of the three food categories. Birds with their names in red have increased in numbers in the target sites from 2017 to 2020. Specifically, the number of oystercatchers increased in all target sites, black-headed gulls in the Baalhoek target site and dunlins in Perkpolder. The bird diet information is from Leopold et al. (2004) and the bird silhouettes are from http://phylopic.org/.

Discussion

The implementations of groins and a managed realignment with the aim of creating low-dynamic habitat were successful in enhancing the habitat value for the benthic macrofauna community. Lowering the hydrodynamics at target sites stimulated sediment import and, as a result, we observed an increase in the benthic macrofauna biomass in the target sites after project implementation (Fig. 7). Moreover, the density of benthos-eating birds, in particular the oystercatchers, increased at some target sites. However, we also found that if the sediment had an extremely high silt content (>70%), then benthic macrofauna biomass was slower to develop than in areas with less extreme silt content. While improving the habitat is important to attract benthic macrofauna, biotic processes such as colonization and succession are also important for determining the evolution of macrobenthic assemblages. Because of this, there may be delays in observing the response of the benthic macrofauna community to changes in their habitat.

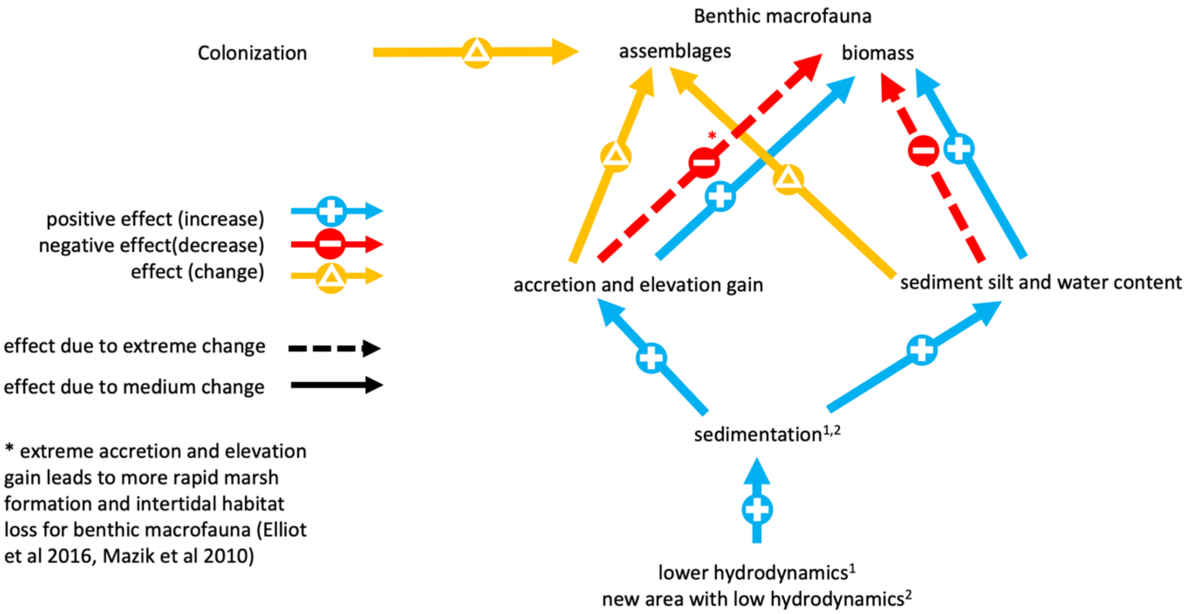

***Figure** 7*: Schematic showing how physical changes due to intervention measures ([1]Knuitreshoek and Baalhoek, [2]Perkpolder) lead to geomorphological changes at an intertidal site, which in turn affect the benthic macrofauna assemblages and biomass. All relationships depicted are derived from this study except those marked with an *. An increase in sediment accretion and siltiness can lead to increase in biomass, but if these changes in geomorphology are too extreme, the effects on benthic biomass can become negative (red arrow). Changes in the hydrogeomorphology also lead to changes in the composition of benthic macrofauna assemblages, however, assemblages are also driven by processes like colonization and succession.

The pros and cons of low-dynamic areas for stimulating benthic macrofauna

One of the core goals of the restoration initiatives behind our case studies was to create low-dynamic intertidal flats, from the principle that low-dynamic areas (i.e. peak current velocity is less than 0.6 m/s) are more species rich than high-dynamic areas (Van Colen et al. 2010, van der Wal et al. 2017) (though not always, see Dutertre et al., 2013). Highly dynamic areas tend to have a lower number of species than less energetic intertidal flats because fewer species can maintain a foothold under these conditions (Warwick & Uncles 1980, Van Colen et al. 2010). Furthermore, coarse sediments in high-dynamic areas are unstable for large burrowers and offer little food to deposit feeders (Donadi et al. 2015), and greater sediment and larval resuspension due to high hydrodynamic stress can reduce recruitment (Bouma et al. 2001). However, the difference between low-dynamic and high-dynamic areas may have more to do with the types of assemblages that these habitats can support than the species richness. Burrowing deposit feeders are favored in low-dynamic areas whereas omnivorous crawling or swimming species are favored in high-dynamic areas (van der Wal et al. 2017). Low-dynamic environments may also come with disadvantageous conditions. For example, bottom-waters may become susceptible to oxygen depletion because of reduced mixing (Dutertre et al. 2013) which could be exacerbated due to rising temperatures. Finally, spatial heterogeniety leads to greater species richness (Ellingsen et al. 2007), and so, if tidal flat restoration iniatives only aim to create low-dynamic areas, we may forego diversity in both the environmental and biological components of the ecosystem at the macro-scale.

In the target sites of our three cases, the low hydrodynamics were accompanied by the accumulation of fine-grained sediment with an exceptionally high silt content in the case of Perkpolder and Knuitershoek Center. High silt content means a food-rich environment for deposit feeders as well as greater bed level stability than coarse sand (Ysebaert & Herman 2002), yet extremely high silt content, especially when resulting from rapid accumulation (Lohrer et al. 2006) and coupled with poor drainage (Dale et al. 2019), can be detrimental to animal functioning. Though low bulk densities can facilitate animal movement (Wiesebron et al., 2021), animals may have to expend a greater amount of energy to maintain their position in highly silty sediment or unclog their feeding apparatus of small mud particles (Lohrer et al. 2006, Mestdagh et al. 2018). The rapid accumulation of extremely silty sediments may have had a negative effect on the development of the benthos community at Perkpolder and Knuitershoek Center, where biomass built up more slowly than other target sites. Therefore, while silt content is beneficial for benthic macrofauna, especially deposit-feeding burrowers, extremely high silt content may be detrimental to the development of benthic macrofauna assemblages on the whole. This needs to be considered when designing low-dynamic areas for restoration purposes.

Bottom-up effects on birds

As benthic macrofauna form the prey base of many other intertidal fauna, an increase in their biomass should cascade up trophic levels and attract predators such as birds. Indeed, we observed an increase in the number of benthos-eating birds at the target sites and, in particular, the oystercatcher numbers increased at all target sites over the project years. We also observed an area-wide shift in benthic macrofauna biomass from polychaetes to bivalves, with the biggest shifts occurring at target sites, and *S. plana* was by far the biggest contributor to the increase in bivalve density and biomass at these sites. Oystercatchers prefer to eat bivalves, and *S. plana* is one of the oystercatcher's most profitable prey (Zwarts et al. 1996). Thus, it is possible that oystercatchers specifically responded to this prey source. However, links between bird assemblages and the availability of their preferred prey are frequently weak (Horn et al. 2020). Instead, bird distribution patterns are more strongly related to abiotic factors such as tidal cycle (Dias et al. 2006), distance to roost (Rogers et al. 2006), and anthropogenic disturbance (Velando & Munilla 2011). Thus, at this point it is still unclear to what extent we can link the observed changes in bird use of the target sites to benthic prey availability. To explain bird observation, we should also consider the geomorphological changes as important factors.

Contextualizing intervention success: a perspective over time and space

Within the scope of our projects, the interventions succeeded at achieving the management goal of increasing benthic macrofauna biomass in the target sites. This was the result of careful design, but such interventions are not necessarily always successful. In fact, at Knuitershoek, a number of groins and channel edge fixation works were already present, but the groins were not sufficiently high to stimulate sedimentation. Instead, these works hindered drainage as evidenced from the pools visible in Fig. 1 which resulted in relatively low sediment bulk densities. In other projects the opposite effect has been reported, with sediment accumulation occurring so quickly that the intended intertidal flat became a marsh in less than ten years (Mazik et al. 2010). The challenge is that a single intervention can have opposing eco-morphological consequences at different locations, due to different hydrodynamics and sediment supply (de Vet et al. 2020). Thus, interventions can help improve a habitat, but only if they are implemented correctly, with the appropriate forethought and hydromorphodynamic modeling of the impact of various designs where needed.

Though both kinds of interventions (groins and managed realignment) engendered an increase in benthic macrofauna biomass, the two types of interventions will have different long-term consequences, especially when they are implemented en masse and under the threat of sea-level rise. The estuaries where these tidal flat interventions are implemented are typically highly impacted in other ways, with continued human disturbance such as dredging to keep channels open to shipping. Managed realignments could help counteract the steepening of the floodplain under sea-level rise by widening the floodplain, thus increasing the accommodation space for intertidal flats (Leuven et al. 2019). Groins, on the other hand, restrict the estuarine channel and might have the opposite effect of managed realignments and steepen the floodplain. For example, the construction of groins in the Yangtze delta resulted in sediment accretion and current dampening between the groins, but the channel deepened and eroded (Luan et al. 2018). Steeper tidal flats restrict the habitat availability to benthic macrofauna and have a negative, long-term effect on benthic macrofauna (Cozzoli et al. 2017). The effects of groins under sea-level rise would certainly be exacerbated if these were implemented en masse. Thus, the fact that the groins were successful in increasing benthic macrofauna biomass at the local scale is not the only factor that should be taken into account when considering the success of the projects. Their impact on the estuarine system should also be considered, as the long-term and large-scale morphological changes may have negative ecological effects that surpass the current short-term and localized benefits.

Conclusion

The engineering modifications of the tidal flats at Knuitershoek, Baalhoek, and Perkpolder led to the creation of habitat with low hydrodynamics and the accumulation of fine, silty sediment, and an increase in benthic macrofauna biomass. Furthermore, the trajectories of both the abiotic and biotic components of the target site ecosystems in all three study locations are moving towards the adjacent reference sites' states. However, the abiotic conditions and the biotic responses at these sites are still in flux. While improving habitat is of crucial importance to attract benthic macrofauna, biotic processes such as colonization and recruitment success also determine the evolution of macrobenthic assemblages (Zajac et al. 1998), especially in the early years post-intervention. Thus, even though the targeted sites experience rapidly changing abiotic characteristics, there may be a delay in the benthic community response (or even a delayed environmental response to intervention, (de Vet et al. 2020). As a result, it may take a longer period to observe how the benthic community responds to their changing environment. Indeed, slow recovery rates of benthic communities have been often observed post-disturbance (Lohrer et al. 2010, de Juan et al. 2014) and recovering benthic communities can diverge from that of the surrounding area and/or even their pre-disturbance state (Van Colen et al. 2010). The existence of these delays in benthic community response necessitates a sound implementation of intertidal flat alterations (without undesirable side-effects) and stresses the importance of monitoring campaigns following the initial impact from the interventions.

Acknowledgements

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Supplementary figures

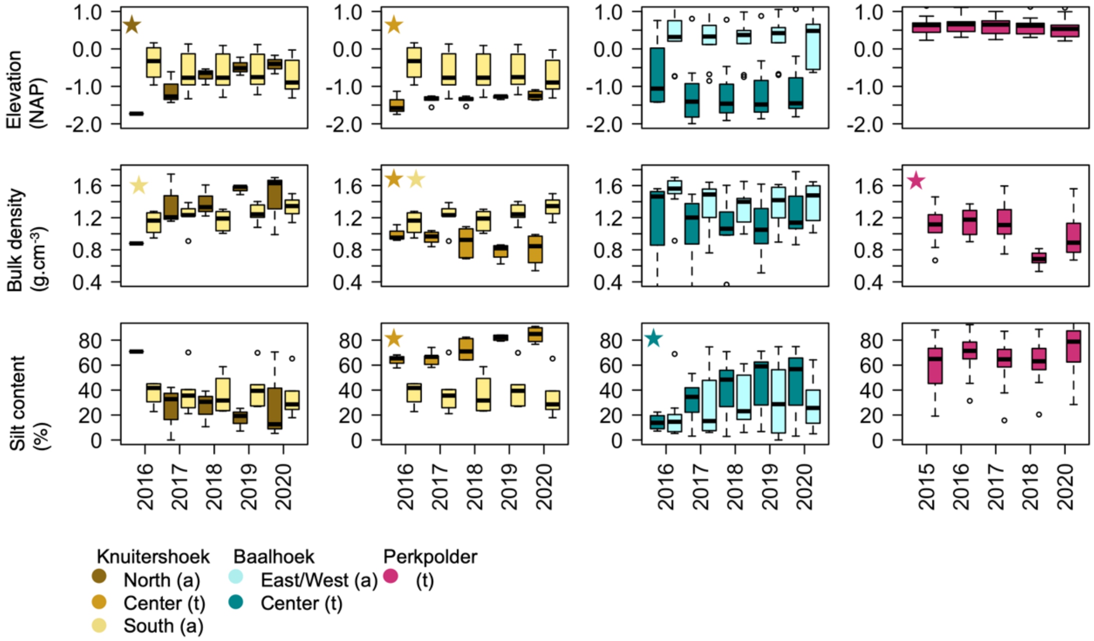

Figure S1: The evolution of the sediment properties at sites in Knuitershoek, Baalhoek, and Perkpolder. In the legend, (t) and (a) indicate whether the corresponding site is a target site (intended area of intervention impact) or an adjacent site (area next to target site). The target sites are shown in contrast to the adjacent sites in Knuitershoek and Baalhoek. We also show the Knuitershoek North adjacent site contrasted with the Knuitershoek South adjacent site because they diverge, largely due to the sand nourishment at Knuitershoek North which occurred in 2016. Statistically significant linear trends are shown by stars. All target sites show the accumulation of soft, silty sediment, with Knuitershoek Center and Perkpolder having the highest silt content overall.

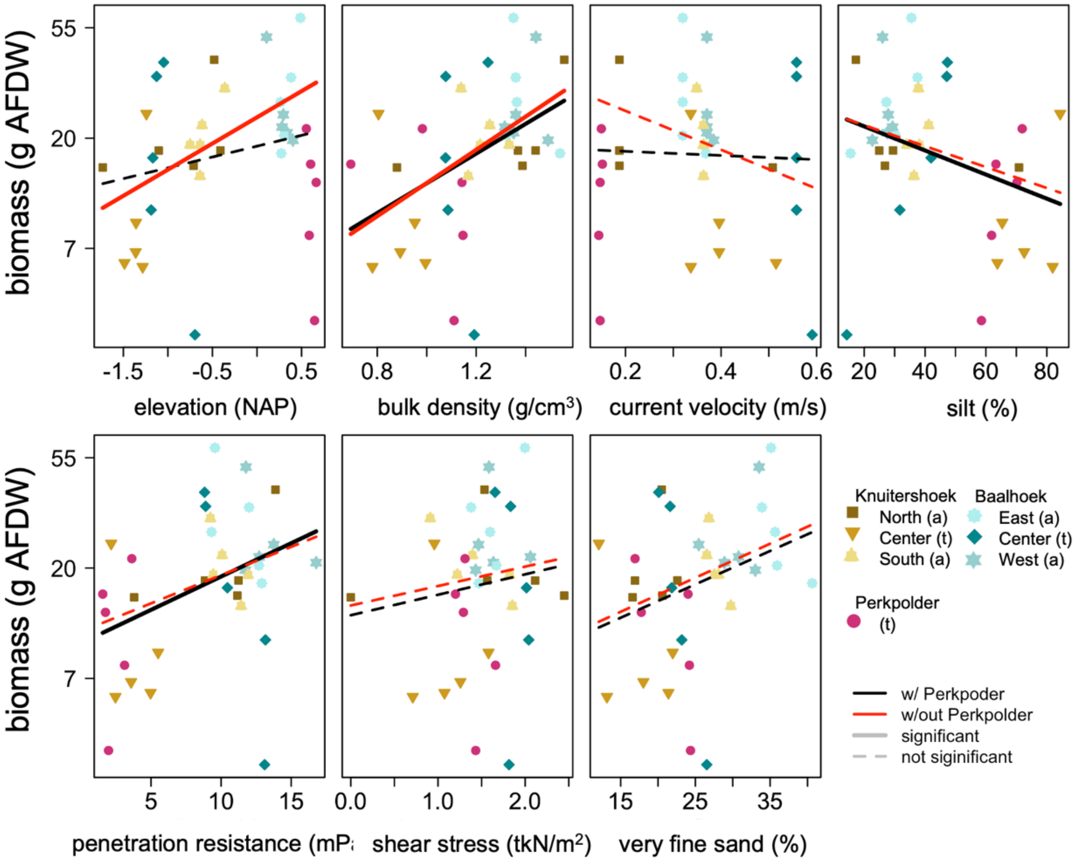

Figure S2: Relationship between biomass (g AFDW) and suite of environmental parameters. The points were site averaged per year. In the legend, (t) and (a) indicate whether the corresponding site is a target site (intended area of intervention impact) or an adjacent site (area next to target site).

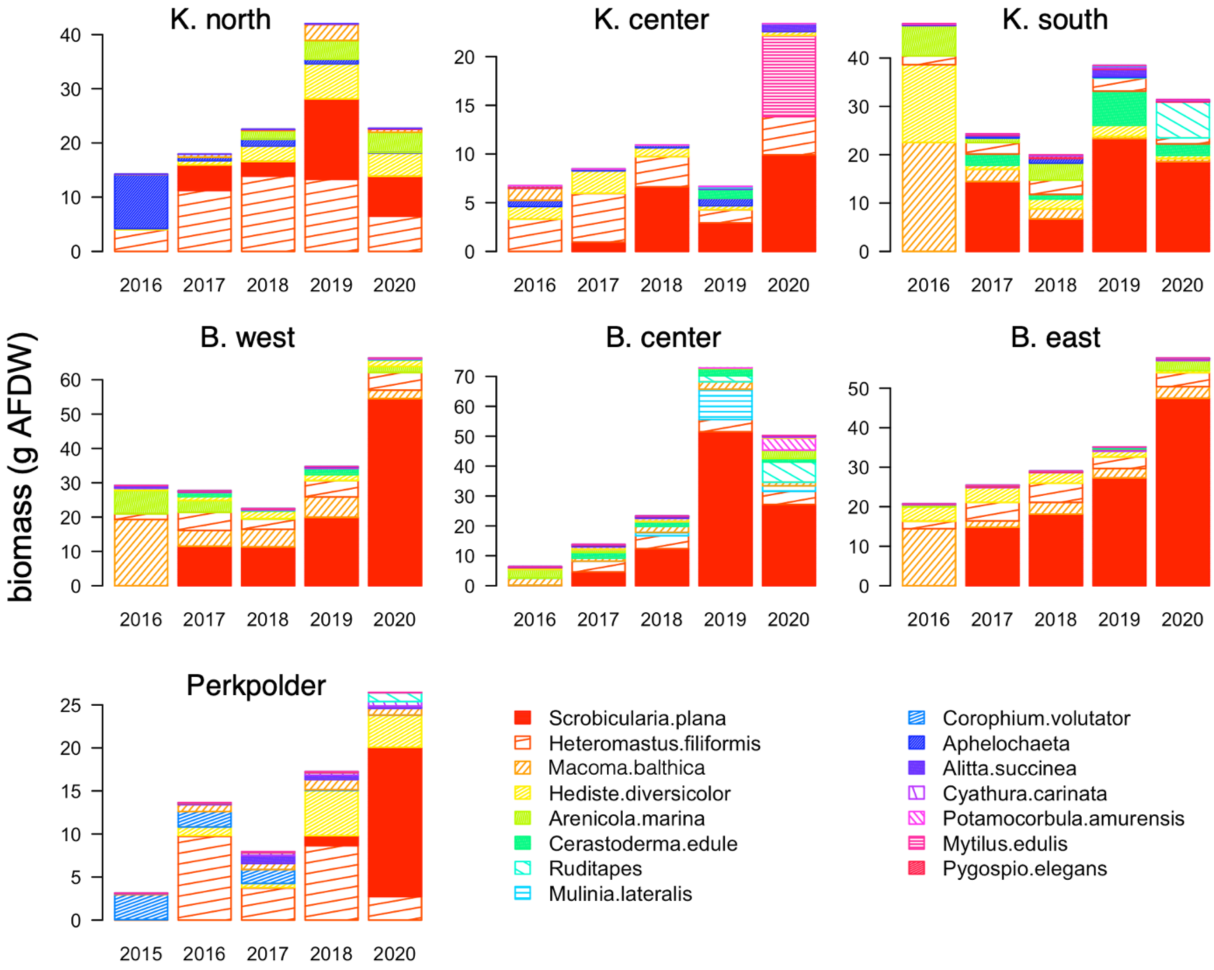

Figure S3: The fifteen most massive species at sites in Knuitershoek (north, center, south), Baalhoek (west, center, east), and Perkpolder. Species biomass (g AFDW) was summed over all sampled points within a site and a given year.

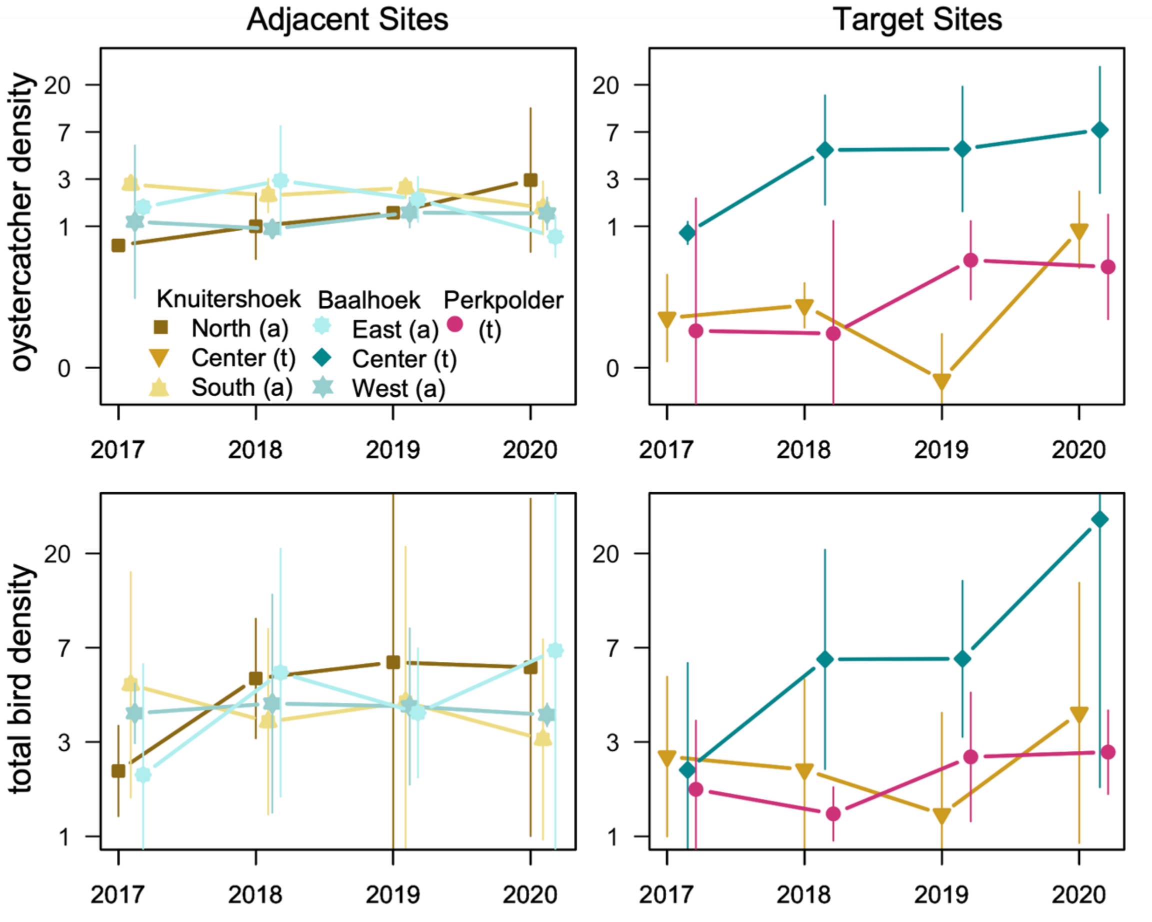

Figure S4: Time series showing oystercatcher densities (top) and the total benthos-eating bird densities (bottom) from 2017-2020, averaged per site over the autumn and winter months (October to February), with standard deviations. The bird densities are in counts per hectare. Note the log scale in the y-axis and that the points have noise added to them along the x-axis for legibility. The left panel shows the time series for adjacent sites, the right panel shows the times series for target sites.


CLAMMED OUT!

Chapter 6

General discussion

Lauren E. Wiesebron

Short summary

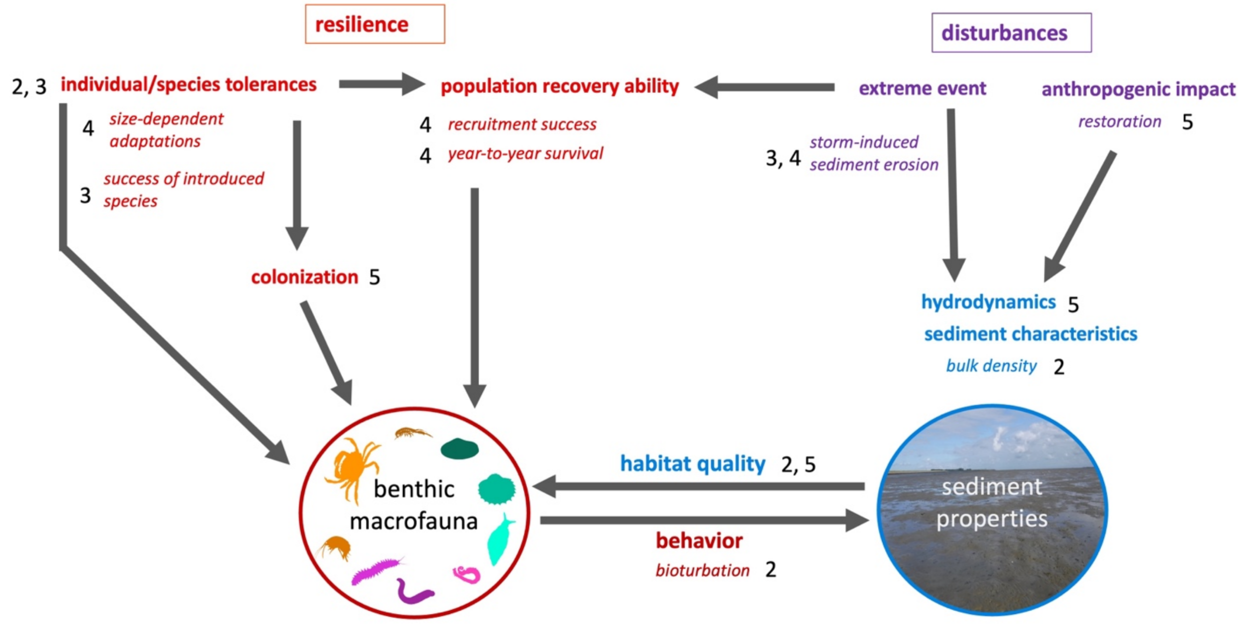

Figure 1: Summary schematic of important traits (under "resilience", in red) and drivers (under "disturbances" in purple, resulting in the "physical environment" in blue) relating to the response of benthic macrofauna to the dynamic intertidal environment. The arrowhead denotes the direction of the interactions. Texts in italics refer to thesis-specific studies. The black numbers next to the text refer to the thesis chapter these processes/interactions are studied. The benthic macrofauna (silhouettes from www.phylopic.org) depicted are three crustaceans, three mollusks, and three polychaetes that are common to the Scheldt.

In this thesis, I examined the response of benthic macrofauna assemblages and behavior to dynamic sediment drivers. I focused on detecting behaviors and traits that confer resilience to benthic macrofauna against disturbances and extremes in sediment dynamics (Fig. 1). In **Chapter 2**, we used a mesocosm experiment to uncover the effects of sediment bulk density, a poorly studied but important sediment characteristic, on benthic macrofauna burrowing and bioturbation behavior. This study shows that bulk density had a strong effect: benthic macrofauna burrowed faster and bioturbated more intensely in softer sediments, regardless of grain size. In **Chapters 3 and 4**, we examined the effects of storm-induced erosion on bivalves, which are vulnerable to storms due to their low mobility. These chapters show how species-specific behaviors (**Chapter 3**) and size-dependent traits (**Chapter 4**) regulate tolerances to extreme sediment erosion, which has consequences for the bivalve population trajectories and long-term species success in a more storm-disturbed intertidal. In **Chapter 5**, we analyzed the concurrent development of the hydrogeomorphology and benthic macrofauna community at three restoration projects in the Netherlands' Western Scheldt. This chapter suggests that while the creation of a low-dynamic habitat can stimulate benthic macrofauna biomass, extremely high silt content, which is typical for low-dynamic habitats, may slow the benthic community development.

Key future research themes following from present studies

The value of including biotic interactions in future experiments

Ecology is the only discipline in the natural sciences that is explicitly about relationships: the science of the interrelationships of organisms and their environment (Eggleton 1939). In this thesis, I focused exclusively on biotic-abiotic interactions, however, these do not cover all the relationships under the ecological umbrella. A second sphere of important relationships that govern animal assemblages are biotic interactions.

Some of the most important biotic interactions (i.e. relationships that organisms have with other organisms) are competition and predation (Wilson 1990, Chase et al. 2002). Intra-specific competition is important for claiming food and space resources (Wilson 1990), such as competition among newly-settled bivalves for food which can lead to low growth and mortality when the recruitment rate is high (Philippart et al. 2003). Inter-specific competition for resources can explain why certain species with similar tolerances do not always coexist. For example, I examined the possible competition between *R. philippinarum* and *C. edule* for habitat and resources which may arise because they are two bivalve species that live at similar depths and eat the same food. Predation is another important biotic interaction. While I examined animal behaviors, like burrowing, in terms of responding to the animal's environment, such behaviors can also be in response to predator threats. For example, bivalves burrow deeper into the sediment to protect themselves from predators, e.g. birds and fish. In addition, biotic interactions are often coupled to the environment (de Fouw et al. 2020). For example, mild winters can lead to low bivalve recruitment on intertidal mudflats, not due to direct climactic effects but because a higher number of predatory shrimp and crab survive the winter and eat the bivalve spat (Beukema & Dekker 2014). Because biotic interactions are important for governing animal assemblages, they should be considered along with biotic-abiotic interactions when examining how assemblages respond to their environment.

Even though biotic interactions are very important in nature, there is a clear advantage to excluding biotic interactions in an experimental setting. When one excludes biotic interactions, it's a lot easier to isolate responses to a stressor which is very important for determining mechanisms and causality. Except for Chapter 5 where I took a multivariate approach to examining the development of a benthic macrofauna community, I focused on single-species responses to environmental drivers. However, in all my experiments I included several species, which means that I could link responses to different behaviors and traits. For example, in the bulk density mesocosm experiment in Chapter 2, I found the same responses across all species (i.e. they all burrowed faster in low bulk density sediment) while other responses were species-specific (i.e. *Macoma balthica* burrowed deeper in low bulk density than in high bulk density sediment). This allowed me to better understand the universality of a response across taxa vs. nuances in a response that is linked to species-specific traits. Such clear mechanistic responses are hard to obtain when one includes biotic interactions in an experiment.

Once mechanistic responses of biota to the environment are isolated, it is important as a next step to include biotic interactions in experiments or observations to better understand how the ecosystem functions a whole. An animal may change their behavior the depending on the community composition. For example the presence of the burrowing crab *Chasmagnathus granulatus* increases the bioturbation intensity of the deposit-feeding polychaete *Laeonereis acuta* because the crab activity causes organic matter to increase within its burrows which is beneficial for the polychaete (Palomo et al. 2003). In addition, biotic interactions may change the response of an organism to a stressor. For example, the erodibility of *C. edule* at the sediment's surface changes depending on their density (Anta et al. 2013), and so density-dependent processes may change *C. edule*'s vulnerability to storm-induced erosion. Because biotic processes can change the way animals respond to their environment, it would be a logical next step to explore these in the context of the responses that I uncovered in this thesis. Investigating whether the vulnerability of benthic macrofauna to storm erosion changes depending on the presence of other animals would be very interesting to explore.

Scaling up disturbances and biotic responses

One must consider the scale of both a disturbance and the response if one wants to obtain a meaningful understanding of abiotic-biotic interactions. In this next section, I will only discuss scale in terms of spatial scale. While temporal scale is also important to consider, it is outside the scope of this thesis. At different spatial scales, the environmental variables which are important in driving macrobenthos community assemblages will change, and this is also true for disturbances.

The biotic response to a disturbance will change depending on the spatial scale of the impact. Storms have the potential to impact one to hundreds of kilometers (Zajac et al. 1998). This spatial scale of impact is several orders of magnitude larger than the one I used in Chapter 3 & 4 flume experiments: a 10 cm wide pot. In addition, spatial scale of storm impact is very unpredictable and can change dramatically on the order of hundreds of meters (de Vet et al. 2020). The recovery process for a *C. edule* population will be very different after a storm that causes a local extinction in 5 m^2 area, vs. one that causes a local extinction in a 50 m^2 area, because the recolonization potential is much larger for a small area than for a big area. Because biotic response to a disturbance will change depending on the scale of the disturbance, it will be important to be better able to predict the spatial scales of storms to better project the biotic responses that I uncovered in this thesis.

In addition, the effect of a disturbance may have a different direction depending on the scale. In Chapter 5, I analyzed the effects of engineering measures which impact two tidal flats. While we saw a positive response of the biota to the creation of low-dynamic habitat, the implementation of groins en masse across the basin could have a negative response to the estuary overall, by steepening the main channel of the Western Scheldt (Luan et al. 2018), which could restrict habitat for benthic macrofauna and have long-term negative effects (Cozzoli et al. 2017). In addition, the masse implementation of low-dynamic habitat restoration could homogenize habitat, leading to similar benthic macrofauna communities, which could decrease ecosystem-scale resilience on the whole estuary (Ellingsen et al. 2007). And so again, it is important to consider how the biotic response changes depending on the scale of impact.

Future outlook: how do we increase the resilience of intertidal ecosystems against a more extreme climate?

Ecosystem resilience stems from biodiversity and functional redundancy

In this thesis, I examined the response of benthic macrofauna to extreme and/or disturbed sediment conditions. The response of a species or individual indicates how resilient it may be to a certain stressors or disturbances. While specific traits and behaviors can confer resilience (the ability to resist and recover from stress) onto an individual or population against a disturbance, I wondered how the concept of resilience is transferred from individual to ecosystem. Though the origins of ecosystem resilience have been long debated, it is widely accepted that functional redundancy within biotic assemblages is a key contributor. At an ecosystem level, resilience is largely conferred by species richness (Yachi & Loreau 1999), and more recently, by functional redundancy (Oliver et al. 2015). Besides providing functional redundancy, high biodiversity has a stabilizing effect on ecosystems faced with disturbances because asynchrony in the response of species to disturbances, regardless of their function (Loreau & de Mazancourt 2013).

An ecosystem will have greater resilience if it contains multiple species which perform the same function. For example, in Chapter 3, I consider the theoretical competition between *C. edule* and *R. philippinarum*. The two species are functionally similar: the two are filter-feeding bivalves that live at similar depths (Zwarts & Wanink 1989, Lee 1996). Because *R. philippinarum* has a greater tolerance for heat than *C. edule*, even though it may be more vulnerable to storms in the future than *C. edule*, perhaps a much warmer environment in the Scheldt means that *R. philippinarum* may take over *C. edule's* niche. From an ecosystem perspective, the replacement of one species by another may mean that, on a population level, *C. edule* was less resilient than *R. philippinarum*, but the ecosystem was resilient overall because it retained a species that performed a similar function *C. edule*. However, if the stressors become too great, an ecosystem might lose this functional group (filter-feeding bivalves) altogether. But all in all, an ecosystem with both *C. edule* and *R. philippinarum* would be more resilient than one with only *C. edule*, because, as I show in Chapter 3, the two species have different tolerances and strategies to cope with extreme disturbances. And so, biodiversity and species with functional redundancy is something to promote within an ecosystem to increase its resilience against environmental disturbances. From a resilience perspective, having invasive species like *R. philippinarum* enter the Scheldt can be seen as a blessing in disguise, especially if it coexists with species with similar functions, like *C. edule*.

To increase resilience of intertidal benthic macrofauna, we need greater habitat quantity, connectivity, and heterogeneity.

An individual's environment greatly affects its resilience. Unsuitable habitat induces stress in an animals and cumulative environmental stressors decrease an animal's ability to tolerate environmental disturbances. For example, *C. edule*'s ability to recover from heat stress was weakened when living in salinities outside of its preferred range (Zhou et al, submitted). On the other hand, living on the edge of one's niche can induce physiological adjustments to stressful conditions which may be an advantage for climate change. For example, seagrass populations living on the edge of their temperature niche may be more tolerant of warming temperatures than seagrass in more suitable conditions due to their local adaptations to higher temperatures (DuBois et al. 2022).

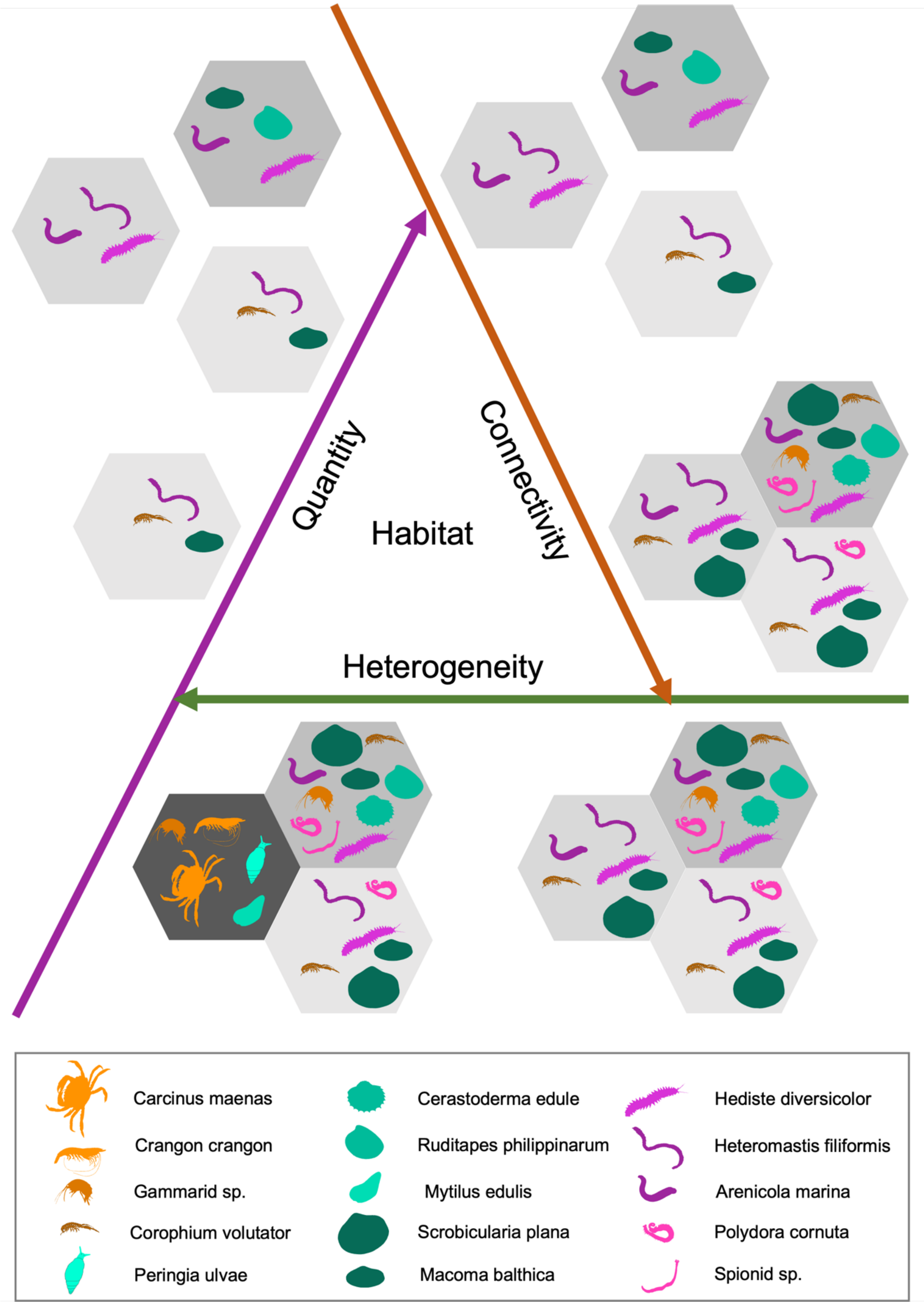
Quantity
Habitat
Connectivity
Heterogeneity
Carcinus maenas
Crangon crangon
Gammarid sp.
Corophium volutator
Peringia ulvae
Cerastoderma edule
Ruditapes philippinarum
Mytilus edulis
Scrobicularia plana
Macoma balthica
Hediste diversicolor
Heteromastis filiformis
Arenicola marina
Polydora cornuta
Spionid sp.

Figure 2: Schematic of how habitat quantity, connectivity, and heterogeneity improve the resilience of the macrobenthic community by promoting species diversity and functional redundancy. Each of the three axes builds upon the previous one, starting at the bottom left corner (low habitat quantity, connectivity, and heterogeneity). In each habitat hexagon, I place species that are commonly found together in the Scheldt intertidal (silhouettes from www.phylopic.org). The colors of the macrobenthic invertebrates indicate their broad taxonomic group: crustaceans (orange), bivalves (green), polychaetes (purple). The closer the species are together in color, the more similar their function. For example, though *S. plana* is larger and lives deeper than *M. balthica*, both species are slow moving, deposit feeding bivalves, and perform similar bioturbation functions (see Chapter 2 for more details on bioturbation modes).

Just as the environment affects an individual's resilience, it also affects the resilience of an ecosystem. Because my thesis dealt with the manipulation of benthic macrofauna's sedimentary habitat to induce a (often negative) response in individuals (in a small-scale experimental setting in Chapters 2, 3, and 4; and in a large-scale experimental setting in Chapter 5), I thought it would be appropriate to end this thesis by considering how we can manipulate intertidal habitat on a large-scale to induce a positive response in intertidal benthic macrofauna. Specifically, I wanted to discuss three habitat attributes that we can manipulate on a landscape scale to increase the resilience of intertidal benthic macrofauna assemblages: quantity, connectivity, and heterogeneity.

(High-quality) habitat quantity

First, and probably most obviously, to increase the resilience of benthic intertidal communities, one must increase the quantity of available, high-quality habitat. Habitat degradation (decrease in habitat quality) and habitat loss greatly weakens ecosystems, and in particular reduces species richness (de Juan & Hewitt 2011), which negatively impacts functional redundancy (Maure et al. 2018). When discussing increasing habitat availability, quantity and quality go hand in hand. Habitat quality is challenging to define as the suitability of the habitat will change species to species. Hall et al. (1997) define habitat quality as the ability of the environment to provide conditions appropriate for individual and population persistence. For example, high hydrodynamics provide low-quality habitat for certain bivalve species as high-dynamic conditions impede their ability to recruit (Bouma et al. 2001). Indeed, as I found in Chapter 4, extreme incidence of storms may lead to local extinction of vulnerable slow-moving bivalves, rendering wave-exposed, high-dynamic locations unsuitable for these species. Furthermore, the quality of a habitat will change species to species, which makes it difficult to assess. In Chapter 5, I concluded that the restoration measures increased the habitat quality in the area between the groins at Buitendijks as we observed a big increase in the biomass of benthic macrofauna, with the caveat that habitat quality was increased only for the animals that were particularly suited to low-dynamic conditions.

Increasing the extent of high-quality intertidal habitat means increasing the overall animal reserves to facilitate the recovery of collapsed local populations. Increasing habitat quantity can also promote the spatial spread of a species and its overall abundances. If a species is spatially widespread, it will have an easier time recolonizing after a small-scale disturbance (Greenfield et al. 2016). Finally, increasing high-quality habitat availability will also increase habitat connectivity, the second ingredient in making intertidal benthic macrofauna more resilient.

Habitat connectivity

Habitat fragmentation decreases species richness (Goodsell & Connell 2002). In addition, spatial connectivity is important for facilitating recovery and recolonization after a disturbance. Because most benthic species have a pelagic larval phase, connectivity between populations is ensured through pelagic dispersal. The degree to which the population of benthic macrofauna self-recruits or is supplied by outside areas can regulate population persistence (Cowen & Sponaugle 2009). Species with high fecundity or larval tidal transport lead to short recovery times after disturbances (Giménez et al. 2020). For example, a sea star with a pelagic larval phase, *Pisaster ochraceus*, had a much higher dispersal potential and recolonized a disturbed 100 kilometer-wide area within a year, whereas *Leptasterias aequalis*, a sea star without a pelagic larval phase, failed to return to the area after three years (Schiebelhut et al. 2022). Thus, maintaining populations of species which have lower dispersal potential will require higher habitat connectivity, either through corridors or the removal of physical barriers. Finally, connectivity changes depending on the scale of examination (Wiens 1989). For example, local populations within a tidal flat may be open and exchanging individuals and recruits, but a tidal basin may be closed from the landscape's metapopulation if the basin inlet is too small. Understanding how connectivity to a restored habitat is facilitated or halted by marine currents (Cowen & Sponaugle 2009) will be important for increasing overall ecosystem resilience, and should be taken into account during large-scale restoration planning.

Habitat heterogeneity

And lastly, habitat heterogeneity has long been theorized to increase biodiversity (MacArthur & Wilson 1967, Hewitt et al. 2005), because a heterogeneous landscape supports a wider variety species, especially at the landscape scale (Goodsell & Connell 2002). Habitat heterogeneity buffers against climate change because different habitats will be differently impacted by disturbances. I discussed in Chapter 3 and 4 that exposed, high-dynamic habitat may be more vulnerable to stormy conditions than sheltered, low-dynamic habitat. However, perhaps exposed, high-dynamic habitat may be less vulnerable to other disturbances, like hypoxia, because of greater water mixing than in low-dynamic waters (Lin et al. 2006). Finally, a heterogeneous landscape increases the likelihood of containing refugia, which will be necessary to help the survival of individuals during disturbances. For example, shaded microhabitat can found to help mussels survive in the intertidal during a hot summer (Li et al. 2021) which can contribute to populations persistence (Han et al. 2020).

Conclusion

Benthic macrofauna are well-suited to their environment, which means that they are well-suited to high variability in their habitat. Perhaps this means that in a more extreme climactic future, benthic macrofauna will be more resilient than other types of species assemblages in environments which are less naturally variable. And so, maybe we ought to be optimistic about the future of benthic macrofauna in tidal flats. But whether or not that is the case, we can increase the resilience of benthic macrofauna, and the intertidal ecosystem, to future climactic extremes by manipulative expansion of their habitat (i.e. through restoration projects). To increase their resilience, we must focus on increasing the amount of heterogeneous, interconnected habitat available to intertidal benthic macrofauna. However, sea level rise and anthropogenic activity are a threat to the most basic of all resilience requirements: habitat quantity. This emphasizes the need for protection and restoration efforts can counterbalance these impacts. Such efforts will greatly help to increase the resilience of intertidal benthic macrofauna in a more climactically extreme future, as long as these are applied in judicious and committed manner.


A-TCHA!

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Curriculum vitae

Lauren Wiesebron was born in Levallois-Perret, France, on November 30th, 1989. Lauren is a marine ecologist and is most interested in how animal communities are shaped by their environment. She has had a diverse scientific career and prior to her PhD, she studied trophic dynamics in forage fish, salmon migration, tidal energy and extreme events, nutrient cycling in the Arctic, coral reef MPAs in Madagascar. She did her PhD at the Netherlands Institute of Ocean Research (NIOZ-Yerseke) from 2018-2023 where she researched how sediment dynamics drive the establishment and survival of intertidal benthic communities. She took a sabbatical in 2019 to do research in Chile under a Fulbright Award to study trophic linkages between forage fish and zooplankton in Northern Patagonia. In 2022, she took part in the SEES cruise to Svalbard to study seaweed adaptations to the warming climate. She is moving to Oslo and has applied for a Rubicon grant to work on the effects of hypoxia on zooplankton behavior in fjords. Aside from science, she is an enthusiastic reader, weaver of self-dyed yarns, balcony gardener, and writer of fantastical fiction (hopefully coming to a bookstore near you in 2025). You can follow her scientific goings-on at www.ecologist.laurenwiesebron.com and her author updates at www.laurenwiesebron.com.

List of publications

L.E. Wiesebron, L. Teeuw, J. van Dalen, L. van Ijzerloo, K. Troost, B. Walles, T. Ysebaert, T. Bouma, Contrasting strategies to cope with storm-induced erosion events: a flume study comparing a native vs. introduced bivalve; Limnology and Oceanography (2022) doi:10.1002/lno.12223

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