

Benthic macrofauna responses to extreme weather events

Towards predicting the effects of climate change

Zhengquan Zhou

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Benthic macrofauna responses to extreme weather events

Towards predicting the effects of climate change

De reactie van benthische macrofauna op extreme weersomstandigheden

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(met een samenvatting in het Nederlands)

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Summary

Extreme weather events are increasing in intensity, duration, and frequency, and threatening tidal flat ecosystems due to global climate change. Benthic macrofauna plays essential roles in biogeomorphic feedback as ecosystem engineers, yet they are prone to extreme environmental fluctuations in storms and drying tidal regimes. Moreover, modern globalization has accelerated the invasion of introduced species, which compete with native species for natural resources. Therefore, studying how benthic macrofauna responds to climate-change-induced extreme weather events may convey an essential message on short-term equilibrium and the long-term development of tidal flat ecosystems.

A mesocosm system was designed and customized in the lab to mimic the heatwaves with contrasting magnitudes and durations on tidal flats. Simulated heatwaves were imposed on the model bioturbator species *Cerastoderma edule* living in different micro-topographies and sediment types, to study the response of bioturbation activities under thermal stress (Chapters 2 & 3). Besides individual-level response, an in-situ experiment was applied to study the effects of repeated storm events on benthic community structure, using a raking treatment to mimic storm-induced sediment disturbance (Chapter 4). Moreover, the effects of compound extreme weather events on species shift were studied by imposing different salinity settings and heatwave profiles on the native *C. edule* and an introduced bivalve *Ruditapes philippinarum* (Chapters 5).

Macrobenthos' response on the individual level is categorized into the “fight, flight, or freeze” framework. Bioturbators increase metabolic rates to “fight” against the thermal stress and maintain optimal physiological conditions (Chapters 2); they burrowed deeper during low tide to escape from (“flight”) the thermal stress, thereby causing more sediment mixings (Chapters 2 & 3); they reduce activity and metabolism (“freeze”) to maintain basic physiological functions under acute extreme stress or long-term intermediate stress (Chapter 5). On the community level, internal environmental stress can select species with specific biological traits, while species with unfitting traits decrease in abundance (Chapter 4). Moreover, compound extreme weather events may create “disturbance-driven establishing windows” that benefit the introduced species to overtake native species (Chapter 5).

Samenvatting

Als gevolg van de wereldwijde klimaatverandering nemen extreme weersomstandigheden toe in intensiteit, duur en frequentie en bedreigen het voortbestaan van intergetijdensystemen. Hierbij spelen benthische macrofauna een essentiële rol met hun bio-geomorfologische zelforganisatie als biobouwer, maar daarnaast zijn zij gevoelig voor de extreme in stormen en droogtetijden. Bovendien heeft de globalisering en klimaatverandering de invasie van invasieve soorten versneld, welke concurreren met inheemse soorten. Het bestuderen van de reactie van bodemdiergemeenschappen op extreme weersomstandigheden is daarmee cruciaal om de korte termijn dynamiek en lange termijn ontwikkeling van intergetijdengebieden te begrijpen.

De invloed van hittegolven met verschillende magnitudes en duur is onderzocht in grootschalige laboratoriumexperimenten. Hierbij zijn kokkels (*Cerastoderma edule*) als modelsoort blootgesteld aan de gesimuleerde hittegolven, waarbij de kokkels leefde in verschillende microtopografieën en sedimenttypen om de reactie van hun bioturbatie activiteiten onder thermische stress te bestuderen (hoofdstuk 2 en 3). Naast de reactie op individueel niveau werd een veldexperiment toegepast om de effecten van herhaalde stormen op de structuur van de bodemdiergemeenschap te bestuderen, waarbij een fysieke verstoring doormiddel van omploegen werd gebruikt om storm geïnduceerde sedimentdynamiek na te bootsen (hoofdstuk 4). Aanvullend is de invloed van een combinatie aan veranderingen in saliniteit en temperatuurstress op de overlevingskans onderzocht voor de inheemse kokkels en een geïntroduceerde tweekleppige Filipijnse tapijtshell (*Ruditapes philippinarum*) (hoofdstuk 5).

De reactie van bodemdieren groter dan 0.5 mm kan verdeeld worden in drie categorieën: **vechten**, **vluchten** of **bevrozen**. Bioturbatoren verhoogde het metabolische niveau om te **vechten** tegen temperatuurstress en daarbij de optimale fysiologische omstandigheden te behouden (hoofdstuk 2), daarnaast **vluchten** zij naar diepere lagen tijdens laagtij en zorgde daarbij voor een toegenomen bioturbatie (hoofdstuk 2 en 3). Echter, onder acute extreme stress of langdurige intermediaire stress **bevrozen** zij de activiteit en metabolisme om de basis fysiologische functies te behouden (hoofdstuk 5). Op gemeenschapsniveau kan langdurige stress zorgen voor soorten met specifieke biologische eigenschappen, terwijl soorten met ongeschikte eigenschappen afnemen in aantal (hoofdstuk 4). Bovendien kan een combinatie van extreme weersomstandigheden ertoe leiden dat invasieve soorten de inheemse soorten verdringen dankzij de verstoring-gedreven vesting kansen (hoofdstuk 5).



Chapter 1 General introduction

Zhengquan Zhou

1.1 The tidal flat ecosystem: being dynamic is the normal status

Have you been to the mud or sand flats near the dike, and what do you see there? Waves, seagrass, algae, or little animals crawling in the mud? Imagine that you are one of the habitats on tidal flats, just like a crab, cockle, or lugworm. What would you experience every day? To search for food, you may need to go through marshes that are tens of your height. And better hurry because you need to lower the risk of dehydration under strong winds or high temperatures. Moreover, it will be very different when the high tides come (again, tens of your height): everything is submerged in the water with elevated water pressure and flushing currents dragging you back and forth. Difficult for us to imagine, yet it is normal for organisms to cope with the constantly changing environment on tidal flats (*see* Fig. 1.1 for views on the tidal flat).

Benthic organisms (also called *benthos*) refer to those little animals living in the tidal flat; they successfully adapt to the dynamic tidal flat environment (Chowdhury et al., 2022; Sukumaran et al., 2021; van der Wal et al., 2017). Little as they are, benthic animals take active parts in the feedback between seawater action and sediment mixing processes due to their large numbers. For example, the mud scud *Corophium volutator* is an abundant species in intertidal ecosystems along the North-Atlantic, and population densities easily reach 100,000 to 140,000 ind./m² during summertime (Möller & Rosenberg, 1982). The process of how sediments are affected by organisms living inside is called *bioturbation*, and these organisms are called *bioturbators* (Kristensen et al., 2012). Bioturbation activities closely correlate to the short-term dynamic of tidal flats, such as sediment erosion, and may affect the long-term landscape formation of tidal flats (Mermillod-Blondin & Rosenberg, 2006; Teal et al., 2008). The interplay between organisms and landscape development is defined as *biogeomorphology*. Studying biogeomorphology is essential to understanding the dynamics of tidal flats and preserving their valuable ecosystem services (Arlinghaus et al., 2022; Corenblit et al., 2011).

1.2 Benthos as ecosystem engineers of tidal flats

Benthic organisms actively change the sediment properties and control the resource availability for other organisms through their unique living styles (Bremner et al., 2006a) (Fig. 1.3). This makes them key *ecosystem engineers* on tidal flats (Wright & Jones, 2006). According to the ways how organisms change the physical and chemical properties of sediments, ecosystem engineering animals on tidal flats can be divided into the following functional groups (Kristensen et al., 2012):

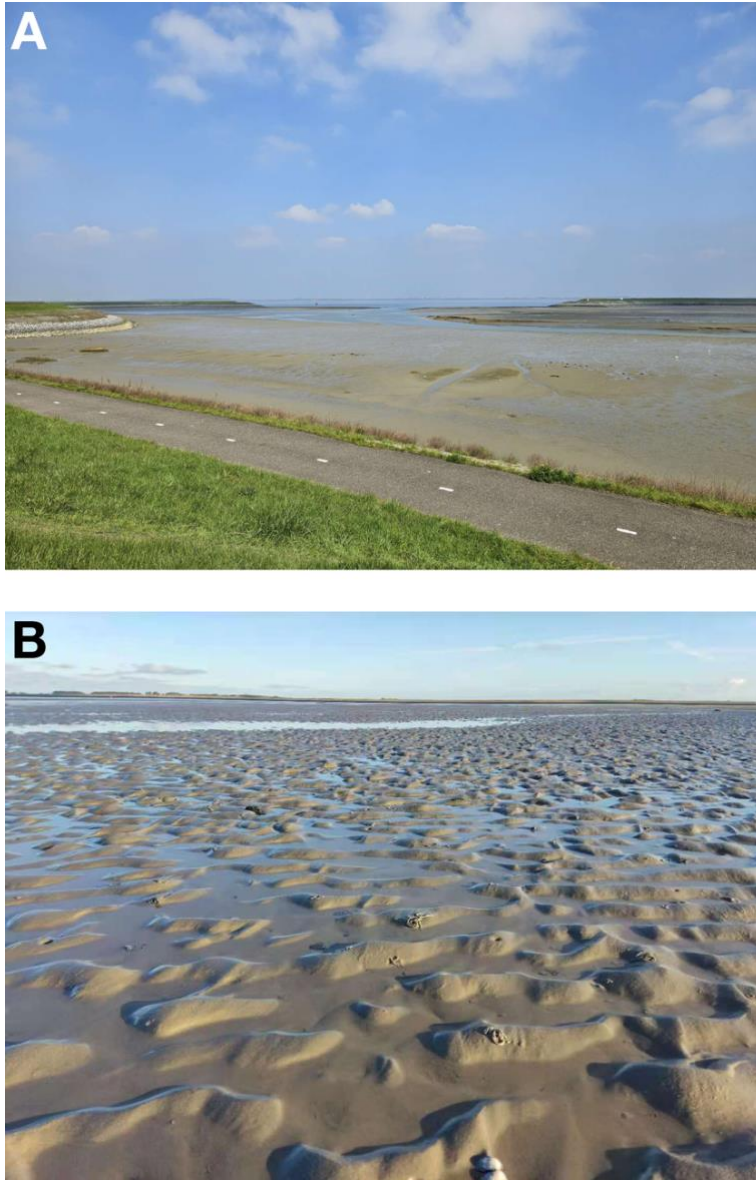


Figure 1.1 Tidal flats in the Netherlands. (A) a developing mud flat in a newly opened polder area at Ossensisse. (B) a sand flat dominated by cockles and lugworms at Hooge Platen. Photos taken by Zhengquan Zhou.

Biodiffusers - animals cause random and constant sediment mixing over short distances. Many diffusers are deposit feeders that weaken the stability of sediments. Therefore, they are also named as *destabilizers*.

Bivalves such as *Scrobicularia plana* (Fig. 1.3A) and *Cerastoderma edule* are typical biodiffusers (Fig. 1.3B). The crustacean amphipods *Corophium volutator* and the worm *Hediste diversicolor* (Fig. 1.3C) are also well-known biodiffusers that can actively change the physical properties of sediments. Moreover, *H. diversicolor* is a gallery diffuser that can build complex burrows that connect deeper sediments with the surface water and air (Scaps, 2002) (Fig. 1.3D).

Regenerators - animals constantly dig and maintain their burrows without changing the average grain size at the surface. This means that regenerators only transfer sediments from the deeper layers back to the surface but do not “digest” them, while the sediments maintain the average grain size.

The shore crab *Carcinus maenas* is a typical regenerator on European coasts (Fig. 1.3E). While digging and foraging, *C. maenas* creates pits or depressions in the surface sediment. These “feeding pits” reduce the sediment stability and potentially cause mortality or removal of non-targeted species by being accidentally exposed to other predators (Botto & Iribarne, 1999; Escapa et al., 2004).

Upward and downward conveyors - vertically oriented animals transport particles upward from the deeper layer or downward from the sediment surface. There is a noticeable difference in the effects of diffusers and regenerators versus conveyors: diffusers and regenerators only transport sediment, but conveyors ingest sediment particles and alter the chemical characteristics, such as binding properties, thus changing the stability of the sediment environment.

The lugworm *Arenicola marina* is a typical upward conveyer at the northwest European coasts (Fig. 1.3F). *A. marina* destabilizes the sediment by creating J- or U- shaped burrows in 20 to 40 cm deep sediments. While burrowing, they swallow fine sediments, ingest the organic matter, and defecate fecal strings at the sediment surface. These continuous reworking activities can gradually deplete fine particulate matter in a bioturbated sediment layer (Wendelboe et al., 2013).

Stabilizers - organisms that increase sediment stability by creating complex, three-dimensional structures on top of the sediment surface, such as reefs or dense patches. They affect biogeochemical resources mainly through bioturbation and bioirrigation processes (Reise 2002;

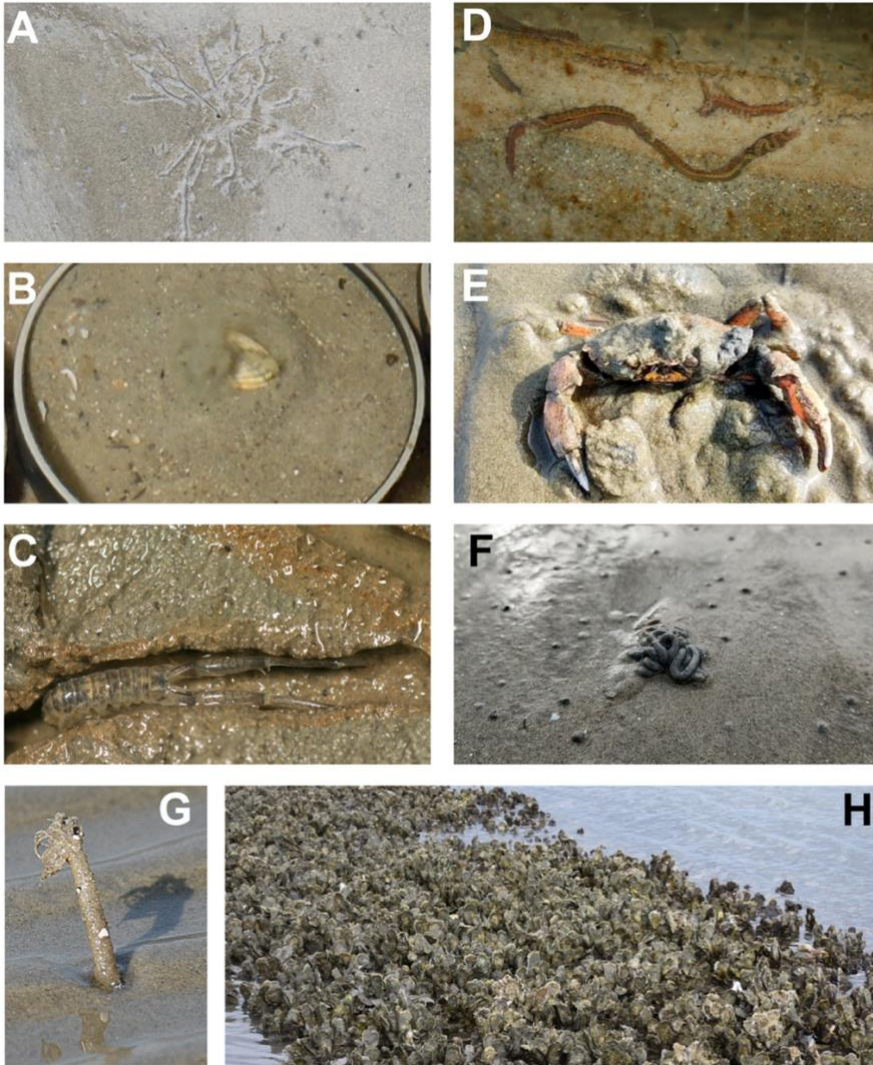


Figure 1.3 Bioturbation outcomes from several animal activities on tidal flats. (A) the feeding traces left by a *Scrobicularia plana*; (B) the burrowing activity of a *Cerastoderma edule* during a mesocosm experiment; (C) a *Corophium volutator* digging “tunnels” in sediments (by Misjel Decleer, 2010); (D) worms *Hediste diversicolor* crawling in the sediments (by Adrian Bischoff-Lang, 2020); (E) a crab *Carcinus maenas* burrowing itself on a sand flat; (F) the pseudo-feces of a lugworm *Arenicola marina*; (G) the extended tube of a sand mason worm *Lanice conchilega* (by Matthias Buschmann, 2007); (H) an oyster reef built by *Crassostrea virginica* (by Linda Walters).

Ciutat et al. 2007; Montserrat et al. 2009), but in high densities they also can increase sediment stability (Donadi et al. 2013).

The reef-building oysters Ostreidae (Fig. 1.3H) and sand mason worms *Lanice conchilega* (Fig. 1.3G) are well-known examples for ecosystem stabilizers. Oyster reefs not only protect the tidal flats underneath their footprint, but also extend their protection beyond the reef's boundaries (Walles et al., 2015). The patches formed by *Lanice conchilega* increase the bed shear stress in front of the patch and reduce the bed shear stress within the patch (Borsje et al., 2014).

1.3 Impacts of global climate change on tidal flats biogeomorphology

Tidal flats constantly evolve due to dynamic feedback between biological and physical factors. However, the physical environmental drivers may change significantly in the years to come due to climate change. Climate change scenarios suggest more frequent and/or prolonged extreme weather conditions, such as heatwaves, storms, and flash floods (see a heatwaves example in Fig. 1.2). Sometimes, a single weather event is not extreme by itself, while if it may co-occur with other weather events, it thereby may result in an extreme condition. These combinations of multiple weather events contributing to extreme environmental hazards are named *compound weather events*. The effects of these extreme events can be particularly strong on benthic organisms living in higher elevations on tidal flats, where they are exposed to environmental changes due to the longer low-tide time (Vafeiadou et al., 2018).

Climate change effects on the tidal flat and its benthic communities may affect the ecosystem services these systems provide, such as carbon sequestration, wave attenuation, coastline stabilization, seafood production and supporting a unique biodiversity including migratory birds. The tidal flat development also affects the development of adjacent ecosystems such as salt marshes that can effectively protect coastal regions by attenuating waves, even under extreme conditions. The existence of expansive healthy salt marshes in coastal ecosystems typically requires vast and stable tidal flats fronting the marsh (Fig. 1.1A&B).

Unfortunately, tidal flats have been reported to decline under the threat of sea level rise and global warming (Murray et al., 2019). Shrinkage of tidal flats may initiate the “coastal squeeze” by shrinking the space (including the habitat for salt marshes) between seawater and artificial concrete sea walls. Hence, deepening the current understanding of how tidal flat biogeomorphology responds to climate change scenarios is urgently needed to preserve their valuable ecosystem services. Understanding the biogeomorphology of tidal flats starts with understanding the effect of climate change on ecosystem engineering by the benthic community and the persistence of these communities.



Figure 1.2 Effects of heatwaves on tidal flats during and after the 2022 summertime. (A) cracked dry sediments on a mud flat at Zuidgords, the Netherlands, in August 2022. (B) dead bivalve shells on a sand flat near Ossensisse, the Netherlands, in October 2022. Photos taken by Zhengquan Zhou.

1.4 Response strategies: fight, flight, or freeze

It is hard for benthic organisms on tidal flats to reverse the increasing global trend of extreme (compound) weather events. Therefore, these organisms must cope with these changes by either “fight” or “flight” responses: i.e., either cope with or escape from the environmental stress. The stress induced by climate change can be acute or chronic, whereas chronic stress weakens the ability to adapt to acute stress (Herbert et al., 2018; Sleight et al., 2018). If the environmental variation surpasses animals’ tolerant thresholds, either in duration or intensity, they will be shocked and “freeze”: they can do nothing and wait until the threats passing by. This “freeze” response may lead to mass mortality events on tidal flats (Coma et al., 2009; McDowell & Sousa, 2019; Seuront et al., 2019).

As benthic species connect closely through biological networks on food webs, either changing response strategies or suffering from massive death will impact the relationship between species and, thereby, the overall ecosystem functioning of tidal flats (Birchenough et al., 2015; Mouritsen et al., 2018). Further, landscape development can be affected through biogeomorphic feedback under the altered species relationship and community function (Cumming, 2011; D’Alpaos et al., 2012).

1.5 Knowledge gap and research questions

Given the ongoing climate change scenarios and the global decline of tidal flat areas, I mainly question how bioturbators respond to climate-change-induced extreme weather events, from individual behavior to community characteristics. Despite the numerous studies on (1) the impact of climate change on benthic animals, including their physiological and behavioral responses to warming seawater temperature (Garrahou et al., 2022; Zhang et al., 2020), altered hydrodynamics (Shi et al., 2021), ocean acidification (Pörtner, 2008), sea-level-rise and coastal squeeze (Alexander et al., 2012; Fujii, 2007), and on (2) the effects of bioturbating activities on sediment mixing and stability, such as critical shear stress (Li et al., 2017; Shi et al., 2020), suspended sediment concentration (de Smit et al., 2021; Soissons et al., 2019), sediment surface roughness (Dairain et al., 2020), and sediment particle mixings (Montserrat et al., 2009), the relationship between these two processes remains inadequately explored. As a result, there is lack of insight into how bioturbation by bioturbators respond to climate change and how this affects biogeomorphic dynamics.

In the future, climate change will increasingly expose tidal flats to more extreme weather conditions. Benthic organisms on tidal flats must decide whether to *fight or flight*. However, it is still poorly known about benthos’ behavioral strategies responding to non-lethal stress induced by climate change. Therefore, it is necessary to study **Question 1: Can extreme weather events change the**

Chapter 1

benthic organisms' bioturbation behavior? If so, what are the potential effects on tidal flat biogeomorphology (Chapter 2, Fig. 1.4, ②)?

Global climate change not only boosts the intensity of extreme weather events but also amplifies their temporal dynamics, such as frequency and duration. For example, the frequency of global marine heatwaves increased by 34% in 1987-2016 compared to 1925-1954 (Oliver et al. 2018). Thus, we intend to study **Question 2: How do the temporal dynamics of extreme weather events affect the organisms' bioturbating behaviors? Does the behavioral change affect the sediment mixing condition (Chapter 3, Fig 1.4, ③)?**

The previous two questions focus on the individual-level response, while there are various biogeomorphic feedbacks on community levels which make it more complex the response of the benthos community to disturbance.

Numerous studies have demonstrated that the burrowing activities of macrofauna can have a significant impact on sediment dynamics. By reducing the critical erosion thresholds and increasing sediment resuspension, bioturbation has been shown to play an essential role in regulating the sediment transport (Ciutat et al., 2006; Cozzoli et al., 2019; Li et al., 2017). However, the increased sediment dynamics caused by storms can substantially reduce the abundance of macrofauna (de Vet et al., 2020; Shi et al., 2021). Despite this, there has been limited research on the relationship between sediment dynamics and species' biological traits, and whether changes in sediment dynamics can trigger changes in macrofauna biological traits. Therefore, it is crucial to explore **Question 3: What is the biogeomorphic relationship between sediment dynamics and benthos composition, and how can this relationship affect the response of benthic communities to extreme weather events (Chapter 4, Fig 1.4, ④)?**

Despite the global climate change that threatens tidal flat organisms, the increasing pace of globalization supercharges the species' transportation across the continents. The introduced species are usually more capable of adapting to broad environmental changes than native species and tend to rapidly occupy ecological niches cleared by abiotic pressures (Gallardo et al., 2016). Many studies predict that tidal flat benthic communities will experience gradual succession under the impacts of climate change (Solan et al., 2020). Yet it can be expected that the short-term extreme weather events may accelerate the species shift by benefiting the introduced species by sterilizing the native species, during which niches are cleared and open. Therefore, it is intriguing to address **Question 4: How do native and introduced species respond to extreme weather events? Can extreme weather events induce benthic community succession on tidal flats (Chapter 5, Fig 1.4, ⑤)?**

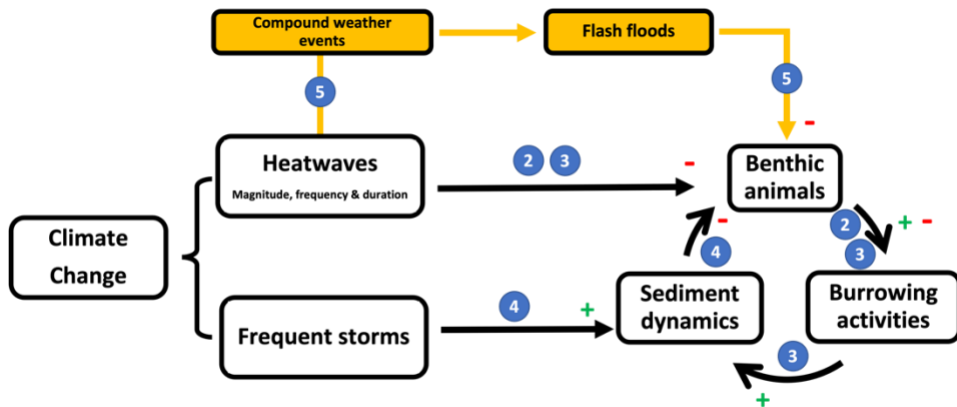


Figure 1.4 Research diagrams and thesis chapters. The chapter numbers are marked on each routine. The red “-” means negative effects, and the green “+” means positive effects. The extreme weather events listed here (heatwaves, frequent storms, and flash floods) are the focal model events in the current thesis, though there are more extreme weather events caused by climate change.

1.6 Thesis outlines

In the following chapters, we study how climate change affects the biogeomorphic process on tidal flats. We focus on the effects of extreme weather events on benthic animal activity and community functions, and the above four questions were addressed using laboratory and field experiments.

Benthic animals’ activities initiate of bioturbation process in tidal flat sediments. Therefore, it is essential to study whether extreme weather events can change the bioturbating activities of benthic animals. To directly measure bioturbators’ movement under heatwaves, in **Chapter 2 (regarding Question 1)**, we applied a mesocosm experiment using the well-known bioturbator species *C. edule*. Different temperature regimes and micro-topographies were mimicked in a newly designed mesocosm system with regular tidal shifts. We also tested a low-cost method using cotton threads to measure the vertical burrowing behaviors of shellfish, and successfully applied it again in Chapters 3 and 5.

In **Chapter 3 (regarding Question 2)**, we extrapolate the extreme weather events to scenarios with more internal variations, such as different frequencies and durations. We summarize benthic organisms’ response strategies as two steps: *i*) more horizontal movements to search for less stressful locations; *ii*) burrowing deeper and hiding in the shelters. Moreover, we measured the bioturbation

Chapter 1

effects under different heatwave frequencies using the luminophore particles. Further, we discussed how these conclusions fit other animals in different habitats.

After examining individual-level effects in previous chapters, we focus on the community level in **Chapter 4 (regarding Question 3)**. Using the tidal mud flat as our model ecosystem, we investigate the impact of storm events on benthic community structure. To quantify the response of macrobenthos to repeated environmental disturbance, we increase sediment dynamics in-situ by employing a raking treatment. In our discussion, we analyze the relationship between sediment dynamics and the response of the benthic community. We also predict how community structure might evolve under more frequent disturbances induced by climate change-related storms.

In **Chapter 5 (regarding Question 4)**, we explore further the effects of compound extreme weather events on species shift using a mesocosm experiment in combination with historical data for population dynamics of native and introduced species. We propose that compound extreme weather events will shape an invasion gap for the introduced species to overtake the native species.



Chapter 2 Thermal stress affects bioturbators' burrowing behavior: a mesocosm experiment on common cockles (*Cerastoderma edule*)

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Chapter 2

Abstract

The intensity of marine heatwaves is increasing due to climate change. Heatwaves may affect macroinvertebrates' bioturbating behavior in intertidal areas, thereby altering the deposition-erosion balance at tidal flats. Moreover, small-scale topographic features on tidal flats can create tidal pools during the low tide, thus changing the heat capacity of tidal flats. These pools could then potentially operate as refuge environments during marine heatwaves. We studied behavior responses to heat waves using the well-known bioturbating cockle *Cerastoderma edule* as a model species. Different temperature regimes (i.e., fluctuating between 20 to 40 °C) and micro-topographies (i.e., presence vs. absence of tidal water pools) were mimicked in a mesocosm experiment with regular tidal regimes. Our results demonstrate that behavioral responses to heat stress strongly depend on the site-specific morphological features. Cockles covered by shallow water pools moved up when exposed to thermal stress, while burrowing deeper into the sediment in the absence of water pools. But in both cases, their migratory behavior increased under heat stress compared to regular ambient treatments. Moreover, long-term cumulative heat stress increased cockles' respiration rates and decreased their health conditions, causing mass mortality after four weeks of gradually increasing heat exposure. Overall, the present findings provide the first insights into how bioturbating behavior on tidal flats may change in response to global warming.

Keywords

marine heatwaves, bioturbators, tidal flats, tidal water pools, surface sediment temperature.

2.1 Introduction

Intertidal ecosystems, such as tidal flats and salt marshes, are highly valuable given their unique ecological and socio-economical functions (Barbier et al., 2011; Costanza et al., 1997). These functions include offering habitats to unique plants and benthic invertebrates (Barbier et al., 2011; Walles et al., 2015), hosting migratory birds (Horn et al., 2020; Mu & Wilcove, 2020), providing nurseries for economically important species (Beukema, 1992; Bezerra et al., 2017), carbon sequestration (Chmura et al., 2003; Herbert et al., 2018; Macreadie et al., 2021), and contributing to coastal protection (Barbier et al., 2008; Möller et al., 2014; Shepard et al., 2011; Zhu et al., 2020). Whereas salt marshes and mangroves are increasingly regarded as an opportunity to realize cost-effective flood-defence systems under climate change (Arkema et al., 2015; Narayan et al., 2016; Zhu et al., 2020), it is increasingly realized that they cannot exist without vast convex-shaped tidal flats fronting them (e.g., see Bouma et al., 2016; Mariotti & Fagherazzi, 2013; van Bijsterveldt et al., 2020). The tidal flat morphology is also recognized as being of key importance for birds feeding on benthos, as the inundation time determines how many hours birds are able to collect food (Hughes, 2004). Unfortunately, tidal flats have been reported to be globally in decline (Murray et al., 2019). Sustainably managing intertidal ecosystems for their unique ecological and socio-economical functions requires a fundamental understanding of the key processes driving the morphology of tidal flats under climate change.

Benthic organisms can profoundly affect the long-term, large-scale morphological development of tidal systems (Brückner et al., 2021), by altering the critical erosion thresholds of consolidated sediments (Cuzzoli et al., 2021; Grabowski et al., 2011, 2011; Widdows & Brinsley, 2002; Willows et al., 1998). The key process by which organisms enhance the erodibility of tidal flats is called *bioturbation* (Darwin, 1897; Kristensen et al., 2012). Bioturbators are widespread across tidal flats, with their distribution determined by multiple environmental factors such as inundation time (Gribsholt & Kristensen, 2003), current velocity (Cuzzoli et al., 2014), grain size (McGonigle & Collier, 2014), and sediment dynamics (Khedhri et al., 2016). Many bioturbators create biogenic fluff layers over consolidated sediment matrixes, with low critical thresholds for erosion (Cuzzoli et al., 2019; Dairain, et al., 2020; Orvain et al., 2003, 2006). However, bioturbation activities are essential for species survival, as they are related to feeding activity and burrowing to escape predation (Cuzzoli et al., 2019; Friedrichs et al., 2009). Therefore, understanding the effects of climate change on the long-term, large-scale morphological tidal flat development starts with studying the bioturbators' behavioral responses.

In the future, climate change is expected to increasingly expose tidal flats to more extreme weather conditions such as heatwaves (Frölicher & Laufkötter, 2018; Oliver et al., 2018). Marine heatwaves occur when the surface sea temperature exceeds seasonal thresholds for consecutive days (Hobday et al., 2016, 2018; Holbrook et al., 2019). Compared to open waters, tidal flats are highly

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vulnerable to elevated seawater temperatures and air temperatures (Alsterberg et al., 2011; Harley et al., 2006; Mouritsen et al., 2018). The latter was clearly seen from the devastating effects of heatwaves in the summer of 2021. For example, the heatwaves that struck the western United States and Canada with a peak temperature of 49.6 °C from 25 June to 1 July (Schiermeier, 2021), were estimated to have killed billions of animals living in tidal areas, including bioturbating benthic animals (Einhorn, 2021; Williams, 2021). Heatwaves may particularly affect the organisms inhabiting higher intertidal areas, which face the most prolonged low water and thus most severe heat stress (Vafeiadou et al., 2018). The extreme temperature fluctuations related to alternating flooding and drying regimes, making temperature acclimatization virtually impossible (Gomes & Bernardino, 2020; Munari, 2011). The only 'escape' for benthic organisms to the heat stress is to seek the most suitable locations, by *i*) adjusting their burrowing behavior, or *ii*) using existing geomorphologic tidal-flat features as refuge environments.

Most nearshore tidal flats harbor complex geomorphological structures like slopes, channels, and ridges (Meager et al., 2005), including isolated shallow depressions that trap pooling water during low tide (Perillo, 2019; Toniolo et al., 2021). The formation of these depressions in the tidal flat can be attributed to mutual effects of currents and sediment properties (Perillo, 2019), movements of bioturbators such as crabs *Neohelice granulata* and shellfish *Meretrix meretrix* (Shi et al., 2020; Toniolo et al., 2021), or anthropogenic activities like bait digging and collections (Meager et al., 2005). Water pools may provide temporary habitats for various marine organisms during low tide (Dethier, 1984; Kunishima & Tachihara, 2020). Moreover, tidal pools could potentially provide refuges to organisms during heatwaves, because a higher pore water content can attenuate thermal diffusion on tidal flats (Kim et al., 2007; Thomson, 2010). On the other hand, heated water is typically low in oxygen, which may impose additional stress on benthic animals during heatwaves, instead of acting as a refuge habitat (Kodama et al., 2018; Pihl et al., 1991; Roman et al., 2019).

It has been well recognized that elevated temperatures can impose lethal conditions for bioturbating benthic fauna (Comaa et al., 2009; Rivetti et al., 2014; Soon & Ransangan, 2019), thereby resulting in mass mortality that may alter community compositions on tidal flats (Gauzens et al., 2020; Seuront et al., 2019; Vinagre et al., 2016; Wernberg et al., 2013). However, it remains poorly understood how tidal flat benthos responds to non-lethal thermal stress. In particular, little is known about *i*) how heatwaves affect bioturbating organisms' behavioral responses on tidal flats, and *ii*) how the behavioral response depends on geomorphological structures like tidal water pools. Hence, we aim to quantify how heatwaves affect bioturbating burrowing behaviors of macroinvertebrates in intertidal areas, using the well-known bioturbator cockle *Cerastoderma edule* as a model species. Using tidal mesocosms, we studied the cumulative impact of a gradually building-up heatwave on cockles living in two contrasting micro-topographies: the presence vs. absence of tidal water pools covering the animals during low tide.

Heatwave conditions were imposed using terrace heaters, to mimic the effect of direct solar radiation onto the mudflat (i.e., referred to below as the “solar-radiation treatment”). This treatment was only imposed during the daytime low tide interval. The air temperature during nighttime low tide and the seawater temperature during high tide were both kept constant at the beginning of the experiment, to mimic the buffering capacity of the environment (referred to below as the ambient heat condition). However, during the second phase of the experiment, the ambient air and water temperature of the climate chamber were also increased to mimic a gradually increasing background temperature. Cockles' burial depth, biomass (ash-free dry weight, AFDW), and respiration rate were measured as response variables at intervals throughout the experimental heatwave.

2.2 Material and methods

2.2.1 Model species *Cerastoderma edule*

The common cockles *Cerastoderma edule* are widely distributed along the European Atlantic coastline (Malham et al., 2012). As a representative suspension-feeding bivalve that lives just below the sediment surface, cockles affect the sediment stability by various vertical and horizontal activities such as shell shaking, adductions, and excreting feces (Ciutat et al., 2007; Vaughn & Hoellein, 2018). Previous studies have shown that the cockles' bioturbation can destabilize cohesive sediment and increase erosion rates (Cozzoli et al., 2019; Dairain, et al., 2020; Li et al., 2017).

In recent years, a number of massive die-offs of cockles have been reported during summer heatwaves (Burdon et al., 2014; Thielges, 2006). In addition, the physiological conditions can also determine cockle's influence on sediment dynamics. For example, Dairain et al. (2020) recently proved that parasitism reduced cockles' metabolic rates, thereby resulting in lower bioturbation potentials.

In our experiment, we collected the common cockles, *C. edule*, for use as a model species. These cockles ($n = 400$) were collected from the Oesterdam, located in Zeeland, the Netherlands, in early October 2019. They were transported to a temperature-controlled room at 20 °C and left in a tank filled with aerated seawater for 24 h acclimation. Then, active cockles were transferred into mesocosms and acclimate to the new environment for another 120 h before starting the experiment. Cockles with similar shell lengths were selected for the experiment (mean shell length was 27.31 ± 1.82 mm; $n = 139$). Most of the cockles immediately dug into the sediment and buried themselves in less than 15 minutes after being introduced to the sediment surface. When individuals were inactive or remained on the sediment surface for 24 h, they were replaced with new individuals.

2.2.2 Mesocosm setups: mimic tidal flats under heatwave conditions

The effect of thermal stress on cockles was tested using a mesocosm lab experiment, in which we imposed a “solar” heatwave using terrace heaters aimed at the tidal flat surface, combined with a delayed “ambient” heatwave by increasing the ambient air and water temperature in the climate chamber at the end of the experiment (*see* following section 2.1). Four tidal mesocosms were used to mimic the tidal cycle on tidal flats. One tidal mesocosm consisted of two water tanks (inner size $110 \times 95 \times 60$ cm) stacked one on top of the other (Fig. 2.1a). The upper tank was filled with a 30 cm-thick sediment layer ($D_{50} = 265.02 \mu\text{m}$, Silt content = 0%) as the typical living environment for cockles (*see* Fig. 2.2a). Due to the large amount of sediment needed for the experiment (ca. 1 m^3), we purchased sea sand from a building material company with similar grain size and silt content to the sediment at the field site where the cockles used in the experiment were collected (*in-situ*, $D_{50} = 260.72 \mu\text{m}$, Silt content = 0%, Oesterdam, $51^{\circ}28'01.4'' \text{ N}$, $4^{\circ}12'49.8'' \text{ E}$). The sediment used in the experiment was exposed to natural sunlight and air for 30 days to eliminate all the live organisms. The lower tank was used as a water reservoir for tidal cycle simulations (for details, *see* Cao et al., (2018)). The water level was restricted by a return-flow pipe (30 cm, Fig. 2.1c), transporting the overflow water back to the lower tank. A regular semi-diurnal tide was mimicked according to the natural conditions of the field site mentioned above. The low tide interval was 5 h, occurring twice daily (*see* Fig. 2.2b).

The four mesocosms were placed in one room, of which two were used for the “solar” heatwave treatment, and two experiencing only “ambient” temperature used as controls. The heatwave mesocosms were equipped with hanging terrace-heaters (Frico, EZ212) to mimic sun irradiation during low tide. To study the effects of heat stress on intertidal sediment with and without pooling water, PVC pots (internal diameter = 10 cm) were used to retain pooling water artificially (Fig. 2.1c). Pots designated to have pooling water were manipulated by removing the top 2 cm sediment, so that a layer of surface water would be trapped in these pots during low tide. Treatments without pooling water were designated within a PVC tube whose top was level with the sediment surface. Each PVC pot represented one experimental replicate, and they were arranged in 2 cols \times 6 rows (i.e., matching the size of the heater) staggered patterns in the upper mesocosm tanks.

2.2.3 Temperature treatments and measurements

The temperature under ‘solar’ heatwave conditions was controlled through feedback between the hanging terrace heater and a temperature sensor positioned on the sediment surface of every heated tank (Fig. 2.1a). When the sediment surface temperature was above the set temperature, the heater was turned off; below the set temperature, the heater was turned on again. A timer switch controlled the activation of the heater for the period 30 minutes prior to the daytime low tide, and shut down 30 minutes

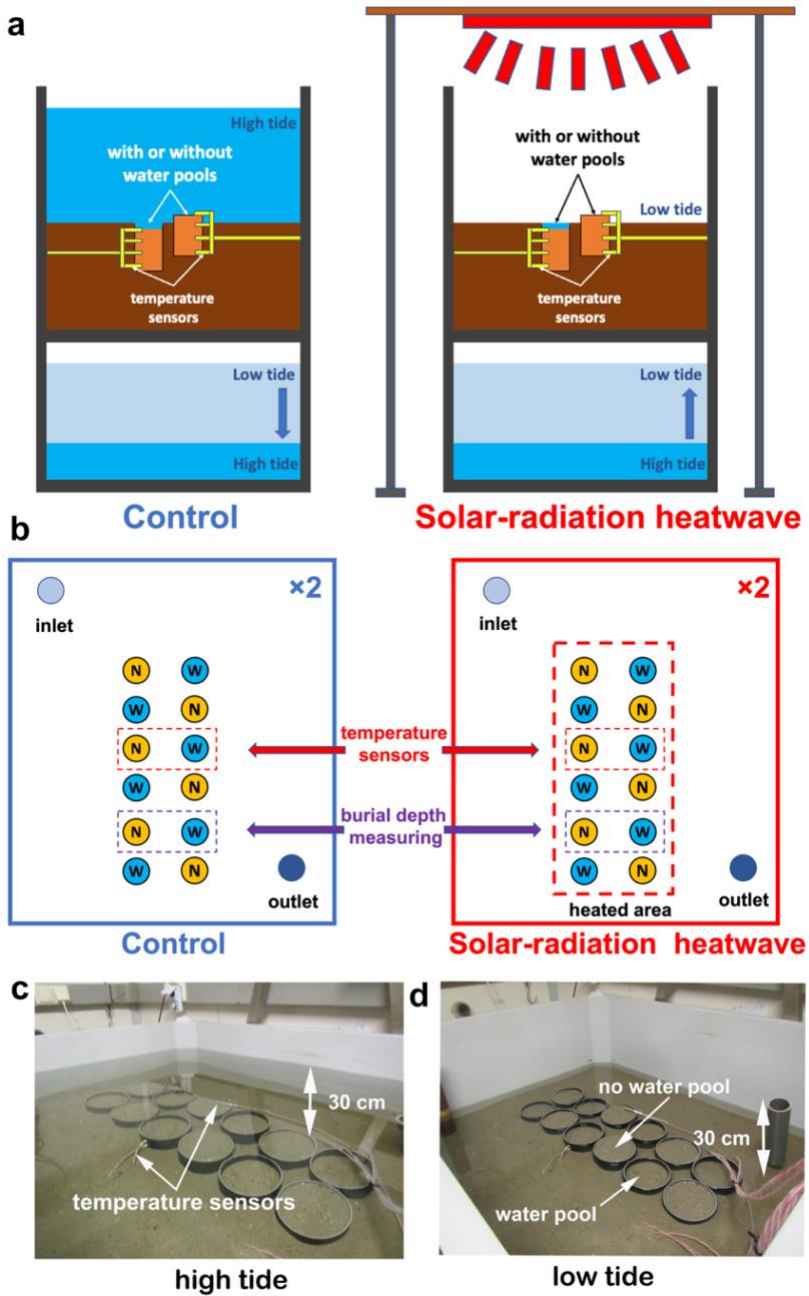


Figure 2.1 Schematic diagrams and photos of the mesocosm experimental design. (a) The mesocosm setup mimicked diurnal tidal cycles on tidal flats for both “control” (left, only exposed to ambient temperatures of the climate chamber)

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and "solar" heatwave (right). The heatwave was mimicked using terrace heaters above the mesocosm units, indicated by red strips). These were only switched on during the daytime low-tide interval. Each unit has regular tidal regimes, indicated by dark blue arrows in bottom tanks. (b) An overhead view of column pot setups in control (left) and heatwave (right) tanks: "W" for with water pools, "N" for without water pools; 4 cockles were randomly placed in each pot. Two PVC pots in each mesocosm tank were chosen to measure the depth profile of temperature, one with a water pool and the other without. The temperature sensors were deployed at 0 cm, 2 cm, 4 cm, 6 cm in the sediment of the PVC pot. (c) A photo shows the "high tide" condition, with continuous water flow (30 cm deep) submerging the pots. (d) A photo shows the "low tide" condition, with the cockles being invisibly buried inside the sediment. Half of the PVC pots had water pools on top, the other half not.

after. As a result, the heatwave temperature conditions fluctuated closely around the set temperature for 6 h per day, covering the 5 h daytime low tide (Fig. 2.2a). Note that the ambient temperature of the mesocosms increased in the second phase of the experiment, which meant a change in control conditions during this phase (Figure 2b). A 12-hour day-night cycle was created using indoor lighting, with no additional lighting device to adjust the light intensity (Fig. 2.2a).

Two systems determined the thermal conditions in the mesocosms: *i)* the "ambient temperature" was controlled by the air conditioning system in the mesocosm room (Fig. 2.2b), while *ii)* the "solar-radiation heatwave temperature" was manipulated by the terrace heaters (Fig. 2.2c). Over five weeks, five different temperature intensities were imposed on the experiment with different combinations of ambient and heatwave temperature settings (*see* Fig. 2a&b, Week I to V, in total 35 days). At the end of the experiment, the heatwave conditions are comparable to marine heatwave temperatures observed during heatwaves in the Netherlands in the summer of 2020 (*see* Appendix 2.1: Fig. A2.1).

To record temperatures throughout the sediment column in the experimental tanks, temperature sensors (PT-100 sensors, TC Direct) were deployed at 0 cm, 2cm, 4 cm, 6 cm depths to record the per-minute temperature profiles (Fig. 2.1a & d). These sensors were faced with a CR10X datalogger (Campbell Scientific, Inc.), and the data was transferred via LoggerNet software (Campbell Scientific, Inc.). During low tide, the temperature sensors at 0 cm measured the temperature at the water-sediment interface for the pots with "water pools". In contrast, they measured the air temperature of the emerged sediment surface in pots without pooling water.

We measured the temperature of only two PVC pots per mesocosm (i.e., one with "water pools" and the other without) to represent the temperatures in all pots of each mesocosm unit (Fig. 2.1d). In this way, we maximized the number of PVC pots available for the behavioral study. These two PVC pots with the temperature sensors did not contain cockles as the PT-100 sensors would obstacle cockles' movements. Whereas control experiments showed that the presence of cockles did alter the warming

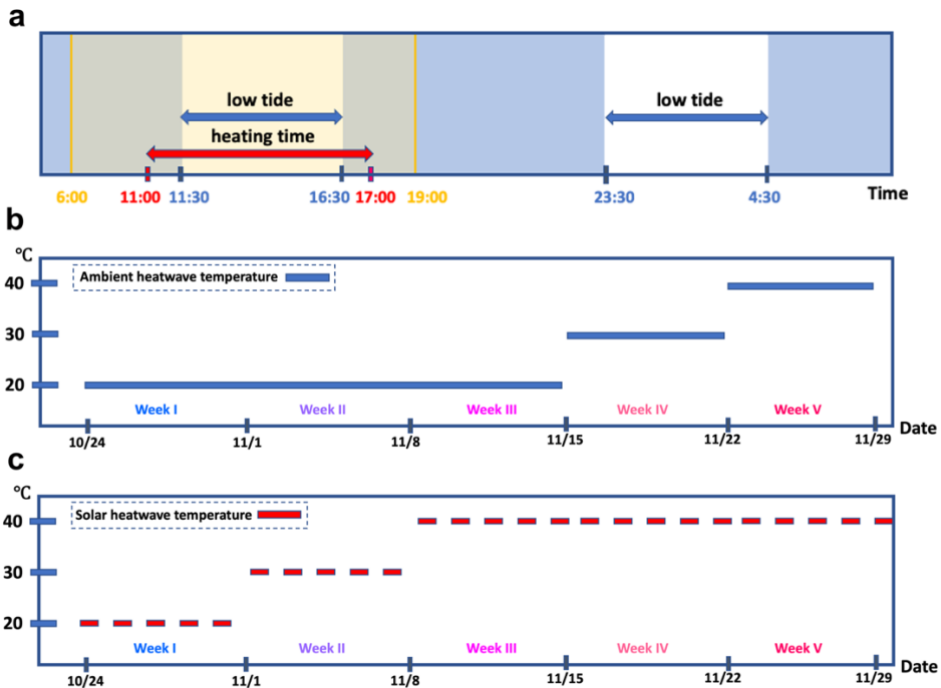


Figure 2.2 Schematic diagrams represent (a) the daily tidal cycles and temperature settings and (b & c) the long-term temperature treatments over the experiment. When looking into the daily cycle settings (a) The daylight period is indicated by a yellow color shade in panel a. Semi-diurnal tides are visualized with the high tide marked as blue area, and the low tide marked as white. The solar heatwave period when the terrace heater is on is marked with a red arrow, spanning the period 30 mins before and after the daytime low-tide interval. (b) The long-term temperature settings of the ambient heatwave treatment, for both the ambient-air and ambient-water temperature. (c) The red dashed lines indicate the temperature of the simulated heat waves maintained by the terrace heaters.

process (see Appendix 2.3: Fig. A2.3a), the mean temperature difference between the presence/absence of cockles during the low tide was around 1 °C. Note that a slight temperature gradient was present within the mesocosms themselves. The mean temperature between pots located at different positions under the terrace heaters showed up to 1.5 °C difference (indicated by the pilot test; see Appendix 2.2: Fig. A2.2). However, the magnitude of this temperature gradient remained constant between ambient and heatwave conditions. Pilot tests also showed that the salinity did not change significantly during the low tide periods in both topographies (see Appendix 2.3: Fig. A2.3b).

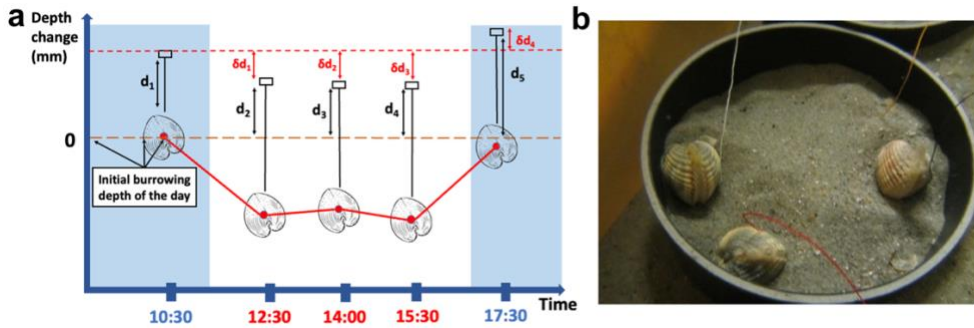


Figure 2.3 Diagrams of burrowing depth measurements. (a) A conceptual diagram for burrowing depth measurements. The absolute length was measured five times every day. The "zero value" was defined as the initial burrowing depth of the day (i.e., "d"). Then, the burrowing depth change was calculated using the first measurement as a reference (i.e., " δd "). (b) Cockles glued to different colors of lines, enabling to measure how deep they buried based on the above-ground line length. Note that the picture was taken shortly after the cockles were placed on the sediment surface, before burial took place.

2.2.4 Cockle maintenance and health condition measurements

We placed four cockles in each pot, giving a total of 160 individuals in four mesocosm tanks, mimicking a density of 512 ind./m² in each PVC pot (Fig. 2.3b). Twice a week, all cockles were fed with instant microalgae (Shellfish Diet 1800, Reed Mariculture Inc.). The algae concentrate was pre-diluted at 10:1 with 100 ml seawater, then fed to each tank homogeneously with a dropper. One-third of the seawater in reservoir tanks was replaced every week to guarantee clean water conditions. Cockles' physiological response to thermal stress was quantified by measuring survival and respiration rates.

Survival: The living states of the cockles was checked before the first burial depth measurement every day. Cockles were recorded as dead if their shells were gaping and they did not react to mechanical stimulation. Dead cockles were removed daily from the PVC pots. Weekly mortality was calculated for each temperature profile.

Oxygen consumption: At the end of each temperature scenario (i.e., at the end of each week), we randomly selected one PVC tube with pooling water and one without in each of the four mesocosms to collect the cockles (i.e., two pots and eight cockles for each mesocosm; 16 in total for the heatwave, and 16 in total for the ambient treatment). Cockles from the same pot were collected and placed into the same respiration chamber (inner \varnothing = 10 cm, inner height = 9 cm) with seawater from respective mesocosms. The sediment temperatures (ca. 1 cm depth) at the collection time were measured manually using an alcohol thermometer. A water bath (Water Bath 12L, VWR) was used to keep the respiration

chambers at a constant temperature. The oxygen concentration ($\mu\text{mol L}^{-1}$) in the respiration chambers was continuously measured using FireSting pro (PyroScience Sensor Technology) for 2 h. Following the respiration measurements, the flesh tissues of cockles were detached from their shells, dried at 60°C for 48 h, and then put in the muffle furnace at 580°C for 2 h to get biomass as AFDW (g). The oxygen consumption rates (OR, in $\mu\text{mol} \cdot \text{h}^{-1}$) of cockles were calculated from the following equation,

$$\text{OR} = \frac{(C_0 - C_1) \times V}{t_0 - t_1} \quad (1)$$

in which t_0 and t_1 (h) are the starting and ending time of measurements; C_0 and C_1 represent the oxygen concentrations ($\mu\text{mol} \cdot \text{L}^{-1}$) at t_0 and t_1 ; V is the seawater volume in the chamber (L) with correction for the sensor volumes.

2.2.5 Burrowing behavior measurements

In each mesocosm tank, one pot with pooling water and one were chosen for continuous measurements of burrowing activity. In these tests, a cotton thread was attached to the shell of each cockle with cyanoacrylate glue to measure changing burial depth of the cockle underground. In each pot, 4 cockles were glued with 4 different thread colors (Fig. 2.3b).

In each week, cockles were allowed to acclimate to the new temperature for two days, and then their burrowing depths were measured over the next 5 days. Five measurements were applied daily to survey cockles' burrowing behavior before, during, and after the heating exposure (Fig. 2.3a). Two of them were 30 mins before and after the low tide at 10:30 and 17:30. Three of them were during the low tide when cockles were directly exposed to thermal stress in heatwave mesocosms (i.e., 12:30, 14:00, and 15:30).

The relative depth change at each time point was obtained by subtracting the first measurement from the following four measurements. Therefore, the relative depth change of the first measurement was always 0 cm at 10:30. The following four measurements used the first as baselines to calculate the burrowing depth change (*see* Fig. 2.3a).

2.2.6 Data analysis

To compare the effects of thermal stress and micro-topographies on cockles' burrowing behavior, we fit a linear mixed-effects model using the "lme4" package (Bates et al., 2015, p. 4) in R 4.1.2 (R Core Team, 2021). In this model, we tested the effects of the heatwave treatment and the presence or absence of pooling water on the standard deviation of the burial depth of each cockle over the heatwave interval. This metric indicated the magnitude of the behavioral response of the cockle to the heated environment. The week was also included as a random effect.

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A rolling window analysis was used to examine the relationship between daytime low-tide temperature and the magnitude of the burrowing position change. The standard deviation of individual position change was used in the analysis (i.e., window size = 3 °C, step size = 0.1 °C) to indicate the daily variance in burial depth of each cockle under the heatwaves. For each step, position change data were first log-transformed, and both the temperature and position change data were summarized for the mean values. Then, the mean values were fit into a linear regression model to test the correlation between heatwave temperature and position change.

A linear regression model tested the effects of temperature on cockles' respiration rates. The ash-free dry weight (AFDW) was $\log(x+1)$ transformed, then multiplied temperature as a product to correlate with the "oxygen consumption" data. Instead of only using temperature, this analysis can constrain the discrepancies of biomass due to random sample selections. Both variables were then fit into the linear model: $y = ax + b$, in which x is the product of temperature (°C) and $\log(\text{AFDW} + 1)$ and y is the oxygen consumption by an hour ($\mu\text{mol O}_2 \cdot \text{h}^{-1}$). All the above analyses were performed using R 4.1.2 (R Core Team, 2021).

2.3 Results

2.3.1 The effects of thermal stress on burrowing behavior

To test the heat stress caused by *i*) the simulated solar heating and *ii*) increases in the ambient temperature during heatwaves, we measured temperatures at 0 cm and 4 cm of the sediment during low tide. Under the same heat stress conditions during low tide, the temperature in water pools (Fig. 2.4a) was lower than that of the exposed sediment surface without water pools (Fig. 2.4c). However, the heat penetrated the shallow water layer, resulting in increased sediment temperatures. When exposed to heat stress during low tide, temperature values at 4 cm depth were lower than the soil surface (i.e., 0 cm) for both topographies with and without water pools (Fig. 2.4a & c). In contrast, the temperature values in the ambient tanks were similar across depths.

To study the behavioral response of bioturbators under heat stress, we measured the burrowing depth changes using threads. The thermal stress affected the burrowing behavior of cockles in both topographies (i.e., presence/ absence of tidal water pools) during different heatwave profiles. Cockles in water pools moved up or surfaced when exposed to thermal stress during low tide (Fig. 2.4b). The pattern of surfacing movement was particularly solid when the heating temperature was high during the fifth week. In contrast, cockles living without water pools burrowed deeper into the sediment when exposed to thermal stress (Fig. 2.4d). These cockles then moved towards the surface as soon as the tide came. The magnitude of change in borrowing depth increased under greater heatwave temperatures.

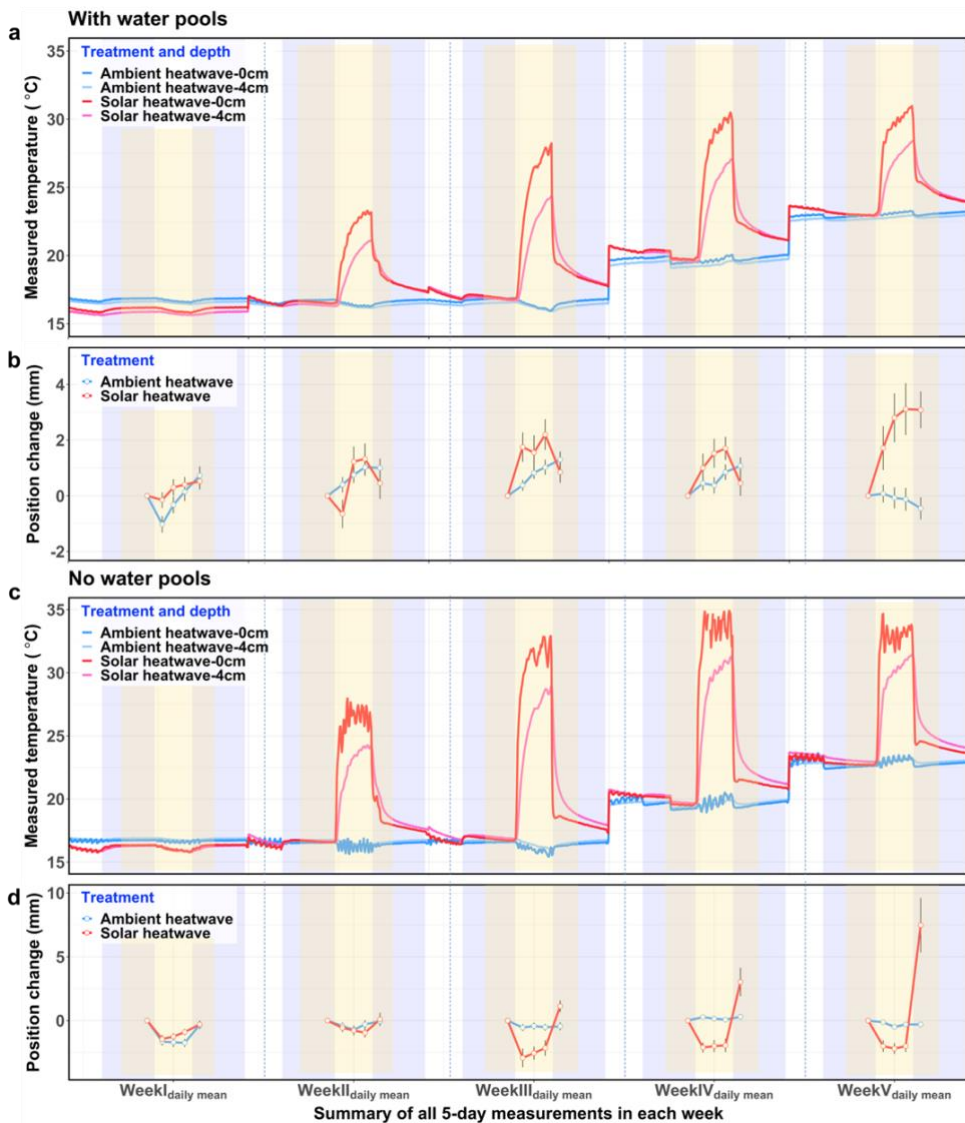


Figure 2.4 Average daily temperature (a, c) and change in the burial depth (b, d) during each week, for tidal flats with (a, b) and without (c, d) pooling water. The dashed lines indicate summarised daily profiles; mean values were calculated for temperature and change in burial depth based on 5-day data in each week. The blue shaded bars represent the period of inundation time during high tide. The yellow shaded bars indicate daytime. Average temperature values were calculated for the sensors placed at 0 cm and 4 cm, representing the depth range where cockles typically live. The position change represents the distance that cockles move. Positive values indicate that the

cockles move upwards relative to their initial position, while negative values indicate movement downwards. Position changes of every individual are aggregated by week to calculate daily mean values. The error bar represents the standard error between individuals in all replicate PVC pots.

2.3.2 Burrowing position and health conditions in response to thermal stress

A linear mixed-effects model was applied to test the effects of thermal stress and micro-topographies on cockles' burrowing position change (*see* Appendix 2.5: Table 2.1 & 2.2). The results show that the presence of heatwaves and water pools can significantly explain cockles' burrowing depth ($t_{\text{water pool}} = 6.03, p_{\text{water pool}} < 0.01$; $t_{\text{heatwave}} = -2.09, p_{\text{heatwave}} = 0.04$). Further ANOVA test on the mixed-effects model showed that interactions between thermal stress and micro-topographies significantly affected the burrowing positions ($F = 28.44, n = 344, p < 0.01$).

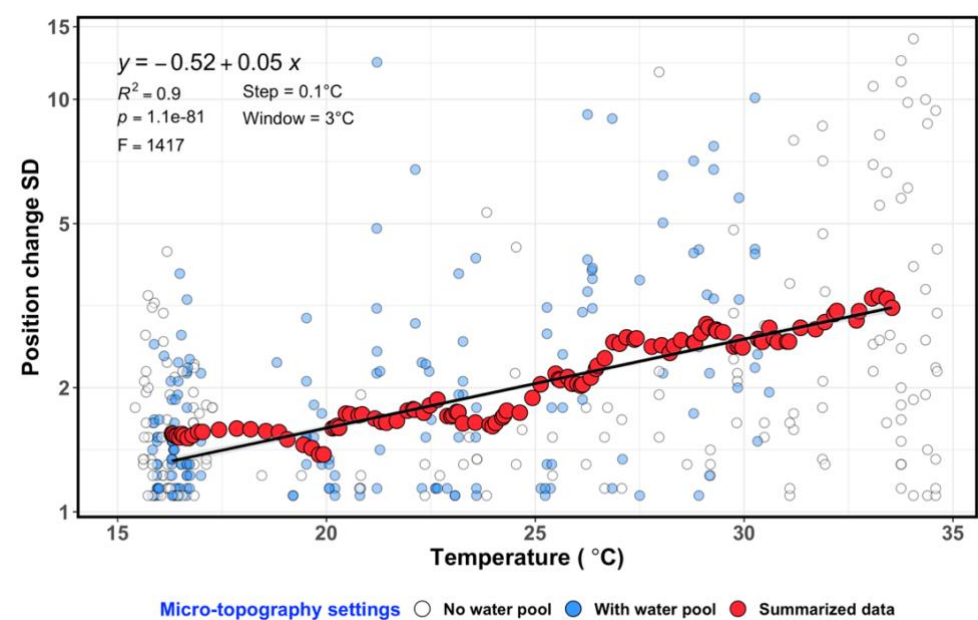


Figure 2.5 The effects of temperature on cockle's burrowing positions. The data points in the graph represent the log-transformed standard deviation of each cockle's daily position change. The white circles stand for cockles living without water pools, while blue circles represent those living in the water pools. The red circles are summarized data calculated by the rolling window analysis. Temperature and standard deviation values are averaged in each window (3 °C) with a step of 0.1 °C.

A rolling window analysis was applied to test the daily variance of cockles' position change (ignoring the direction of movement) under the heatwaves (Fig. 2.5). It clearly shows, *i*) that the overall mobility significantly increased with temperature ($F = 1417$, $n = 344$, $p < 0.01$), and *ii*) that this trend appeared to be constant for both the treatments with/without pooling water, despite the opposite direction of movement between treatments, and higher temperatures in the pots without pooling water (Fig. 2.4).

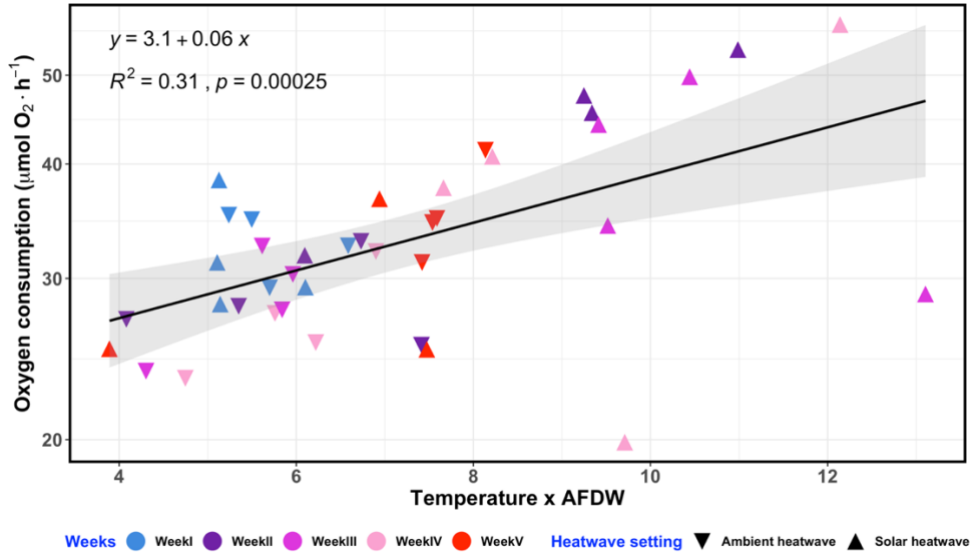


Figure 2.6 The effects of the thermal stress on cockles' respiration rates. The grey shaded bar shows the 95% confidence intervals of the linear regression model. The product of temperature and AFDW was the independent variable, and oxygen consumption per hour was the dependent variable. The temperature was the mean value during respiration measurements, and AFDW was the total ash-free dry weight of all surviving cockles in the same respiration chamber. In this plot, oxygen consumption data were log-transformed, and AFDW data were $\log(x+1)$ transformed.

A linear regression model tested the interactive effects of temperature and biomass on respiration rates. Thermal stress significantly increased cockles' respiration rates ($F = 16.37$, $n = 39$, $p < 0.01$), while they showed larger variance as the heatwaves were stronger (*see* Fig. 2.6 for upward triangles). Specifically, some cockles consumed more oxygen under thermal stress, but others consumed less oxygen because of dying conditions. Moreover, oxygen consumption was also determined by biomass. Even if the temperature at Week V was high, oxygen consumptions were low due to fewer surviving individuals (i.e., lower measured biomass). No cockles died in the ambient mesocosm units, while the death rates in the heatwave mesocosms were low until Week V (*see* Appendix 2.4: Fig. A2.4).

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The heatwave reached its highest intensity in Week V (*see* Fig. 2.4 for details), thus resulting in mortality rates of 50% and 62.5% in topographies with and without water pools, respectively. This indicated a mass mortality event at the end of the simulated heat waves.

2.4 Discussion

In-depth knowledge of how macrofaunal behavior is affected by climate-change-induced heat waves is key to understanding how bioturbation may affect sediment stability on tidal flats in the future (Sturdivant & Shimizu, 2017). To our knowledge, the present study is the first to demonstrate that heat stress increases the burial activity of the common cockle, *C. edule*, and thus their bioturbation potential. That is, *i*) cockles burrow deeper in sediment that is heated by solar radiation during low tide, followed by an upward movement towards the surface as soon as the high tide arrives, while *ii*) cockles living in tidal water pools move up and sometimes even surface when exposed to low-tide thermal stress, reburying at the start of the next low tide. Overall, mobility increases with the magnitude of heat stress, regardless of topography. Finally, cockles' respiration rate increases while health condition decreases with the increasing duration of the heat stress. This results in higher mortality during prolonged heat stress.

2.4.1 Reasons for mortality of bioturbators under heatwaves

Bivalve populations can experience mass mortality due to multiple causes such as predation, diseases, pollution, and overfishing (Beukema & Dekker, 2005; Malham et al., 2012). Current climate change scenarios pose extra pressures on the physiological conditions of bivalves. Recent studies show that the duration and intensity of marine heatwaves are increasing due to global warming effects (Frölicher et al., 2018). Meanwhile, increasing bivalve mortality has been reported worldwide, most of which has correlated with heatwaves in late summer or early fall (Malham et al., 2012; Ortega et al., 2016). In addition to the high temperature, the specific causes of mass mortality during heatwaves may also be indirect, related to other factors such as hypoxia and pathogens (Burdon et al., 2014).

Hypoxia - Thermal stress may expose marine organisms to external and intrinsic hypoxia. On the one hand, higher temperatures reduce the amount of dissolved oxygen in the water due to physical processes (Song et al., 2019). Moreover, the dissolved oxygen decreases in warmer seawaters due to greater oxygen consumption by micro-organisms with accelerated metabolisms breaking down organic matter (Degerman et al., 2012). On the other hand, animals can have limited oxygen uptake capacities at low or high borders of thermal thresholds (Pörtner, 2001). Both types of hypoxia can decrease bivalves' metabolic rates, leading to lower body conditions and eventually massive mortality (Anestis et al., 2007;

Soon & Ransangan, 2019). Many studies confirmed that heatwaves cause hypoxia events and finally result in mass mortality of bivalves, such as *C. edule* (Burdon et al., 2014), *Mesodesma mactroides* (Fiori & Cazzaniga, 1999), *Crassostrea virginica* (Ivanina et al., 2013), *Corbicula fluminea* (Vohmann et al., 2010), and *Mytilus edulis* (Seuront et al., 2019). Hypoxia may also explain the behavioral responses of cockles in our experiment: the upward movement of cockles in water pools cannot be directly attributed to the thermal stress as they move in the direction of the heating source. The heating underneath standing water may cause anoxia in the sediment, driving the animals upwards to an oxygenic environment. This is in line with findings of Riedel et al. (2014), who showed that most species increased movement under mild hypoxia ($< 2 \text{ mL O}_2 \cdot \text{L}^{-1}$), then emerging from the sediment surface under moderate ($< 1 \text{ mL O}_2 \cdot \text{L}^{-1}$) to severe hypoxia ($< 0.5 \text{ mL O}_2 \cdot \text{L}^{-1}$), finally showing violent movements and death under anoxia conditions (Stachowitsch et al., 2007). However, hypoxia should not be a problem for species living in the surface sediments of emergent tidal flats that are fully exposed to air during low tide. In this experiment, increased respiration rates and reduced health conditions for cockles living outside of pooling water in surface sediment should be attributed to direct thermal stress (see Fig. 2.4).

Pathogens - High temperatures may decrease the enzymatic and phagocytic activities in bivalves, leading to less resistance to pathogens such as parasites (Longshaw & Malham, 2013; Thieltges, 2006). Increased infection levels may cause direct or indirect mortality. For example, trematode parasites who utilize cockles as the first or second intermediate hosts reduce their burrowing activities, leading to mass mortality (Thieltges, 2006). In the case of a non-lethal trematode parasite infection, the reduced cockle bioturbation may enhance sediment stability (Dairain et al., 2020). The cockles used in this experiment were all healthy individuals burrowed rapidly. Dead individuals were removed daily, and the seawater in the tanks was renewed in time to ensure a clean environment for the cockles to survive. If present, the effects of parasites should have been consistent across treatments, as all cockles were collected from the same area. Most parasites reduce bivalves' burrowing behavior and cause surfacing on tidal flats (Dairain et al., 2020; Thieltges, 2006). Since the cockles in the ambient treatments did not show surfacing or mass mortality tendencies, it is unlikely that parasites had a dominant effect in our study. Due to the specific life history, parasites usually take several months to develop into mature individuals (Lucius et al., 2017; Thieltges, 2006). Therefore, the experiment was likely to have been too short for parasites to develop into a problem, even if the animals were infected at the start. Nevertheless, the effects of parasitism on the bioturbation process under heatwaves deserve further investigation in future studies (e.g., using flumes or luminophores).

Surfacing behavior - Our experiment provides insights into how bivalves may expose themselves to the risks of dislodgement and predators under the heatwaves by surfacing behaviors. The

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exact process depends on the topography of sediment surface, *i*) cockles living in emerged sediments surfaced after the high tide comes, or *ii*) cockles living in water pools gradually surfaced during the low tide under the heatwaves.

2.4.2 Mass mortality and community effects

High temperatures may also directly affect the health conditions of cockles, eventually translating into mass mortality, as observed in the last week when the solar and ambient heatwave were combined. Studies have shown that older cockles (i.e., > 1 year old) were more vulnerable to heatwaves than juveniles (Beukema & Dekker, 2020). It is speculated that the mass mortality of cockles during the heatwave can result in a sharp decline in adult individuals before the spawning season. On the other hand, the surviving cockles with poor health conditions may have become too weak to survive the harsh winter. Nevertheless, these adverse effects do not necessarily decrease the cockles' recruitment rates in the subsequent year, as winter temperatures and predators also determine overall recruitment (Beukema & Dekker, 2020). However, mass mortality is likely to result in a younger age structure of the cockle populations and open ecological niches for other invasive species that better tolerate high temperatures, such as the invasive Manila clam, *Ruditapes philippinarum* (Dang et al., 2009). As the duration and magnitude of marine heatwaves increase under current global warming scenarios (Frölicher & Laufkötter, 2018), cockles will have to adapt to the thermal stress or migrate to higher areas with lower mean temperatures.

2.4.3 Implications for sediment stability in the face of global warming

Bioturbation by macrozoobenthos generally reduces the sediment stability of the benthic boundary layer, thereby increasing erosion (Cuzzoli et al., 2021; Dairain et al., 2020; Shi et al., 2020). These bioturbation activities can result from various species-specific living styles and feeding behaviors, such as mobile grazing that disturbs the sediment surface (e.g., *Hydrobia ulvae*) (Andersen et al., 2002; Orvain & Sauriau, 2002) or deposit-feeding via moving up and down in the sediment (e.g., *Corophium volutator*) (Gerdol & Hughes, 1994). Besides, the shells of the benthic organisms can also have physical effects (i.e., corrasion or ballistic impact) on sediment erosion rates (Amos et al., 2000). The model species used in our experiment, *C. edule*, is known to increase sediment erodibility by burrowing behavior (i.e., valve shaking or adductions, (Ciutat et al., 2006; Cuzzoli et al., 2020). The intensity of cockles' burrowing behavior determines the quantity of bio-disturbed sediments (Rakotomalala et al., 2015), and shifts in burrowing depth (i.e., cockles moving up and down more frequently) is a critical factor to predict sediment stability (Ciutat et al., 2007; Dairain et al., 2020). As shown in Fig. 2.5, cockles'

daily vertical movements significantly increased with temperature, which translates into more sediment bioturbation and may eventually be expected to increase sediment erodibility.

Present results revealed that the effect of heatwaves on the benthos behavior varies between areas with tidal water pools versus well-drained areas. To further unravel the consequences of these behavioral changes for bio-mixing, the use of luminophores should be considered. This requires some technical challenges to be resolved (Fang et al., 2019; Montserrat et al., 2009), such as minimizing the suffocation of organisms by luminophore applications, resolving edge effects in image analysis, and selecting a proper luminophore-application technique to avoid low-temperature shock resulting from the frozen sediment-luminophore mixtures. Flumes may provide an opportunity to measure sediment erosion after long-term exposure to temperature treatments (de Smit et al., 2021; Li et al., 2017), provided that the pots used for the temperature treatments are adjusted to the size of the flume.

The current study highlights how cockles move towards different directions in contrasting sediment topographies under the same magnitude of heat stress: upward in sediments underwater pools versus downward in well-drained sediments. Thus, the initial morphology of the landscape may be expected to affect the magnitude by which heatwaves impact the biogeomorphic influences. At the landscape scale, sediment type will also determine the magnitude of the heatwave-induced bioturbation effect, with the most substantial effects to be expected on cohesive muddy systems, versus little to no effect in the case of non-cohesive sandy systems (Li et al., 2017; Soissons et al., 2019). Future studies should identify to what extent the observed changes in burial behavior may differ concerning grain size distribution and sediment bulk density. In general, the effect of sediment bulk density on benthos behavior remains poorly studied (Wiesebron et al., 2021).

2.5 Conclusions and outlook

In addition to demonstrating a solid behavioral response in enhanced animal mobility under heatwaves, our experiments also show that cockles can withstand high temperatures for a reasonable period, whereafter mass mortality occurs following long-term exposure to high temperatures. Based on these observations, the effects of bioturbators on sediment stability during a heatwave can be expected to have two phases: *i*) an initial phase with enhanced erosion due to the increasing bioturbation activities under thermal stress; *ii*) a second phase with reduced erosion because of reduced health conditions and mass mortality of the animals. The first phase should occur during typical short heatwaves. Only in the case of a long-duration heatwave should the second phase be expected to occur. Mass mortality will open niches for other, potentially more heat-resistant invasive species after very long-term heatwaves, resulting in new equilibrium conditions of coastal ecosystems (Reise, 1991; van Colen et al., 2010). Studying the sequence of erodibility-affecting processes and how these vary between different

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environmental settings, like surface topography, are critical to understanding the tidal flat dynamics under global warming. And behavioral studies, as presented here, form a neglected but crucial step in obtaining such insights.

Appendices

Appendix 2.1 Temperature measurements in the field

The HOBO sensors (Onset Computer Corporation) were deployed to measure the temperature of air and sediment at Paulina polder, Netherlands (51°21'01.6" N, 3°43'41.9" E). Two sensors were fixed on bamboo sticks to measure the air temperature near the sediment surface. The distance from the sediment surface was 15 cm. The other two sensors were deployed at 3 cm depth in the sediment to measure the temperature of sediment. The results of both measurements (near-surface and 3-cm depth temperature) were the mean values of 2 replicates. The elevation of the location was 0.73 ± 0.01 m, and the grain size of the sediment was 68.47 ± 2.90 μm (top 1 cm).

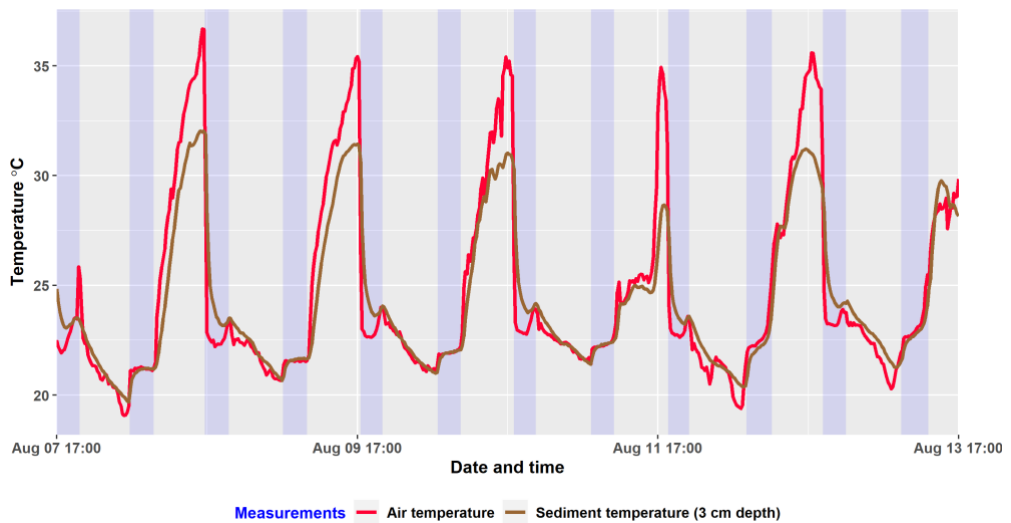


Figure A2.1 Air and sediment temperature profiles during summer heatwaves 2021 at Paulina polder, Netherlands. The blue shades represent inundation during high tide, and gray shades for exposure time during low tide.

Appendix 2.2 Temperature distribution under the terrace heater

A pilot functioning test for temperature profiles was applied before the experiment started. Three temperature sensors (PT-100 sensors, TC Direct) were placed under the terrace heaters (Frico, EZ212) to test their heating effects (Fig. A2.2a). The heater was turned on 0.5 h before low tide, and then the data were collected 1 h after the low tide (i.e., till the water in the sediment was drained) for another 1 h. The set temperature of the terrace heater was 30 °C. The mean temperature values (i.e., within 1 h) at different positions under the heater were similar, varying between 25.19 ± 1.08 °C to 26.70 ± 2.03 °C (Fig. A2.2b).

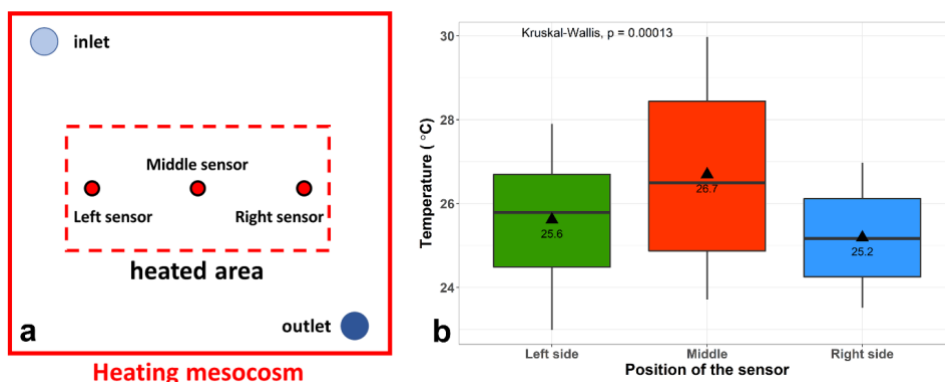


Figure A2.2 A diagram of the functioning pilot test for the terrace heater. (a) The position of the temperature sensors for the pilot heating test. This diagram shows the top view of a mesocosm tank. The rectangular dashed line area is the vertical projection of the heater on the sediment surface. (b) The temperature of different positions under the terrace heaters. The black triangles indicate the mean values during measuring periods (1 h). The distance between the heater and sediment was 40 cm. The p -value indicates different heating processes (i.e., temperature variance during the same heating period) between the middle part and two ends. However, the average heating temperatures are similar, ranging around 26 °C.

Appendix 2.3 Pilot tests on temperature measurements and salinity change

In this pilot, we used four mesocosm units in 2 climate rooms (i.e., two mesocosms in each room) to test the interference of cockles with temperature and salinity change. Each mesocosm was applied heaters on top with two PVC pots inside, one with and the other without overlying water pools. Each mesocosm was treated with four cockles per PVC pot, and the other did not contain any cockles. Therefore, there will be two replicates for both topographies with/ without cockles under heat stress. The pilot test was conducted for two days. During the low tides, pore water samples were obtained in the surface sediments of each PVC pot for further salinity analysis. Due to sampler size limitations, pore water samples were collected in the upper 3–4 cm sediments. The salinity was tested by a conductivity meter at 25 °C (CDM 230, MeterLab).

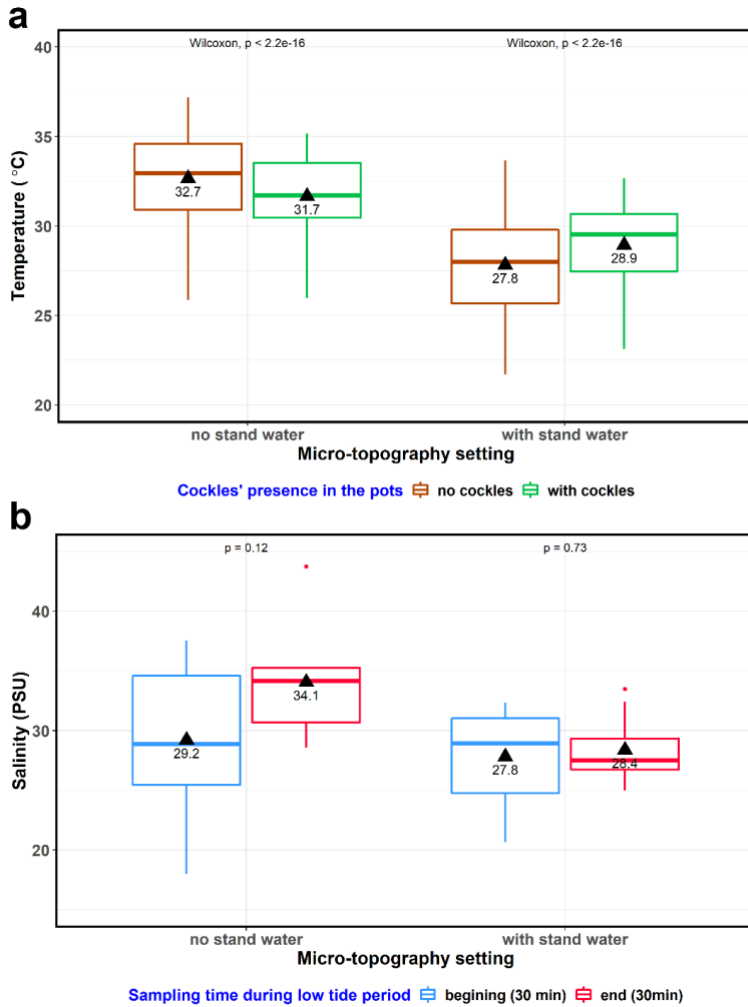


Figure A2.3 Temperature and salinity change under the heat stress during low tide. (a) Temperature change at 4 cm depth of both topographies under the heat stress during low tide, with/ without the presence of cockles. (b) The salinity change of pore water in sediments from both topographies, 30 mins after the beginning and before the end of low tides.

Appendix 2.4 Cockles' survival rates during the experimental periods

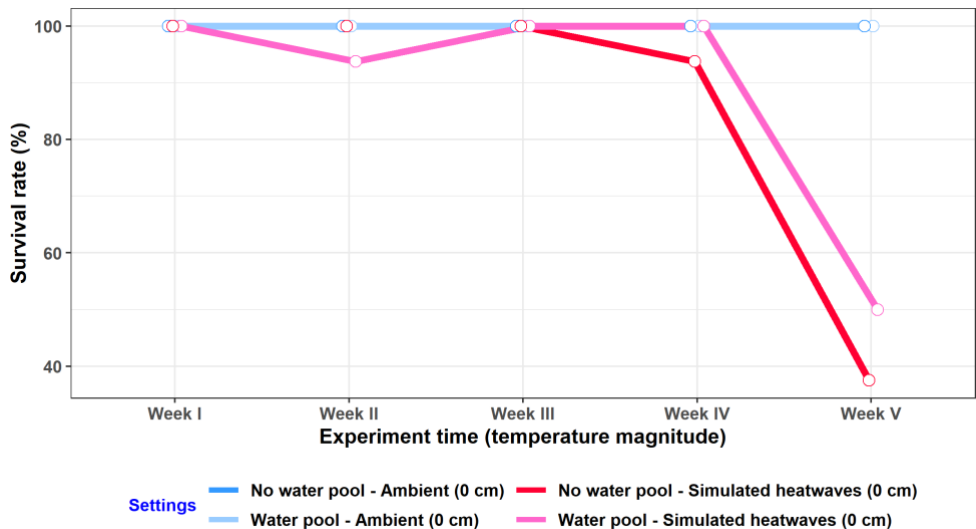


Figure A2.4 The average survival rates observed for different heatwave regimes in the absence/presence of tidal water pools (i.e., representing contrasting tidal-flat topographies). The red lines (dark and light) represent the heatwave treatment. The blue lines (dark and light) represent ambient temperature treatment.

Appendix 2.5 Statistics of the linear mixed-effects model**Table 2.1** Linear mixed model fit statistics. The *t*-tests used Satterthwaite's method.

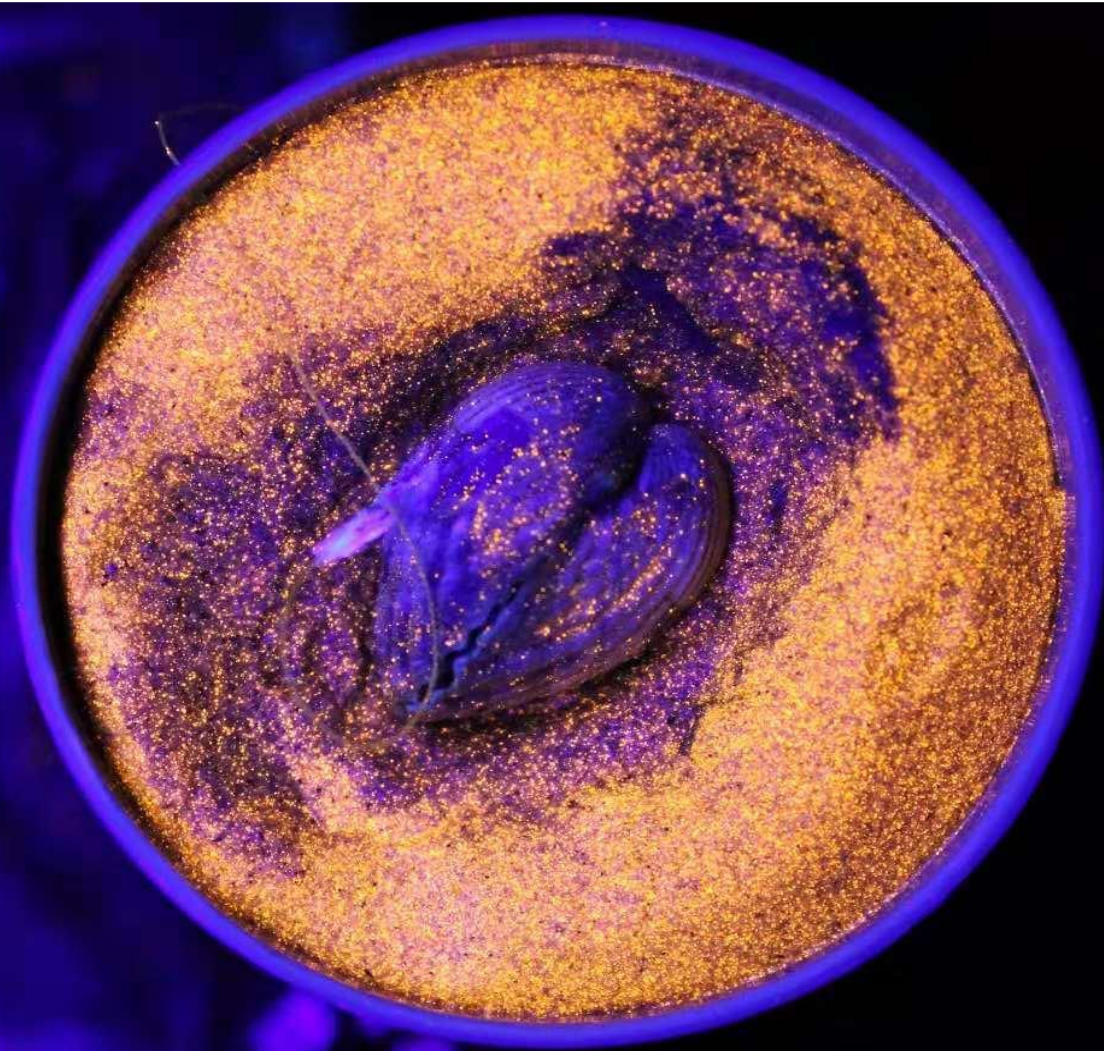
	Estimate	Std. Error	df	<i>t</i> -value	<i>p</i> (> <i>t</i>)	
(Intercept)	-0.37	0.16	6.20	-2.31	0.06	.
with water pools	0.71	0.12	3857.99	6.03	1.84E-09	**
with heatwave	-0.25	0.12	3861.09	-2.09	0.04	*
with water pools: with heatwave	0.90	0.17	3859.13	5.33	1.02E-07	**

Notes: *** for $p < 0.01$, ** for $p < 0.05$, and . for $p < 0.1$.

Table 2.2 Type III Analysis of Variance with Satterthwaite's method

	Sum Sq.	Mean Sq.	Num. DF.	Den. DF.	F-value	<i>p</i> (>F)	
water pools	1294.56	1294.56	1.00	3859.13	187.53	1.02E-41	**
heatwaves	37.55	37.55	1.00	3860.64	5.44	0.02	*
water pools: heatwaves	196.31	196.31	1.00	3859.13	28.44	1.02E-07	**

Notes: *** for $p < 0.01$, and ** for $p < 0.05$.



Chapter 3 Temporal dynamics of heatwaves are key drivers of sediment mixing by bioturbators

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Abstract

Heatwaves affect tidal flat ecosystems by altering the bioturbating behavior of benthic species, with potential consequences for sediment oxygenation, particle mixing, and erodibility. Although the frequency and duration of heatwaves are expected to increase under global warming scenarios, we lack insights into how heatwaves' temporal dynamics affect bioturbating behaviors. Using the widely distributed bioturbator *Cerastoderma edule* as model species, we quantified how heatwaves with identical heat-sum but different temporal dynamics (i.e., 3-day vs. 6-day heating and normal temperature cycles) affect bioturbating behaviors and the sediment mixing processes in tidal mesocosms. Our results show that short but frequent 3-day heatwave cycles increased the magnitude of bioturbating behaviors, thereby resulting in more bio-mixed sediment than observed under infrequent prolonged 6-day heatwave cycles. This unexpected result could be ascribed to the weakening health condition indicated by a high death rate (47.37%) under 6-day heatwave cycles than in 3-day and no-heatwave control cycles. Present findings reveal that the impact of heatwaves on sediment bioturbation will strongly depend on the temporal dynamics of future heatwaves: bioturbation will be enhanced unless the heatwave duration exceeds species resistance and increases mortality.

Keywords

heatwaves; temporal dynamics; bioturbation; burrowing behavior; *Cerastoderma edule*

3.1 Introduction

Bioturbation is the process of sediment reworking by living organisms (Darwin, 1897). Bioturbators are classified as ecosystem engineers (Jones et al., 1997; Wright & Jones, 2006) because they can excessively modify the physical properties of sediments (e.g., compaction, bulk density, and particle distribution) and the diffusion rate of chemical compounds (Braeckman et al., 2010; Cozzoli et al., 2021; Kristensen et al., 2012) via foraging (Wrede et al., 2018) and building behaviors (Borsje et al., 2014). From terrestrial fields to deep-sea sediments, bioturbation plays a significant role in changing the surface landscape of our planet (Meysman et al., 2006). Across the globe, tidal flats are one of the most renowned ecosystems dominated by a wide range of bioturbating benthic species (Teal et al., 2008; van der Wal et al., 2017), and hence the focus of the present study.

The physical conditions for living on tidal flats are typically harsh in that they constantly change due to tidal cycles of drying and inundation. By interacting with physical forces from currents and waves, some bioturbators actively flush their burrows to refill oxygen and nutrients (Hedman et al., 2011; Mermillod-Blondin & Rosenberg, 2006). These burrows thus become networks to promote chemical exchange at water-sediment interfaces (i.e., benthic-pelagic coupling). Moreover, bioturbators loosen the sediment and increase the surface roughness (Li et al., 2017; Widdows & Brinsley, 2002). Hydrodynamic forces may reshape these biologically induced topographies during tidal inundation, resulting in enhanced sediment resuspension and erosion (Cozzoli et al., 2019; Dairain et al., 2020; Montserrat et al., 2009). For example, the common cockle *Cerastoderma edule* can affect sediment stability through vertical and horizontal movements such as shell shaking, adductions, and excreting feces. These bioturbating activities can lead to more erosion in cohesive sediment (Le Hir et al., 2007; Li et al., 2017; Widdows et al., 2000). Understanding the effect of benthic bioturbators on sediment erodibility is essential, as short-term transitions between erosion and accretion may affect the long-term stability of tidal flat ecosystems (e.g., see Bouma et al., 2016; Shi et al., 2021).

Tidal flat ecosystems worldwide are declining and may be increasingly threatened by global change processes (Murray et al., 2019). Recent studies show that 50% of the ocean surface water may suffer from marine heatwaves by the late 21st century (Holbrook et al. 2019). Tidal flat ecosystems are expected to be much more prone to such heatwaves since the surface sediments can experience a daily temperature difference of more than 10 °C during the low-tide emersion time (Bouchet et al., 2007; Johnson, 1965; Y. Li et al., 2019), despite that the seasonal variation can be more than 30 °C from summer to winter (Murphy & Reidenbach, 2016). Gouletquer et al. (1998) even measure a daily temperature increment of 23 °C in the oyster reef. Bioturbators living on tidal flats are prone to extreme temperature fluctuations, particularly those inhabiting higher intertidal areas (Pansch et al., 2018). Occasional exposure to heatwaves can decrease the health conditions of the benthic bioturbators living

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on tidal flats (Coma et al., 2009; Paireud et al., 2014; Rivetti et al., 2014). Thermal stress typically promotes the bioturbators' metabolic rates (Anestis et al., 2007; Vinagre et al., 2016), which positively relates to their moving behavior (Cozzoli et al., 2019). More movements may increase sediment bio-mixing and a reduced critical erosion threshold on the tidal flat scale (Cozzoli et al., 2020). Thus, to predict the future fate of tidal flat ecosystems, it is necessary to better understand how future heatwaves affect benthos' bioturbation behaviors.

Like most abiotic stresses and disturbances in the natural environment, the effect of heatwaves may be expected to depend on their magnitude, duration, and frequency (Donohue et al., 2016). To date, most heatwave studies only focus on magnitude (i.e., the effects of the heatwave intensity; Gauzens et al., 2020; Laufkötter et al., 2020; Perkins-Kirkpatrick et al., 2017), even though variation in duration and frequency may impose more complex outcomes. For example, Seuront et al. (2019) show that 100% mortality for the mussel *Mytilus edulis* occurred at lower temperatures with increasing duration of exposure to heatwaves. Global warming not only leads to a higher heatwave intensity, but also amplifies the temporal dynamics of heatwaves. That is, the duration and frequency of marine heatwaves have increased by 17% and 34%, respectively, in the years 1987-2016 compared to the years 1925-1954 (Oliver et al., 2018). Thus, in addition to experiments quantifying the effects of heatwave intensity on bioturbation behavior and changes in tidal flat sediments, studies are needed to quantify the impact of temporal dynamics.

To gain insight into the effects of heatwave temporal dynamics on the bioturbation process, we conducted a mesocosm experiment with contrasting “short” and “long” heatwave cycles. Both cycles consist of 12-day heating and 12-day recovery phases, while the temporal distribution of heating and recovery treatments are different: the “short-duration” heatwaves consist of alternating 3-day heating and normal temperature periods; the “long-duration” heatwaves consist of alternating 6-day heating and normal temperature periods (Figure 1). The control treatment is kept constantly under ambient temperatures of 20 °C. The heatwave temperature was 35 °C during daytime low tides. In each mesocosm, a regular semi-diurnal tide was mimicked with a 5-hour low tide during the day and 5 hours at night. We used the widely distributed common cockle *Cerastoderma edule* as a model bioturbator species. Cockles' burrowing depth, sediment mixing, and survival were measured to study the bioturbation response patterns under different heatwave profiles.

3.2 Material and methods

3.2.1 Mesocosm setups

A mesocosm experiment was performed in a climate room to simulate natural heatwaves on tidal flats. One tidal mesocosm unit consists of 2 water tanks stacked together (inner dimensions: 110 ×

95 × 60 cm). The upper tank was filled with 30 cm-high sand ($SD_{50} = 265.02 \mu m$) as a basement that contained the experimental treatments; the lower tank was used as a water reservoir for simulations of tidal cycles (for details, *see* Cao et al., 2018). The experimental treatments created a high tide by pumping water from the lower reservoir tank into the upper tank. The water height was adjusted by a return-flow pipe (30 cm height), transporting the overflow water back to the lower tank. Low tide was created by turning off the pump to drain all water into the lower reservoir tank. A regular semi-diurnal tide was mimicked according to the natural conditions where cockles were collected (Oesterdam, 51°28'01.4" N, 4°12'49.8" E). The low tide period was 5 h occurring twice daily during both day and night, giving a total of 10 h low tide per day (Fig. 3.1a).

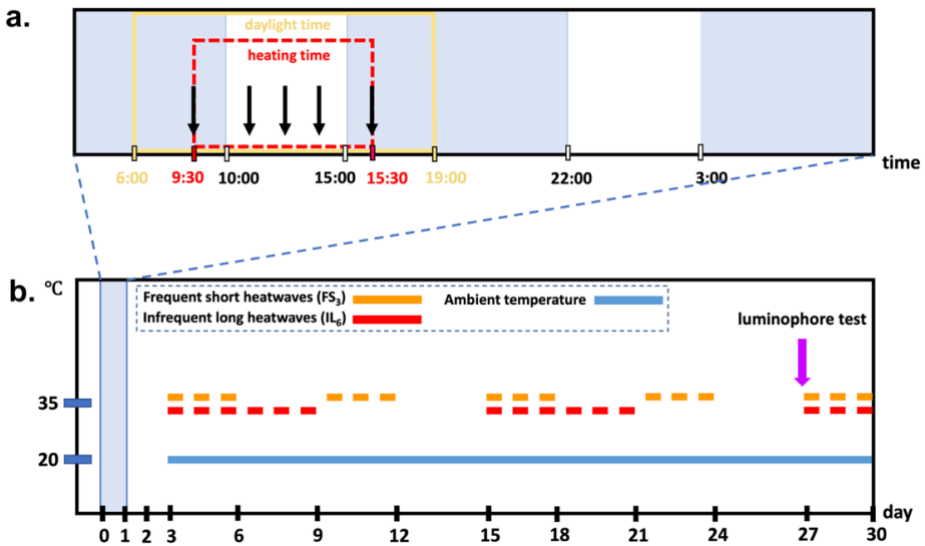


Figure 3.1 Schematic representation of the daily tidal regime (a) and simulated heatwave treatments (b). In the daily tidal regime (a), daylight time is indicated by a yellow color on the time axis. In contrast, nighttime is marked as black. Semi-diurnal tides (42% low tide time) were mimicked (i.e., high tide marked as blue shades, low tide marked as white rectangles). In panel a, the times at which burrowing depth measurements were taken are indicated by black arrows. The ambient air temperature was constant at 20 °C (b, indicated by the solid blue line). The heaters were only turned on during the daytime low-tide period, as indicated by the dashed lines starting half an hour before and ending half an hour after low-tide (a, the red frame). The maximal temperature of the simulated heatwave was 35 °C. Two heatwave temporal profiles were applied, a frequent short-duration heatwave (b, 3-day cycles) and a less frequent long-duration heatwave (b, 6-day cycles). Both heatwaves followed a 3-day heatwave to measure bioturbation effects using luminophores. The purple arrows indicate when luminophore tablets are deployed during the low tides.

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PVC pots (67 mm inner diameter, 3 mm wall thickness, 100 mm height) were filled with sieved sediment (mesh size $\varnothing = 1000 \mu\text{m}$, sediment $\text{SD}_{50} = 158 \mu\text{m}$) and placed in the upper mesocosm tanks for holding the cockles to be used in the experiment. These pots were made by cutting long 5000 mm PVC pipes into a shorter uniform size, then adding ventilated bottom covers at one end. There are three types of experimental pots: *i*) “heatwave” pots with cockles inside that experienced a 3-day cycle or the 6-day cycle heatwaves (FS₃ and IL₆; details in next section), *ii*) “control” pots with cockles inside and were under ambient temperatures, and *iii*) “blank” pots that contained no cockles under ambient temperature, to only measure the tidal effects on sediment mixing. There were 40 “heatwave” pots; 20 replicates for each heatwave profile. The “control” pots had 20 replicates, and the “blank” pots had ten replicates. All pots were evenly distributed in four mesocosms, two with heaters on top and two without under ambient temperature.

3.2.2 Imposing heatwaves: Temperature setting and measurement

Four mesocosms were placed in the same climate room, of which two were used for simulated heatwave treatment and the other two as ambient temperature controls. According to temperature measurements in the field during the 2020 summertime heatwaves (*see* Appendix 3.1, Fig. A3.1a), we set the maximal temperature of the sediment surface at 35 °C and the ambient temperature at a constant 20 °C. Terrace heaters (Frico, EZ212) were used to mimic solar irradiation during low tide. A thermal probe was placed on top of the sediment to control the heater temperature by real-time measurements: when the temperature of the sediment surface reached 35 °C, the heater was turned off; when it dropped below 35 °C, it was turned on again.

Due to delays in the control system, the actual mean temperature was $32.23 \pm 1.61 \text{ }^{\circ}\text{C}$ (*see* Appendix 3.1, Fig. A3.1b, red lines); the actual mean ambient temperature was $16.42 \pm 0.35 \text{ }^{\circ}\text{C}$ (Fig. A3.1b, blue lines). The daily operating time of the heater was controlled by a time switch to match the daytime low tide period, starting to heat half an hour before the daytime low tide till half an hour after the daytime low tide (Fig. 3.1a). The heaters were turned off during the night.

To measure the temperature profiles in each tank, two extra PVC pots (no cockles inside) were made to hold the temperature sensors (PT-100 sensors, TC Direct). These sensors were deployed at fixed depths of 0 cm, 3 cm, and 6 cm to record the per-minute temperature profiles in the PVC pots, and they were used to represent the temperature profiles of all pots in the same tank. All temperature sensors were connected to a CR10X datalogger (Campbell Scientific, Inc.), and the data was transferred via LoggerNet software (Campbell Scientific, Inc.). During low tides, the temperature sensors measured the temperature of drained sediment in PVC pots; during high tides, all sensors were submerged and measured water temperature instead.

To determine a reasonable magnitude and duration for the artificial heatwaves in our experiment, we obtained 70 years of temperature data from the Royal Netherlands Meteorological Institute (KNMI) at Schiphol (near Amsterdam), Netherlands. The “high-temperature event” was summarized as when the daily maximum temperature was above 30°C for more than two days. In the past 70 years, there were 42 high-temperature events lasting more than 2 days, 35 of which lasted 2-3 days, 5 of which lasted for 4-5 days, and 2 of which lasted more than 6 days. (see Appendix 3.2, Table 3.1). Therefore, two heating treatments were applied to mimic: *i*) frequent short-duration (i.e., FS₃) heatwaves consisting of 4 repeating cycles of 3-day heating within between 3-day recovery at normal temperatures; *ii*) infrequent long-duration (i.e., IL₆) heatwaves consisting of 2 repeating cycles of 6-day heating within between 6-day recovery at normal temperatures (Fig. 3.1b). The overall heatwave exposure had an identical duration for FS₃ and IL₆ during the day, with 5 h per day for 12 days. The FS₃ and IL₆ heatwave treatments ended with a 3-day heatwave to measure bioturbation using luminophores (see section 2.5). The ambient control was maintained at a constant temperature of 20 °C over the whole period.

3.2.3 *Cerastoderma edule* as model species to study bioturbation

The common cockle *Cerastoderma edule* is widely distributed along the European Atlantic coastline. The cockles used in this experiment were collected from Oesterdam, the Netherlands, in late September 2020. They were transported to a temperature-controlled climate room set at 20 °C and left in a tank filled with aerated seawater for 120 h acclimation. Then, living cockles were transferred into PVC pots filled with sediment and placed in the tidal mesocosms, allowing them to acclimate to the new environment for another 72 h before starting the heatwave treatments. Each PVC pot under FS₃, IL₆, and the control treatment received one live cockle taken from a population with a mean shell length of 32.00 ± 1.80 mm and a mean wet tissue weight of 0.91 ± 0.21 g (mean \pm SD; $n = 50$). When individuals were inactive or remained on the sediment surface for 24 h, they were replaced with new individuals. All cockles were fed twice a week with instant microalgae (Shellfish Diet 1800, Reed Mariculture Inc.). The algae concentrate was pre-diluted at 10:1 with 100 ml seawater, then fed to each tank homogeneously with a dropper. One-third of the seawater in the reservoir tanks was replaced every week to guarantee good water quality throughout the experiment. Dead cockles on the sediment surface were removed every day. We used a metal tweezer gently moving around their siphons to check whether cockles had died and burrowed in the sediment. Cockles that did not respond to these physical stimuli were recorded as dead.

3.2.4 Burrowing behavior measurements

We use bivalves' burrowing behavior as an indicator of vertical bioturbation activity. A cotton thread was glued (superglue CA10, F.T Products) on the cockle's shell to measure the cockle's burrowing behavior. The other end of the line is tied with a knot to make different measurements comparable for the same cockle. The thread was gently pulled straight to measure the distance between the knot and the sediment surface. This method was adopted from Auffrey et al. (2004) and has been tested to have no effects on the burrowing activities of bivalves. Moreover, we have successfully applied this method to detect the significant impact of heatwaves on the cockles' burrowing behavior (Zhou, et al., 2022). Five measurements were performed daily. The first and last measurement occurred half an hour before and after the 5-hour low tide at 9:30 and 16:30. The other three measurements occurred during the low tide at 10:30, 12:30, and 14:30, during which the sediment with cockles was directly exposed to solar radiation in the heating mesocosms (Fig. 3.1a). The relative depth change of each measurement point is calculated by subtracting the first measurement value from the absolute length. Therefore, the relative depth change of the first measurement was always 0 cm at 9:00. The following four measurements used the first one as a baseline to calculate the burrowing depth change.

3.2.5 Quantifying the sediment mixing process using luminophores

We used luminophores (Environmental Tracing Systems Ltd., UK) to quantify sediment particle transportation in each PVC pot. Luminophores are inert natural sediment particles dyed with luminescent paint and are often used to track bioturbation effects (Wiesebron et al., 2021). The median grain size (SD50) of the luminophores was 41 μm . The color of the luminophores was "magenta red" under normal ambient light, with shining luminosity in a dark environment under UV light. Sieved ($\phi = 1000 \mu\text{m}$) ambient sediment (SD50 = 158 μm) and luminophores were mixed at a volume ratio of 10:1 with water (i.e., water weight was determined by the bulk density of ambient sediment). Then, the sediment-luminophore-water mixture was poured into PVC molds of $70 \times 70 \times 0.5 \text{ mm}$ (i.e., inner diameter = 67 mm) and froze at -20°C to make luminophore "tablets".

Luminophore tablets were placed on top of each PVC pot during low tide for all treatments, namely, "heatwaves (i.e., FS₃ and IL₆)", "control", and "blank". After this deployment, a final 3-day heatwave treatment was applied to both the FS₃ and IL₆ "heatwave" pots, but not to the no-heatwave "control" and "blank" pots (Fig. 3.1b). When the experiment ended, the PVC pots with luminophores were horizontally sliced using a metal spade along depth gradients (i.e., every 0.5 cm till 3.0 cm, then 1.0 cm per slice till 5.0 cm). The luminophore area in each slice was used to indicate the horizontal bioturbation activities.

Every slice was photographed under UV light using a digital single-lens reflex camera (Canon EOS with 18-55 mm EFS objective). The camera was mounted on a fixed stand to guarantee the same shooting distance. The JPEG images were saved as 2304×3456 pixels. These images were processed using a custom script of ImageJ 2 and R 4.0.0 software. Firstly, the images were subdivided into RGB stacks, and the brightness threshold of red 128-255 was used to distinguish the image pixels in red luminophores and sediment. Then, the total number of luminophore pixels in each slice was counted ($S_{\text{bioturb-depth}}$, cm^2). Only pixels within the circular region in the center frame of the photo (within the PVC tube) were analyzed. A buffer margin of 5mm from the edge within the tube was also excluded to minimize edge effects due to the cutting process.

Since luminophores were applied on top of the sediment, the luminophore counts in photographs taken from the top view of below-ground sediment slices provide a quantitative indicator of the bioturbation activity in an individual PVC core. Due to limitations of the slicing tool, in all cores, the first two sediment slices taken at a depth of 0.5 cm and 1 cm were disturbed by edge effects and thus neglected. As $< 1\%$ luminophore pixels were observed in slices taken below 3 cm (i.e., at 4 cm and 5 cm depth), these slices were also neglected. As a result, the luminophore counts in photographs taken from the top of the sediment slices at 1.0, 1.5, 2.0, 2.5, and 3.0 cm were used to calculate the average bioturbation areas with the following equation:

$$S_{\text{bioturb}} = \sum_{i=1}^n \left(\frac{\text{Pixels}L_i}{\text{Pixels}S_i} \times 100\% \times S_{\text{pvc}} \right) / n \quad \text{Eq.1}$$

where S_{bioturb} is the depth-averaged bioturbated surface area in each PVC core (cm^2); i is the slice number (i.e., 5 slices in each core); $\text{Pixels}L_i$ and $\text{Pixels}S_i$ refer to the luminophore pixel amount and the total pixel amounts of sediments in slice i , respectively; S_{pvc} refers to the cross-sectional area of one PVC pots (i.e., 35.24 cm^2); n is the number of layers averaged ($n = 5$ for all cores).

3.2.6 Data analysis

Survival percentage: The number of living cockles during the experimental period was divided by the total number of replicates (excluding replicates lost due to the accident, *see* Appendix 3.3) to calculate the survival percentage for FS₃, IL₆, and ambient control treatments.

Burrowing depth: The burrowing depth measurement was an indicator of vertical bioturbation activities. A linear mixed-effect model was used to test the effects of heatwave treatments on cockles' burrowing depths: *Burrowing depth change* ~ *Heatwave Treatment* + *Day* + (*1* | *Individual number*). The heatwave treatments and experimental days are fixed factors, while the individual serial number is a random factor nested within the fixed factors. Finally, a post-hoc Tukey HSD analysis was applied to check the effects of different heatwave cycles on burrowing depth change.

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Luminophore tests: We used luminophore tests to get quantitative proxies for bioturbation activities. That is, we calculated first the depth-specific bioturbation area ($S_{\text{bioturb-depth}}$, cm^2) for each 5-mm slice along a 1- to 3-cm depth profile and used these data to derive the depth-averaged bioturbation area (S_{bioturb} , cm^2) in each PVC core. Since the luminophore tests were only applied once at the end of the experiment, we could not do a time-series analysis.

The effects of heatwave treatments on the depth-specific bioturbation profiles were tested using a two-way analysis of covariance (ANCOVA): *Bioturbation areas* ~ *Heatwave treatment* + *Depth*, followed by a Tukey HSD analysis for post-hoc analysis. The effects of heatwave treatments on the depth-averaged bioturbation areas were first checked by the Kruskal-Wallis test, and then a Wilcoxon rank sum test was used as a post-hoc analysis.

The data points and error bars indicate *mean* \pm *standard error* in all plots. The data analysis was performed by R 4.0.0 (R Core Team, 2021).

3.3 Results

3.3.1 Cockles' response to thermal stress: mortality and behavior

Repeated exposure to heatwaves (defined as temperatures $\geq 35^\circ\text{C}$) can lead to the death of cockles. The 3-day cycle heatwaves (FS_3) resulted in a 72.73% survival rate (*see* Appendix 3.3, Fig. A3.2). Even though the total number of heating days was the same, the 6-day cycle heatwaves (IL_6) resulted in a lower survival rate at 47.37% (Fig. A3.2). The same applies when comparing the survival rate of IL_6 to the survival rate in the absence of any thermal stress (no-heatwave controls, 100 % survival). The method of behavioral measurement can detect significant differences in the burrowing depth under different heatwave settings (significance levels are shown in Fig. 3.2). The burrowing behavior of cockles was affected by thermal stress (Fig. 3.2). During low tide, the cockles burrowed deeper into the sediment when exposed to heatwave conditions (Fig. 3.2b). Upon the return of the high tide, the cockles then moved towards the surface. On ambient temperature days between heatwaves the behavior of cockles that had earlier experienced heatwaves returned to movement patterns similar to those seen in cockles in the permanently ambient temperature treatments (Fig. 3.2a). The statistical results for Fig. 3.2 are shown in Table 3.2 and Table 3.3 in Appendix 3.4.

3.3.2 Bioturbation effects: the area of disturbed sediments

Cockles' activities always introduced the surface particles into up to 3 cm sediment layers, resulting in similar overarching patterns as shown in Figure 3. The horizontal bioturbation areas differed between treatments: the bioturbating areas under FS_3 were the largest, and those under IL_6 were the

smallest. This trend was consistent from 1.0 cm to 2.5 cm depth (Fig. 3.3). The statistical results for Fig. 3.3 are shown in Table 3.4 and Table 3.5 in Appendix 3.5.

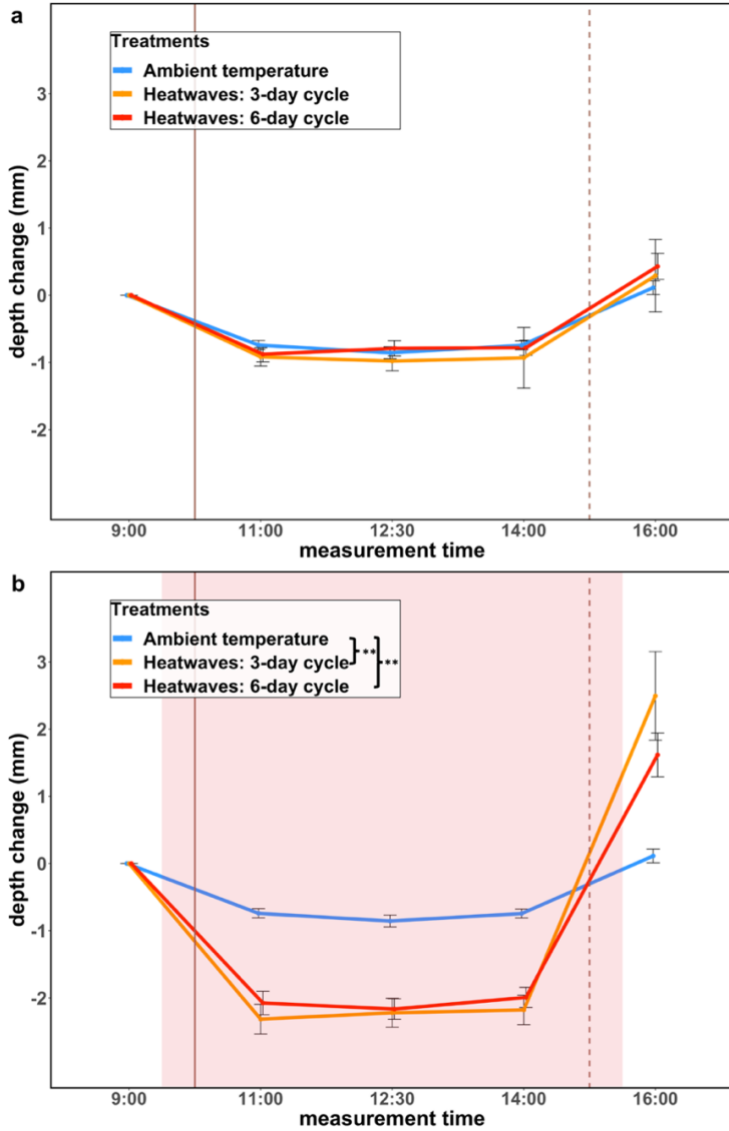


Figure 3.2 Daily average burrowing position as measured during the non-heatwave cycles (a) and heatwave cycles (b). Different line colors indicate temperature settings, as shown in the legends. The red shades represent the period of the heating treatment. The solid brown lines represent the beginning time of low tides (start of sediment exposure);

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the dashed brown lines represent the beginning time of high tides (start of sediment submersion). Data from individual measurements were averaged daily by each heatwave and recovery cycle. In the plot, each point represents the mean values of the measured alive individuals. The calculation was based on 72 to 540 recordings in panel a, and 95 to 540 recordings in panel b, depending on the survival individuals under the control/heatwave treatments. The ambient control measurements (blue lines) in panels a and b are identical based on all daily recordings in each heatwave/cycle setting. Positive depth change values indicate cockles move upwards, while negative values indicate moving downwards. The error bars represent the standard errors of individual measurements during all repeated cycles. The difference in depth changes between control and heatwave treatments were tested using one-way ANOVA. The significant level $p < 0.01$ was marked by “***” on the right side of the figure legends.

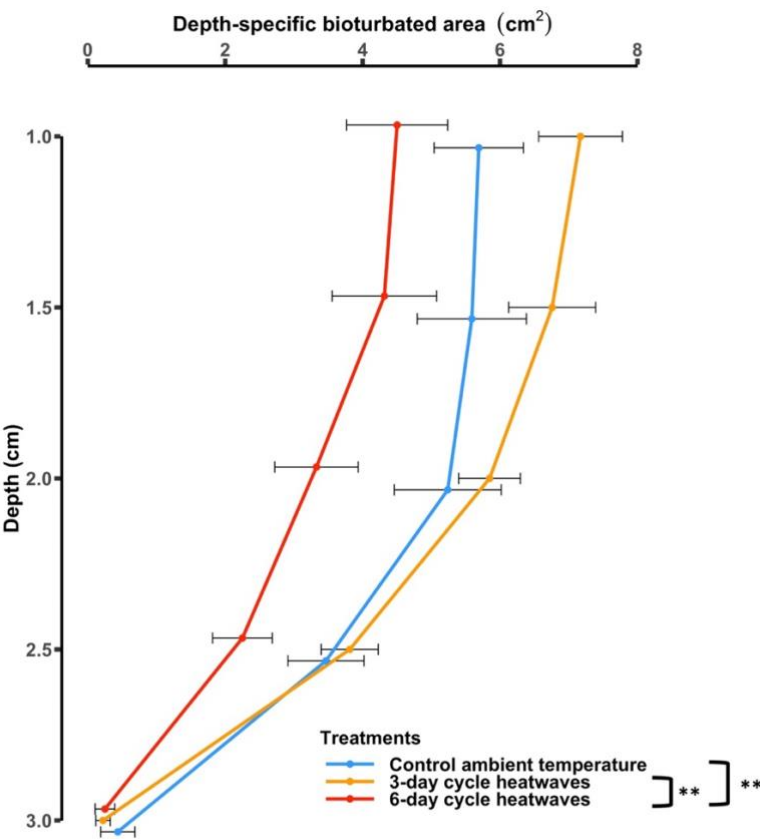


Figure 3.3 The depth-specific bioturbated area ($S_{\text{bioturb-depth}}$, cm^2) for contrasting heatwave treatments. The bioturbation areas were calculated using luminophore pixel counting data. Each point represents 8 to 10 data recordings in the plot depending on the number of successfully processed PVC pots. Only 1.0 to 3.0 cm profiles were displayed since most

of the bioturbation process happened within this range. The top 1cm layer results were discarded after slicing due to pervasive edge effects. Each data point represents the mean values of the measured replicates. The error bars represent the standard errors between replicate PVC pots at each depth. The significant level of $p < 0.01$ was indicated by “***” in the figure legend.

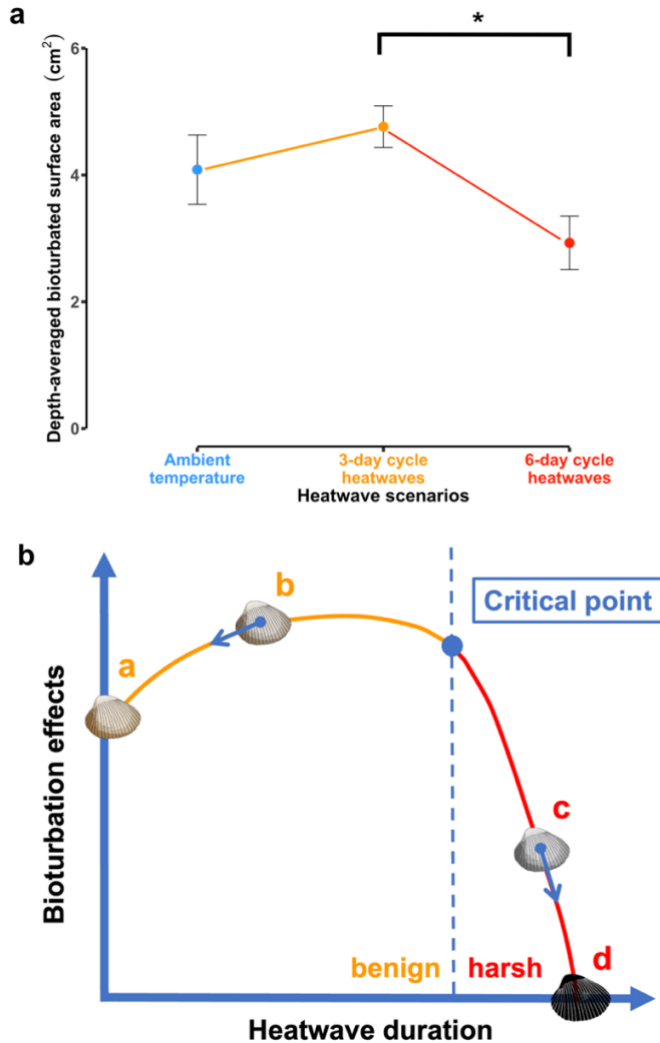


Figure 3.4 Diagrams showing how the heatwave duration may determine bioturbation effects. a) Experiment data that summarizes heatwave effects on the depth-averaged bioturbated area. Each data point represents the mean values of the measured replicates. The 3-day cycle heatwaves result in more bioturbation areas than those under ambient

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temperatures. The 6-day cycle heatwaves decrease depth-averaged bioturbated areas compared with ambient temperatures. Each data point represents the mean values of the measured replicates. The error bars represent the standard errors between replicate PVC pots. The significant level of $p < 0.05$ was indicated by “*” in the figure. b) A conceptual figure showing how cockles’ behavioral response can determine the bioturbation under heatwaves. The x-axis indicates the duration of heatwaves. The y-axis shows the bioturbation intensity in tidal flat sediment. When the heatwave duration does not pass the critical point of bioturbators’ thermal tolerance thresholds, the bioturbation can be enhanced due to more movements (status “a” to “b”). After the heatwaves, bioturbators’ condition may still recover (as indicated by the blue arrow on “b”). When the heatwave duration lasts too long, bioturbators’ health conditions are reduced, leading to reduced bioturbation effects (status “a” to “c”). In the worst case, the bioturbator may no longer be able to recover (as indicated by the blue arrow on “c”), resulting in mass mortality (status “d”).

The heatwave duration significantly impacted the amount of bio-disturbed sediments (Table 3.4, ANCOVA, $F = 12.01$, $Df_{\text{treatments}} = 2$, $p < 0.01$). Post-hoc analysis showed that the 6-day cycle heatwaves (IL₆) significantly decreased the size of bio-disturbed areas compared with that under 3-day cycle heatwaves (FS₃) (Table 3.5, Tukey HSD, $t = -4.81$, $Df_{\text{treatments}} = 2$, $Df_{\text{depths}} = 4$, $p < 0.01$). However, the 3-day cycle heatwaves imposed similar bioturbation effects with those under control ambient temperatures (Table 3.5, Tukey HSD, $t = 1.82$, $Df_{\text{treatments}} = 2$, $Df_{\text{depths}} = 4$, $p = 0.17$).

Heatwave treatments significantly changed the depth-averaged bioturbated area (Kruskal-Wallis test, $\chi^2 = 7.2884$, $df = 2$, $p\text{-value} = 0.03$). Further post-hoc analysis indicated that the 6-day cycle heatwaves significantly decreased the depth-averaged bioturbated area compared to that under 3-day cycle heatwaves (*see* Fig. 3.4a, Wilcoxon rank sum test, IL₆ – FS₃, effect size $r = 0.63$, $N = 17$, $p = 0.02$).

In summary, the 6-day cycle heatwaves (IL₆) imposed higher mortality than the 3-day cycle heatwaves (FS₃) (Fig. A3.2) and decreased cockles’ bioturbation ability (Fig. 3.3), thus significantly reducing the size of the depth-averaged bioturbation area (Fig. 3.4a). FS₃ heatwaves boosted vertical (Fig. 3.2b) and horizontal (Fig. 3.3) bioturbation activity, yet the total bioturbated areas did not show a significant difference with those under ambient temperature after three days of sediment reworking (Fig. 3.4a).

3.4 Discussion

Studying bioturbation under heatwaves is essential to understand the effects of global warming on the tidal flat sedimentary environment, as bioturbation is known to affect both the sediment mixing and the erodibility of tidal flats. In the present study, we show for the first time that bioturbation effects under global warming strongly depend on the frequency and duration of the heatwaves. That is, repeated short heatwaves can increase bioturbation activity while not causing much mortality. In contrast, the less frequent long-duration heatwaves decrease the overall bioturbation activity as it increases bioturbators’ mortality, thereby causing less sediment mixing. Predicting climate-change effects on tidal flat

functioning requires insights into the frequency and duration of future heatwaves and in-depth studies on the behavioral responses and mortality consequences of key bioturbating species, as demonstrated in the current study.

3.4.1 Thermal tolerance of organisms in the face of climate change

In our experiment, cockles that suffered from 3-day repetitions of heating treatments showed more vertical movement than those under ambient temperatures. This response can be seen as a strategy in which bioturbators adjust their burial depth and use the sediment as a thermal refuge during the heatwave (Munguia et al., 2017; Payette & McGaw, 2003). Other bivalve species also adapt their burial depth to elevated temperatures. For example, a mesocosm experiment showed that *Ruditapes decussatus* burrowed deeper into the sediment under simulated heat stress of 29 °C to 8 cm depth (Domínguez et al., 2021). Compared with *C. edule*, *R. decussatus* typically buries deeper into the sediment, potentially down to 20 cm (Macho et al., 2016). Therefore, we summarize the response strategies by which benthic organisms cope with extreme temperatures with the following two strategies: *i*) either employing more horizontal movements to search for locations with less stressful temperature conditions; or *ii*) burrowing deeper to use deep layers of the sediment as a shelter to escape the extreme heat stress. The trade-offs between these two strategies will likely depend on a species' physiological limitations and energy consumption. For example, the maximal burrowing depth of bioturbating bivalves is mainly limited by their siphon size (*i.e.*, physiological limitation) (Zwarts & Wanink, 1989). However, higher filtration costs due to enhanced movements will typically increase the energy consumption of these bivalves (Sobral & Widdows, 2000).

These strategies can be regarded as regulatory behaviors that are stimulated by the environmental conditions of microhabitats. Microhabitats are usually local habitats with less harsh environmental conditions than those at larger spatial scales. Many intertidal ectotherms have developed a range of behavioral strategies to search for suitable microhabitats and adapt to temperature variations (Muñoz et al., 2005; Williams, 1984). In cooler environments, most freshwater insect larvae avoid freezing by actively staying in the water body that will not freeze; lizards will shuttle between the sun and shade to maintain their body temperature in an optimal range (Diaz & Cabezas-Diaz, 2004; Lencioni, 2004). In a warmer environment, snails may actively search for sheltered microhabitats on rocky shores to escape direct sunlight and stabilize their body temperatures during daytime emersion; capitellids may burrow deeper to escape warm temperatures that exist in natural soft sediments (Lardies et al., 2001; Tsubokura et al., 1997). The movement behaviors demonstrated by cockles in our experiments could be considered an example of the wide range of thermoregulatory movement responses commonly practiced by ectotherms.

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Tidal flat invertebrates may cope temporarily with thermal stress through thermoregulatory behaviors such as burrowing. However, when the thermal stress (e.g., magnitude, duration, etc.) surpasses critical thresholds, these response strategies may fail and lead to severe physiological stress or even mass mortality (Fig. 3.4b). The findings by Deldicq et al. (2021) also support the conceptual summary shown in Fig. 3.4b, in that foraminifera reduced their activity by up to 80% under high-temperature regimes (i.e., 36 °C) and the photosynthetic activity of their sequestered chloroplasts significantly decreased. When the heatwave duration is long enough to create mass mortality (50% death rate in this experiment), organisms cannot escape from the continuous accumulation of heat stress via different behavioral strategies. The resulting mass mortality can potentially cause large-scale species distribution shifts (Fiori & Cazzaniga, 1999; Paireud et al., 2014; Wernberg et al., 2013). Due to the mass mortality of adult individuals, the age structure of native species tends to be younger in the following year (Beukema & Dekker, 2020; Magalhães et al., 2016). This implies that if the duration of heatwaves strongly increases under climate change scenarios, there will not be enough adults to produce larvae. As a result, native species with poor temperature tolerance will not persist, thereby giving up their niche to more heat-tolerant invasive species (Molnar et al., 2008). Both native species depletion and invasive species replacement can result in functioning shifts of the whole tidal flat ecosystems.

3.4.2 Implications for bioturbation in tidal flat ecosystems

Our experiment provides novel insights into the effects of heatwaves on tidal flats by demonstrating that the temporal scale of heatwaves is a key factor in driving the overall bioturbation outcome (Fig. 3.4b). High temperature promotes bioturbation rates via increased metabolism (Cozzoli et al., 2019; Ouellette et al., 2004; Pörtner, 2008). In this experiment, repeated short-duration heatwaves increased cockles' burrowing activities, as shown in their daily burrowing depth change. Studies have shown that bioturbation activities result in higher erodibility dependent on sediment type and suspended particle content (Li et al., 2017; Willows et al., 1998). Thus, more erosion can be expected under short-duration heatwaves. Moreover, bioturbating activities promote sediment mixing and chemical resource exchange (Mermillod-Blondin & Rosenberg, 2006; Sturdivant & Shimizu, 2017). To our surprise, the luminophore tests yielded a similar bioturbation effect between the control and FS₃ heatwaves. This similarity might be due to the relatively long 3-day action duration before slicing and the limited volume of the PVC pots. Cockles living in the small PVC pots thus had sufficient time to disturb most of the sediments. Nevertheless, previous studies indicated that enhanced burrowing activities under short-duration heatwaves potentially resulted in a deeper oxygen penetration (Sturdivant et al., 2012; Weissberger et al., 2009), which will further change the bottom chemical conditions for microbial communities and other organisms (Jørgensen & Des Marais, 1990).

However, temperature regimes beyond physiological thresholds can impede bioturbators' activities to reduce the animals' energy consumption (Pörtner, 2001; Vianna et al., 2020; Wu et al., 2017). For example, the mudflat foraminifera *Haynesina germanica* can contribute most to sediment reworking under moderate temperatures between 6 and 30 °C, yet significantly reduce activities by 75% under extremely high temperatures (i.e., 32-36 °C, Deldicq et al., 2021). The opportunistic deposit-feeding polychaete *Capitella sp.* burrowed significantly deeper at 21 °C than at 15 °C; however, they suffer from mortality at 32 °C (Przeslawski et al., 2009). Similar responses were observed in our experiment: the bio-disturbed area under the IL₆ heatwave was significantly lower than the ambient control temperature, though cockles' burrowing depth varied during the heatwaves.

Heatwaves are usually fragmented by mild temperature periods, during which the organisms may recover from the thermal stress (Pansch et al., 2018; Woodin et al., 2013). The tolerance landscape theory by Rezende et al. (2014) states that species-specific tolerance thresholds are determined by the stress event's intensity and duration. In addition, our study revealed the importance of the heatwave temporal dynamics in determining bioturbators' thermal tolerance thresholds. Present findings are conceptualized in a generic schematization as Fig. 3.4b. Although our experiment settings indicate significant effects of heatwave duration and frequency in soft sediments, the current conceptualizations can be enlarged to other species and broader habitats. For example, the study by Seuront et al. (2019) showed that the mussel *M. edulis* living on rocky shores suffered a 100% mortality when exposed only once to 41 °C for 6 h, while they also suffered a 100% mortality when exposed five times to 32 °C for 6 h. Moreover, another rocky-shore species *Littorina littorea* also showed a similar response pattern to heatwaves that the temperature at which its heat coma occurred declined significantly with repeated daily exposures (Clarke et al., 2000). These results together indicate that the temporal dynamics of the heatwaves are one of the determining factors for the species sustainability in tidal flat ecosystems, especially under the current global change scenarios featured by increasing frequency and duration of heatwaves.

The present novel findings show that it is the combination of heatwave frequency and duration that determines the outcome of ecosystem functioning like bioturbation. We thus call for action to gain a broader knowledge based on how key bioturbating species respond to the interaction between heatwave frequency and duration, and its meaning for multiple other key species inhabiting tidal flats. This is the only way toward quantifying in detail the conceptualized relationship (Fig. 3.4b) at the community level.

Appendices

Appendix 3.1 Temperature measurements in the field

The HOBO sensors (Onset Computer Corporation) were deployed to measure the temperature of air and sediment at Paulina polder, Netherlands (51°21'01.6"N 3°43'41.9"E). Two sensors measured air temperature 15 cm above the sediment surface. The other two sensors were deployed at 3 cm depth in the sediment to measure the temperature of the sediment. Both measurements (near-surface and 3-cm depth temperature) were the mean values of 2 replicates. The location's elevation was 0.73 ± 0.01 m, and the grain size of the sediment was 68.47 ± 2.90 μm (top 1 cm).

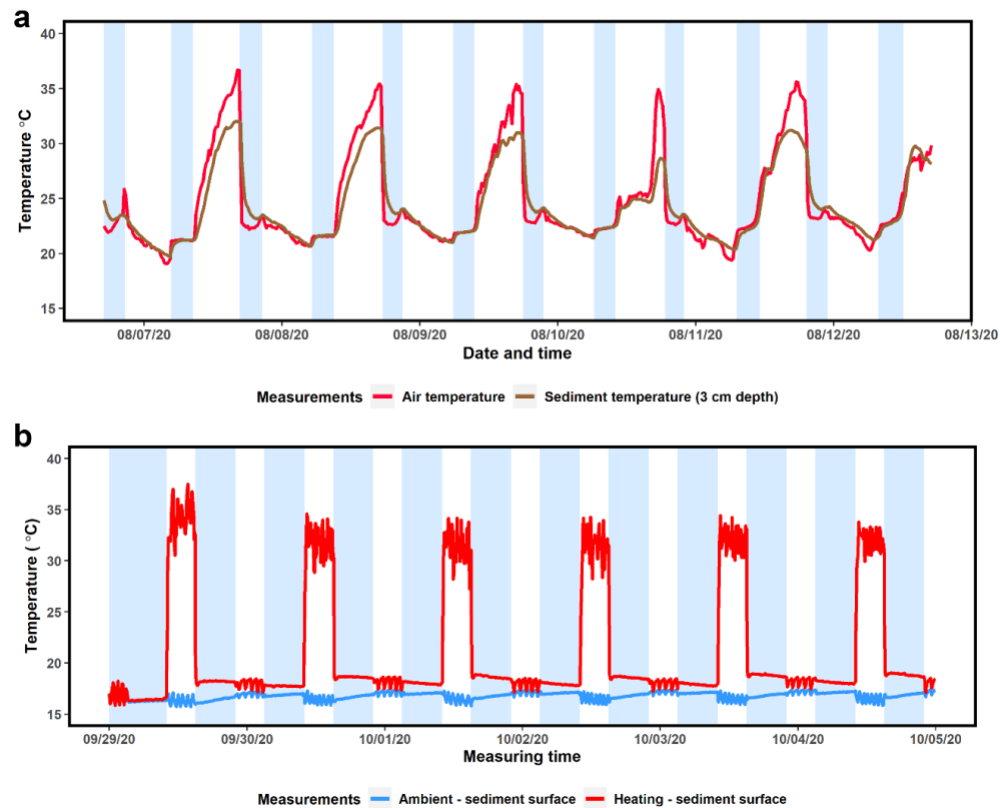


Figure A3.1 Heatwave field data during summer 2021 (a) and simulated heatwaves in mesocosm tanks (b). The blue shades represent inundation during high tides, and white rectangles for exposure time when low tides. The field data shows air and sediment temperature profiles during summer heatwaves 2021 at Paulina polder, Netherlands (a). The mesocosm data shows sediment surface temperatures during a pilot test before the experiment.

Appendix 3.2 Historical temperature data from Schiphol, the Netherlands

A 70-year dataset of daily air temperature at Schiphol is available from Royal Netherlands Meteorological Institute (KNMI). The air temperature was measured at 1.5 m elevation NAP (Amsterdam Ordnance Datum) and recorded to an accuracy of 0.1 °C. The “high-temperature event” was summarized when the daily maximum temperature was above 30°C for more than 2 days. The numbers of 30-35 °C high-temperature events in the dataset are shown in the table.

Table 3.1 The occurrence of high-temperature events in the past 70 years at Schiphol, the Netherlands.

temperature (°C)	high-temperature durations (days)		
	2-3	4-5	> 6
≥ 30	35	5	2
≥ 31	17	4	0
≥ 32	9	0	0
≥ 33	4	0	0
≥ 34	2	0	0
≥ 35	1	0	0

Appendix 3.3 Time series variation of cockles' survival rate

The cumulative survival rate is the ratio of the dead number to the total number of cockles. The designed replicate number is 20 at the beginning of the experiment. However, on Day 2 of the experiment some of the heaters failed, leading to the loss of replicates 9 and 1 of the FS₃ and IF₆ heatwaves, respectively. As a consequence, the lost replicates were not included in the experiment. In the end, 8 out of 11 and 9 out of 19 cockles survived the FS₃ and IF₆ heatwaves, respectively.

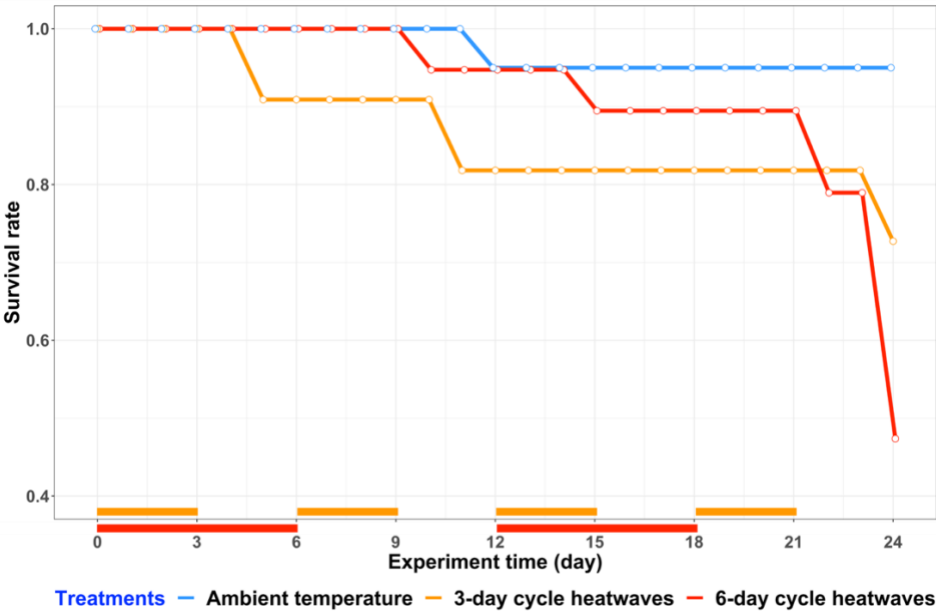


Figure A3.2 The survival rates of cockles under both heatwave settings during the experimental periods. The heatwave cycles are marked on the x-axis to show the duration of two heatwaves. In this figure, the blue lines indicate cockles only exposed to ambient temperature; orange lines represent the cockles under 3-day cycle heatwaves, and red lines represent cockles under 6-day cycle heatwaves.

Appendix 3.4 Statistical analysis for burrowing depth measurements

Table 3.2 The nested ANOVA analysis of the burrowing depth change under different heatwave cycles using a linear mixed-effect model. The *heatwave treatment* (FS₃, IL₆, and Control) and *day* are fixed factors, and *individual number* is a random factor nested in *heatwave treatment* across *day*. The significant level of $p < 0.01$ was indicated by “***”.

	Sum Sq.	Mean Sq.	Num. DF	Den. DF	<i>F</i> - value	<i>Pr</i> ($> F$)
non-heatwave cycles						
Heatwave treatments	5.628	2.8139	2	3601	0.8299	0.4362
Days	224.855	8.6483	26	3601	2.5505	2.55e-05 **
heatwave cycles						
Heatwave treatments	242.83	121.415	2	3807	24.1797	3.67e-11 **
Days	529.05	20.348	26	3807	4.0523	2.49e-11 **

Table 3.3 Post-hoc Tukey HSD analysis for the effects of heatwave treatments on burrowing depth change during heatwave cycles. This test was based on the nested ANOVA analysis in Table 3.2. The significant level of $p < 0.01$ was indicated by “***”.

	Estimated	Std. Error	<i>z</i> - value	<i>Pr</i> ($> z $)
FS ₃ - Control	-0.62055	0.11796	-5.261	2.87e-07 **
IL ₆ - Control	-0.56236	0.10375	-5.42	1.78e-07 **
IL ₆ – FS ₃	0.05818	0.14239	0.409	0.683

Appendix 3.5 Statistical results for luminophore tests

Table 3.4 Analysis of covariance (ANCOVA) for the depth-specific bioturbated areas. The heatwave treatment (FS₃, IL₆, and Control) was an independent variate, and depth was a covariate. The significant level of $p < 0.01$ was indicated by “***”.

	Sum Sq.	Df	<i>F</i> -value	<i>p</i> (> <i>F</i>)
(Intercept)	5680.9	1	229.41	< 2.2e-16 **
Treatments	594.6	2	12.005	1.67e-05 **
Depths	4384.5	4	44.264	< 2.2e-16 **
Residuals	3169.7	128		

Table 3.5 Post-hoc analysis for the effects of heatwave treatments on depth-specific bioturbated areas using the Tukey HSD Test. The significant level of $p < 0.01$ was indicated by “***”.

	Estimate	Std. Error	<i>t</i> -value	<i>p</i> (> <i>t</i>)
FS ₃ - Control	1.924	1.056	1.823	0.16616
IL ₆ - Control	- 3.277	1.023	- 3.205	0.00476 **
IL ₆ – FS ₃	- 5.201	1.081	-4.81	< 1e-03 **



Chapter 4 Sediment dynamics shape the mobility traits of macrofauna on tidal flats

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Abstract

Tidal flats are valuable biogeomorphic ecosystems where the short-term sediment dynamics and the long-term bed level evolution partly result from the interaction between organisms and physical sediment transport processes. Under climate change, tidal flats may expect to be increasingly threatened by intensifying sediment dynamics due to sea-level rise and more frequent storms. Since it is nearly impossible to replicate the sediment disturbances caused by climate change, we simulate intensified sediment dynamics by using plow rake as a proxy treatment to repeatedly disturb the sediments. This was done for four intertidal zones, representing two contrasting inundation times and two contrasting wind exposure levels. Long-term daily sediment dynamics (using Acoustic Surface Elevation Dynamics sensors, A-SED) and biophysical changes including topography, macrobenthos community, and sediment chlorophyll-*a* were compared between biweekly raked plots and the control plots that were only affected by natural hydrodynamics. Our results showed that tidal flat topography eroded by more than 2 cm after six times biweekly raking treatments. Species mobility traits across all plots correlated closely with the SED-measured daily sediment dynamics. Moreover, the enhanced dynamics reduced the presence of macrobenthos with limited mobility traits, while those with more moving abilities remained stable in abundance. Overall, present findings indicate varying degrees of resilience among biogeomorphological systems when faced with sediment dynamics: tidal flats with high sediment dynamics and mobile macrofauna appear to be highly resilient to enhanced sediment dynamics; in contrast, tidal flats with limited sediment dynamics and less mobile macrofauna are vulnerable and potentially facing a community shift towards dominant species with mobile traits.

Keywords

tidal flat resilience; biogeomorphology, macrobenthos, mobility traits, frequent storms

4.1 Introduction

Macrobenthos are crucial elements of intertidal ecosystems because of their significant contributions through various pathways, including physical and chemical influences on the sediment matrix (Meysman et al., 2006; Murray et al., 2002). Especially, these intertidal benthic organisms can function as stabilizers that enhance the sediment stability or destabilizers that increase the sediment erodibility (Alves et al., 2017; Dairain, et al., 2020; Wright & Jones, 2006). Sediment stabilization is typically caused by organisms building epibenthic structures like tubes or reefs that protect the sediment from the impact of the hydrodynamics (Borsje et al., 2014; Walles et al., 2015). Sediment destabilization commonly originates from *bioturbation*, defined as the process by that animal behaviors cause active sediment transports (Kristensen et al., 2012; Meysman et al., 2006). The composition of community traits is significantly influenced by abiotic factors (van der Wal et al., 2017), and changes in the trait composition are frequently utilized to assess how the macrobenthic community reacts to environmental pressures, including both natural and anthropogenic processes (Bremner et al., 2006; van der Linden et al., 2012).

The unvegetated tidal flats that harbour benthic organisms are ecosystems subject to various environmental pressures and biogeomorphic feedbacks resulting from hydrodynamic forces (de Vet et al., 2017; Wang & Temmerman, 2013). Despite the ecological significance of tidal flats, the total area has decreased by 16% from 1984 to 2016 due to both climate change and anthropogenic influences (Murray et al., 2019), and these vital ecosystems are becoming increasingly vulnerable to storms and sea-level rise (Cazenave & Cozannet, 2014; FitzGerald et al., 2008; Hinkel et al., 2014). The prevailing global sea level rise may increase the wave height and tidal amplitude, intensifying the daily bed-level stress resulting in potentially more dynamics (de Dominicis et al., 2020). While storms significantly increase the tidal amplitude and current speed, leading to massive sediment erosion and resuspension events (Janssen et al., 2019; Zhu et al., 2020). In the end, storms and sea level rise may thus result in more intense sediment dynamics of intertidal flats and cause severe and even irreversible impacts on benthic organisms inhabiting them (Nacem et al., 1994; Shi et al., 2021).

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Several studies indicate that enhanced sediment dynamics caused by storms decrease the overall population of macrofauna. According to Shi et al. (2021), the occurrence of a typhoon at a distance of over 1,400 km from the research location could cause sediment erosion of up to 10 cm and lead to a decline of nearly 50% in both the abundance and the biomass of clams inhabiting the tidal flats. Besides, Bouma et al. (2001) demonstrate that sediment dynamics can significantly impact the passive resuspension of early recruits, and the existence of low-dynamic zones is crucial for the establishment of bivalve populations during their initial recruitment stage. Although it is known that increased sediment dynamics either from storms or average natural conditions can have negative impacts on benthic organisms, there is still uncertainty about how daily sediment dynamics can shape the biological traits and community structures of benthic macrofauna. This is important for gaining a better understanding of ecosystem resilience under current global change scenarios, as climate change-induced extreme weather events become more frequent (AghaKouchak et al., 2020; Ummenhofer & Meehl, 2017) and tidal amplitude increase will enhance the daily sediment dynamics of tidal flats.

Studying the effects of sediment dynamics and climate change is a challenging task since it often requires a considerable amount of time to observe changes occurring naturally, which can take several decades. Therefore, an *in-situ* experiment was conducted using plow rakes to simulate the physical disturbance in sediments and increase sediment dynamics on tidal flats. Our hypothesis is that increased bed-level dynamics alter the benthic community structure by eliminating species with limited mobility. The experiment involved applying raking treatments six times biweekly at two Dutch tidal flats in the Scheldt estuary, with contrasting inundation periods and wind exposures. Replicate raked and control plots were established at low and high elevations to compare areas with different inundation periods.

4.2 Methods and materials

4.2.1 Locations: where to conduct the experiment

An *in-situ* experiment was conducted on the Dutch tidal flats at Paulinapolder and Groot Buitenschoor, located along the coast of the Westerschelde estuary (Fig. 4.1a&b). Paulinapolder (the following referred to as *Sheltered*) is sheltered from the prevailing southwest wind direction, which results in limited waves compared to the water height (*see* Appendix 1: Fig. A4.1a); Groot Buitenschoor (the following referred to as *Exposed*) is more exposed to the prevailing wind conditions resulting in higher waves compared to the water height (Fig. A4.1a). Considering the gradients in wave intensity over the tidal flat transect, the experiment was conducted at the low inundated salt marsh boundary (*Exposed_{low}* / *Sheltered_{low}*; landward edge) and the high inundated seaward edge (*Exposed_{high}* / *Sheltered_{high}*; channel-ward edge) of the two tidal flats. The elevations and emersion times of four different intertidal sites were shown in Table 4.1. To measure the daily Surface Elevation Dynamics (SED) with a high vertical and temporal resolution, one acoustic SED sensors (A-SED) was deployed at each experimental site during a long-term campaign between 2019-2021 (*see* details about the A-SED in Willemsen et al. 2022).

Table 4.1 The elevations and daily emersion times of four different sites, two located in a sheltered area and two in an exposed area. The values are expressed in relation to the Dutch ordnance level (NAP, the zero value being close to mean sea level) and are presented with mean values and standard deviations. The daily emersion time is expressed as a percentage, with higher percentages indicating longer periods of time during which the site is in low tide and the sediments are exposed to air.

Location	Sites	Elevation (NAP)	Daily emersion percentage
Paulinapolder	<i>Sheltered_{low}</i>	-0.31 ± 0.02 m	49%
Paulinapolder	<i>Sheltered_{high}</i>	0.74 ± 0.01 m	64%
Groot Buitenschoor	<i>Exposed_{low}</i>	1.11 ± 0.04 m	66%
Groot Buitenschoor	<i>Exposed_{high}</i>	2.14 ± 0.01 m	87%

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The wave forcing and tidal level of each location were measured during the experimental period in 2019, using one pressure sensors (OSSI-010-003C; Ocean Sensor Systems) deployed 5 cm above the tidal flat surface of each site. The measuring interval and burst period were 15 min and 7 min, respectively. The wave analysis was based on pressure fluctuations, measured with a frequency of 5 Hz.

4.2.2 Raking treatment: to mimic disturbance induced by frequent storms

We used a plowing rake to simulate increased bed-level dynamics under environmental changes on the tidal flat sediments (shown in Fig. 4.1e), the physical disturbance was repeated six times every other week from March to June 2019 (Week 1 to Week 11, Fig. 4.1f). This period encompasses the typical recruitment period of macrobenthos. There were two raked plots and two control plots at each elevation of each tidal flat. Each experiment plot encompassed an area of $2 \times 2 \text{ m}^2$, with a central sampling area of $1.5 \times 1.5 \text{ m}^2$ to minimize the edge effects during the sampling work. All plots were set parallel to the shoreline.

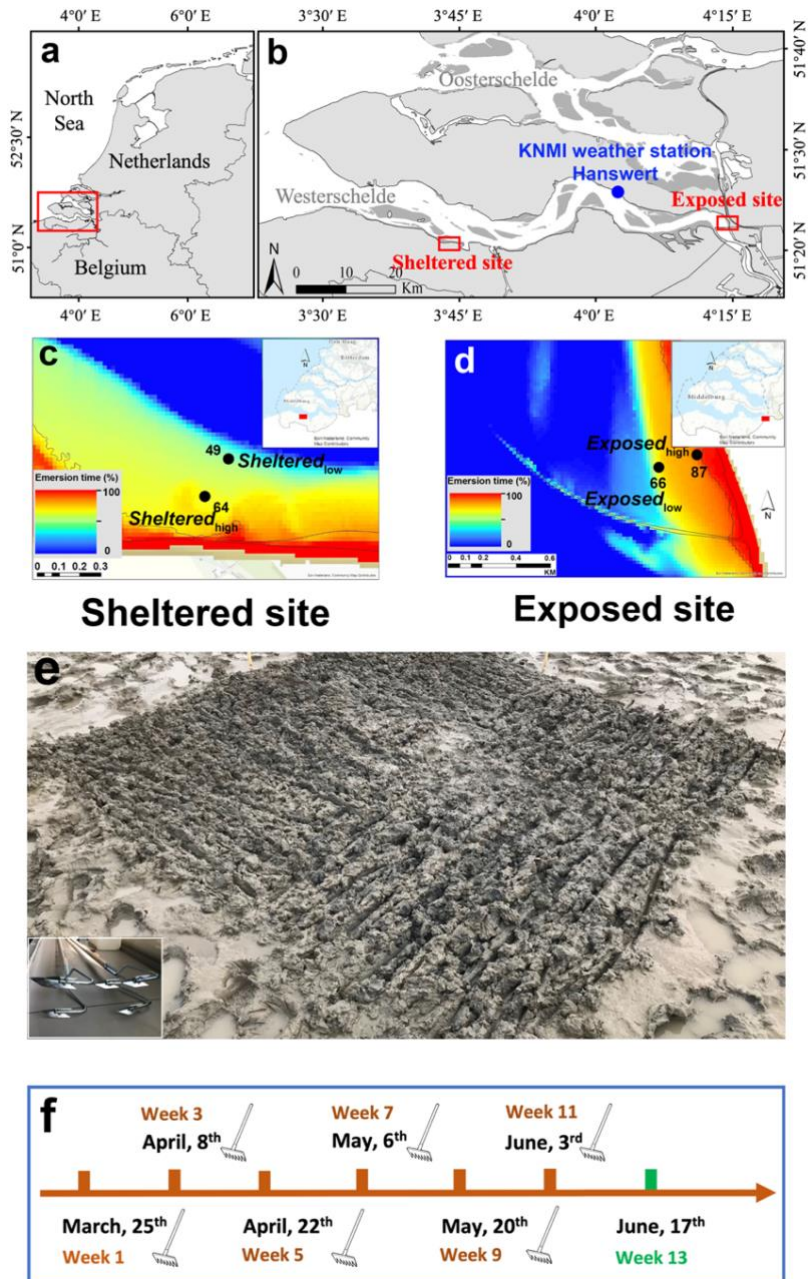


Figure 4.1 Overview of experiment location and treatments. a) the location of Western Scheldt in Western Europe; b) the geographical distribution of the two chosen tidal flats and the Hansweert Royal Netherlands Meteorological

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Institute (KNMI) weather station in the Western Scheldt; c) and d) shows the emersion times of the exposed and sheltered sites, respectively; 0% means being inundated for 24 h, and 100% means being emerged for 24 h. e) an *in-situ* photo of the raked plot at *Exposed* site, with a picture of the plow rake used in this experiment. f) the experiment schedule for treatment and sampling work. The raking treatment was applied every two weeks from Week 1 to Week 11 (in total, six times, as indicated by the rake symbol); the green ticks and labels refer to the sample harvest.

Before the artificial disturbance, the micro-topography was measured in each plot by setting up a 200 cm sedimentation erosion bar (SEB) at the corner of each raked plot (*see* details about SEB in Nolte et al. 2013). The height between the sediment surface and the SEB meter was measured every 10 cm across the plot before each raking treatment. After taking the SEB measurements the raking treatment was applied. The experiment plots were first raked parallelly and then perpendicularly to the shoreline to mimic a homogeneous physical disturbance on sediments (Fig. 4.1e). The raking depth was about 10 cm, the same as the plowing rake length.

4.2.3 Sampling work: measuring biogeomorphic features

Before each raking treatment, we collected four sediment samples in each plot using a 20 ml syringe, two for grain size (3 cm height) and two for chlorophyll-*a* (1 cm height) measurement. After collection in the field, sediment samples were stored in an icebox to preserve their integrity. Samples intended for chlorophyll-*a* measurements were immediately frozen at -80 °C, while those designated for grain size measurement were stored at -20 °C until further analysis. The chlorophyll-*a* in sediments was measured after extraction in the Specord 210 spectrophotometer (Analytik Jena GmbH). To measure sediment grain size, the samples were placed in a freeze dryer for 72 h and then sieved through a 0.5 cm mesh to remove organisms and rocks. Then, grain size composition was measured using the Mastersizer 2000 analyzer (Malvern Panalytical Ltd.).

To monitor changes in macrobenthos communities between the control and raked plots, macrobenthos samples were taken at the end of the experiment (Fig. 4.1f). In each plot, three sampling cylinders ($\varnothing = 10$ cm) were extracted from the sediment to a depth of 30 cm. To monitor the depth

change of macrobenthos in response to the raking treatment, each core was sliced into three pieces along depth gradients, which are 0-5 cm, 5-10 cm, and 10-30 cm. These three depths correspond to *i)* the upper active layer: easily disturbed in natural conditions, also without raking; *ii)* the lower active layer: rarely disturbed other than by raking; *iii)* the inactive layer: never being disturbed. All specimens were identified at the lowest taxonomic level and subsequently classified into different mobility traits according to a classification table by Queirós et al. (2013). Then, mobilities scores were given to each species as, “1” for organisms that live in fixed tubes; “2” indicates limited movement; “3” indicates slow, free movement through the sediment matrix; “4” indicates free movement via burrow system. After counting the abundance, the benthic animals were dried for 48 hours at 80 °C and then burned in a muffle oven (510 °C) for 3 hours to measure the ash-free dry weights (AFDW).

At the end of the campaign, we took five cores in each plot for the Oscillatory-Channel Resuspension flume to measure the critical erosion threshold of the tidal flat (OsCaR, *see* details in de Smit et al. 2021). The flume consists of two cylindrical columns connected to a horizontal channel into which the sediment core is inserted from below. The erosion threshold was measured by gradually increasing the oscillatory velocity until the sediment resuspension rate exceeded a critical value of 0.06 g m⁻² s⁻¹ (de Smit et al., 2021).

4.2.4 Data analysis

We retrieved statistical A-SED indices from the daily A-SED time series to describe the typical local sediment dynamics using the methods from Grandjean et al. (2022). We calculated the return time of the daily bed level dynamics at each site, which represents the frequency that specific magnitude changes are likely to occur. Moreover, the auto-correlation function (ACF) was used to indicate the long-term surface elevation persistence in time. The correlation length is an essential proxy for how fast conditions change for organisms, an indicator how much environmental fluctuations species can cope with. A higher value of the correlation length indicates that the physical environment, such as sediment

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dynamics, takes a longer time to change and is hence more suitable for organisms at that location. So, return time is a proxy for the short-term bed level changes and ACF for the long-term bed level changes.

The topographic measurements with the SEB were summarized as *mean \pm standard errors* by treatments (raked vs. control). The “zero value” was the first SEB measurement in Week 1. Then, the net topography changes in following weeks were calculated using the first measurement as a reference.

The abundance data were firstly converted to total individuals per square meter, then summarized by sampling depth and species traits to test the effects of frequent physical disturbance on species abundance. This dataset did not pass the Shapiro test for normality; therefore, an unpaired Wilcoxon test was used for statistical analysis. The total abundance of each mobility trait was summarized by correlation length to display the effects of raking treatments on community traits. All data analyses were performed using the R 4.0.0 (R Core Team, 2021).

4.3 Results

4.3.1 Topographic response to frequent disturbance

We measured the daily and long-term topographic changes using A-SED sensors to study the sediment dynamics at each site. On the short-term, *Exposed_{low}* is the most dynamic location in terms of sediment dynamics, and experienced the most significant waves as well for the relative shallow water depth (see Appendix 1: Fig. A4.1b). In contrast, the *Sheltered_{low}* is the location with the least sediment dynamics observed. While *Sheltered_{high}* experienced the least wave impact given the relative high water depth, and this location still experiences the most sediment dynamics for the sheltered locations perhaps due to tidal forcings. For the long-term, *Exposed_{high}* experienced the most sudden changes in surface elevation as indicated by the least autocorrelation length of 29 days (see Appendix 4.2: Fig. A4.2). In contrast, *Sheltered_{low}* was the most stable location on the long-term with the longest autocorrelation length at 122 days (Fig. A4.2).

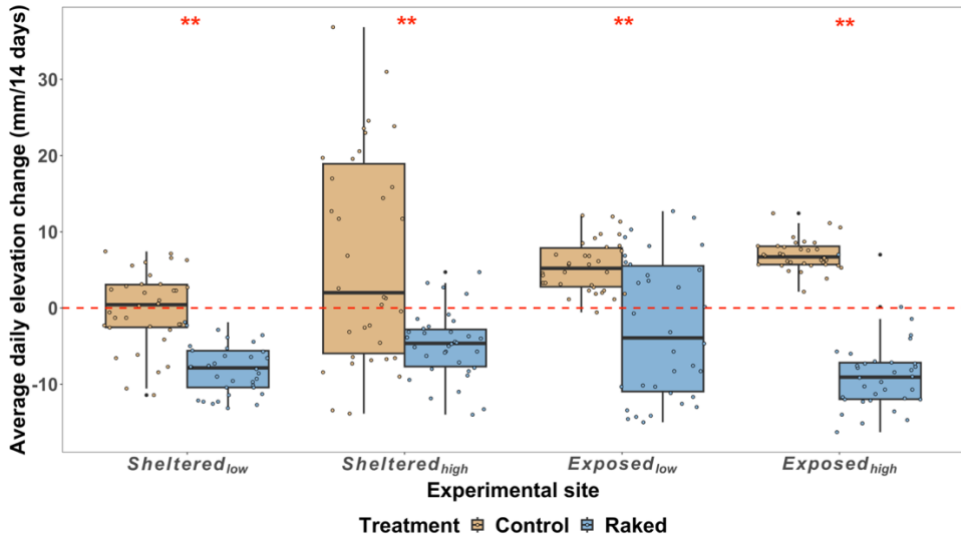


Figure 4.2 The average daily micro-topography difference between control and raked plots measured by sediment erosion bars. The average daily change of micro-topography was calculated by the biweekly measurements divided by 14 (days of two weeks). Each box plot contains 34 data points. The red dashed line shows no elevation change at 0 mm/14 days. The difference between control and raked plots is tested using the Wilcoxon test. The significant levels of $p < 0.01$ between control and raked plots were indicated by “***”.

The repeated physical disturbances by raking resulted in significant sediment erosion at all experimental plots (Appendix 4.3: Fig. A4.3, *see* red dashed lines). Most erosion occurred within the first three times of raking, except for the site *Sheltered_{high}*, which was more resistant in the beginning. The site *Exposed_{low}* experienced the most erosion, up to 2.5 cm. The raking treatment significantly increased the daily erosion depth with larger impacts at the exposed sites compared to the sheltered sites (*see* Fig. 4.2 the red dashed line is a reference of no elevation change at 0 mm/14 days; $F_{\text{Sheltered_low}} = 1031$, $p_{\text{Sheltered_low}} = 2.84\text{e-}08$, $F_{\text{Sheltered_high}} = 851.5$, $p_{\text{Sheltered_high}} = 0.00081$, $F_{\text{Exposed_low}} = 851.5$, $p_{\text{Exposed_low}} = 0.00081$, $F_{\text{Exposed_high}} = 1137$, $p_{\text{Exposed_high}} = 7.31\text{e-}12$).

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The critical erosion threshold (U_{\max}) measured with the OsCaR flume showed only a significant difference between the raked and control plots for $Exposed_{\text{low}}$ (see Table 4.2, $F = 52$, $p = 0.007$). The chlorophyll-*a* content and grain size within the surface sediment layer did not experience significant change after the raking treatment (Appendix 4.4: Fig. A4.4). Except that the chlorophyll-*a* content decreased with increasing times of raking treatments at $Exposed_{\text{low}}$.

Table 4.2 A summary of critical erosion thresholds by the OsCar flume measurements. U_{\max} is the maximum current speed that induces erosion of the cohesive sediment underneath. The w - and p -values are parameters from the Wilcoxon test for the U_{\max} values between control and raked treatments. The significant level of $p < 0.01$ was indicated by “**”.

Sites	Control U_{\max} (cm/s)	Raked U_{\max} (cm/s)	w	p	
$Sheltered_{\text{low}}$	23.36 ± 5.85	22.47 ± 8.26	27	0.432	
$Sheltered_{\text{high}}$	27.08 ± 5.55	26.70 ± 8.01	26	0.689	
$Exposed_{\text{low}}$	20.09 ± 4.08	18.41 ± 1.93	44	0.471	
$Exposed_{\text{high}}$	27.57 ± 2.32	24.06 ± 1.20	52	0.007	**

4.3.2 Macrofauna succession after frequent disturbance

The species presence and composition at each location are listed in Appendix 4.5, Table A4.1. Analyses of species trait analysis revealed that free-moving species (e.g., *Corophium volutator*) contributed most of the macrofauna abundance at the exposed sites. In contrast, species with limited- or slow-moving ability shared most proportions of the macrofauna at the sheltered sites (Fig. 4.3). Specifically, high-mobility species ($M_i = 4$) showed higher abundance at both $Exposed_{\text{low}}$ and $Exposed_{\text{high}}$ with lower correlation lengths (i.e., more dynamic areas). In comparison, low-mobility species ($M_i = 2$) showed higher abundance at both $Sheltered_{\text{low}}$ and $Sheltered_{\text{high}}$ with higher correlation lengths (i.e., slowly changing areas).

The total abundance of macrofauna in the surface 0-5 cm sediments decreased in a trait-specific way after repeated raking six times (Fig. 4.4). The six-time repeated raking treatments significantly reduced the abundance of low-mobility species in 0-5 cm sediments ($Mi = 2$ and 3 , $F_{Mi=2} = 2378.5$, $p_{Mi=2} = 0.0078$, $F_{Mi=3} = 356.5$, $p_{Mi=3} = 0.00999$). The high-mobility species significantly increased in the 6-10 cm sediments ($F_{Mi=4} = 568.5$, $p_{Mi=4} = 0.016$), though they did not experience a significant change in the top 5 cm depth (Fig. 4.4).

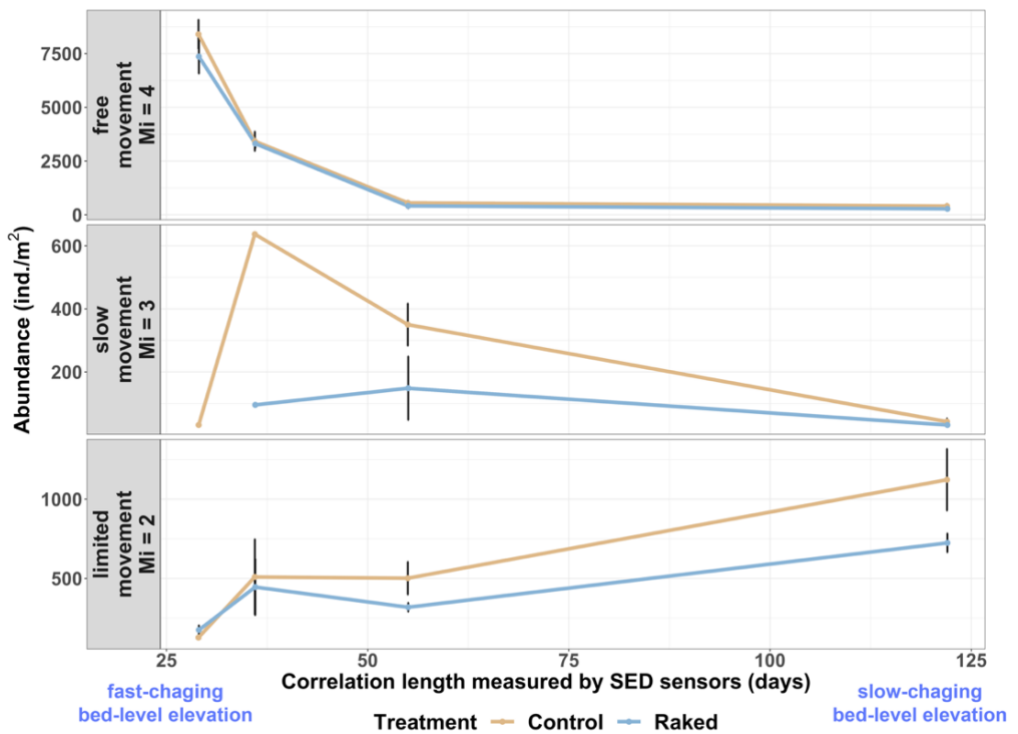


Figure 4.3 The relationship between the correlation length and the species abundance as categorized by mobility traits. Low correlation length values indicate a fast-changing bed-level elevation and strong sediment dynamics, while high correlation length values indicate a slow-changing bed-level elevation and weak sediment dynamics. “Mi” represent the mobility index score (species mobility increase from 1 to 4, “1” for organisms that live in fixed tubes;

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“2” indicates limited movement; “3” indicates slow, free movement through the sediment matrix; “4” indicates free movement via burrow system); the mobility score 1 was not shown because no samples belonged to this category. Each point represents 3 to 5 data recordings in panel a and c, and 1 to 4 recordings in panel b, depending on the species trait presence. The error bars represent the standard errors between replicate cores; the error bar was not shown if only one data point existed.

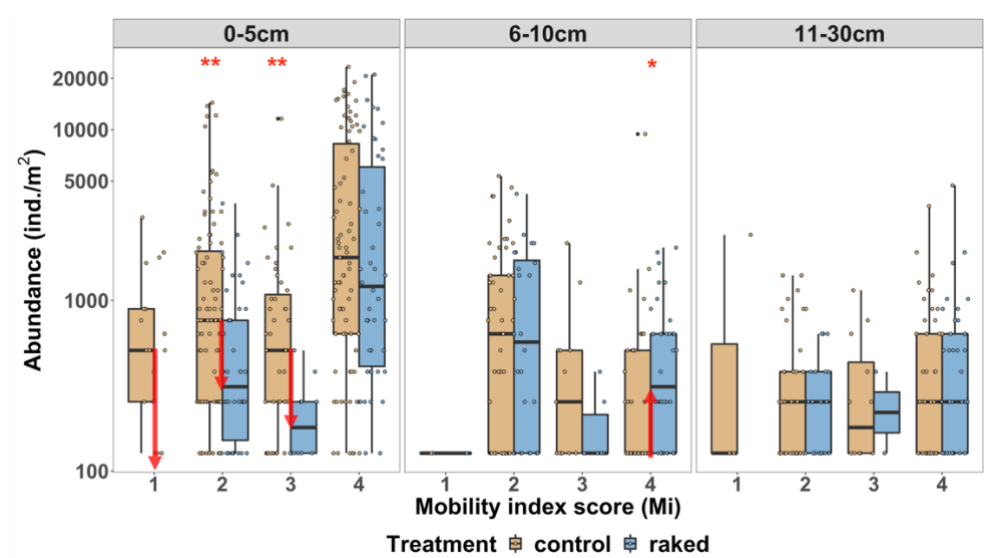


Figure 4.4 Effects of raking treatments on species abundance with different mobility traits. The facet name indicates the sampling depth below the sediment surface. The x-axis in each facet shows the mobility trait as indicated by the mobility index score (species mobility increase from 1 to 4, “1” for organisms that live in fixed tubes; “2” indicates limited movement; “3” indicates slow, free movement through the sediment matrix; “4” indicates free movement via burrow system). The y-axis indicates the log-transformed species abundance. The red arrows indicating significant changing trends of trait-based abundance in respective depths. The difference between control and raked plots is tested using the Wilcoxon test. The significant level of $p < 0.05$ was indicated by “*”. The significant level of $p < 0.01$ was indicated by “**”.

4.4 Discussion

An in-depth understanding of community resilience is important to predict the ecosystem resilience to future climate change, especially as tidal velocities and more frequent storms are expected to influence the daily bed level dynamics. In the current experiment, we increased the physical disturbance to mimic enhanced sediment dynamics by a raking treatment. We observed a significant elevation decrease of up to 2.5 cm after a 12-week repeated physical disturbance for site *Exposed_{low}*, which may be explained by the high return time of bed level changes (Appendix 2: Fig. A4.2). While *Sheltered_{high}* hardly eroded in the beginning, comparable to the low return time of bed level changes. Moreover, the enhanced bed level dynamics mimicked by raking disturbance decreased the abundance of low mobility macrobenthic species, yet high mobility burrowed deeper into the sediments (Fig. 4.4). The traits of the macrobenthic community are closely linked to the internal environmental variability of a location. Specifically, locations that experience frequent high-magnitude changes in bed level tend to have a higher abundance of species with high mobility. Overall, community shifts are critical in determining the ecological resilience of intertidal ecosystems under potential climatic scenarios, including tidal amplitude increase and more frequent storms.

4.4.1 Sediment dynamics as ecological indicators

The present study reveals that both short-term and long-term sediment dynamics are an essential indicator for tidal flats' internal environmental variance and ecological stability. Previous studies signify many other factors that may indicate the stability of the tidal flat ecosystems, such as the critical erosion thresholds (Bale et al., 2006; de Smit et al., 2021), chlorophyll-*a* (Morys et al., 2016), and sediment grain size (Garwood et al., 2015; van der Wal et al., 2017), though these factors did not show an overall significant difference between raked and control plots after six raking treatments in 12 weeks. However, significant bed level erosion was observed at all locations after six raking-recovery cycles. Moreover, the raking treatments significantly affected the benthic macrofauna: species with

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limited mobility were removed from the surface layer of 0-5 cm sediments, while mobile species burrowed deeper into 5-10 cm sediments.

Most benthic organisms inhabit in the top 10 cm of sediments, making them vulnerable to disturbance at the sediment-water interface (Poole & Stewart, 1976; Weston, 1990). Several studies also indicate that the effects of storms on macrofauna depend on their mobility traits (Pages 2013). For example, the low-mobility bivalve *Meretrix meretrix* ($M_i = 2$) was dislodged up to 50% of their density and biomass during extreme physical disturbance caused by storms (Shi et al., 2021). However, highly mobile species, such as the fish *Sarpa salpa*, can escape from the storm's disturbance (Pagès et al., 2013). Therefore, benthic species that inhabit locations with high return times of bed level dynamics are generally less sensitive to physical disturbances. The diverse response to disturbance may change the species structure of macrofauna on tidal flats, thus changing the ecosystem functions. For example, the high density (6000 ind./m²) of the amphipod crustacean *Corophium volutator* increased the nitrogen removal to 1.5-fold via burrowing activities compared with sediments with no *C. volutator* (Pelegrini 1994).

Further, the time-series SED data showed that the raking treatment was in the range of elevation change at all experiment sites, except for the site *Exposed_{low}* (Fig. A4.2a). In addition, *Exposed_{low}* was the only site with a significant difference in critical erosion thresholds between raked and control plots (Table 4.2). The SEB results show that the raked plots suffered more vigorous long-term erosion than the non-raked treatments; this more substantial erosion removed the raking-loosened mud from the surface of tidal flats, resulting in sediments with higher critical shear stress. Therefore, we speculate that the effects of physical (raking) disturbance depend on the natural tidal flat dynamics. The raking treatment constantly causes erosion, but the recovery potential for the critical erosion thresholds differs between areas where the natural sediment dynamics differ. If the (raking) disturbance depth is within the natural elevation variance, we expect that the surface 0-5 cm sediment can quickly recover to pre-disturbance characteristics; otherwise, there will be a significant difference in the critical erosion thresholds. In the end, we summarize that changes under climate change in sediment dynamics may shift

species composition, thereby being crucial for the internal environmental variance and can change the ecosystem functioning.

4.4.2 Translating environmental variance into community resilience

In general, external disturbance plays an important role in shaping the community assembly, though the community experience natural dynamics in species abundance due to intrinsic relationships such as competition and predations (Turner, 2010). Species that cannot withstand the predominant disturbance regime will be filtered out so that the remaining community will gradually adapt to prevailing environmental conditions due to the filtering for specific living styles (Diaz et al., 1998). As such, ecosystems have *memories* in that the experience of environmental variables may influence the present community structure, thus defining their resilience to future environmental change (Johnstone et al., 2016).

Ecosystem resilience usually refers to the capacity to undertake disturbance yet not permanently lose the key ecological structures and functions (O'Brien et al., 2018). Extreme weather events, such as frequent storms and floods, are usually stochastic external disturbance that surpasses the ecosystem memory (Johnstone et al., 2016; Turner et al., 2020), but will indirectly influence the bed level dynamics. The present *in-situ* experiment reveals the relationship between internal environmental variance and community resilience to external disturbance: *i*) increasing sediment dynamics filter species with high mobility traits along time, while species with low mobility traits decrease in abundance (Fig. 4.5a, based on results in Fig. 4.3); *ii*) community resilience to sediment dynamics correlates positively with the dominant mobility trait (Fig. 4.5b, based on results in Fig. 4.4). The ACF indicates how quickly environmental conditions change for organisms that need to cope with environmental fluctuations (Grandjean et al., 2022; van Belzen et al., 2022). Specifically, exposed sites with lower ACF (i.e., faster-repeating changes in the bed level evolution) are dominated by more mobile species such as *Corophium* sp. (see species list in Appendix 4.5). In contrast, sheltered tidal flats with high ACF (i.e., slowly changing bed levels) are dominated by less active species, such as shellfish and worms (Table A4.1).

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The raking treatment was applied multiple times, overlapping with the spat season (from March to June). We hypothesize that mobile species are recruited even with disturbance from multiple times raking during the spat season, while less mobile species cannot recover in the two-week interval.

The interplay between disturbance (short-term dynamics) and recovery (long-term evolution of bed level) determines the development of many ecosystems (White & Jentsch, 2001). However, the disturbance pattern is changing because of the current global climate change scenarios (Turner et al., 2020). The present study highlights the potential of decreasing ecosystem resilience under climate-change-induced extreme weather events and tidal amplitude increase, with the exact impact depending on ecosystem memory shaped by the internal environmental variance. Therefore, regular monitoring of the environmental conditions will provide essential knowledge to predict the spatial and temporal vulnerability of ecosystem functioning and help lower the risks of biodiversity loss.

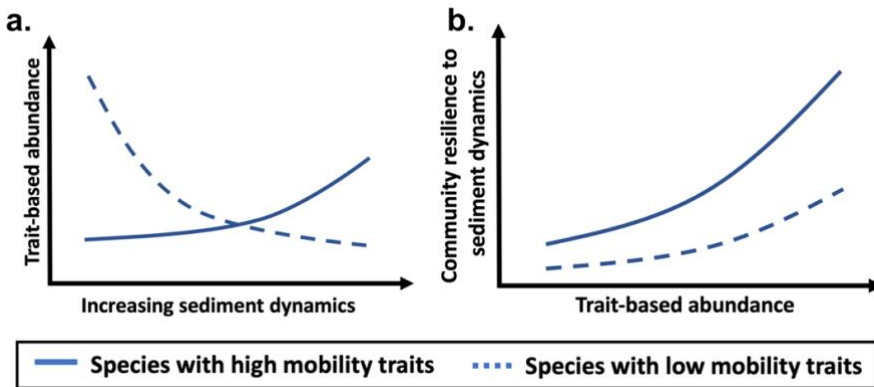


Figure 4.5 A conceptual figure illustrating how sediment dynamics determine community resilience against the storm-induced sediment dynamics. a) the filtering effects of sediment dynamics on species' biological traits; b) dominant species traits determine the community resilience to increased sediment dynamics induced by storms. The solid lines represent species with specific biological traits that may help to endure the prevailing environmental stress, and the dashed lines represent the less-tolerant species in response to the environmental stress.

4.4.3 Outlook on long-term implications

Extreme weather events can dramatically impact ecosystem functioning and biodiversity (Ummenhofer & Meehl, 2017). Storms may become more frequent and intensified under the current global warming scenarios (Bevacqua et al., 2019). Tidal amplitude increase is likely to expect under sea-level rise, causing potential increased in tidal velocities and enhanced sediment dynamics. Our experiment shows that tidal flats with limited sediment dynamics may suffer more in terms of species loss compared to tidal flats with inherent high sediment dynamics. Under projected changes we may expect that: *i*) macrofauna in less dynamic areas may shift towards more mobile species, despite being already vulnerable to disturbances; *ii*) macrofauna in more dynamic tidal flats are expected to be able to cope with more frequent disturbances, as long as the disturbances remain within the range they can cope with. The selection of the mobile trait may lead to more bioturbation on tidal flats, which typically enhances erodibility. For that reason, the selection of mobile traits may negatively impact the stability and ecological services of tidal flats in the long-term decadal shifts.

Our experiment provides initial insights into how biogeomorphic features of tidal flats respond to the disturbance induced by climate change scenarios. We can conclude that *i*) the biogeomorphic system of tidal flats with high sediment dynamics and inhabited by mobile macrofauna appear to be resilient to increased sediment disturbances; *ii*) the system with limited sediment dynamics and less mobile macrofauna will be highly impacted and likely to shift in the benthic community towards hosting more mobile species. This study also provides essential support for policy-makers in keeping up with global change regarding tidal flat restoration. Since sediment dynamics play a vital role in biogeomorphic feedbacks, artificial constructions (e.g., breakwaters, sheltering dykes, and cultivating oyster reefs) may reduce the disturbance intensity, thereby causing more sedimentation and recruitment of benthic macrofauna. For example, the nature restoration project named “Buitendijkse Maatregelen NPW (Natuur Pakket Westerschelde)” is expected to create 300 hectares of wave-sheltered mudflats by constructing breakwaters and groynes in Western Scheldt, the Netherlands. The construction and renovation of breakwaters indeed decreased hydrodynamics, promoted sediment accretion, reduced sediment

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dynamics, and provided habitats for various benthic organisms, thereby enhancing the food availability for migratory birds (Grandjean et al. 2022; Wiesebron et al. submitted).

Appendices

Appendix 4.1 The wind and wave conditions of the chosen tidal flats during the experimental period

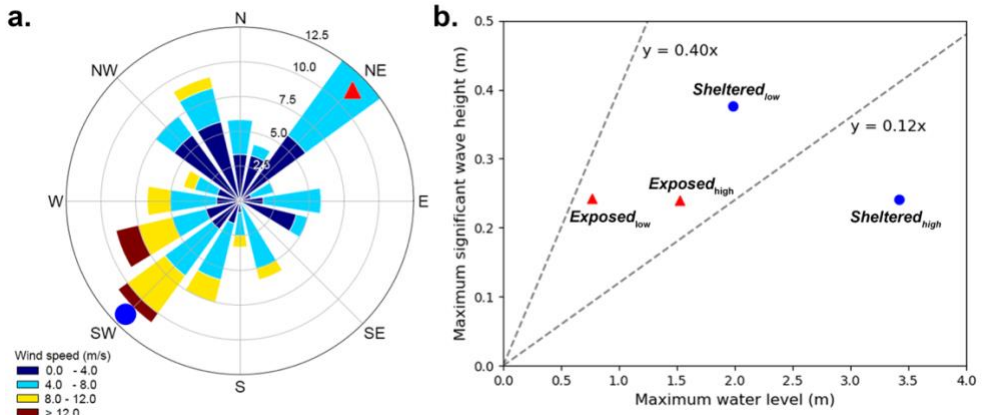


Figure A4.1 The wind and wave condition of the experimental tidal flats. a) A wind rose map of the chosen tidal flats during the experimental period. The red triangle represents the *Exposed* sites, and the blue circles represents the *Sheltered* sites. Daily wind data (March 1st, 2019 – June 30th, 2019) were retrieved from the nearby Hansweert Royal Netherlands Meteorological Institute (KNMI) weather station (see Fig. 4.1b), which is located at the middle position of the two chosen tidal flats. The prevailing wind direction was southwest, with a mean wind speed of 5.2 m/s. b) Observed relationship between maximum significant wave height and maximum water depth. The two dashed lines are the thresholds of wave exposures at the Western Scheldt generated from *in-situ* measurements by Zhu et al., (2020). In general, the two *high* inundated sites suffered less wave exposure than the two *low* inundated sites according to their positions regarding the two dashed lines.

Appendix 4.2 The A-SED sensor data indicating the sediment dynamics on experimental sites

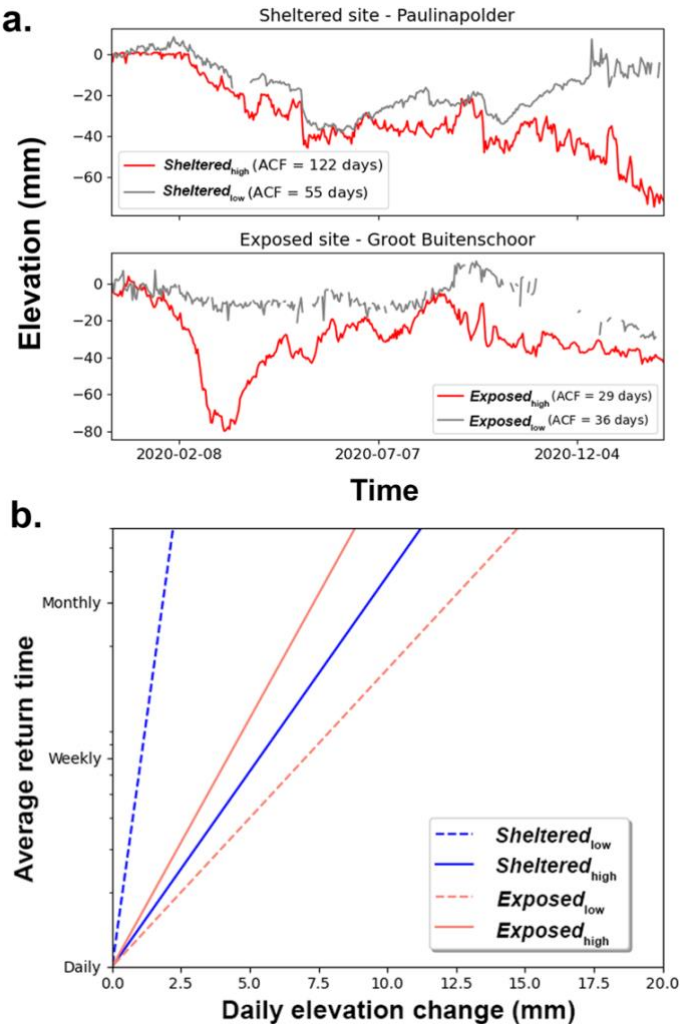


Figure A4.2 The A-SED sensor data about micro-topography change of the experimental sites. a) the long-term time-series of bed-level elevation with in red the higher inundated sites and the grey lines indicate the low inundated sites. ACF indicates the correlation length derived by the auto-correlation function. b) the average return time of daily elevation change, the return time indicates how often a specific daily elevation change may occur.

Appendix 4.3 The micro-topography change

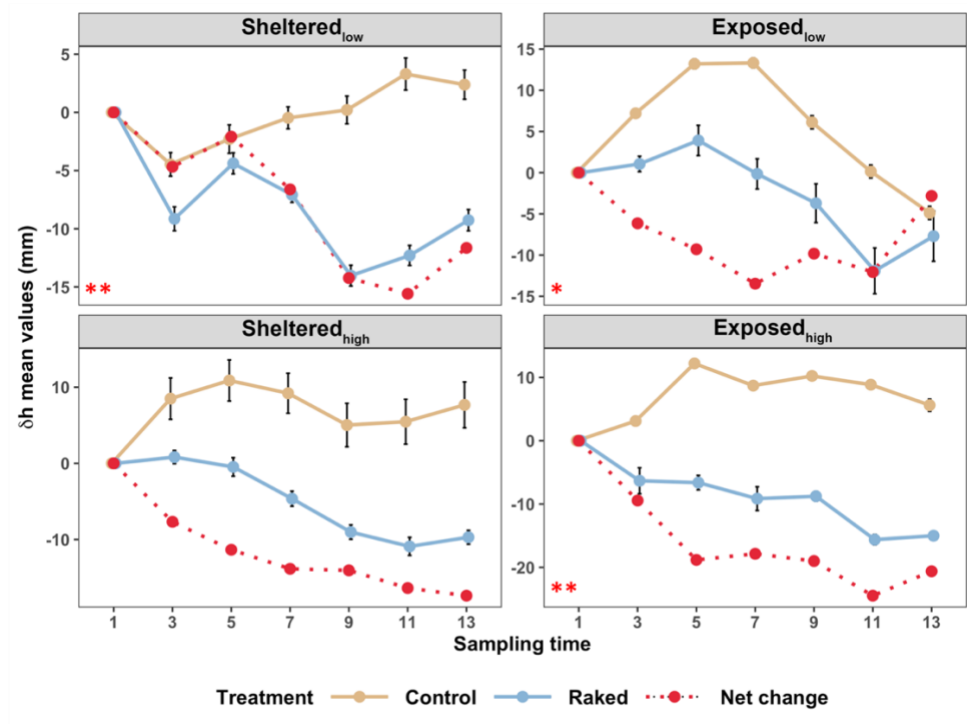


Figure A4.3 The time-series change of micro-topography measured by sediment erosion bars. Each data point shows the net elevation changes using measurements in Week 1 as a reference (net change in Week 1 was 0 mm). The error bars represent standard errors. The net change values were calculated using mean values in raked plots minus the ones in control plots. The difference between control and raked plots is tested using the Wilcoxon test. The significance levels are indicated by “*” for $p < 0.05$ and “**” for $p < 0.01$.

Appendix 4.4 the time-series change of *Chlorophyll-a* and grain size

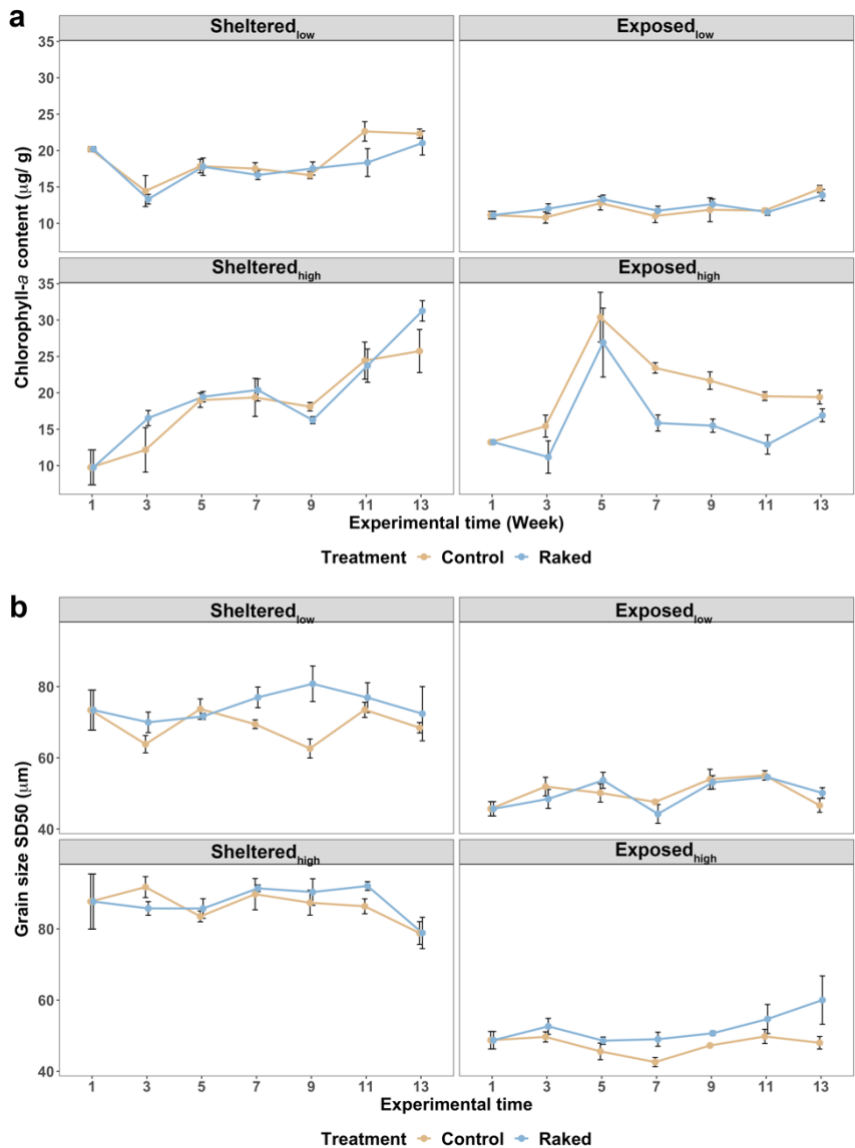


Figure A4.4 The time-series variation of chlorophyll-*a* (a) and grain size SD50 (b) at 0-1 cm and 0-3 cm sediments, respectively. The error bars represent standard errors.

Appendix 4.5 Species presence list and respective mobility score (Mi)

Table A4.1 A summary of macrobenthos species presence in respective experimental sites. Mobility scores (Mi) were listed as, “1” for organisms that live in fixed tubes; “2” indicates limited movement; “3” indicates slow, free movement through the sediment matrix; “4” indicates free movement via burrow system.

Species	Class	M _i	Exposed _{low}	Exposed _{high}	Sheltered _{low}	Sheltered _{high}
<i>Abra alba</i>	Bivalvia	2		+		+
<i>Abra tenuis</i>	Bivalvia	2			+	
<i>Alitta succinea</i>	Polychaeta	4	+	+	+	+
<i>Brachyura</i> sp.	Malacostraca	4			+	+
<i>Capitella</i> sp.	Polychaeta	2		+		+
<i>Carcinus maenas</i>	Malacostraca	4			+	+
<i>Cardiidae</i> sp.	Bivalvia	2				+
<i>Cerastoderma edule</i>	Bivalvia	2			+	+
<i>Cirratulidae</i> sp.	Polychaeta	2			+	
<i>Corophium</i> sp.	Malacostraca	4	+	+	+	
<i>Crab</i> sp. juvenile	Malacostraca	4			+	+
<i>Crangonidae</i> sp.	Malacostraca	4			+	+
<i>Cyathura carinata</i>	Malacostraca	2	+	+	+	+
<i>Eteone</i> sp.	Polychaeta	3			+	+
<i>Hediste diversicolor</i>	Polychaeta	4	+	+	+	
<i>Heteromastus filiformis</i>	Polychaeta	2	+	+	+	+
<i>Lanice conchilega</i>	Polychaeta	1			+	
<i>Limecola balthica</i>	Bivalvia	2	+	+	+	+
<i>Modiolula phaseolina</i>	Bivalvia	2			+	
<i>Nereididae</i> sp.	Polychaeta	4		+	+	+
<i>Oligochaeta</i> sp.	Oligochaeta	3	+	+	+	+
<i>Peringia ulvae</i>	Gastropoda	3				+
<i>Phyllodoce mucosa</i>	Polychaeta	3			+	
<i>Retusa obtusa</i>	Gastropoda	3				+
<i>Ruditapes philippinarum</i>	Bivalvia	2				+
<i>Sabellida</i> sp.	Polychaeta	1		+		
<i>Scrobicularia</i> sp.	Bivalvia	2	+		+	+
<i>Spionidae</i> sp.	Polychaeta	1			+	
<i>Tellinoidea</i> sp.	Bivalvia	2		+		+



Chapter 5 Compound extreme weather events create establishing windows for introduced bivalves

Submission in preparation.

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Abstract

Extreme weather events such as heatwaves and flash floods are increasing in frequency due to global climate change. While many studies have investigated the potential impact of high temperature and salinity fluctuations on benthic animals in tidal flats, few have explored how these stressors affect the relationship between competitive species, including the potential establishment of introduced species in response to extreme short-term events. This study examines the differential effects of heatwaves and salinity changes on the survival, burrowing behavior, and respiration rates of native and introduced bivalve species. Specifically, the non-indigenous species *Ruditapes philippinarum* and the native species *Cerastoderma edule* were cultivated in four salinity settings under five temperature scenarios. The results show that *R. philippinarum* exhibits lower mortality than *C. edule* under high temperatures ($> 35^{\circ}\text{C}$), especially in lower salinity settings (10 and 20 PSU), and can survive longer under heatwaves. Meanwhile, *C. edule* is more sensitive to thermal stress than *R. philippinarum*, as indicated by its stronger regulatory pattern in respiration rates. Interestingly, the burrowing behaviors of the two species did not differ significantly, indicating that they share similar ecological functions under future climate change. However, if heatwaves coincide with other stressors - in this study, strong freshwater inputs - compound extreme weather events may widen the establishment window for introduced species and increase their abundance, potentially driving community succession on tidal flats in future climate change scenarios. Overall, these findings provide valuable insights into how compound extreme weather events could impact the establishment and abundance of introduced species, with important implications for understanding community dynamics on tidal flats in a changing climate.

Keywords

heatwaves, mass mortality, alien species, tidal flat ecosystems, community succession

5.1 Introduction

Global climate change is a prevalent threat to the well-being of organisms in many ecosystems (Scholze et al., 2006; Turner et al., 2020). On the one hand, individual organisms may alter their biological traits, such as behaviors, productivity, and physiological characteristics, to cope with the constantly changing climate (Pörtner & Farrell, 2008; Scapini et al., 2019). On the other hand, these species-level responses can affect the community-level interactions such as predator-prey and competition relationships in the ecosystems, leading to altered ecosystem functions through food webs in both bottom-up and top-down directions (Weiskopf et al., 2020). Therefore, understanding the responses of individual species to climate change provide an essential indication to understand the direction of ecosystem development.

Besides long-term gradual impacts like rising temperature and acidity, climate change causes more frequent extreme weather events, such as heatwaves, prolonged droughts, and rain-fed flash floods, with the latter two affecting the salinity in estuaries (Kendrick et al., 2019; Smith, 2011). These extreme events usually change the benign environment into harsh conditions in a short time and create pulse impacts on organisms (Harris et al., 2018). The detrimental effects of climatic events are not necessarily caused by a single extreme environmental event; combinations and interactions of these extreme events can pose threats as “compound events” (Leonard et al., 2014; Ridder et al., 2022). Studies have shown that coastal salinity can fluctuate from freshwater (near 0 ppt) to hypersaline seawater levels in tidal pools (>150 ppt) under the effects of compound events such as heavy rains, run-off waters, and low tides in conjunction with high temperatures (McAllen et al., 1998). In addition, extreme events can have combined effects on habitat stability with temporal and geographical lags (Kornhuber et al., 2019; Zscheischler et al., 2018).

Besides global climate change, the increasing pace of globalization enhances the transportation of introduced non-indigenous species across continents (Molnar et al., 2008). For example, non-indigenous species can be deliberately introduced for economic purposes or accidentally delivered by ballast water in cargo ships or seagoing freighter (Bailey, 2015; Breber, 2002). The successfully settled non-indigenous species are usually more capable of adapting to environmental changes than native competitor species and tend to rapidly occupy ecological niches cleared by abiotic pressures (Gallardo et al., 2016). The development of the future community will depend on the balance between surviving individuals and the spatfall recolonization of native and introduced species (Troost, 2010). To our knowledge, it is poorly known how compound extreme weather events can affect the relationship between competitors in ecosystems, especially between native and introduced species.

The high density ascertains native species to persist in extreme weather events by retaining a stable niche occupancy even if many individuals die (Schreiber et al., 2002; Tricklebank et al., 2021),

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which might be referred to as “density-based buffering effects” in response to environmental changes. The more extreme the weather event, the fewer (native) adult individuals will survive, leaving more empty niches for introduced species to settle and establish (González-Moreno et al., 2015). However, this “density buffering” will disappear if compound extreme events vastly surpass the physiological thresholds that native species can withstand in short periods (Seuront et al., 2019; Soon & Zheng, 2019). In such a scenario, the native species may suffer mass mortality (Soon & Ransangan, 2019). Once the native species loses its dominance in abundance, it may be difficult for the community to return to its original state even after prevailing environmental conditions return to the pre-disturbance state (Jacquet & Altermatt, 2020). From this perspective, we propose that the compound extreme weather event may be regarded as an “establishing window” that opens niches for an introduced species to win over the original native species in species abundance. Specifically, the more frequent short-term compound extreme weather events (e.g., heatwaves, drought events, and rain-fed flash floods) may benefit the introduced species by weakening the native species or creating mass mortality events that empty more niches, though global climate change encompasses a relatively long-term timeframe to cause community succession.

In this study, we use the tidal flat as a model ecosystem to explore the effects of extreme events on benthic organisms living in sediments with highly dynamic tidal regimes (Coma et al., 2009; Smale et al., 2019; Vafeiadou et al., 2018). Specifically, we investigate how different combinations of extreme weather events can create windows of opportunity for introduced species to establish themselves. Benthic organisms play a critical role in the functioning of tidal flats. Their bioturbating behavior affects the biogeomorphology of the ecosystem, while they also constitute an essential component of the food web, serving as a food source for many migratory bird and fishes. We thus use benthic macrofauna as model organisms to study how compound extreme weather events may affect the relative survival of native and competing introduced species.

In the Netherlands, the introduced species *Ruditapes philippinarum* was captured at Eastern Scheldt in 2008 and largely increased in population since 2014, living in similar environment as the native cockle *Cerastoderma edule* (see Appendix 5.1; Foekema et al., 2014). Due to the high fecundity and colonization potential of *R. philippinarum*, they may compete with *C. edule* found in the same sediment with a similar filtering feeding behavior (Foekema et al., 2014). The population size of *R. philippinarum* rapidly grew from 27 ind./m² in 2014 to ca. 81 ind./m² in 2020 per station (Appendix 5.1: Fig. A5.1). Between 2014 and 2020, there was an increase in the cumulative daily maximum temperature above 30 °C, from 5.9 °C to 27.9 °C. However, during the heatwaves in 2020, the cockle *C. edule* experienced mass mortality (unpublished observation from Wageningen Marine Research).

Studies have shown that extreme temperature and salinity changes can have significant impacts on the physiological health, behavior, and species distribution of benthic macrofauna on tidal flats (Chappon & Seuront, 2011b; Damme et al., 2005; Harley & Helmuth, 2003). In addition to this, heatwaves have become more frequent, longer, and more intense, which poses added stress on the biodiversity of marine ecosystems on tidal flats (Dolbeth et al., 2021; Oliver et al., 2018). Extreme weather events such as flash floods and rainstorms that cause lower salinity can also affect the distribution of the macrobenthos (Little et al., 2017; Miththapala, 2013). To study the effect of these compound extreme events on bivalves in tidal flats, we simulated the combined impact of heatwaves and salinity changes in the mesocosm as an idealized model system. In this study, we used competing bivalve species, native *C. edule*, and introduced *R. philippinarum*, as model organisms to test our assumptions of “establishing window”. We measured the mortality rate and oxygen consumption as a proxy of the physiological condition and metabolic response under the compound stress of temperature and salinity. Additionally, we measured burying behaviors to evaluate the ecological functions of both species in tidal flat ecosystems.

5.2 Material and methods

5.2.1 Model species

To investigate how competitive species respond to extreme weather events, we selected the common cockle *C. edule*, and the Manila clam *R. philippinarum*, as our model species. *C. edule* is a native species dominant in tidal flat ecosystems along the European Atlantic coastline and holds significant economic importance for the fishing industry (Malham et al., 2012), although its natural stock has experienced several collapses due to mass mortality events (Burdon et al., 2014). *R. philippinarum*, originally from the Indo-Pacific coasts, was introduced to Europe and successfully established itself as one of the most commercially exploited bivalves in European tidal flats (Drummond et al., 2006). Since its introduction to Europe in 1972, *R. philippinarum* has been expanding rapidly and has been found to have a higher thermal tolerance window than *C. edule* (Drummond et al., 2006; He et al., 2022).

In August 2021, we collected 400 individuals of each species from the tidal flat Oesterdam, the Netherlands. Then, these organisms were transported to a room with a constant ambient temperature of 20 °C and kept in a tank filled with air-saturated seawater for 7 days. During this acclimation phase, dead individuals are removed daily, and 1/3 of the water was changed halfway through the time. When the experiment started, individuals with similar body lengths for each species were transferred into the experimental mesocosms. The average shell lengths of the experimental individuals were 31.70 ± 1.5 mm ($n = 20$) and 37.30 ± 2.1 mm ($n = 20$) for *C. edule* and *R. philippinarum*, respectively.

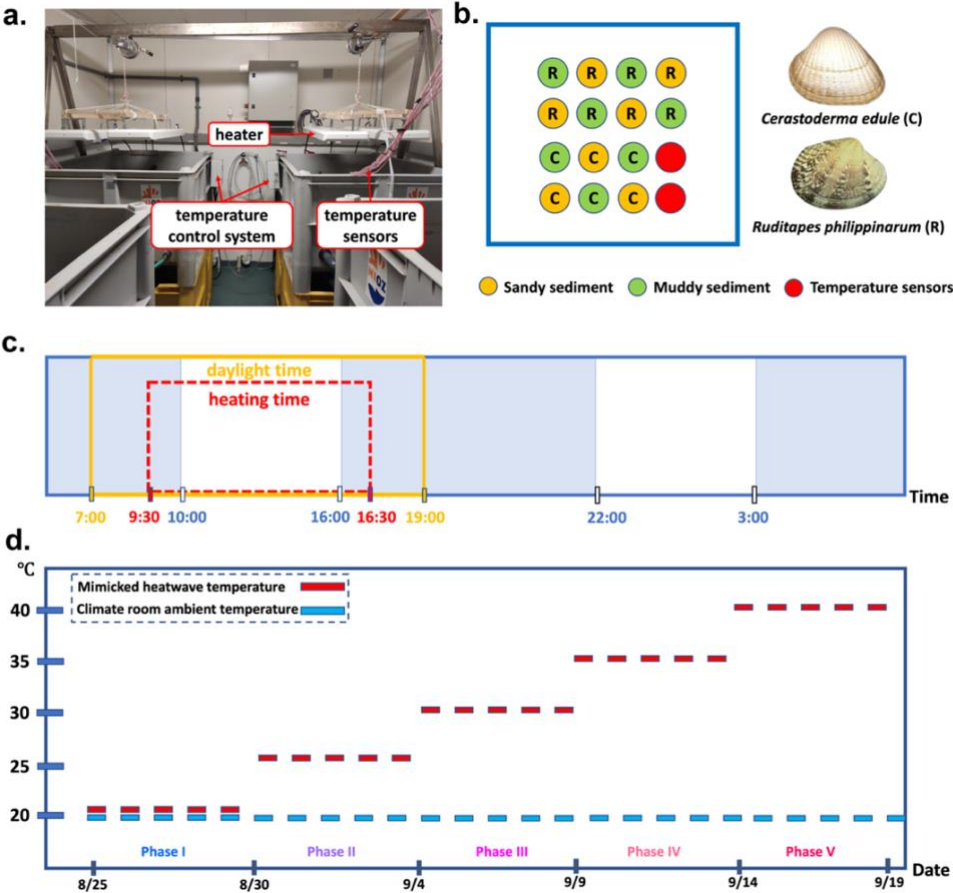


Figure 5.1 Experimental design and treatment settings. a) a photo of the climate room and mesocosms: “heater” was used to mimic the heatwaves; “temperature control systems” manipulated the temperature of mimicked heatwaves; “temperature sensors” measured the temperature in the PVC pots. b) model species and their allocation in the mesocosm tank. c) daily schedule of heating time (red color), day-night cycle (yellow color indicates daylight time), and tidal regimes (blue color indicates high tide time; white color indicates low tide time). d) temperature settings during the experiment, including the 5-day cycles of heatwave increments (red) and ambient temperature (blue).

5.2.2 Environmental treatments: imposing heatwaves and salinities

We used seawater from Eastern Scheldt, the Netherlands, which had a monthly average salinity of 30.21 ± 0.2 PSU in 2021 according to the Royal Netherlands Meteorological Institute (KNMI) weather station at Lodijkse Gat. Studies have shown that coastal areas can experience extreme events such as

floods and heavy rainfall that decrease the regional salinity by 5-10 PSU (Voynova et al., 2016). To mimic different scenarios of freshwater input, we established four salinity settings of 5, 10, 20, and 30 PSU, representing "brackish water," "heavily affected by flash floods," "high freshwater input," and "no effects of freshwater input," respectively. The surface sediments can experience daily temperature fluctuations exceeding 10 °C during low-tide emersion time on tidal flats, despite seasonal variations that can exceed 30 °C from summer to winter. To replicate the effects of heatwaves, we set the maximum sediment surface temperature at 40 °C based on temperature measurements taken during the 2020 summertime heatwaves (Appendix 5.2: Fig. A5.2), while keeping the ambient air and tidal-water temperature both constant at 20 °C.

5.2.3 Mesocosm technical settings: mimicking tidal flat environment with heatwaves

Tidal cycles - The tidal cycles were simulated using double-layer mesocosm units. Each mesocosm unit consists of two tanks stacked together (inner size 110 × 95 × 60 cm); the upper tank was used for the experimental area, and the bottom tank was used for the water reservoir to create tidal regimes (details *see* Zhou et al., 2022). All mesocosm tanks were placed in two separate climate rooms to minimize the random effects. Each room contained two mesocosm units with two terrace heaters on top to regulate the upper tank exposure temperature and two mesocosm tanks that were directly exposed to the ambient temperature (Fig. 5.1a). For each mesocosm unit, the same regular semi-diurnal tide was mimicked according to the tidal regimes at the location where bivalves were collected. The low tide interval was 6 h, occurring twice daily during daytime and nighttime (Fig. 5.1c).

Heatwaves - Two terrace heaters hung on top of each mesocosm to simulate tidal flat heatwaves (see "heater" in Fig. 5.1a). The heaters were 40 cm above the sediment surface and connected to thermal sensors that measured the sediment surface temperature. The temperature control system allowed the heaters to heat the sediment surface to a set temperature value, and stop heating as soon as this temperature was reached. If the temperature fell below the set value, the heaters turned on again (for details *see* Zhou et al., 2022). The heaters were active for 7 hours daily, covering the 6-hour daytime low tide period from 9:30 to 16:30 (Fig. 5.1c).

All the mesocosm units were divided into two heatwave treatment groups, *i*) the ambient control group, which was only exposed to the climate room ambient temperature; *ii*) the heatwave group, which was exposed to daytime heating treatment and the ambient temperature during non-heating periods. To simulate the heatwave, we gradually increased the temperature from 20°C to 40°C with a 5°C increment every five days (Fig. 5.1d), creating five phases of simulated heatwaves: Phase I (20°C), Phase II (25°C), Phase III (30°C), Phase IV (35°C), and Phase V (40°C) (*see* Fig. 5.1d). The climate room ambient temperature was constant at 20 °C. We measured the surface sediment temperature in one coarse

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and one fine sediment PVC pot to represent the temperature profiles in each mesocosm unit. Temperature sensors (PT-100 sensors, TC Direct) were deployed at the sediment surface of the two PVC pots to record the per-minute temperature data via a CR10X datalogger (Campbell Scientific, Inc.).

Salinity and sediments - Seawater with four salinity settings was randomly filled into the bottom tanks in two rooms. The four salinities 5, 10, 20, and 30 PSU were obtained by mixing freshwater with filtered seawater. Each salinity setting had a mesocosm unit with ambient temperature treatment and the other with heated treatment. The seawater was changed every ten days to maintain a clean environment for bivalves. The day and night profiles were manipulated by the ambient light in the climate rooms, with 12 h day-night cycles (Fig. 5.1c).

In the upper tank, PVC pots (internal diameter = 10 cm, height = 15 cm) were used as experimental replicates to keep bivalves. All PVC pots were arranged in 4 cols \times 4 rows staggered patterns (in total 16 pots) in each tank, with two types of sediments (Fig. 5.1b). The sediments were firstly sieved through a 0.5 cm mesh, then put in the -20 °C refrigerated storage for 48 h as defaunation. The grain sizes indicated by D50 were 265.02 μ m and 120.06 μ m, referring respectively to coarse and fine sediments.

5.2.4 Bivalve maintenance and measurements

Replication and maintenance - We placed 4 *C. edule* or 3 *R. philippinarum* in each PVC pot, mimicking the abundance of 512 ind./m² and 384 ind./m², respectively, in each PVC pot considering the body size of the two species. In each mesocosm unit, every PVC pot contained only one species with one sediment type. Therefore, each species had 192 individual replicates for two heating treatments in four salinity settings (N = 24 per treatment). The bivalves were fed with instant microalgae (Shellfish Diet 1800, Reed Mariculture Inc.) twice a week. The algae concentrate was diluted with seawater at 10:1 (seawater: concentrate), then homogeneously added to the upper mesocosm tanks. We daily check if bivalves were dead or alive. We used a metal tweezer gently moving around bivalves' siphons to check whether they had died yet still were buried in the sediment. Bivalves that did not respond to these physical stimuli were recorded as dead. Dead individuals were removed from the tank daily and the daily survival number was recorded.

Burrowing depth - Borrowing depth change of each bivalve was measured to study the compound stress of temperature and salinity on bivalve moving behavior (as indicators for bioturbation). A cotton string was firstly glued (superglue CA10, F.T Products) on bivalves' shells, and a knot was made at the other end of the string so that the length from the posterior end of the cockle to the knot was fixed for each cockle. This method was adopted from Auffrey et al. (2004) and has been tested in our

previous studies to *i*) have no effects on the burrowing activities of bivalves (Zhou, et al., 2022); *ii*) be able to detect significant impacts of thermal stress on the cockles' burrowing behavior (Zhou et al., 2023).

To measure the burrowing depth of each bivalve, the string is gently pulled straight, and the distance between the knot and the sediment surface is recorded. The burrowing depth is measured four times daily: at 9:00 and 17:00 during high tide, and at 12:00 and 14:00 during low tide. The relative depth change of each measurement point is calculated by subtracting the first measurement value from the absolute length. Therefore, the relative depth change of the first measurement was always 0 cm at 9:00. The following four measurements used the first one as a baseline to calculate the burrowing depth change.

Respiration rates – The mortality rate was high under the compound stress of temperature and salinity during the four-week heatwave experiment, which prevented us from collecting adequate replicates to investigate the combined impact of temperature and salinity on bivalves' metabolism. To address this, new bivalves were collected for an additional respiration test. Four replicate individuals of each species were then placed in PVC pots in mesocosm tanks with four salinity settings, the same setting as the previous four-week experiment. The bivalves were subjected to a 40°C simulated heatwave for a total of 18 hours during the daytime low tide, over the course of three consecutive days. Following this, each bivalve was collected and placed in a respiration chamber (bottleneck Ø = 35 mm, volume = 100 ml) with seawater from the respective mesocosms. The respiration chambers with bivalves were then placed in a water bath (Water Bath 12L, VWR) to maintain a constant temperature at 20 °C, while the oxygen concentration ($\mu\text{mol L}^{-1}$) in the chambers was continuously monitored using FireSting pro (PyroScience Sensor Technology) for 1.5 hours. After completing the respiration measurements, the bivalves' flesh tissues were detached from their shells, dried at 60 °C for 48 hours, and then put in the muffle furnace at 580 °C for 2 hours to obtain biomass as AFDW (g). The oxygen consumption rates (OR, in $\mu\text{mol} \cdot \text{h}^{-1} \cdot \text{g}^{-1}$) of bivalve individuals were calculated from the following equation (Ong et al., 2017),

$$\text{OR} = \frac{(C_0 - C_1) \times V}{\text{AFDW} \times (t_0 - t_1)} \quad (1)$$

in which t_0 and t_1 (h) are the starting and ending time of measurements; C_0 and C_1 represent the oxygen concentrations ($\mu\text{mol} \cdot \text{L}^{-1}$) at t_0 and t_1 ; V is the seawater volume in the chamber (L) with correction for the sensor volumes.

5.2.5 Data analysis

Survival percentage - The number of daily alive bivalves were divided by the total number of replicates to calculate the survival percentages for the four salinity scenarios under ambient control and heating treatments. To calculate the accumulative daily mean temperature, we first determined the mean

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heating temperature during low tide periods and subtracted the mean ambient temperature. This was done for each day of the study period. Cumulative sums were then calculated every five days to provide a more comprehensive understanding of the temperature trends over time. The potential establishing conditions of the introduced species were identified by comparing the survival percentage of *R. philippinarum* and *C. edule* under different conditions of salinity and accumulative daily mean temperature: *Survival percentage difference = Survival percentage *R. philippinarum* – Survival percentage *C. edule*.*

Movement intensity - The daily variance (standard deviation) of burrowing depth change was calculated by species and salinity. The variance values were plotted along time series, then fitted into a linear regression model: $y = a^{bx}$, in which x was *experimental time* and y was the *daily variance of burrowing depth changes*. The coefficient b was used to determine the movement intensity of bivalves. All the above analyses were performed using R 4.1.1 (R Core Team, 2021).

5.3 Results

5.3.1 Survival and mortality

The daily survival percentages of bivalves under compound stress caused by temperature and salinity changes were clearly species dependent (Fig. 5.2). At an extremely low salinity of 5 PSU (brackish water), both species' survival percentages decreased to 0 within the first two phases (20 and 25 °C) of heating treatments, up to 25 °C. Without the effects of heatwaves, *R. philippinarum* survived five days longer than the native *C. edule*. However, under the effects of heatwaves, *R. philippinarum* survived only two days longer. In scenarios mimicking “severe impacts of flash floods” at 10 PSU, higher temperatures increased the survival of the temperate species *R. philippinarum* but decreased the survival of *C. edule*. Both species' survival decreased to 0 in the fifth heating phase (40 °C). In the scenario of “high freshwater input” at 20 PSU, heatwaves severely decreased the survival of *C. edule*, but *R. philippinarum* was barely affected. In normal salinity conditions of 30 PSU, simulated heatwaves slightly decreased the survival of *C. edule*, while *R. philippinarum* had 100% survival until the end of the experiment.

R. philippinarum can adapt wider range of salinity and temperature variation than *C. edule* as indicated by the smaller dark blue areas in Fig. 5.3. *C. edule* exhibits a higher mortality percentage than *R. philippinarum* in low salinity conditions (<10 PSU) even under low accumulative daily mean temperature (53.2 °C). Moreover, high accumulative daily mean temperature (370.7 °C) causes higher mortality percentage for *C. edule* than *R. philippinarum* event at lower salinity stress of 30 PSU. The negative impact of low salinity on both species was more significant than that of high temperature, as demonstrated by the dark areas shown in Fig 5.3a at 5 PSU across all thermal stress levels.

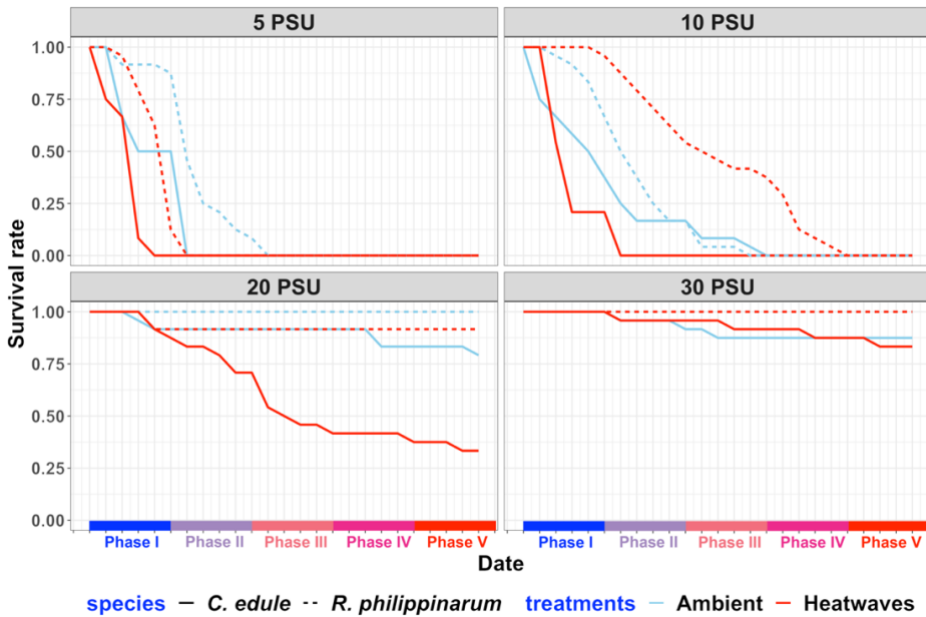


Figure 5.2 Time-series variations of survival rates during the experimental period. The x-axis shows the experimental phases (Phases I to V), and the y-axis indicates the mortality rate. The four facets represent four salinity settings (PSU = Practical Salinity Unit, which is approximately equivalent to 1 mg/g of salts). The red lines indicate the heatwave treatment, and the blue lines indicate ambient temperatures. The solid lines represent the native species *C. edule*, and the dashed lines represent the alien species *R. philippinarum*.

5.3.2 Burrowing behaviors and respiration rates

At normal salinity conditions of 30 PSU, both the native species *C. edule* and the introduced species *R. philippinarum* displayed increased movement intensity with heating treatment, but the increase was greater in *C. edule* compared to *R. philippinarum*. In the “high freshwater input” scenario at 20 PSU, the simulated heatwaves resulted in a decrease in movement for both bivalves (Fig. 5.4a). However, when exposed to the “heavily affected flash flood” scenario at 10 PSU, the simulated heatwaves only slightly weakened the movement ability of the two bivalves compared to the other salinity settings. In brackish conditions of 5 PSU, both *R. philippinarum* and *C. edule* showed an increase in movement intensity when exposed to simulated heatwaves, but the increase was more pronounced in *R. philippinarum* than in *C. edule*. Overall, these results suggest that both species exhibit a similar response pattern under the combined effects of temperature and salinity.

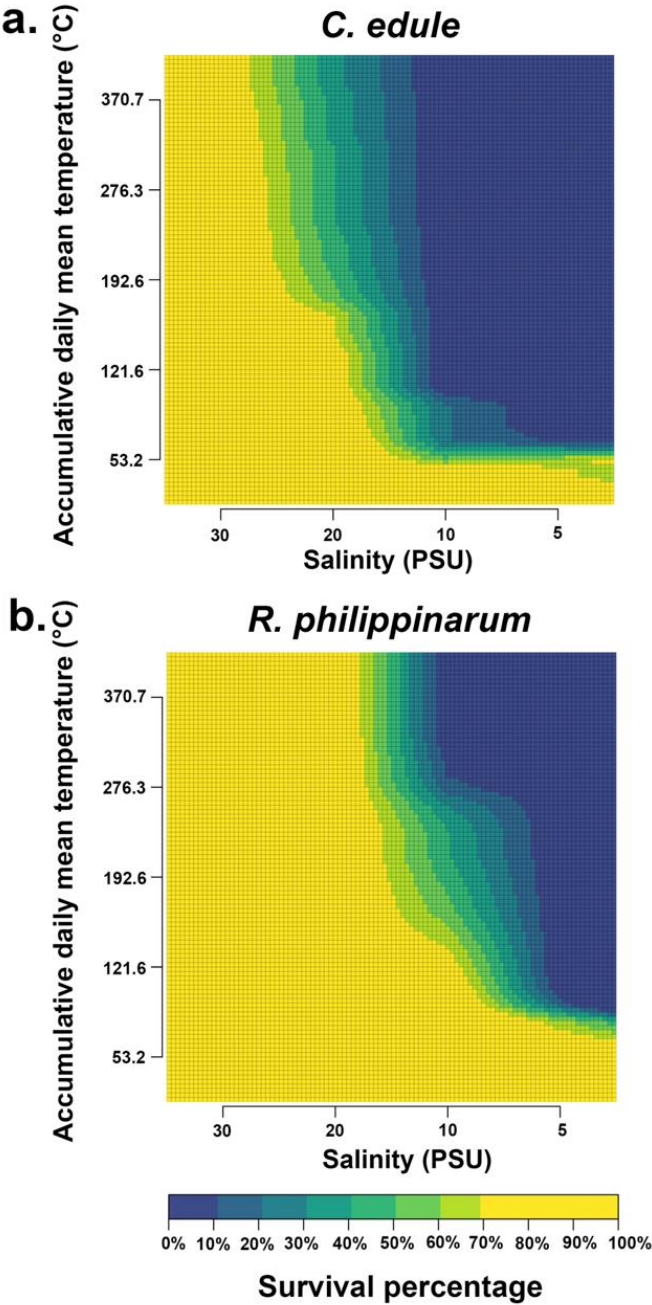


Figure 5.3 Extrapolated contour plots of survival percentages of *C. edule* and *R. philippinarum* under compound effects of salinity and temperature. The x-axis indicates the salinity stress (measured by practical salinity unit, PSU),

Compound events create establishing window

and the y-axis shows the accumulative daily mean temperature difference between heating and ambient treatments (°C). Salinity stress was varied from 5 to 30 PSU, and the accumulative daily mean temperature difference ranged from 53.2 °C to 370.7 °C. The color scale indicates survival percentages of both species, with blue indicating low survival and yellow indicating high survival.

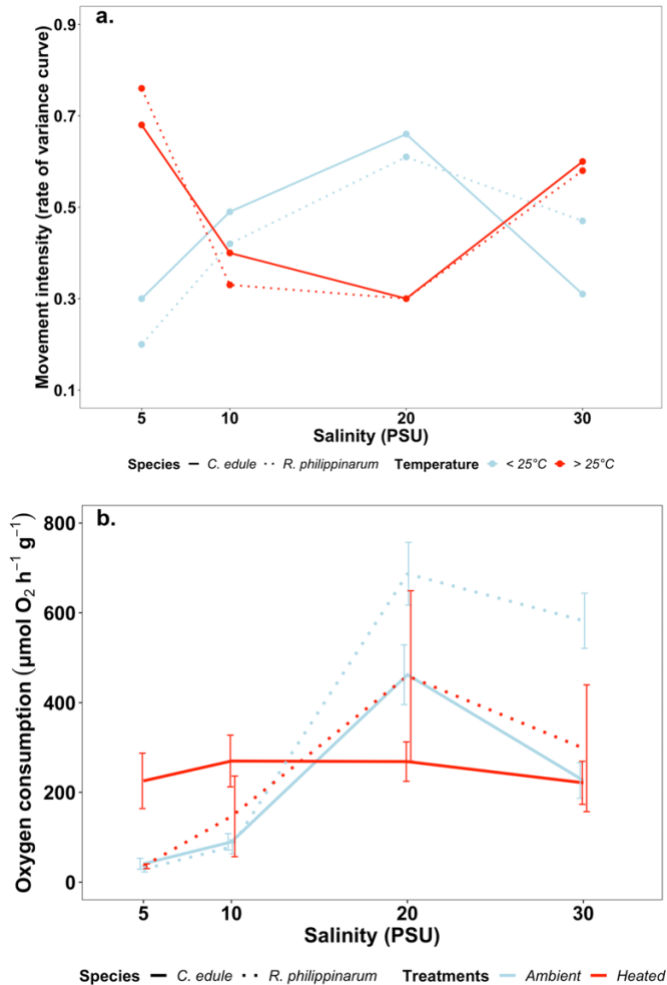


Figure 5.4 Movement intensity (a) and respiration rates (b) of bivalves in different salinity settings, with or without simulated heatwaves. In both figures, the solid lines represent the native species *C. edule*, and the dashed lines represent the introduced species *R. philippinarum*. In figure (a), the movement intensity is represented by the slope of the time series lines that show the daily variance of bivalve burrowing depth changes. In figure (b), the y-axis

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indicates the oxygen consumption weighted by ash-free dry weight during the 3-day thermal stress test. Each point represents 2-7 replicates, and the error bars represent the standard errors.

To gain further insight into how compound stressors affect the physiological conditions of bivalves, we measured their respiration rates under thermal stress in four salinity settings. In the "high freshwater input" scenario at 20 PSU, both species showed a significant decrease in oxygen consumption when exposed to simulated heatwaves (Fig. 5.4b). However, at 10 PSU, the heating treatment had opposite effects on the oxygen consumption of the two species, increasing it for both species, but to a greater extent in *C. edule* than in *R. philippinarum*. When exposed to simulated heatwaves in brackish conditions at 5 PSU, the respiration rates of *C. edule* increased while those of *R. philippinarum* decreased under normal salinity conditions of 30 PSU. Overall, these results suggest that *C. edule* is more sensitive to thermal stress compared to *R. philippinarum*, as indicated by its stronger regulatory pattern. Moreover, we found that the burrowing activities of *C. edule* follow similar variation patterns with its respiration rates.

5.4 Discussion

Global climate change results in more frequent extreme events such as e.g., heatwaves, strong rainfall events and flash floods (Debortoli et al., 2017; Frölicher et al., 2018). To assess if compound extreme weather events may create establishing windows, we tested as model system the compound effects of heatwaves and salinity variations on the mortality of two competitor species. The results show that native species *C. edule* suffered from higher mortality than the introduced species under heatwave conditions, and that this became more pronounced when the habitat conditions were less suitable for both species as mimicked by reducing the salinity as compound stress. Below we discuss how the mass mortality of native species in such compound stressor events may open an establishing window for the introduced species to thrive.

5.4.1 Disturbance-driven establishing window as accelerator of invasions

The mortality results suggest that when compound extreme events affect two prevailing habitat conditions, introduced species may have a competitive advantage over native species due to their broader range of adapting abilities, as shown by the yellow color in Fig. 5.5, which represents a survival percentage difference of 70% and 90% between *R. philippinarum* and *C. edule*. As the old Dutch saying states, "de ene zijn dood is de ander zijn brood", meaning the death of one is the bread (i.e., opportunity) of another. The reduction in adult native individuals may lead to a decrease in larval yield (Beukema & Dekker, 2005; González-Moreno et al., 2015), opening an "establishing window" for the introduced

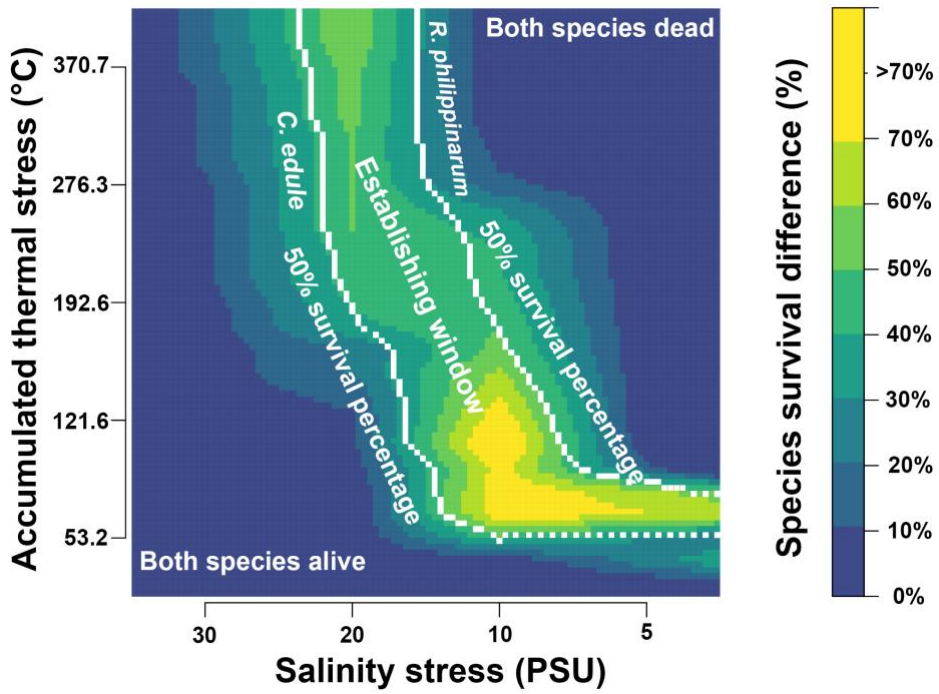


Figure 5.5 An extrapolated conceptual figure based on experimental data explaining the disturbance-driven establishing window under compound stress by salinity and temperature. The x-axis shows increasing salinity stress (measured by practical salinity unit, PSU), the y-axis shows the increasing thermal stress represented by the accumulative daily mean temperature difference between heating and ambient treatments (°C). The white reference lines indicate 50% survival percentages for both species under the compound stress of salinity and temperature. When the salinity and thermal stresses are low, both species are alive; when salinity and thermal stresses are high, both species are dead. The color scale indicates the difference of survival percentage between *R. philippinarum* and *C. edule*, with yellow indicating higher survival percentage of *R. philippinarum* over *C. edule*, which can be seen as the “establishing window”.

species to settle during the following spat seasons. This period can thus be defined as a “disturbance-driven establishing window,” during which the survival of native species is reduced due to the extreme disturbance, while non-indigenous species are better able to survive and potentially outcompete native species due to higher survival percentage (*see* the reference lines of 50% survival percentage in Fig. 5.5).

The species invasion process is composed of several stages: *i*) species introduction and transport, *ii*) establishing a self-sustained population, *iii*) spreading across the habitats, and *iv*) reaching

similar levels of abundance with local species and impacting the native ecosystems (Theoharides & Dukes, 2007). In the context of this research, the concept of a “disturbance-driven establishing window” suggests that extreme disturbances have the potential to benefit introduced species in the establishing stage (i.e., stage *ii*) and beyond (i.e., stages *iii* and *iv*). That is, it is advantageous for all stages that benefit from a decreased native species’ abundance, by allowing the introduced species to occupy more available resources with lower biotic resistance, leading to a higher chance of successful establishment. Such “disturbance-driven establishing windows” may be found across various ecosystems, from marine to freshwater, forest to grasslands, and natural to urban areas. However, existing examples are mainly derived from single stressors, yet not compound events as shown in the current experiment.

Marine ecosystems - Storm surges and wave actions can leave communities susceptible to invasion. Following Hurricane Omar in 2008, extremely large sediment loads resulted in the burial of native seagrass beds in Dominica, which led to the establishment of invasive seagrasses, including *Halophila* spp (Steiner et al., 2010). In New Zealand, a heatwave significantly increased the mortality rate of native mussels more than non-native mussel species (Petes et al., 2007). Sorte et al. (2010) found that only non-native species of the epibenthic fouling community from California were able to tolerate the heatwave simulated in a laboratory mesocosm.

Forest ecosystems - Invasive grasses, such as *Bromus* spp, are widespread in western North America and may be suppressed temporarily by drought but can recover rapidly and invade areas where the pinyon pine *Pinus* spp. or juniper *Juniperus* spp. died off (Kane et al., 2011). Droughts facilitate the invasion of *Tamarix ramosissima* into riparian zones in southwestern North America, outcompeting the native *Populus deltoides* (Sher et al., 2000).

Grassland ecosystems – White et al. (2001) found that extreme heatwave events decreased the native biomass of plants with C4 photosynthesis and increased the invasibility of plants with C3 photosynthesis in a grassland system. Similarly, Song et al. (2010) showed that a heat wave led to a decrease in the biomass of a native herbaceous species *Wedelia chinensis* but not its non-native congener *Wedelia trilobata*.

Freshwater ecosystems - The the 2003 European heatwave and severe flood events were temporally correlated with the increases in non-native and eurytolerant macroinvertebrates in France’s Rhône River (Daufresne et al., 2007). The smaller native lizard species in the Bahamas faced local extinction due to predation by introduced lizards, which occurred only after storm events had decreased the population sizes of the native species (Schoener et al., 2001).

Urban ecosystems – Droughts promoted the invasion of the introduced fish species *Cichlidae* sp. at San Juan, Puerto Rico located in the Caribbean Sea; while body size and abundance of the native species *Agonostomus monticola* decreased during the droughts (Ramírez et al., 2018). In West Africa, studies have found a significant negative correlation between *Rattus rattus* and *Mastomys natalensis* relative abundances, indicating a potential native-to-invasive species turn over under the unexpected disturbance (Hima et al., 2019). The replacement of *M. natalensis* by *R. rattus* in Southern Benin cities could have significant public health consequences since *M. natalensis* is the main cause of annual epidemics of Lassa hemorrhagic fevers in West Africa and the virus has not been found in *Rattus* spp (Hima et al., 2019).

While still rarely studied, the occurrence of compound stressors may increase with climate change. We expect that compound extreme events may increase the occurrence of disturbance-driven establishing window, and hence act as accelerator of invasions. Since the establishment of non-native species can have significant impacts on ecosystem functioning and native species diversity, there is need to focus more study on the effect of compound stressors as accelerator of invasions.

5.4.2 Why compound stresses may become increasingly important for species invasion

The establishment of introduced species is determined by various factors, including dispersion and habitat suitability (Occhipinti-Ambrogi, 2007). In our experiment, we employed different salinity and temperature settings to replicate various habitat conditions resulting from compound events such as heavy rainfall, run-off water, low tides, and high temperature heatwaves on tidal flats. Anthropogenic activities may further increase the frequency and magnitude of salinity changes (Rivera-Ingraham & Lignot, 2017). For example, the inflow of rivers into the sea temporally fluctuates due to the freshwater utilization and wastewater discharge by cities around estuarine areas (Flörke et al., 2018; van Rooijen et al., 2005). According to a modelling study by Xu et al. (2018), the salinity of coastal waters off north-eastern Chongming Island will increase from < 0.45 to 20-24 PSU if the runoff of Yangtze River discharge decreases from 27,856 m³/s to 14,832 m³/s. Moreover, the frequency, magnitude, and duration of heatwaves are increasing (Oliver et al., 2018). Through our return time analysis of a 70-year temperature dataset from Schiphol weather station in the Netherlands, we discovered that the occurrence rate of daily maximum temperatures reaching 30 °C decreased from once every 647 days in the 1950s to once every 75 days in the 2010s (Appendix 5.3: Fig. A5.3). Combining this trend with the experiment results suggest that the worsening of extreme events such as heatwaves under future climate change scenarios, will create more frequent disturbance-driven establishing window that will accelerate community succession.

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The combinations and interactions of extreme weather events can pose threats as compound events (Leonard et al., 2014; Ridder et al., 2022), while it does not necessarily mean that multiple extremes occur simultaneously in the same location. Extreme events such as heatwaves and flash floods can have temporal and geographical lags, yet their combined impacts on habitat stability can still be significant. For example, a flash flood occurred in Limburg, the Netherlands, on July 15th, 2021, causing 12,000 people to evacuate in the south of Limburg overnight and excessive freshwater input into the Western Scheldt Estuary (NL Times, 2021). Then, a heatwave event happened at the beginning of August (*see* Appendix 5.2 for our in-situ measurements). The surface sediment temperature reached more than 30 °C as logged by our in-situ temperature sensors (Appendix 5.2: Fig. A5.2). Despite this temporal separation, this may have a compound effect impact on the ecosystem, in case the salinity effect has a delay-time. Such delay-time may easily occur, as shown by Lyu et al. (2020) for the Yangtze River. The total length of Yangtze River is around 6300 km covering a basin area of 1.8×10^6 km². The average travel time of the flood crest from Yichang City to Jianli City (347 km) was 1.1 days after the construction of the Three Gorges Dam (Lyu et al. (2020)). Consequently, if flash floods happened in the upper/middle reaches, causing salinity changes, the lower reaches would experience these salinity changes several days later. It is thus possible that lower reaches meanwhile suffer from a heatwave. Therefore, compound effects of multiple extreme weather events may occur, even if they do not happen on the same geographical and temporal scale, emphasizing the need to study the effect of compound stressors as accelerator of invasions.

5.4.3 Including disturbance-driven establishing windows in species distribution models

The results of the current experiment suggest that species invasion may be accelerated by compound extreme events resulting from climate change, as many regions of the world are expected to experience a higher frequency of such events in the future (Bevacqua et al., 2019; Ridder et al., 2022). Species invasion is one of the main causes of biodiversity loss, and understanding their potential spread is crucial to effective management (Crooks & Rilov, 2009; Rato, 2021). Species distribution models (SDMs) are predictive tools that identify relationships between observed occurrences and environmental predictors by using statistical models or theoretically derived response curves (Srivastava et al., 2019). Researchers have used SDMs to investigate the potential for spread and the environmental factors that favor or limit the establishment of invasive species such as the kelp *Undaria pinnatifida* (Báez et al., 2010), the mussel *Mytilus galloprovincialis* (Assis et al., 2015), and the coral *Tubastrea coccinea* (Carlos-Júnior et al., 2015). However, building a robust SDM for species invasion is not an easy task as there are many uncertainties associated with these projections, particularly when projecting species distributions under environmental disturbances (Melo-Merino et al., 2020). Despite the potential of

SDMs to estimate and project invasion risk, these models may give us a conservative estimate of species and communities shift due to their reliance on average conditions (Srivastava et al., 2019). As indicated by the current experiment, future modelling work on species invasion and distribution should consider the occurrence and frequency of compound extreme weather events as potential accelerator of the spreading of invasives.

5.4.4 Anticipating species succession scenarios

The burrowing depth data from our current experiment suggests that the bioturbation potential of *R. philippinarum* and *C. edule* may be similar under compound extreme events, as both species showed comparable trends in burrowing depth changes. This finding is consistent with studies by Soissons et al. (2019), which confirm that these two species share comparable ecological functions in shaping sediment properties due to similar biological traits. Although these two species contribute similarly to ecosystem function, community succession may still arise in future climate change scenarios featuring increasingly frequent compound extreme events, due to the varying functional traits of other species (Bremner et al., 2006b; Sterk et al., 2013). For instance, the basket clam *Potamocorbula amurensis*, originally from the north-eastern Pacific, has been observed in Europe since 2018, with high abundances of up to 382 ind. /m² at Bath, the Netherlands (Dumoulin & Langerart, 2020). *P. amurensis* can adapt to a wide salinity range from 2 to 28 PSU after proper acclimation (Paganini et al., 2010). Furthermore, their ability to release heat-shock proteins (i.e., hsp70) ceased only in 0.5 PSU salinity after a heat shock at 37°C for 30 minutes (Werner, 2004). During its previous invasion of the United States, *P. amurensis* was the primary cause of the dramatic reduction in summertime phytoplankton abundance and altered the original trophic structure (Wilkerson et al., 2006).

Understanding how these species may interact under future climate scenarios is critical not only for predicting potential shifts in community structure and functioning, but also for assessing potential economic impacts. (Doney et al., 2012; Harley et al., 2006). If *R. philippinarum* continues to expand and outcompete *C. edule* under future warming and more frequent extreme weather events, it could have significant consequences for the fishing industry and the wider ecosystem (Beukema & Dekker, 2005; Bidegain et al., 2015). On the other hand, if the non-native *P. amurensis* becomes dominant, it could lead to further ecological disruption and changes in higher trophic structures (Nicolini & Penry, 2000). Therefore, it is important to continue monitoring these species and conducting experiments to better understand their responses to environmental stressors (Beukema & Dekker, 2020). By doing so, we can anticipate and potentially mitigate the impacts of community succession and species invasion in tidal flat ecosystems.

Appendices

Appendix 5.1 Variation in *R. philippinarum* abundance from 2014 to 2021

Between 1990 and 2021, Wageningen Marine Research conducted annual research to analyse the abundance of bivalves in the Eastern Scheldt region of the Netherlands during April and May. The introduced species *R. philippinarum* appeared in this area in 2014, but body-size data was unavailable for 2016. To focus on relevant data, we selected stations that met three criteria: *i*) stations where both *C. edule* and *R. philippinarum* were present; *ii*) stations where *R. philippinarum* had been consistently captured since 2014 (as not all stations had *R. philippinarum* present in the dataset every year); *iii*) adult species with a body size greater than 1.5 cm. Among the available stations, only 9 met these criteria and were selected for analysis to examine the variation of population abundance of *R. philippinarum*. To contextualize these findings, maximum daily temperature data recorded at Vlissingen, the Netherlands, from 2014 to 2021, were obtained from the Royal Netherlands Meteorological Institute (KNMI).

The abundance data of *R. philippinarum* were calculated by averaging the total count based on the number of sampling stations for each year. Temperature values that exceeded 30 °C were first reduced by 30, and then the sum was calculated for each year. The mean abundance and the cumulative sum of temperature exceeding 30 °C were matched by year and fitted into a linear regression model $y = ax + b$, where x is the summed temperature, and y is the mean abundance.

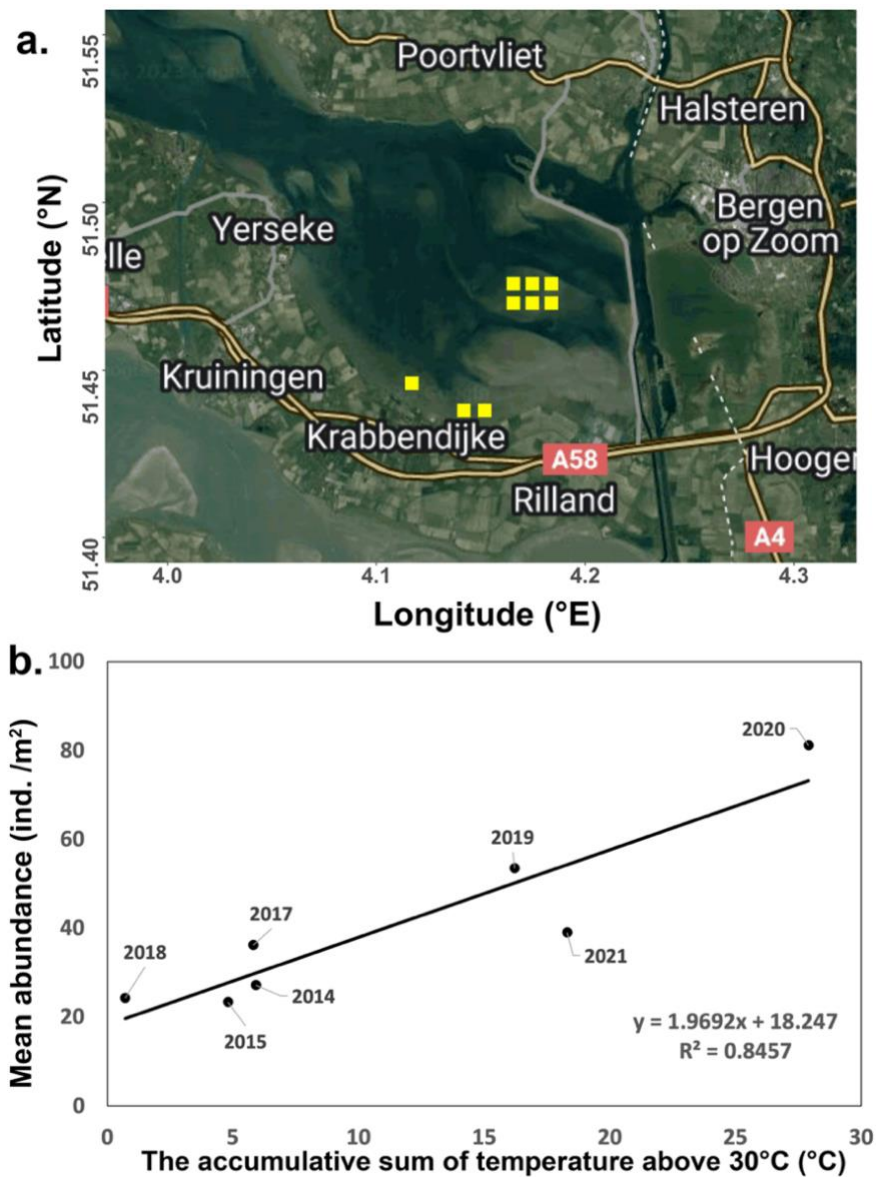


Figure A5.1. Sampling stations of *R. philippinarum* at Eastern Scheldt (a) and the abundance variations in response to high temperatures (b). In Figure (a), the yellow squares represent the sampling stations where *R. philippinarum* were collected from 2014 to 2021. In Figure (b), the x-axis represents the cumulative temperature sum above 30 °C, and the y-axis indicates the mean abundance of *R. philippinarum* per station for each year.

Appendix 5.2 Temperature measurements in the field

The HOBO sensors (Onset Computer Corporation) were deployed to measure the temperature of air and sediment at Paulinapolder, Netherlands (51°21'01.6"N 3°43'41.9"E). Two sensors measured air temperature 15 cm above the sediment surface. The other two sensors were deployed at 3 cm depth in the sediment to measure the temperature of sediment. Both measurements (near-surface and 3-cm depth temperature) were the mean values of 2 replicates. The location's elevation was 0.73 ± 0.01 m, and the grain size of the sediment was 68.47 ± 2.90 μm (top 1 cm).

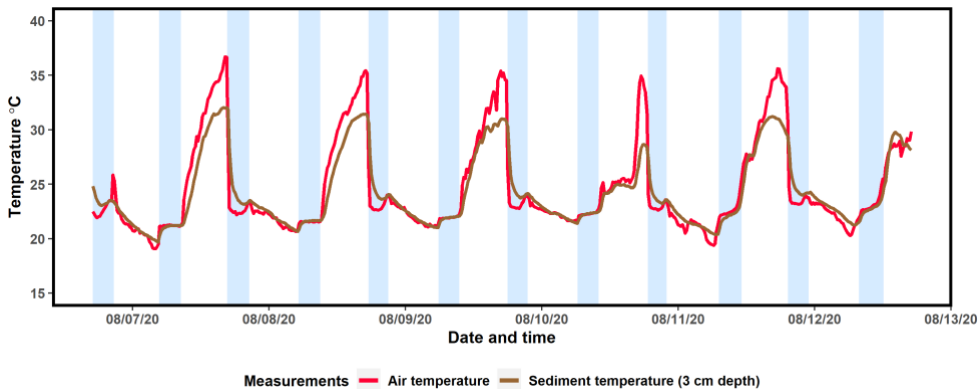


Figure A5.2 Heatwave field data during summer 2021 at Paulina polder, Netherlands. The blue shades represent inundation during high tides and white rectangles for exposure time when low tides.

Appendix 5.3 A 70-year temperature dataset revealing a shorter return time of heatwaves

The hourly air temperature data for 70 years (1951-2020) at Schiphol, the Netherlands, were available from the Royal Netherlands Meteorological Institute (KNMI). The data were divided into four parts, each containing data for 20 years except for the last decades (2010-2019). The return time of high temperature was used as a proxy of the heatwave frequency, as the return time indicates how often a specific temperature may occur. For the data shown here, the return time of temperature was calculated in a step size of 0.1 °C. Then, the return time values of the same temperature were summarized as mean values. The return time mean values were log-transformed and fit into a linear regression model: $y = ax + b$, in which x is temperature and y is the log(return time).

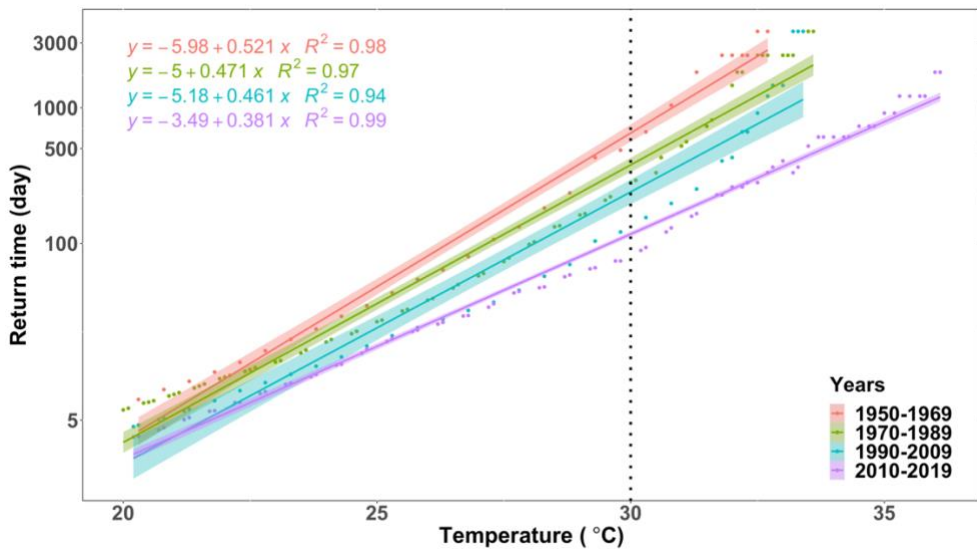


Figure A5.3 Return time analysis for 70-year time series temperature data at Schiphol, the Netherlands. The temperature data were divided into five parts, as shown in the legend, and fitted into relative regressions lines. The regression equations and R squares are listed using the same colors. The y-axis indicates the log-transformed return time values, which has been transformed into days.



Chapter 6 General discussion

Zhengquan Zhou

6.1 Individual-level response to the environmental disturbance

Benthic macrofauna can indicate habitat conditions due to their sedentary living style and sensitivity to physical or chemical disturbance (Donadi et al., 2015; Sukumaran et al., 2021). The current climate change scenarios are threatening the macrofauna by enhanced environmental disturbances in multiple abiotic factors such as temperature (Helmuth et al., 2002), hydrodynamics (Cahoon, 2006), sediment dynamics (Wiesebron et al., 2022; Zhou, Wu, et al., 2022), salinity (Debortoli et al., 2017), etc. Moreover, modern globalization has accelerated the invasion of introduced species, which compete with native species for natural resources (Bailey, 2015; Gallardo et al., 2016). Therefore, studying how benthic macrofauna, including both native and invasive species, respond to extreme weather events conveys important messages about the ecosystem resilience and long-term morphological development of tidal flats.

We now know that under extreme weather events such as heatwaves, macrobenthos increase the movement activities and search for suitable places to escape environmental pressure on tidal flats (Chapters 2, 3 & 5). The exact movement pattern does not only depend on the topography of the sediment surface (Chapter 2) but is also determined by the temporal dynamics of the environmental disturbance (Chapter 3). The respiration rate measurements in Chapter 2 and Chapter 5 indicate that the behavior performance is closely related to the respiration rate: higher respiration rates correlate with more active movement behaviors. If the environmental stress exceeds the metabolic tolerance thresholds, macrobenthos will suffer from mass mortality due to excessive respiration-related energy consumption (Chapter 2)

The work of this thesis confirms that extreme weather events change benthic behavior, and that this may be related to regulation of their metabolic rates. The metabolic response depends mainly on the respiratory chain and the tricarboxylic acid cycle, which requires adequate capacity of the oxygen supply (Anestis et al., 2007). However, extreme weather events, such as heatwaves and salinity changes, may harm the oxygen convey pathways and lower the oxygen supply capacity (Helmuth & Hofmann, 2001; Williams, 1984). The regulatory response of these basic biotechnical mechanisms can only fluctuate within a limited range. Yet, they affect various biological performances, such as feeding behaviors, movement patterns, reproductions, social interactions, and even migration tendencies (Chapperon & Seuront, 2011a; Pörtner, 2001; Scapini et al., 2019). These biological traits further

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determined how individual organisms contribute to ecological functions at a population scale with a higher density (Bremner et al., 2006b; Wrede et al., 2018). Therefore, we may discuss the findings of this thesis on a broader scale of ecological functions by linking the animals' behavioral changes to metabolism, and use this to make general predictions for the effects of climate change on community functions (Cozzoli et al., 2018), even though this will in remain in part rather speculative.

6.2 Response strategies regarding intensity and duration

As mentioned in the first chapter of this thesis, one of the pathways that maintains the optimal status of physiological functioning (i.e., homeostasis) under environmental stress is the “fight or flight” response. The American physiologist Walter Bradford Cannon first described the *fight-or-flight* theory, which states that when an animal is faced with a threat, it will either fight the threat (if it believes it can win) or flee from it (Cannon, 1914). This response mechanism is controlled by the sympathetic nervous system (of the vertebrates) and triggered by the release of epinephrine, norepinephrine, and other hormones (via endocrine systems), which prepare the body for action by increasing heart rate, blood pressure, and muscle strength (Wortsman, 2002).

The nervous system of macrobenthos varies depending on the species. In general, they possess a decentralized nervous system, with a diffuse network of nerves and ganglia distributed throughout their body (Müller, 2006; Yurchenko et al., 2018). Although benthic organisms have simpler nervous systems than vertebrates, hormones play a crucial role in regulating behavior in response to various external stimuli (Jobson et al., 2021; Lye et al., 2005). For example, the hormone serotonin (5-hydroxytryptamine) can decrease oysters' mortality during air exposure by modulating the physiological redox process (Dong et al., 2017). Additionally, the hormone melatonin has been found to play a role in the circadian rhythm of certain shellfish species, such as the blue mussel (Chapman et al., 2020). Other hormones, such as dopamine and octopamine, have also been found to regulate various behaviors in shellfish, such as movement and aggression (Aiello et al., 1981; Jones, 1983).

Throughout the study of this thesis, we consistently observed the *fight-or-flight* response in our model species under two sets of conditions: *i)* low to intermediate stress over a prolonged period, and *ii)* high stress over a short to intermediate duration (as depicted by the yellow shades in Fig. 6.1). For instance, during low tide, cockles resorted to “flight” by burrowing deeper into the sediments to evade the thermal stress, as described in Chapters 2, 3, and 5. If the thermal stress is too pervasive to escape, cockles exhibited a heightened metabolic rate when faced with thermal stress to “fight” and maintain optimal physiological conditions, as evidenced by increased respiration rates in Chapters 2 and 5. When the temperature exceeded 30°C and persisted for more than five days (Intensity IV and V in Chapter 2), cockles surfaced and attempted to move out of the PVC pot during simulated high tides.

Future studies may conduct more detailed experiments to study the underlying mechanisms how bioturbators' movements respond to temperature. One of the methods is using the Q_{10} value to measure the temperature sensitivity of a process,

$$Q_{10} = \frac{R_2}{R_1}^{10^{\circ\text{C}/(T_2 - T_1)}}$$

where R_1 and R_2 are the changing rates of the process, T_1 and T_2 are the temperature in Celsius degrees or Kelvin. For most biological systems, the Q_{10} value is about 2 to 3 (Reyes et al., 2008).

In addition to the fight-or-flight response, we also observed the "freeze" response in organisms when faced with environmental stress that exceeds their physiological thresholds. The "freeze" response is a defensive mechanism some animals use when confronted with a predator or other threat (Blanchard et al., 1968). This response is characterized by a temporary cessation of movement and a decrease in heart rate, blood pressure, muscle tone, and metabolic rate (Hagenaars et al., 2014), making the animal less visible or detectable to predators and providing a survival advantage (Bracha et al., 2004). However, in this thesis, I define the "freeze" response slightly differently. When environmental stress exceeds an organism's optimal range, the organism is forced to reduce activity and metabolism to maintain basic physiological functions. This response typically occurs when the model species are subjected to acute extreme stress or long-term intermediate stress, as evidenced by the surfacing of cockles in Chapters 2 and 3 (depicted by the red shades in Fig. 6.1).

Mass mortality in organisms can occur under two scenarios: when subjected to extreme stress in an intermediate timeframe or when exposed to intermediate to high stress over a prolonged period, as depicted in the grey shades of Figure 6.1. For example, even though the heating temperature was relatively mild at 25°C, the cockle *C. edule* experienced mass mortality in just ten days after a sudden drop in salinity to 5 PSU (as described in Chapter 4, extreme low salinity was the dominant stress). Long-lasting intermediate-high stress is also demonstrated by the results of 6-day cycle heatwaves, which resulted in a significantly lower survival rate of 47.37% compared to that under 3-day cycle heatwaves (presented in Chapter 3). The occurrence of mass mortality can lead to the clearance of ecological niches previously occupied by native species, creating opportunities for introduced species to establish and spread in a new environment, as discussed in Chapter 5. However, it is important to note that while introduced species may initially benefit from these opportunities, their success may negatively impact the long-term stability of the ecosystem due to shifts in functioning traits and community structures.

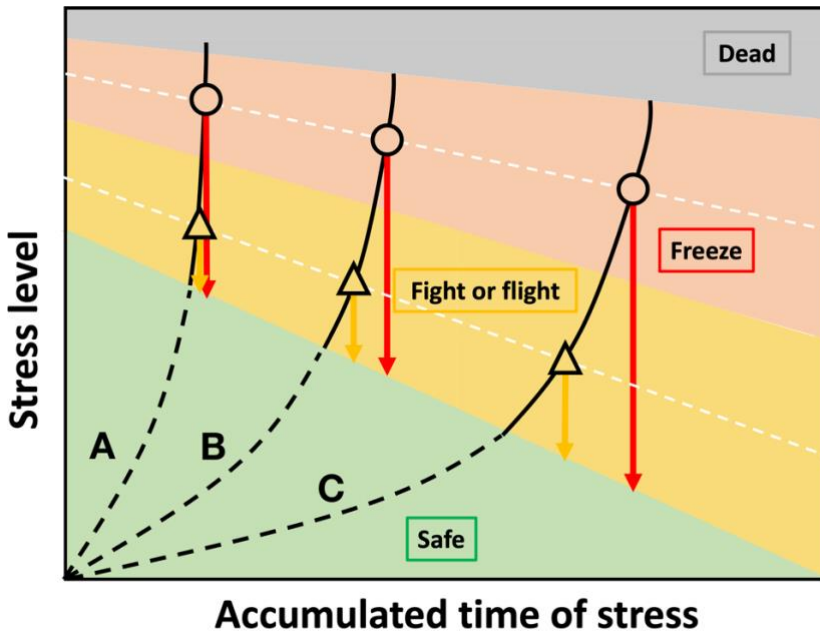


Figure 6.1 An illusion of the fight, flight or freeze response. The x-axis represents the duration of the environmental stress, and the y-axis represents the stress level of organisms in the environmental stress. Different colors represent the response of benthic animals: green is for the “safe” status when the stress is within organisms’ optimal physiological thresholds; yellow is for the “fight or flight” response when organisms increase their metabolic rates and activities to adapt to the stress; red is for the “freeze” response when organisms reduce activities or stay dormant; “grey” is for mortality when organisms under stress which is beyond the physiological limits in magnitude and duration. The curves represent how species with different traits react to the stress along time. Three different curves labeled A, B, and C represent species with stress-sensitive, intermediate-sensitive, and stress-tolerant traits, respectively. The circles in the figure indicate that environmental stress is the dominant factor that determines the organisms’ response, while the triangles indicate that biological traits play a more significant role in determining the response pattern to the stress. The arrows represent the environmental resistance that species face when attempting to recover to a “safe” phase. Figure drawing was inspired by Yaakub et al. (2014).

6.3 Community-level response regarding biological traits

The thriving of intertidal communities relies on complex biological interactions such as predator-prey relationships, competition, facilitation, and mutualism (Liautaud et al., 2020). Species’ biological traits (e.g., feeding type, living styles, morphology, size, etc.) play an essential role in these interactions and contribute actively to ecosystem processes such as assimilation, nutrient cycle, and

productivity (Kuipers et al., 1981). The surrounding environment can strongly influence species traits on the community level since abiotic factors determine the species distributions and assemblage composition on various spatial and temporal scales on tidal flats (Bremner et al., 2006b). As the raking experiment shows in Chapter 4, the daily sediment dynamics functions as an environmental filter in selecting species with specific mobility traits to cope with the inner variance of living conditions. Specifically, the wind-exposure sites encompassed species with high mobility, such as *Corophium volutator* ($Mi = 4$, free movement via burrow system). In contrast, species mainly dominated the wind-sheltered sites with limited mobility, such as *Macoma balthica* ($Mi = 2$, limited movement) and *Heteromastus filiformis* ($Mi = 2$, limited movement). This *in-situ* experiment confirmed that species with high mobility (i.e., higher Mi values indicating higher levels of mobility) are better adapted to the simulated storm disturbance and may have a better chance of survival, while those with unfitted traits (i.e., lower Mi values indicating lower levels of mobility) decreased in abundance. Therefore, in long-term temporal scales (i.e., years to decades), climate-change-induced extreme events may increase the taxonomic similarity among macrofauna and lead to the homogenization of species traits (Woodward et al., 2015).

However, other factors such as intra-species relationships (Chapter 5), pathogens (*see* discussion in Chapter 1), and human activities can also interfere with climate change, thereby affecting the development of biological traits and community structures in complex ways (Leonard et al., 2014). For example, as the temperature increases due to climate change, tidal flat organisms better adapted to higher temperatures will generally outcompete those with lower optimal temperature ranges (Dolbeth et al., 2011). This could increase the proportion of heat-tolerant traits in the community over time. Moreover, high temperatures can increase the growth and reproduction rate of pathogens such as parasites and bacteria (see discussion in Chapter 2), promoting pathogens' transmission between macrofauna (Mouritsen et al., 2018); migratory birds may change the migration timing or routes due to the altered thermal regimes (Albright et al., 2010; Buehler et al., 2008), thus resulting in shifts of the predator-prey balance (Horn et al., 2020; van der Meer et al., 2001). Species with lower temperature tolerance do not have to be demolished, instead, they can migrate towards regions with more favorable conditions (Harvey et al., 2021), or evolve to have more plasticity in their thermal tolerance thresholds (Nguyen et al., 2011). Complex as these effects are, if we focus on species traits and community functions, major effects of extreme weather events on benthic macrofauna can be summarized as *i*) an increased mortality rate for species with unfit traits, *ii*) the community function develops to be more adaptive to dominant disturbance, *iii*) species shifts to habitats with better suitability. The former two affect the internal population dynamics of macrofauna, while the species shift determines the spatial community distribution.

Macrofauna usually positions at lower trophic levels, consume the organic matter in sediments, and function as an energy supply to higher trophic levels (Raffaelli, 2006). Thus, under the impact of climate change and subsequent extreme weather events, local fluctuations in population dynamics and functional traits can be conveyed to regional or even global scales through food webs and flyways (Cozzoli et al., 2018; Robinson et al., 2009). Facts are that the species distribution has already shifted due to the increasing water temperatures: in Britain and Ireland, ‘southern’ species (e.g., the top-snails *Osilinus lineatus* and *Gibbula umbilicalis*) have undergone north and north-eastern range extensions from the 1950s to 2000s (Mieszkowska et al., 2006); in Spain, the southern distribution limit of *Macoma balthica* shifted at least 300 km to the north (from 1972 to 2007), due to the increased respiration-related maintenance rates or even starvation under frequent exposure to high temperatures above 30 °C (Jansen et al., 2007).

6.4 Disturbance frequency and ecosystem memories

Besides duration and intensity, the frequency of environmental disturbance also plays an important role in determining the impacts of extreme weather events on tidal flat ecosystems (Perkins-Kirkpatrick et al., 2017). In this context, “frequency” refers to the probability of return occurrence regarding a threshold value near the upper (lower) end of the observed range of a weather variable (Ridder et al., 2022). Several studies have demonstrated that changes in the frequency of extreme weather events tend to closely align with the shape of their statistical distribution (Ballester et al., 2010; Rhines & Huybers, 2013). Moreover, the intensity of extremes is sensitive to changes in the shape of the probability distribution due to the change of variance and skewness (*see* Fig. 6.2, adapted from Ummenhofer & Meehl, 2017). Therefore, extreme weather events can occur more frequently with higher severity due to increased mean extreme values. Thus, policymakers and coastal managers must thoroughly consider *i*) the specific intensity threshold and *ii*) the probability of occurrence when evaluating the impacts of extreme weather events (Sippel et al., 2015).

Changing the disturbance frequency affects how well an ecosystem can recover and adapt to new disturbances by filtering out certain function traits (Bonada et al., 2007; Turner et al., 2020). For example, the repeated raking experiment suggests that more frequent storms that increase the sediment dynamics will shift benthic macrofauna towards more mobile traits (Chapter 4). This is analogue to feedbacks observed for plants, as seen in boreal North America where the moist soils in black spruce ecosystems create thick organic layers that remain after fires, providing ideal conditions for black spruce regeneration (Johnstone et al., 2010). Black spruce and moss have traits that support plant-soil-microbial feedbacks, which help cycle nutrients slowly and build deep organic soils (Johnstone et al., 2016). However, the climate-driven increases in fire frequency and intensity promote decreasing organic layers

in soils and make it ideal for deciduous trees to grow (Alexander et al., 2012). These trees have traits that support quick growth and nutrient cycling, and they can help establish a deciduous forest with its unique plant-soil-microbial feedbacks that perpetuate the alternate ecosystem dominated by deciduous trees (Alexander et al., 2012; Johnstone et al., 2016).

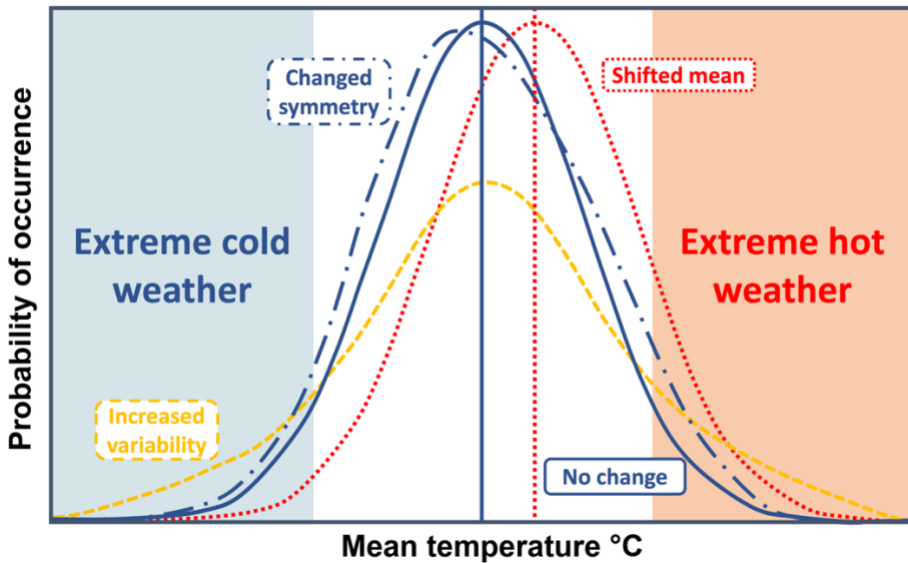


Figure 6.2 A schematic figure showing how changes in temperature distribution can impact extreme conditions. The dark blue solid line indicates a profile without distribution changes (the vertical solid line represents the mean value). The red dashed line shows a future distribution with shifted mean value, resulting in more extreme hot weather but less extreme cold weather (the vertical dashed line represents the shifted mean value). The dark blue dashed line indicates an altered distribution shape, leading to similar cold and extreme hot weather scenarios. The yellow dashed line shows an increased variability profile leading to increased cold and hot extreme weather. Reproduced from data and figures by Ummenhofer & Meehl, (2017) and IPCC (Field et al., 2012).

In Chapter 4, it was argued that the current resilience of an ecosystem is determined by its community structure and functions, which together form the *ecosystem memories*. These “memories” play a crucial role in shaping the future resilience and states of the ecosystem towards extreme events (see Fig. 6.3). To thoroughly understand the resilience of an ecosystem, it's necessary to elaborate further the concept of ecosystem memories, which are usually maintained by two types of disturbance legacies: *information and material legacies* (Franklin et al., 2000; Johnstone et al., 2016). The information legacy is adaptations to long-term historical disturbance regimes expressed by the characteristics of species'

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functioning traits (Johnstone et al., 2016). The results of the 3-month raking experiment is an example showing how changes in disturbance regimes form information legacies. Material legacies are individuals or matters that last after one disturbance events (Monger et al., 2015). The decreasing organic layers in black spruce ecosystems in boreal North America is an example of the material legacies (Johnstone et al., 2016). Material legacies usually survive a short-term disturbance and convey the past ecosystem characteristics into the future. However, climate-driven extreme events may change the frequency, intensity, or spatial attributes of disturbance, resulting in the misalignment between information legacies and environmental conditions (Harris et al., 2018; Millar & Stephenson, 2015). The increasing frequency of extreme weather events under future climate change scenarios will exacerbate misalignments and trigger critical ecosystem transitions, leading to significant disruptions in their equilibriums (Thibault & Brown, 2008).

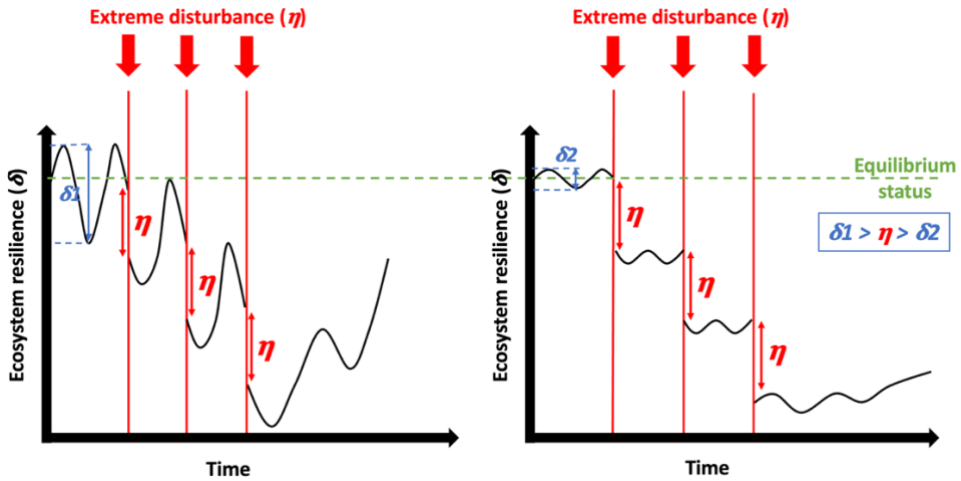


Figure 6.3 A conceptual figure illustrating how ecosystem memories determine future resilience under extreme events. The green dashed line in the figure represents the average ecosystem resilience under an equilibrium state, assuming no extreme events induced by climate change. η refers to the disturbance magnitude of an extreme weather event. $\delta 1$ refers to ecosystems with high variability of resilience. $\delta 2$ refers to ecosystems with low resilience variability. Ecosystems with high resilience variability (δ) are more resistant to repeated disturbances (with the same magnitude η) than those with low resilience variability.

6.5 Synthesis and outlook

The impact of extreme weather events on bioturbators can be complex and is influenced by various factors, such as the site's morphology and the disturbance regime's temporal dynamics. Some species may be able to adapt their burrowing behaviors to cope with short-term disturbances, while long-term and cumulative stress can lead to mass mortality and the introduction of new species. Recurring disturbance patterns can over time affect the life-history strategies of benthic species that can occur on specific tidal flats, leading to changes of survival and regeneration strategies that are specifically tuned to the disturbance regime. These responses ultimately affect the long-term biogeomorphic feedback and development of the tidal flat ecosystem.

Given the complex responses of bioturbators to extreme weather events, our research findings provide empirical evidence for the importance of considering these effects when modelling bioturbation. Our results demonstrate that extreme weather events may impact the outcome of bioturbation at both the individual and community levels. To model bioturbation effectively, future research should consider several bioturbation responses. *Firstly*, bioturbator behavior can change directly in response to extreme disturbances. *Secondly*, the intensity of bioturbation depends on the characteristics of extreme weather events, such as their frequency, duration, and magnitude. *Finally*, environmental disturbance can shape community structure, particularly regarding species composition, when the disturbance exceeds ecosystem memories. Thus, modelling work must account for these bioturbation responses to extreme weather events to predict how ecosystems will respond to future disturbances.

The development of species' life-history traits and community succession under repeated impacts of extreme events are key legacies of recurrent disturbances. Understanding the current conditions of tidal flat ecosystems requires accounting for time lags and ecosystem memory. As global climate change continues, uncovering the hidden trends of community development and ecosystem resilience is crucial. For instance, our study found that compound extreme weather events can result in mass mortality of native species *C. edule* and the subsequent opening of niches for the introduced species *R. philippinarum*, while bioturbation outcomes may remain unchanged. However, increasing frequencies of heatwaves and flash floods in current global change scenarios could potentially allow newly settled bivalve species (e.g., *Potamocorbula amurensis* appeared in the Netherlands since 2019, Dumoulin & Langerart, 2020) to take more niches due to their high tolerance to temperature and salinity changes (from own experimental tests with *P. amurensis* in 5 and 30 PSU, under 40 °C). Similarly, the Great Barrier Reef in Australia transformed corals' response to heat stress following a marine heatwave in 2016, which resulted in less recurrent bleaching in 2017 for hundreds of reefs (Hughes et al., 2019).

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The predictions we make today will likely become the future that ecosystems inherit, and the future will undoubtedly become a critical part of ecological history. It is no longer sufficient to study individual climate-driven events in isolation from other temporally- or geographically-connected disturbances. To comprehensively understand the complex and dynamic nature of tidal flat responses to global climate change, it is necessary to engage in *i)* long-term monitoring to consider the cumulative effects of recurring extreme events and environmental stressors; *ii)* experimental studies to understand underlying physiological and behavioral responses and species interactions; *iii)* conceptual and physical modelling that is supported by the experimental results.

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Acknowledgment

On a summer Friday night in 2022, I was chilling in De Keete's living room, watching TV while people chatted away, and ads playing in the background. That's when Matteo Meli, a guest researcher at NIOZ, dropped by with a beer in hand and asked, "Zhengquan, what do you think of the meaning of all this?" Well, perfect timing for musicians to think about the meaning of life (Matteo played guitar and bass in a band). I reluctantly answered that some parts of life are bound to be wasted. Matteo looked at me for a moment and then looked away. The conversation ended just like that, going nowhere meaningful.

This question still crosses my mind, particularly when I'm stuck with my Ph.D. research: what is the meaning of this all?

Thinking back to 2015, I was an intern in an experiment with Laura Soissons, who was then a Ph.D. candidate from NIOZ, working at the Yantai Institute of Coastal Zone Research, Chinese Academy of Sciences. That was the first time I heard of NIOZ, but I never thought I would one day be a Ph.D. candidate at NIOZ as well. Thanks to Baoquan Li and the China Scholarship Council, I had the opportunity to complete my master's degree at the Chinese Academy of Sciences and pursue my Ph.D. study in the Netherlands.

In September 2018, I sat with my supervisor Tjeerd Bouma in his office, and I knew I would be working on the topics of global climate change effects on benthic animals. Tjeerd looked at me with sharp eyesight and said, "You will finish 4-5 papers for your thesis." I feel impressed by Tjeerd's destined words, but honestly, I had no idea what this topic entails. I have two more supervisors, Tom Ysebaert and Brenda Walles. In the beginning, the supervisor team met me every other week to discuss my thesis content and experiment design. Quite a "nice" start; thinking retrospectively, I don't quite understand them, and they sometimes cannot get my points due to my poor language skills, despite their rich experience with guiding students. Thanks to their patient guidance, I started conducting *in-situ* raking experiments the following spring and came up with a plan for the next heating experiment.

The rookie year was very fancy. My dear colleague and friend Jaco de Smit took me out to the field so that I could see and experience the nature of Dutch tidal flats for the first time. Jaco was like a ninja - jumping, running, sliding – while I could barely walk with an unfitting wader. He also helped me with the OsCar flume and raking experiments with internship student Prasha Maithani.

Tim Grandjean was a lifesaver - always ready to chat in the office and lend a hand with experiments, even though he was busy writing his Ph.D. proposal. Since I couldn't drive then, I often begged Tim to help in the field. One time, we went to take benthos samples near the border of Belgium and saw some weird naked guys lurking in the marshes. I was shocked by the wild culture and asked what they were up to. Tim just smiled and kept driving as if it was a normal occurrence.

Towards the end of my first year, I started to realize the topic of my Ph.D.: how bioturbation affects sediment properties under climate change events. Thanks to Brenda's fantastic idea, we started the heating experiment and measured the burrowing behavior of cockles. In early 2020, I completed the first heating experiment with the help of internship student Cristian Martin, who assisted me with the experiment setup and some extra field sampling work. Unfortunately, the corona lockdown began, and

Cristian had to switch topics and focus on modeling so that he could work from home. Jim van Belzen helped me manage a tough talk with Cristian and assisted him in finishing his master's thesis.

The corona lockdown was a challenging time. We had to learn how to work efficiently from home and had limited access to the lab and fieldwork. However, the online OEI-meeting was a fantastic platform for getting feedback on my data processing and manuscript. Meanwhile, Min Zhang and Zhiyuan Zhao were important partners in De Keete. After dinner, we often walked together, and sometimes Thiri Naing would join us. We chose different daily routes, circling Yerseke, and discussed our work and lives during lockdown. We also daydreamed about what we could do after the lockdown, such as finding a suitable location in the village for a barbecue.

Eventually, the lockdown ended, and we could return and work at NIOZ again. I started my second heating experiment, and Natalie Steiner offered great help in testing the luminophore methods. We initially planned to design an experiment in the field with a greenhouse device, but we ended up with a cooling shelter after several attempts during the summertime, hilarious. Then, we designed a mesocosm experiment to control the variables better and focused on the effects of the temporal dynamics of heatwaves on cockles' burrowing behavior. Natalie helped me with endless sediment slicing and photography until we became too exhausted to talk in the lab. Moreover, internship student Simon Hof helped process samples from the raking experiments. By winter 2020, we had almost completed the heating experiment and obtained enough data to process and write for the second corona lockdown.

The year 2021 began with the rejection of my first paper, which was quite disheartening. I wanted to let it go, but Tjeerd insisted we keep trying journals with higher impact factors. Greg Fivash excellently helped me with data processing and visualization. He would fix my coding errors in seconds and improve my manuscript's grammar as a native speaker. I was also fortunate to work with three more internship students: Max Wieler offered great help in building the greenhouses with his practical experience; Janneke de Bresser quickly learned how to identify benthos species and conducted thorough literature reviews on bioturbators; and Quinn Bommelé, who worked hard on building mesocosms and taking measurements. Thanks to their help, I successfully completed all the planned experiments for my thesis, and I could focus more on writing the manuscript at the beginning of 2022.

The writing wasn't as smooth as I expected, and I needed to conduct extra experiments to satisfy the reviewers. Fortunately, Francesco Cozzoli returned to NIOZ and offered me much help in creating conceptual figures using simple coordinate plots to show how organisms respond to external stress. Chatting with Francesco was always enjoyable. Though I don't smoke, I joined him in the yard of De Keete for discussions on bioturbation, food, culture, and other topics.

Dunia Rio Yunes provided valuable feedback on the thesis introduction and discussion. Dunia is a good listener and generous with sharing ideas, and we had many enjoyable discussions on paintings, music, books, politics, etc. When I felt depressed about thesis writing, she told me that finishing was more important than perfection, and all we needed to do was to get the thesis done first.

I often exchanged ideas with other Ph.D. colleagues such as Lauren Wiesebron, Tim Hermans, Rosanna van Hespén, Carolina Camargo, Roeland van de Vijzel, Victor Malagon Santos, Loreta Cornacchia, Archontoula Valsamidou, Coco van Starrenburg, and Chiu Cheng, learning from their experiences and feelings on finalizing the Ph.D. work and thesis. Chiu once told me he could only write one or two sentences for the whole afternoon when he got stuck; the point was not to be overwhelmed by those disappointing feelings. Meanwhile, I went to the field with Marte Stoorvogel, Victoria Mason,

Eleonora Saccon, Mingxuan Wu, and Ting Zhang and joined their fieldwork. I also took those opportunities to refresh my mind from tiring data processing and writing.

So, what do all of these mean? During the Ph.D. study, I often felt depressed, and memories of the good days during high school, university, and mater periods came back to me, giving me the strength to move on. These experiences and memories will serve as new energy sources and hope in my future life.

Aside from the supervisory team, the Ph.D. study was only possible with great help from the support staff. Jeroen van Dalen, Lennart van IJzerloo, and Daniel B. Blok helped me start all the experiments and always offered kind assistance in the field or mesocosms. Arne den Toonder and André den Herder patiently helped me build up the electrical systems in the mesocosm room. Peter van Breugel kindly taught me how to measure sediment grain size. Yvonne Maas and Jurian Brasser taught me how to measure chlorophyll-a samples and salinity. Pieter van Rijswijk and Anton Tramper offered their technical expertise in respiration measurements. Jan Peene took over the nutrient measurements at lightning speed. Adri Knuijt kindly helped with data subsets and archiving. Christine de Zeeuw and Miranda Manders provided a welcoming atmosphere at the reception and arranged cars on schedule so I wouldn't miss any field trips.

In the past five years, I have resided in De Keete, the guest house where I have found inner peace and shared many happy hours with numerous international friends. I extend my heartfelt appreciation to Jan Megens for his magical touch in arranging my accommodations and daily life and Suzanne Thoen for being like an elder sister and sharing warm conversations with me. I also thank my basketball brothers, Haobing Cao, Long Jiang, Junlin Ren, Mingxuan Wu, Jing Feng, and Qi (Ricky) Liu. I hope we will continue to have opportunities to play basketball together. I am also grateful to my dinner and poker game buddies, Heyue Zhang, Lixia Zhao, Kang Zhang, Yvxi Ma, Xuerong Wu, and Ting Zhang, for their companionship and the fun time we spent. Special shout-out to X.mao Rijk and her husband, Norbert Rijk, for their hospitality in hosting me on Friday nights, treating me like their own child, and serving me delicious Sichuan-style cuisine while sharing lots of fun and laughter. Moreover, Mishu, the smart cat with a furry belly, always greeted me at the front gate and listened to my footsteps when I returned from the labs in the evenings. Unfortunately, Mishu is no longer in De Keete, as she disappeared after a heavy winter snowfall in 2021.

I would like to express my deepest gratitude to Chenyan Zhang, who has been my most important partner and solid source of company during the hardest time of my Ph.D. study.

Finally, I would like to write in Chinese to thank my family and friends in China since most of them do not speak English.

在外几年，我看到了更广阔的世界，但也失去了和你们相处相伴的时间。感谢我的母亲，教会我要把荷兰当作自己的家，不要总拿自己当外来人。感谢我的姥姥、姥爷，视频里总是问我吃穿住行是不是舒心。感谢我的二姨、小姨、舅舅、舅妈，在我缺席的日子里照顾、陪伴我的母亲。感谢弟弟妹妹们的挂念，你们也要努力加油。感谢我的发小，杜宸、王伟卿、张崇圣和李欣洋，总说回去喝两杯，却因为疫情一直没回去。感谢各位好友，心烦的时候能和你们一起打游戏、聊天真的很棒。

寥寥数年，有得有失，不求闻达，但求无愧。

Curriculum Vitae

Zhengquan Zhou was born in Zaozhuang City, Shandong province, China on July 17th, 1992. Zhengquan is a benthic ecologist who studies how environmental stress affect the benthic conditions in coastal areas, regarding the health conditions and community structures of benthic organisms living in the deposits. He conducted his PhD research at Department of Estuarine and Delta Systems, Royal Netherlands Institute for Sea Research (NIOZ), and will defend his thesis at the Utrecht University. He obtained his MSc at the Yantai Institute of Coastal Zone Research, Chinese Academy of Sciences, and BSc at Yantai University.



He has backgrounds in shellfish aquaculture, macrobenthos taxonomy, and his current research interests are: *i)* investigating the mechanisms through which the temporal dynamics of extreme weather events influence bioturbation processes, as well as the behavioral responses of bioturbators to extreme weather events such as heatwaves; *ii)* evaluating the impacts of extreme weather events and anthropogenic incidents on the benthic environment health, based on population traits and species diversity of macrobenthos; *iii)* exploring the influence of tidal flat sediment dynamics on the ecological functions and community stability of macrobenthos, and predicting the tendency of community succession under the compound stress of climate change and anthropogenic activities; *iv)* forecasting the contribution of benthic organisms to the development of ecosystem resilience on tidal flats by influencing sedimental processes such as changing critical erosion thresholds, grain size, bulk density, and surface roughness.

List of Publications

Zhou, Zhengquan, Tjeerd J. Bouma, Gregory S. Fivash, Tom Ysebaert, Lennart van IJzerloo, Jeroen van Dalen, Bas van Dam, and Brenda Walles. "Thermal stress affects bioturbators' burrowing behavior: A mesocosm experiment on common cockles (*Cerastoderma edule*).*" Science of the Total Environment* 824 (2022): 153621.

Zhou, Zhengquan, Natalie Steiner, Gregory S. Fivash, Francesco Cozzoli, Daniel B. Blok, Lennart Van IJzerloo, Jeroen Van Dalen, Tom Ysebaert, Brenda Walles, and Tjeerd J. Bouma. "Temporal dynamics of heatwaves are key drivers of sediment mixing by bioturbators." *Limnology and Oceanography* (2023).

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Li, Baoquan, **Zhengquan Zhou**, Bingjun Li, Quanchao Wang, Xiaojing Li, and Linlin Chen. "Size distribution of individuals in the population of *Asterias amurensis* (Echinodermata: Asteroidea) and its reproductive cycle in China." *Acta Oceanologica Sinica* 37, no. 6 (2018): 96-103.

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Li, Baoquan, Tjeerd J. Bouma, Quanchao Wang, Laura M. Soissons, Francesco Cozzoli, Guanghai Feng, Xiaojing Li, **Zhengquan Zhou**, and Linlin Chen. "Effects of key species mud snail *Bullacta exarata* (Gastropoda) on oxygen and nutrient fluxes at the sediment-water interface in the Huanghe River Delta, China." *Acta Oceanologica Sinica* 38, no. 8 (2019): 48-55.

Li, Baoquan, Xiaojing Li, Tjeerd J. Bouma, Laura M. Soissons, Francesco Cozzoli, Quanchao Wang, **Zhengquan Zhou**, and Linlin Chen. "Analysis of macrobenthic assemblages and ecological health of Yellow River Delta, China, using AMBI & M-AMBI assessment method." *Marine pollution bulletin* 119, no. 2 (2017): 23-32.