



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



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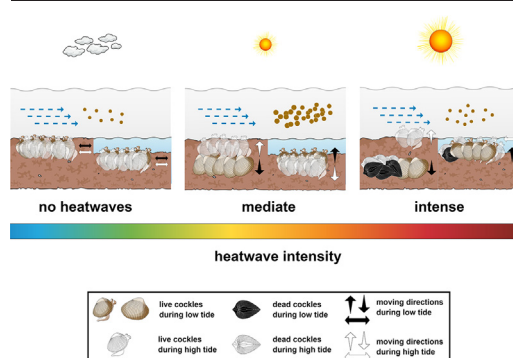
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HIGHLIGHTS

- Heatwaves greatly enhanced cockles' burrowing activities during low tide
- Cockles burrowed deeper into the sediment in the absence of water pools during low tide.
- Cockles covered by shallow water pools moved up when exposed to thermal stress.
- Long-term cumulative heat stress reduced health conditions and can lead to mass mortality.
- Observed changes in behavior can have major consequences for the biogeomorphology of tidal flats

GRAPHICAL ABSTRACT



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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 and 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.

1. Introduction

Intertidal ecosystems, such as tidal flats and salt marshes, are highly valuable given their unique ecological and socio-economical functions

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(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 and 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., 2020a). Whereas salt marshes and mangroves are increasingly regarded as an opportunity to realize cost-effective flood-defense systems under climate change (Arkema et al., 2015; Narayan et al., 2016; Zhu et al., 2020b), it is increasingly realized that they cannot exist without vast convex-shaped tidal flats fronting them (e.g., see Bouma et al., 2016; Mariotti and 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 (Cozzoli et al., 2021; Grabowski et al., 2011; Widdows and 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 and Kristensen, 2003), current velocity (Cozzoli et al., 2014), grain size (McGonigle and 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 (Cozzoli et al., 2018, 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 (Cozzoli 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 and 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 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 and 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 and 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 and 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. Material and methods

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 and Hoellein, 2018). Previous studies have shown that the cockles' bioturbation can destabilize cohesive sediment and increase erosion rates (Cozzoli et al., 2018, 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 min 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. 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 × 95 × 60 cm) stacked one on top of the other (Fig. 1a). The upper tank was filled with a 30 cm-thick sediment layer (D50 = 265.02 μm, Silt content = 0%) as the typical living environment for cockles (see Fig. 1a). Due to the large amount of sediment needed for the experiment (ca. 1 m³), 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, D50 = 260.72 μm, Silt content = 0%, Oesterdam, 51°28'01.4" N, 4°12'49.8" 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. 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. 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. 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 × 6 rows (i.e., matching the size of the heater) staggered patterns in the upper mesocosm tanks.

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. 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 min prior to the daytime low tide, and shut down 30 min 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. 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 (Fig. 2b). A 12-h day-night cycle was created using indoor lighting, with no additional lighting device to adjust the light intensity (Fig. 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. 2b), while ii) the “solar-radiation heatwave temperature” was manipulated by the terrace heaters (Fig. 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 1: Fig. A1).

To record temperatures throughout the sediment column in the experimental tanks, temperature sensors (PT-100 sensors, TC Direct) were deployed at 0 cm, 2 cm, 4 cm, 6 cm depths to record the per-minute temperature profiles (Fig. 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. 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 obstruct cockles' movements. Whereas control experiments showed that the presence of cockles did alter the warming process (see Appendix 3: Fig. A3a), 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: Fig. A2). 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 3: Fig. A3b).

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. 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 Ø = 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 12 L, VWR) was used to keep the respiration chambers at a constant temperature. The oxygen concentration (μmol 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 μmol h⁻¹) of cockles were calculated from the following equation,

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

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 (μmol L⁻¹) at t_0 and t_1 ; V is the seawater volume in the chamber (L) with correction for the sensor volumes.

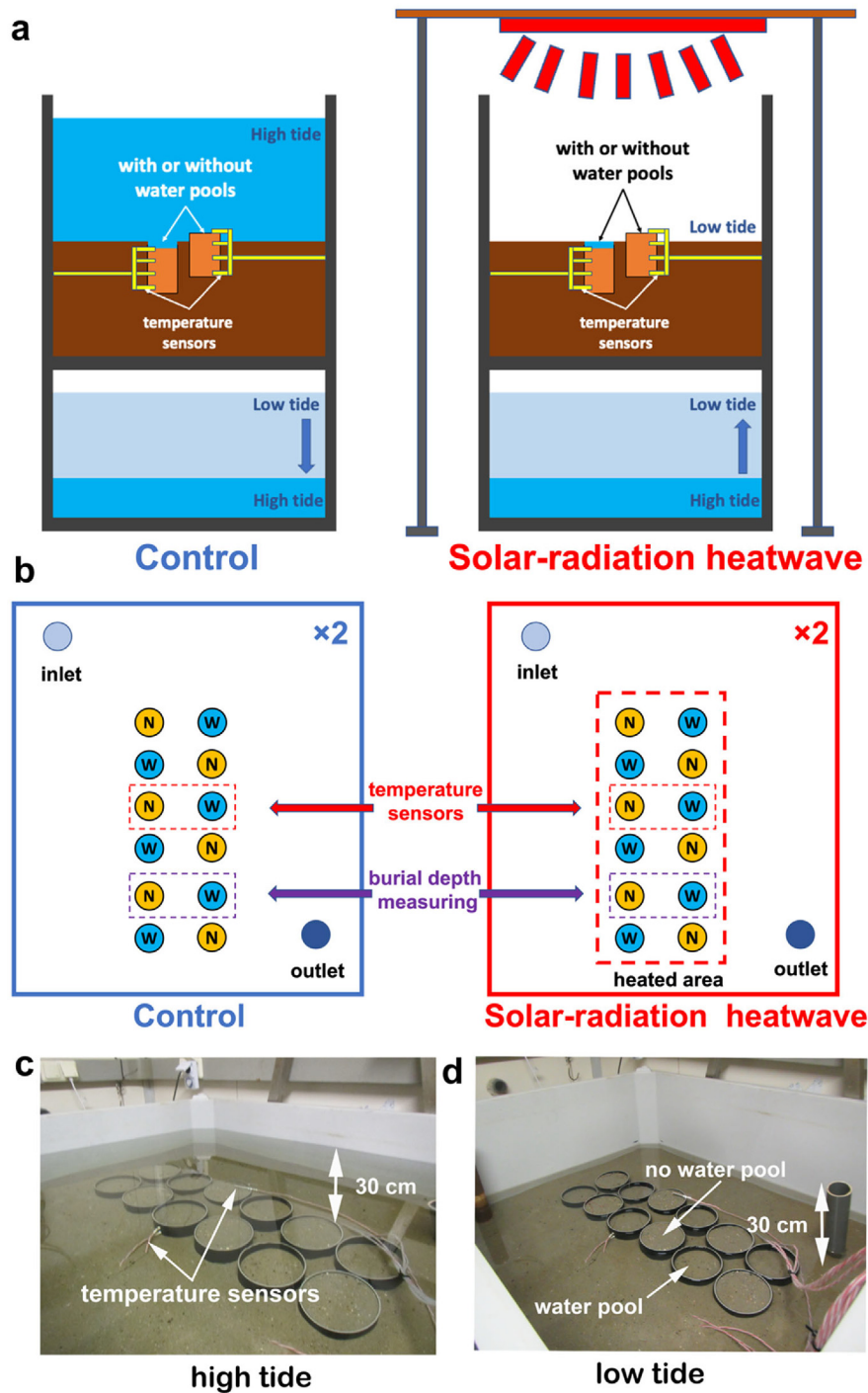


Fig. 1. Schematic diagrams and photos of the mesocosm experimental design. (a) The mesocosm setup mimicked diurnal tidal cycles on tidal flats for both “control” (left, only exposed to ambient temperatures of the climate chamber) and “solar” heatwave (right). The heatwave was mimicked using terrace heaters 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.

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. 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. 3a). Two of

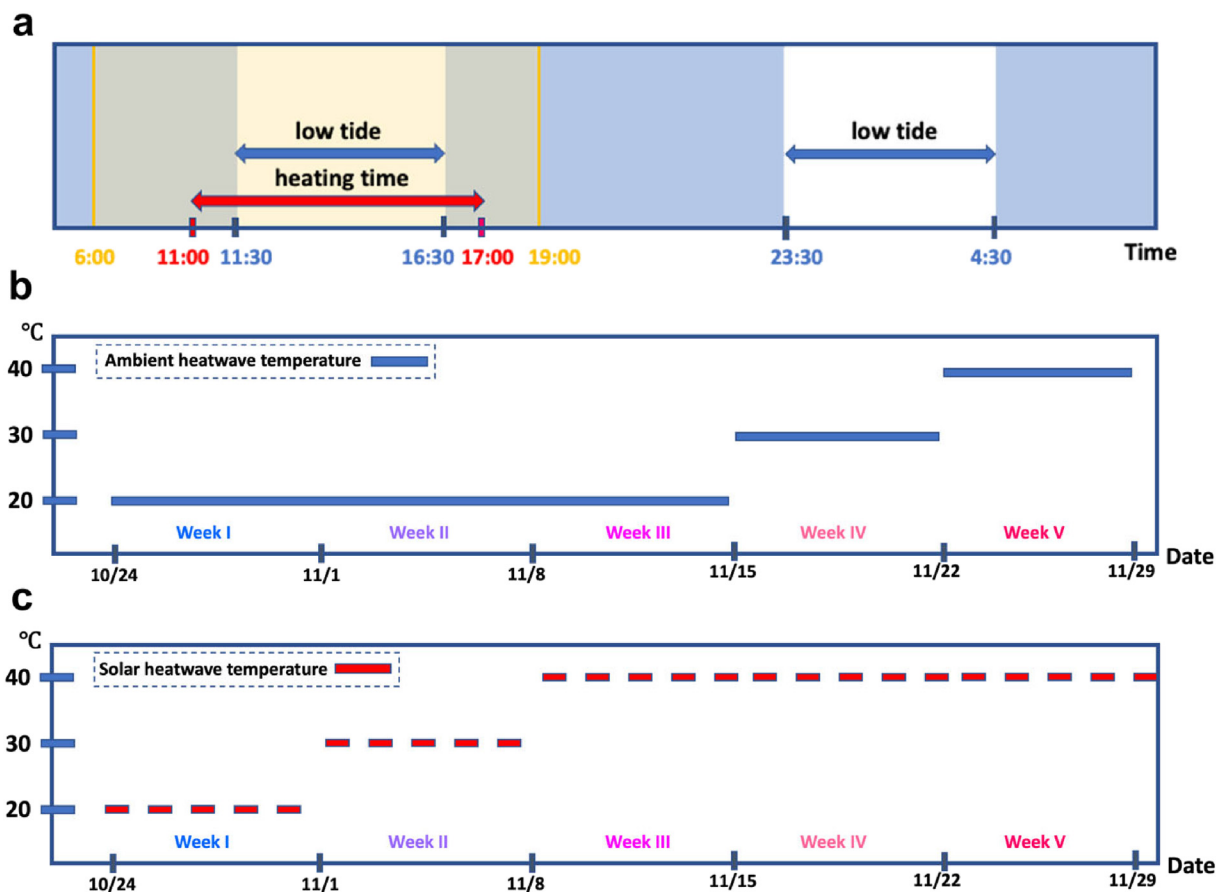


Fig. 2. Schematic diagrams represent (a) the daily tidal cycles and temperature settings and (b & c) the long-term temperature treatments over the experiment. When looking into the daily cycle settings (a) The daylight period is indicated by a yellow colour shade in panel a. Semi-diurnal tides are visualized 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 min 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.

them were 30 min 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. 3a).

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.

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).

3. Results

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. 4a) was lower than that of the exposed sediment surface without water pools (Fig. 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

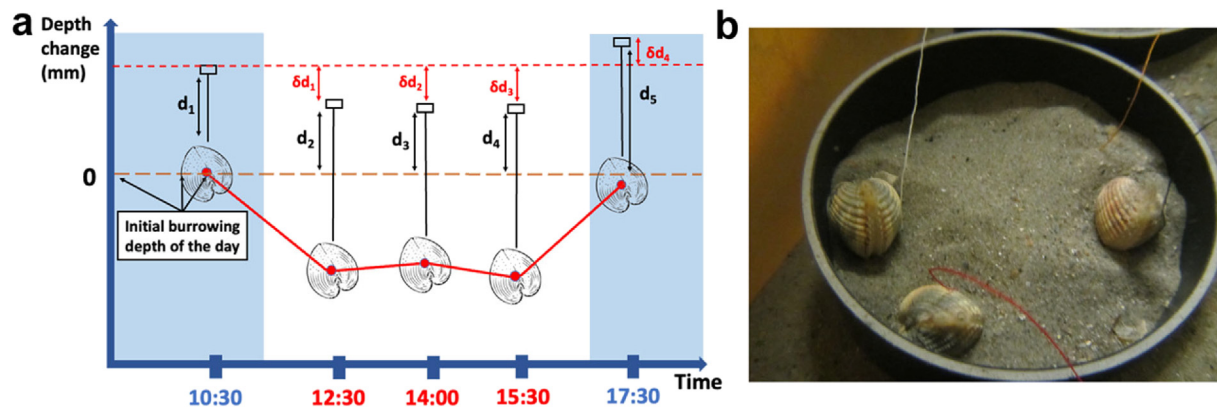


Fig. 3. Diagrams of burrowing depth measurements. (a) A conceptual diagram for burrowing depth measurements. The absolute length was measured five times every day. The “zero value” was defined as the initial burrowing depth of the day (i.e., “ d ”). Then, the burrowing depth change was calculated using 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.

water pools (Fig. 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. 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. 4d). These cockles then moved towards the surface as soon as the tide came. The magnitude of change in burrowing depth increased under greater heatwave temperatures.

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 5: Tables 1 & 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 ($F = 28.44$, $n = 344$, $p < 0.01$).

A rolling window analysis was applied to test the daily variance of cockles' position change (ignoring the direction of movement) under the heatwaves (Fig. 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. 4).

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. 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 4: Fig. A4). The heatwave reached its highest intensity in Week V (see Fig. 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.

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 and 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.

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 and 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 microorganisms with accelerated metabolisms breaking down organic matter (Degerman et al., 2012). On the other hand, animals can have limited

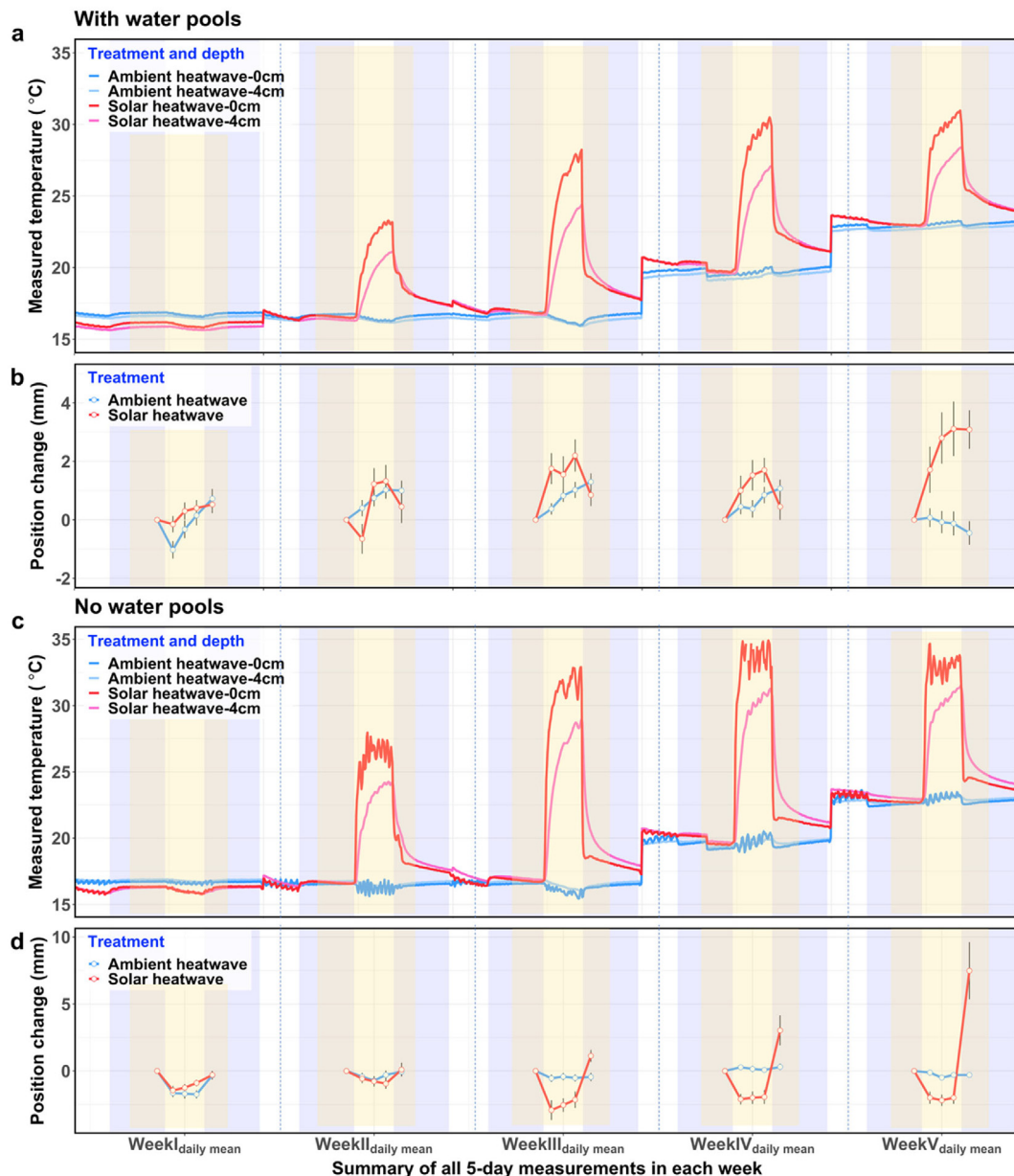


Fig. 4. Average daily temperature (a, c) and change in the burial depth (b, d) during each week, for tidal flats with (a, b) and without (c, d) pooling water. The dashed lines indicate summarized daily profiles; mean values were calculated for temperature and change in burial depth based on 5-day data 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.

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 and 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 and 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 can not 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. 4).

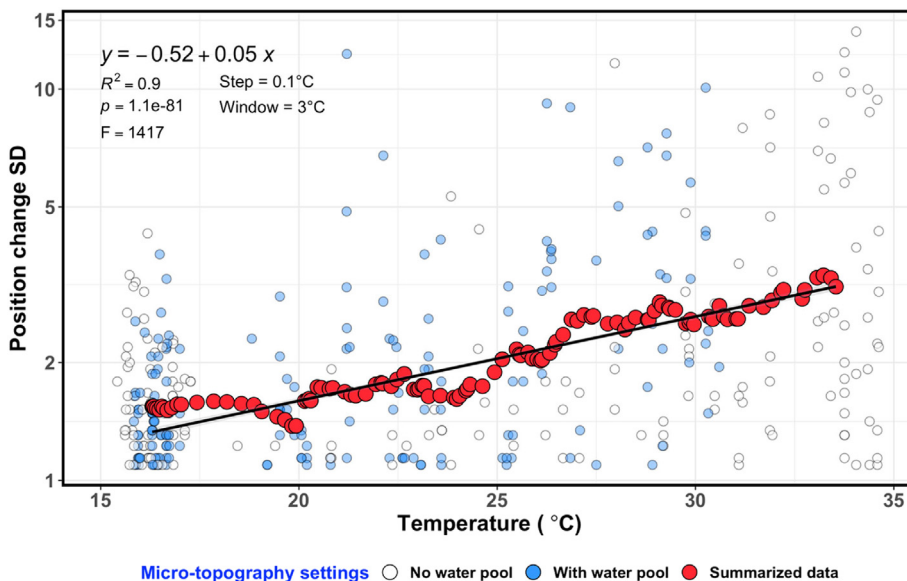


Fig. 5. The effects of temperature on cockle's burrowing positions. The data points in the graph represent the log-transformed standard deviation of each cockle's daily position change. The white circles stand for cockles living without water pools, while blue circles represent those living in the water 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.

Pathogens - High temperatures may decrease the enzymatic and phagocytic activities in bivalves, leading to less resistance to pathogens such as parasites (Longshaw and 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 (Loos-Frank, 1969; 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).

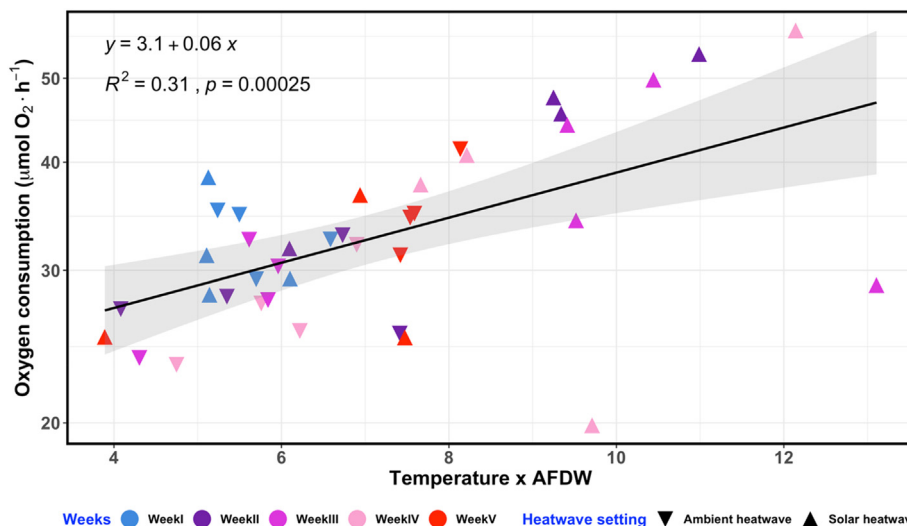


Fig. 6. The effects of the thermal stress on cockles' respiration rates. The gray shaded bar shows the 95% confidence intervals of the linear regression model. The product of temperature and AFDW was the independent variable, and oxygen consumption per hour was the dependent variable. The temperature 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.

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 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.

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 and 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 and 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 et al., 2018), cockles will have to adapt to the thermal stress or migrate to higher areas with lower mean temperatures.

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 (Cozzoli 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 and Sauriau, 2002) or deposit-feeding via moving up and down in the sediment (e.g., *Corophium volutator*) (Gerdol and Hughes, 1994). Besides, the shells of the benthic organisms can also have physical effects (i.e., corrosion 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; Cozzoli 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. 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).

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 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.

CRedit authorship contribution statement

Zhengquan Zhou: Conceptualization, Investigation, Methodology, Data curation and analysis, Visualization, Writing - original draft. Tjeerd J. Bouma: Conceptualization, Methodology, Visualization, Writing review and editing, Funding acquisition, Project administration. Gregory S. Fivash: Statistics, Data curation, Visualization, Writing review and editing, Language proof. Tom Ysebaert: Conceptualization, Investigation, Methodology, Writing review and editing. Lennart van IJzerloo: Investigation, Data curation, Software, Methodology. Jeroen van Dalen: Investigation, Methodology, Mesocosm realization. Ing. Bas van Dam: Software, Methodology. Brenda Walles: Conceptualization, Investigation, Methodology, Writing review and editing.

Declaration of competing interest

The authors have no conflicts of interest to disclose and have all approved this submission.

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Appendix 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

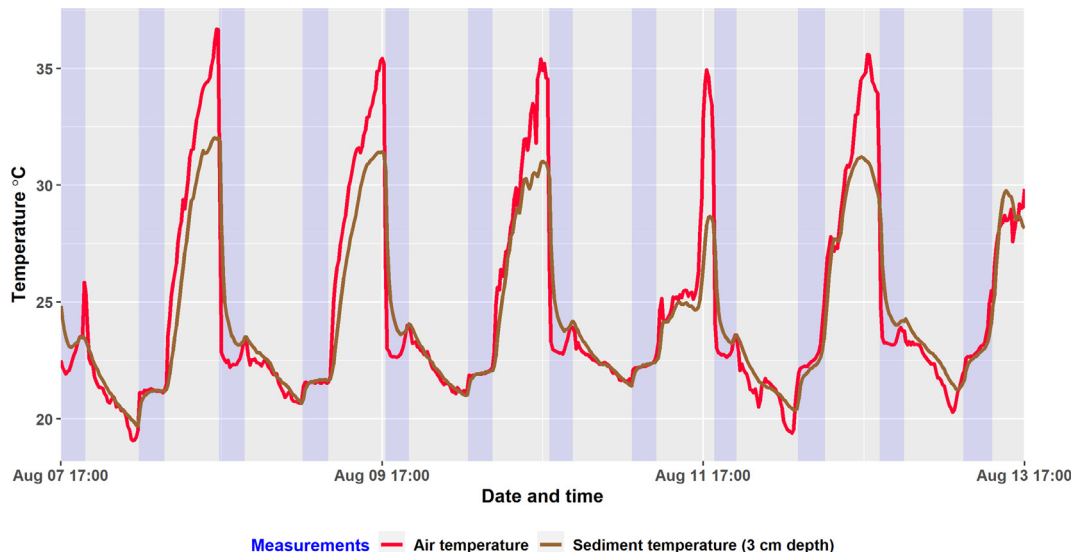


Fig. A1. Air and sediment temperature profiles during summer heatwaves 2021 at Paulina polder, Netherlands. The blue shades represent inundation during high tide, and gray shades for exposure time during low tide. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

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 μ m (top 1 cm).

Appendix 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. A2a). 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

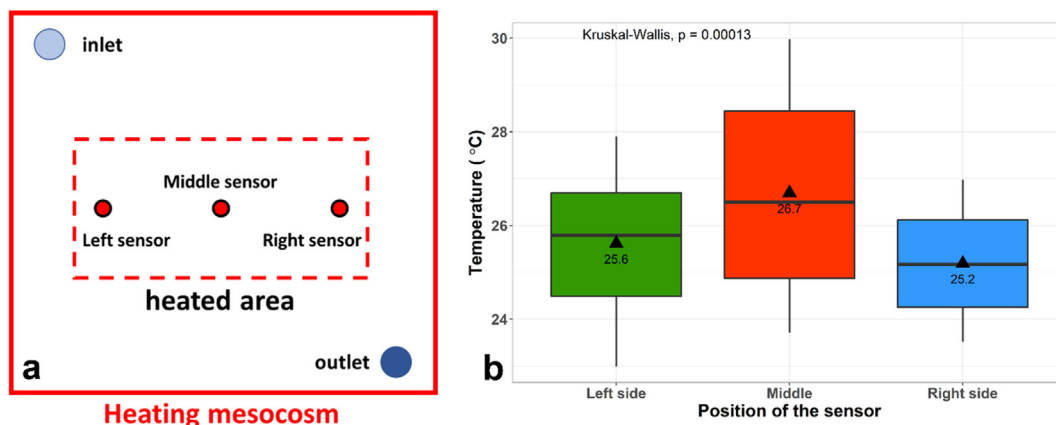


Fig. A2. A diagram of the functioning pilot test for the terrace heater. (a) The position of the temperature sensors for the pilot heating test. This diagram shows the top view of a mesocosm tank. The rectangular dashed line area is the vertical projection of the heater on the sediment surface. (b) The 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.

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. A2b).

Appendix 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).

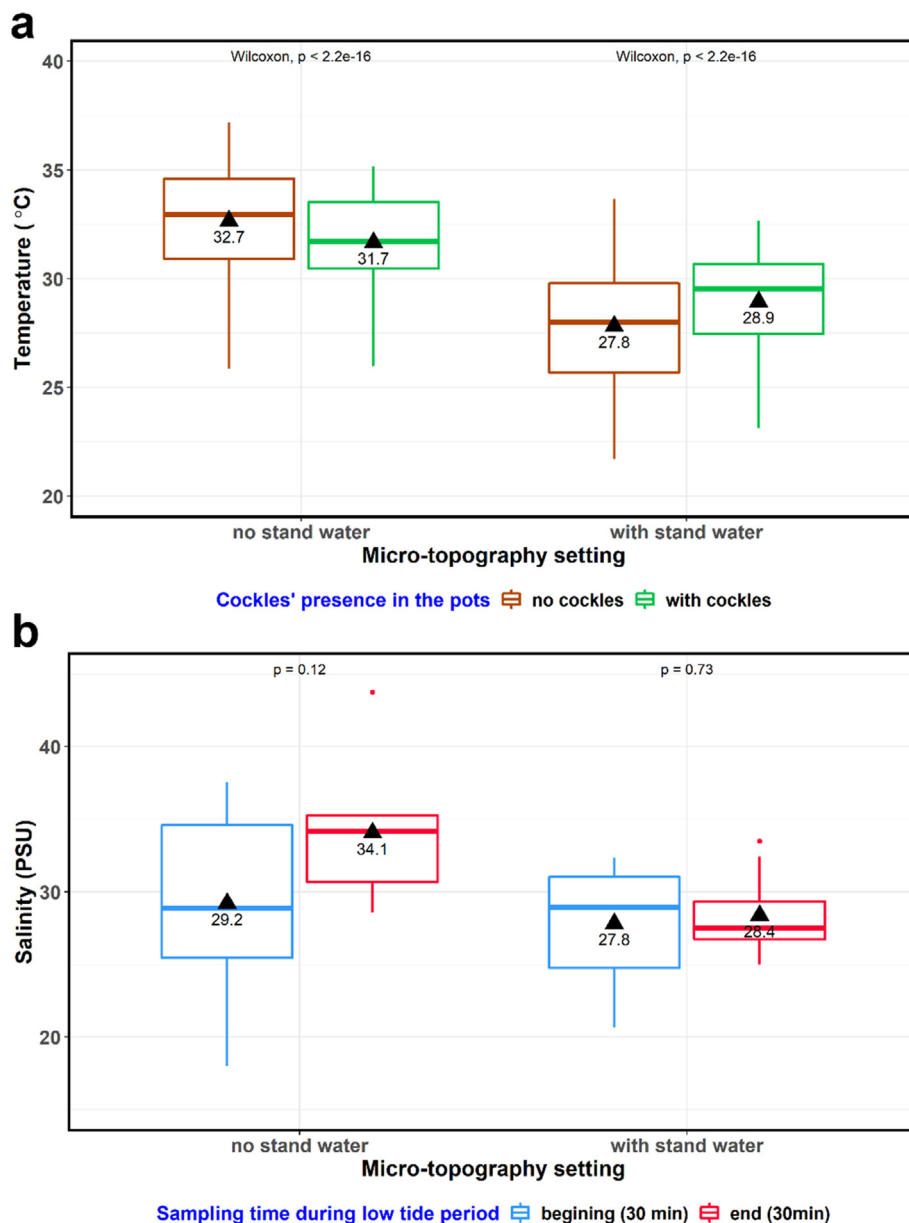


Fig. A3. Temperature and salinity change under the heat stress during low tide. (a) Temperature change at 4 cm depth of both topographies under the heat stress during low tide, with/without the presence of cockles. (b) The salinity change of pore water in sediments from both topographies, 30 min after the beginning and before the end of low tides.

Appendix 4. Cockles' survival rates during the experimental periods

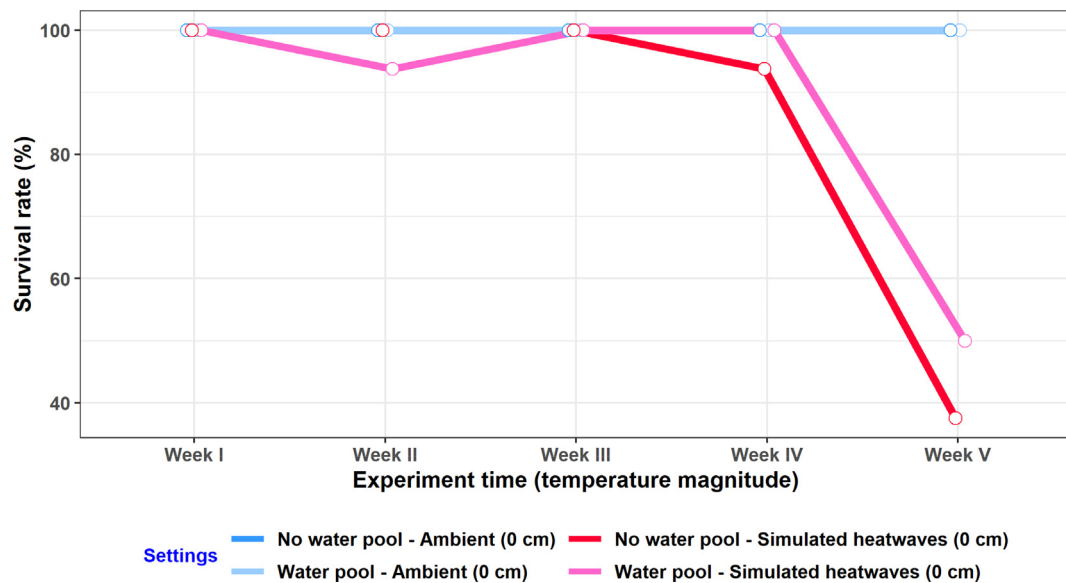


Fig. A4. The average survival rates observed for different heatwave regimes in the absence/presence of tidal water pools (i.e., representing contrasting tidal-flat topographies). The red lines (dark and light) represent the heatwave treatment. The blue lines (dark and light) represent ambient temperature treatment. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Appendix 5. Statistics of the linear mixed-effects model

Table 1
Linear mixed model fit statistics. The t-tests used Satterthwaite's method.

	Estimate	Std. Error	df	t-value	p (> t)	
(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
Type III Analysis of Variance with Satterthwaite's method.

	Sum Sq.	Mean Sq.	Num. DF.	Den. DF.	F-value	p (>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 $p < 0.05$.

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