

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

Lauren Wiesebron¹, Lilian Teeuw¹, Jeroen van Dalen¹, Lennart van Ijzerloo¹, Karin Troost², Brenda Walles², Tom Ysebaert^{1,2}, Tjeerd Bouma^{1,3,4}

¹Royal Netherlands Institute for Sea Research, Department of Estuarine and Delta Systems (EDS), Utrecht University, Yerseke, The Netherlands

²Wageningen University & Research, Yerseke, The Netherlands

³University of Applied Sciences, Vlissingen, The Netherlands

⁴Faculty of Geosciences, Utrecht University, Utrecht, The Netherlands

Abstract

Storm-induced erosion events may alter the diversity of tidal flat communities by selecting species that can better tolerate such disturbances. Introduced and invasive species are highly adaptable to a wide range of abiotic characteristics, and this adaptability may make them better able to withstand erosion events. With a novel flume method, we compared the ability of two bivalve species to resist storm-induced erosion: *Cerastoderma edule*, a native species to the Scheldt estuary in the Netherlands, and *Ruditapes philippinarum*, an introduced species that is successful in the Netherlands and worldwide. We used three sediment erosion rates to simulate storms of increasing severity. At the 10.6 and 15.9 cm h⁻¹ sediment erosion rates, all *R. philippinarum* were surfaced, whereas only half *C. edule* were surfaced. However, after being brought to the sediment surface, *C. edule* were more readily transported by currents and waves than *R. philippinarum* due to differences in their shell shape. We concluded that the two bivalve species had different strategies to avoid mortality by severe storm erosion: *C. edule* avoided being surfaced and *R. philippinarum* avoided being transported. In this case, it appears that extreme storms favor the specific adaptations of a native species over the broad adaptability of a non-indigenous one. Indeed, *C. edule* may be more likely to survive moderately extreme storms than *R. philippinarum*, though the most extreme storms would be equally devastating to both species.

Bivalves are key components of intertidal marine ecosystems: not only do they serve as food for many birds and fish (Hiddink et al. 2002; Bocher et al. 2014), but they also perform vital ecosystem services such as oxygenating the sediment and creating habitat for deeper living organisms (Thrush et al. 2006; Gray and Elliott 2009). Under daily hydrodynamic forcing, slow-moving adult bivalves are safe from erosion due to their size and burrowing depth (Yeo and Risk 1979; Hunt 2004). However, extreme storms can erode

10–15 cm of sediment on intertidal flats in a single event (see de Vet et al. 2020; Hu et al. 2015, 2017; Zhu et al. 2019), thereby not only threatening shallow-buried juvenile bivalves, but also adults. Severe storm-induced erosion can decrease macrofaunal abundances (de Vet et al. 2020), cause long-term community structural change (Ong and Krishnan 1995), and large bivalve mortality events (Rees et al. 1977; Yeo and Risk 1979; Cadée 2016; Shi et al. 2021). Indeed, exposure of bivalves to the sediment surface can increase the risk of mortality by predation (Hiddink and Wolff 2002), desiccation (Kurihara 2003), and transport to unfavorable habitat (Cadée 2016). In addition, the majority of storms in temperate regions occur in the autumn and winter which coincides with low temperatures and food scarcity that can send bivalve into a dormant, or quasi-hibernating, state (Newell and Bayne 1980). Bivalves in a dormant state have reduced mobility (Haider et al. 2020) which makes them even more vulnerable to storm-induced erosion than if they were actively able to burrow further down into the sediment. As the frequency and intensity of storms may increase with climate change (Stocker et al. 2014), they could shape

*Correspondence: lauren.wiesebron@nioz.nl

This is an open access article under the terms of the [Creative Commons Attribution](#) License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

Additional Supporting Information may be found in the online version of this article.

Author Contribution Statement: L.W., T.B., T.Y., and B.W. conceived of the study. L.T., J.v.D., and L.v.I. performed the stormy flume experiment. L.W. performed the racetrack flume experiment. K.T. contributed field data and suggested data interpretation. L.W. analyzed the data and wrote the first draft of the manuscript.

tidal flat communities by selecting for species that are less vulnerable to disturbances from storms.

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

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

While the spatial overlap between the two species is increasing in the Scheldt, studies have shown that *R. philippinarum* prefers habitat with less hydrodynamic forcing than *C. edule* (Bouma et al. 2001; Bidegain and Juanes 2013; Cozzoli et al. 2014). However, a habitat preference for lower hydrodynamic forcing does not necessarily translate to a lower tolerance toward rare extreme events of high hydrodynamic forcing, like storms. Indeed, invasive and introduced species can frequently tolerate a wide range of abiotic conditions (Lenz et al. 2011), and *R. philippinarum*

has demonstrated high physical tolerance to extreme temperature and salinity (Brusà et al. 2013) which can translate to lower mortality risk from non-environmental factors like predation (Domínguez et al. 2021b). The flexibility shown by *R. philippinarum* to other abiotic stressors may manifest in greater resilience to storm-induced erosion events than *C. edule*, despite its preference for a habitat with calmer hydrodynamics.

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

Methods

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

Manipulating sediment erosion rates is important to better understand bivalve vulnerability to storm-induced erosion, because storms do not all have the same intensity. As storms of higher intensity can induce larger volumes of sediment erosion than storms of a lower intensity (Hu et al. 2017; de Vet et al. 2020), the proportion of surfaced bivalves in a population is likely to increase with the intensity of a storm. We may also observe threshold effects, where once a certain sediment erosion rate is reached, all the individuals of a population are surfaced. Racetrack flumes have been used to study the erodibility of newly settled bivalves to great success (Hunt 2004;

Lundquist et al. 2004; St-Onge and Miron 2007), however, it is difficult to mimic extreme sediment erosion rates in a racetrack flume with a controlled intensity. For example, Hunt (2004) caused only 0.5–1 cm of erosion using a racetrack flume, whereas we wished to be able to mimic intense storms where much larger volumes of sediment can be quickly eroded (5–15 cm, cf. de Vet et al. 2020; Hu et al. 2017). In our experiment, we used a custom-made flume (Fig. 1a,b) where we could control the sediment erosion rate precisely, which was ideal for examining the effects of varying intensity of storm-induced erosion on adult bivalve erodibility.

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

We used three sediment erosion rates to simulate different levels of storm intensity: 5.3, 10.6, and 15.9 cm h^{-1} . The final erosion rate represents the upper limit of storms that we have observed in the Scheldt estuary in the past 30 years (Hu et al. 2017; de Vet et al. 2020). By using three different sediment erosion rates, we could test whether there was an interaction between erosion rate and species on bivalve erodibility.

Bivalve collection and experimental set-up

We collected at least 50 adults per species between 25 and 35 mm in length at Oesterdam, a sandy site in the Eastern Scheldt (51.46670, 4.22139), on a biweekly basis. Because their shell morphologies were different, we selected *R. philippinarum* and *C. edule* that had the same dry weight (shell and flesh mean: 5.2 g and SD: 1.2 g) instead of the same shell length. *R. philippinarum* had a greater shell length than *C. edule* (mean: 30.9 mm and SD: 2.4 mm vs. mean: 28.1 mm and SD: 2.1 mm), but *C. edule* had a greater shell width and height than *R. philippinarum* (*C. edule* shell width mean: 25.5 mm and SD: 1.4 mm vs. *R. philippinarum* mean: 23.2 mm and SD: 1.9 mm, and *C. edule* shell height mean: 21.1 mm and SD: 1.5 mm vs. *R. philippinarum* mean: 17.0 mm and SD:

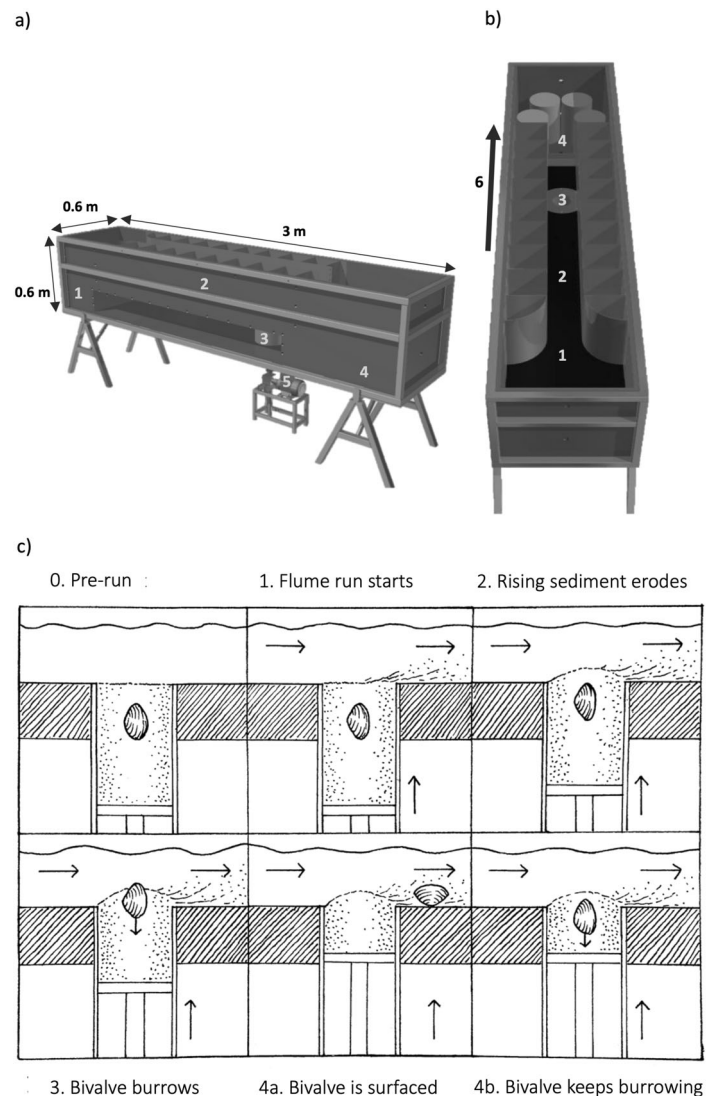


Fig. 1. Schematic of the storm erosion flume showing (a) the exterior, (b) top view with: (1) front basin and cooling system; (2) flume channel; (3) sediment core; (4) back basin, pumps, and circulation tubes; (5) cart with pneumatic piston to raise the sediment core; (6) direction of water through flume channel. The water flows through the main channel (2) of the flume, over the sediment core (3), and is then circulated back with tubes running beneath the main channel. A constant water flow of 40 cm s^{-1} was generated by three pumps at the end back basin of the flume (4). A Lauda WKL 3200 recirculating chiller with a stainless-steel cooling spiral was used to counteract the heating of the water by the pumps (1). (c) A schematic drawing showing the functioning of the flume during a run to test the erodibility of a bivalve. The sediment core is pushed upwards into the 40 cm s^{-1} water flow (Panels 1, 2, 3). As the sediment overlying the bivalve is eroded (Panel 2), the bivalve needs to burrow down into the sediment to escape being surfaced (Panel 3). The speed of sediment erosion is determined by the upwards movement of the sediment. If the bivalve's burrowing speed is slower than the upwards movement of the sediment core the bivalve is surfaced (Panel 4a). If the bivalve is faster, it remains burrowed (Panel 4b). The run ends when the bivalve is surfaced or after 60 min.

1.7 mm). The narrow size range ensured that there was no size effect on erodibility. The bivalves were stored in baskets in tidal tanks in a climate-controlled room with an air temperature of 9°C, for at least a week to ensure acclimatization to laboratory conditions before being used in the experiments. This temperature was chosen to mimic the mean November and December air temperature. Each tidal tank system was composed of two 1.2 × 0.8 m tanks stacked on top of each other (Cao et al. 2018). Unfiltered water from the Eastern Scheldt estuary, which has a salinity of 31 ppt, was pumped from the bottom tank up to the top tank to simulate tidal conditions. High tide conditions (5 cm water above experimental units) lasted 6 h and occurred twice a day. High tide was imposed by pumping water to the higher basin, using a free-fall overflow system for the return flow. The latter kept the water well-oxygenated. The water temperature in the tidal tanks was around 9°C in November 2019 and around 7.5°C in January 2020 when the experiment ended, which was 1–2° warmer than the water in the Scheldt. There was no sand in the tidal tanks and the bivalves were kept in baskets, with around 30 individuals per basket. We changed the water once a week. Since the bivalves are filter feeders, we fed them with an algal concentrate (Shellfish Diet from Reed Mariculture) 5 mL per tank twice per week to supplement the food contained in the raw Eastern Scheldt water.

The day before the experiment, we selected 12 individuals randomly from the two species (six per species). The 12 individuals were placed on top of 12 cores to burrow. Each core was made from a sawed-off PVC pipe (30 cm length, 11.5 cm width) with a removable bottom cap, and was filled to 10 cm below the rim. We filled the experimental cores with a single sediment which had a comparable grain size distribution to the sediments from the collection location at the Oesterdam. The Oesterdam sediment had an average grain size ranging between 250 and 270 μm and the sediment used in the experiments had an average grain size of 246 μm. The field and experimental sediments mainly consisted of medium (250–500 μm; 40%–45%) and fine (125–500 μm; 40%–60%) sand. The 12 cores were kept in a tidal tank in the same mesocosm room that the bivalves were stored and set to the same tidal cycle as the other tanks. The morning after placing the 12 bivalves (six per species) on top of the 12 cores, we checked the dormancy of the bivalves by noting if any had remained lying on the sediment surface. We then selected one core that had a burrowed (i.e., active) individual for each flume run (maximum three flume runs a day).

Estimating species-specific dormancy rates

We monitored the proportion of dormant individuals in our collected bivalve populations from November 2019 to January 2020 because we were interested in whether winter-induced dormancy would impact the erodibility of the bivalves. We considered “dormancy” the hibernation state that bivalves can enter in cold winter conditions (Newell and Bayne 1980) when it may experience food scarcity and even starvation (Haider

et al. 2020). The state that we call dormancy throughout the paper can also be caused by environmental stressors, like hypoxia (Storey and Storey 1990). It is characterized by low metabolic activity (Haider et al. 2020), thus dormant bivalves stayed on top of the sediment and did not burrow. *C. edule* are also known to have their burrowing capacity inhibited by parasites, but as infected *C. edule* are usually found on top of the sediment in the field (Thieltges 2006), we hopefully avoided infected cockles by only collecting burrowed individuals. It is also possible that the dormant state was partly a response to the stress of acclimation to the mesocosm environment. Whatever the cause, we kept track of the number of *C. edule* and *R. philippinarum* that were dormant over the season. As we only used burrowed individuals for our flume experiments, dormancy did not impact our experiments. However, dormancy could impact the erodibility of bivalve populations in the field, as dormant bivalves may be passively surfaced by a storm by being unable to escape erosion by digging.

To track the proportion of dormant individuals, on the mornings of days we conducted flume experiments we counted the number of unburrowed individuals out of the 12 individuals (six per species) that were laid out on cores 24 h prior. Because we collected new bivalves every 2 weeks, this allowed us to better understand if dormancy changed over the course of the late fall-early winter season (12 November 2019 to 15 January 2020). Please see Supplementary Table S1 for the dates that we checked bivalves for dormancy.

Storm erosion flume runs with increasing intensity of sediment erosion

Experiments were conducted in the custom-made flume (Fig. 1a,b). The flume was filled with seawater to a height of 15 cm, which minimized turbulence within the flume. During each run the current velocity was 0.40 m s⁻¹. In addition, the water used in the flume was chilled overnight in 1000 L tank to a temperature of 3–5°C before being used to simulate winter water temperatures. While we acclimated the bivalves to the flume conditions for 30 min before each run, the bivalves may have experienced some shock due to the water temperature difference between the tidal tanks (7.5–9°C) and the flume environment (3–5°C), which may have affected their ability to burrow into the sediment.

We performed 50 flume runs (25 *C. edule* and 25 *R. philippinarum*) over the course of 6 weeks (See Tables S1 and S2 for a summary of the dates and number of bivalves used during flume runs). During each run, a sediment core containing a single bivalve was used. We conducted three trial types with three sediment erosion rates: 5.3 cm h⁻¹ (10 single-individual runs per species), 10.6 cm h⁻¹ (eight single-individual runs per species), and 15.9 cm h⁻¹ (seven single-individual runs per species). We could perform a maximum of three runs per day because we needed to drain and refill the flume chamber from the chilled water storage tank after every run to minimize warming of the water due to

pump friction. The run ended after 60 min had elapsed or when a bivalve was transported outside of the core. A bivalve was considered to be surfaced when it was completely exposed on top of the sediment. The flume runs were recorded with a camera to assess bivalve behavior within the flume and confirm the time of erosion. We retrieved the bivalve after the run was complete for morphological measurements.

Racetrack flume runs to measure bivalve transport speed once surfaced

To gain a better understanding of whether the fate of the bivalves may be different once surfaced, we measured the transport speed for both species under currents and waves. We used the NIOZ racetrack flume, a large flow channel (17.5 m length, 3.25 m width) where waves and a constant unidirectional flow of up to 0.60 m s⁻¹ can be generated. We inserted a 30-cm-wide × 40-cm-long × 10-cm-deep bed of sand in the test section, which we flattened in between runs. Before each run, we deposited six bivalves (three of each species) in a line perpendicular to the current on top of the sand. We performed separate trials to test the effects of current speed and increasing wave height on bivalve transport. We used four levels of current velocity (i.e., 0.089, 0.114, 0.135, and 0.168 m s⁻¹) and four levels of wave height with a constant underlying current velocity of 0.089 m s⁻¹ (i.e., 3.6, 5, 5.6, and 6.4 cm). We used six new bivalves (three per species) for each run, and performed two runs per current speed or wave height setting. During each flume run, we measured the speed at which the bivalves were transported across the sand.

Statistical analysis

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

Our model was as follows:

$$\text{Surfacing}_i \sim \text{Binomial}(p_i)$$

$$p_i = \frac{e^{\beta_0 + \text{ErosionRate}_i \times \text{Species}_i + \text{Date}_i + \text{WaterTemperature}_i}}{1 + e^{\beta_0 + \text{ErosionRate}_i \times \text{Species}_i + \text{Date}_i + \text{WaterTemperature}_i}} \quad (1)$$

where Surfacing_{*i*} is *i*th observation of surfacing, *p_i* is the probability of surfacing occurring, and β₀ is the model intercept.

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

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

$$\begin{aligned} \text{Transport}(y=0)_i &\sim \text{Binomial}(p_i) \\ p_i &= \frac{e^{\beta_0 + \text{CurrentOrWaves}_i + \text{Species}_i}}{1 + e^{\beta_0 + \text{CurrentOrWaves}_i + \text{Species}_i}} \\ \text{Transport}(y>0)_i &\sim \text{Lognormal}(\mu_i) \\ \mu_i &= e^{\beta_0 + \text{CurrentOrWaves}_i + \text{Species}_i} \\ E(\text{Transport}_i) &= (1 - p_i) \times \mu_i \end{aligned} \quad (2)$$

where Transport(*y*=0)_{*i*} is the *i*th observation of untransported bivalves and Transport(*y*>0)_{*i*} is the *i*th observation of transported bivalves, and *E*(Transport_{*i*}) is the expected mean of the lognormal hurdle model of bivalve transport speed. CurrentOrWaves was the current speed in the model for experiments where the flow rate in the flume increased without waves, and CurrentOrWaves was wave height in the model for experiments where the wave increased and the flow was fixed at 0.089 m s⁻¹.

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

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

Table 1. Model formula (Model), coefficients (Coef.), standard errors (Std. Error), confidence intervals for the coefficient (2.5% and 97.5%), test statistics (Test Stat.), and *p* values (*p*) for the intercept and covariates. We present models of bivalve surfacing, dormancy, surfacing time, and transport in current and waves. The transport models have two parts: the first part is a logistic regression describing the probability that a bivalve remains untransported (transport, $y = 0$) and the second part describes the speed of the transported bivalve (transport, $y > 0$). For all models, we indicate in the model formula if the generalized linear model required a link (either "logit" or "log") function. The test statistic for the logistic regressions was Wald's χ^2 statistic and for the lognormal and normal Megressions was a *t*-statistic. We present the test statistic along with its associated degrees of freedom (df). In all models, "species" is a categorical variable and modifies the model intercept when significant. The reference level for the "species" covariate is *R. philippinarum*, which means that model predictions for *R. philippinarum* include the model intercept without modification from the "species" coefficient. The intercept for model predictions for *C. edule* are modified with the "species" coefficient.

Model	Response	Covariate	Coef.	Std. Error	2.5%	97.5%	Test Stat.	<i>p</i>
Logit (surfacing) ~ intercept + sediment erosion rate × species + water temperature + date								
	Surfacing	Intercept	4.01	3.37	−2.61	11.00	1.40 (df=1)	0.75
		Sediment erosion rate	0.63	0.22	0.28	1.20	8.00 (df=1)	0.005
		Species	−6.00	1.95	−10.95	−3.02	9.40 (df=1)	0.002
		Water temperature	−1.58	0.86	−3.48	−0.02	3.40 (df=1)	0.06
		Date	−0.02	0.06	−0.13	0.09	0.081 (df=1)	0.78
Logit (dormancy) ~ intercept + sediment erosion rate + species × date								
	Dormancy	Intercept	−1.00	0.30	−1.63	−0.49	13.1 (df=1)	<0.001
		Species	−2.20	0.60	3.52	−1.1	13.5 (df=1)	<0.001
		Date	0	0	0	0.006	1.40 (df=1)	0.23
		Species×date	0.03	0.02	0	0.05	3.80 (df=1)	0.04
(Surfacing time) ~ intercept + sediment erosion rate + species + water temperature + date								
	Surfacing time	Intercept	37.81	14.98	−2.61	11.00	2.52 (df=19)	0.02
		Sediment erosion rate	−1.07	0.47	0.28	1.20	−2.28 (df=19)	0.03
		Species	1.53	4.69	−10.95	−3.02	0.37 (df=19)	0.74
		Water temperature	−2.13	3.19	−3.48	−0.02	−0.66 (df=19)	0.51
		Date	−0.03	0.22			−0.13 (df=19)	0.89
Logit (transport, $y = 0$) ~ intercept + current speed + species								
	Transport, $y = 0$	Intercept	−15.79	4.29	−26.19	−8.93	10.60 (df=1)	0.001
		Current speed	97.07	27.05	53.38	162.02	10.30 (df=1)	0.001
		Species	3.78	1.18	1.81	6.59	6.60 (df=1)	0.01
Log (transport, $y > 0$) ~ intercept + current speed + species								
	Transport, $y > 0$	Intercept	−8.61	3.01	−11.75	−5.59	−5.52 (df=15)	<0.001
		Current speed	58.49	19.77	38.62	78.46	5.76 (df=15)	<0.001
		Species	2.39	0.73	2.11	3.35	8.62 (df=15)	<0.001
Logit (transport, $y = 0$) ~ intercept + wave height + species								
	Transport, $y = 0$	Intercept	−13.41	4.62	−24.97	−6.19	8.4 (df=1)	0.004
		Wave height	2.39	0.82	1.10	4.42	8.6 (df=1)	0.003
		Species	5.37	1.78	2.65	9.86	9.1 (df=1)	0.002
Log (transport, $y > 0$) ~ intercept + wave height + species								
	Transport, $y > 0$	Intercept	−7.04	1.35	−9.78	−4.29	−5.21 (df=28)	<0.001
		Wave height	1.19	0.22	0.75	1.64	5.43 (df=28)	<0.001
		Species	1.61	0.38	0.83	2.38	4.2 (df=28)	<0.001

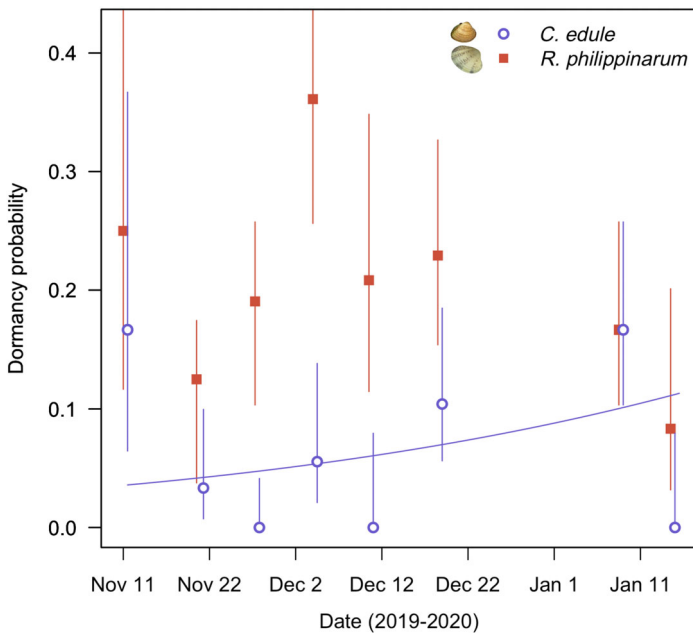


Fig. 2. The probability of dormancy for *C. edule* (circles) and *R. philippinarum* (squares) as a function of days since the beginning of the experiment (12 November 2019) until the end of the experiment (15 January 2020). We observed the dormancy of 12 individuals (six per species) each day that we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

Lancelot 2012) and “binom” (Dorai-Raj 2014). See Table 1 for details on model fits.

Results

Species and seasonal effects on dormancy

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

Species and sediment erosion rate effects on bivalve surfacing

R. philippinarum (84% surfaced on average) were more easily surfaced than *C. edule* (28% surfaced on average) (Fig. 3). For both species, the surfacing probability of the individuals increased with the sediment erosion rate (Wald $\chi^2(1) = 8$, $p = 0.005$). In fact, all *R. philippinarum* were surfaced at the two highest erosion rates and 60% were surfaced at the slowest one (5.3 cm h⁻¹). On the other hand, no *C. edule* were surfaced at the 5.3 cm h⁻¹ speed, but 25% were surfaced at

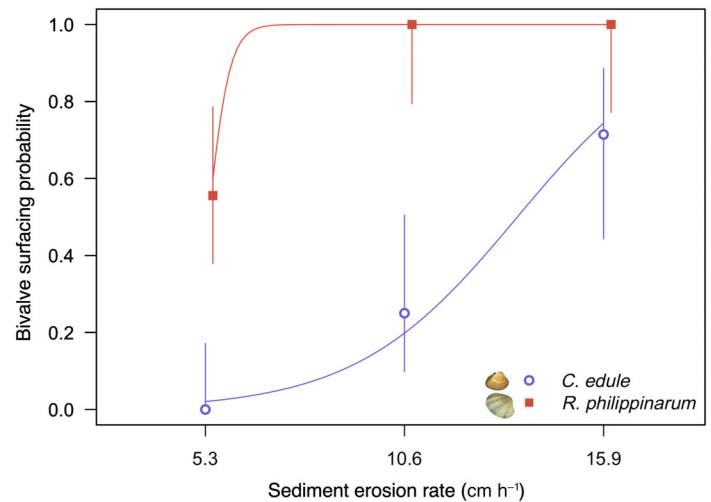


Fig. 3. The surfacing probability (fitted lines) of *C. edule* (circles) and *R. philippinarum* (squares) as a function of sediment erosion rate, with 0 = no individuals surfaced and 1 = all individuals surfaced. We tested bivalve erodibility at three different sediment erosion rates: 5.3, 10.6, and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

the 10.6 cm h⁻¹ erosion rate and 71% were surfaced at the 15.9 cm h⁻¹ erosion rate. We observed active burrowing behavior in all bivalves used in the flume.

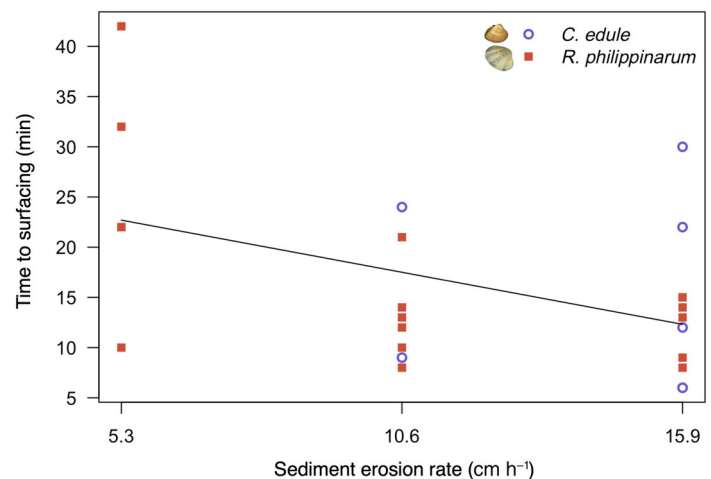


Fig. 4. Time (minutes) elapsed in the flume until bivalve surfacing as a function of sediment erosion rate (cm h⁻¹) and species: *C. edule* (circles) and *R. philippinarum* (squares). We tested bivalve erodibility in the flume at three different sediment erosion rates: 5.3, 10.6, and 15.9 cm h⁻¹. In this linear regression, we treated erosion rate as a continuous variable. The line represents the model fit ($y = 27.9 - 0.9x$, $R^2 = 0.21$). Please note that there were no *C. edule* that were surfaced at an erosion rate of 5.3 cm h⁻¹ and that the total number of *C. edule* that were surfaced was low, especially at an erosion rate of 10.6 cm h⁻¹ ($n = 2$). As these non-surfacing animals could obviously not be included in this analyses, our statistical power for detecting a species effect on the surfacing time was low.

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

Bivalve transport speed

Once at the sediment surface, *C. edule* were transported faster than *R. philippinarum* ($\sim 11 \times$ faster transport as a function of currents $t(15) = 8.62$, $p < 0.001$ and $\sim 5 \times$ faster transport as a function of wave height with an underlying current speed of 0.089 m s⁻¹, $t(28) = 4.23$, $p < 0.001$) and had lower entrainment velocity (fluid velocity that causes initiation of bivalve movement) than *R. philippinarum* (Fig. 5). For example, at a current velocity of 0.168 m s⁻¹, transported *C. edule* had a speed of 3.7×10^{-2} m s⁻¹ whereas transported *R. philippinarum* had a speed of 3.3×10^{-3} m s⁻¹. Furthermore, *C. edule* initiated movement at a current speed of 0.135 m s⁻¹ (no waves) and a wave height of 3.6 cm with an underlying current speed of 0.089 m s⁻¹, whereas *R. philippinarum* initiated movement at a greater current speed (0.168 m s⁻¹ with no waves) wave height of 5.6 cm, again with an underlying current speed of 0.089 m s⁻¹ (Fig. 5). In addition, a greater proportion of

C. edule were transported than *R. philippinarum* at a same wave height or current speed (Wald's $\chi^2(1) = 6.6$ for current and 9.1 for waves, $p \leq 0.01$ for both). For example, at a wave height of 5.6 cm, 100% of *C. edule* were transported, whereas 50% of *R. philippinarum* were transported. We observed *R. philippinarum* sliding across the sand, whereas *C. edule* rolled.

Discussion

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

Contextualizing the experiments in the natural setting

While our experiments offer insight into the response of bivalves to extreme sediment erosion, it is very challenging to predict when and where these events occur in a natural setting. This is because the occurrence of extreme erosion events is the result of the combination of different time- and space-varying processes (e.g., waves, tidal flow, wind-driven flow, and sediment strength) that determine the potential for sudden bed-level changes (Fan et al. 2006; Zhu et al. 2019; de Vet et al. 2020). In addition, the storm's timing in relation to the tidal cycle, and thus the depth of the water column (Shi et al. 2017), is very important for determining a storm's impact (de Vet et al. 2020). And so, the return time of an extreme erosion event is difficult to determine. In addition, the largest bed-level changes occur during a short fraction of the tidal period. For example, a 2014 storm in the Western Scheldt caused 12 cm of erosion, but only when the water was shallow which was 20% of the tidal cycle, with no erosion occurring during the other 80% (Zhu et al. 2019). This means that though a storm may last several days, the sudden erosion of the tidal flat and transport of benthic macrofauna may occur in short bursts spread over a single or several tidal cycles. Furthermore, storm impacts are extremely spatially heterogenous. During a 2016 storm in the Western Scheldt, points that experienced ~ 20 cm and ~ 0.5 cm of sudden erosion were separated by only 300 m (de Vet et al. 2020). Typically, the lowest parts of tidal flats have a higher occurrence of extreme erosion than the highest parts of tidal flats. For

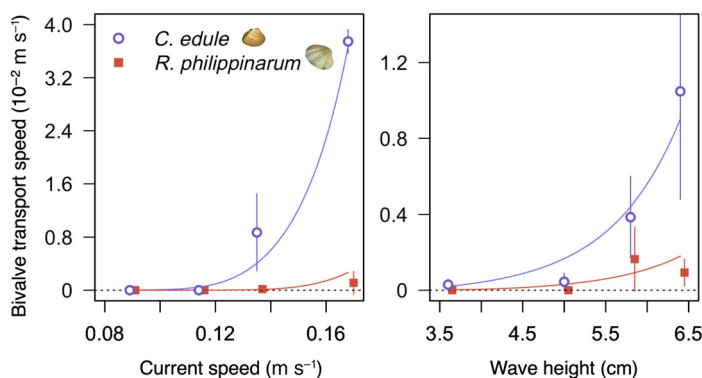


Fig. 5. The transport speed of bivalves *C. edule* (circles) and *R. philippinarum* (squares) in the racetrack flume with (left) increasing current speed and no waves and (right) increasing wave height at a current speed of 0.089 m s⁻¹. The line represents the model fit and the circles represent the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

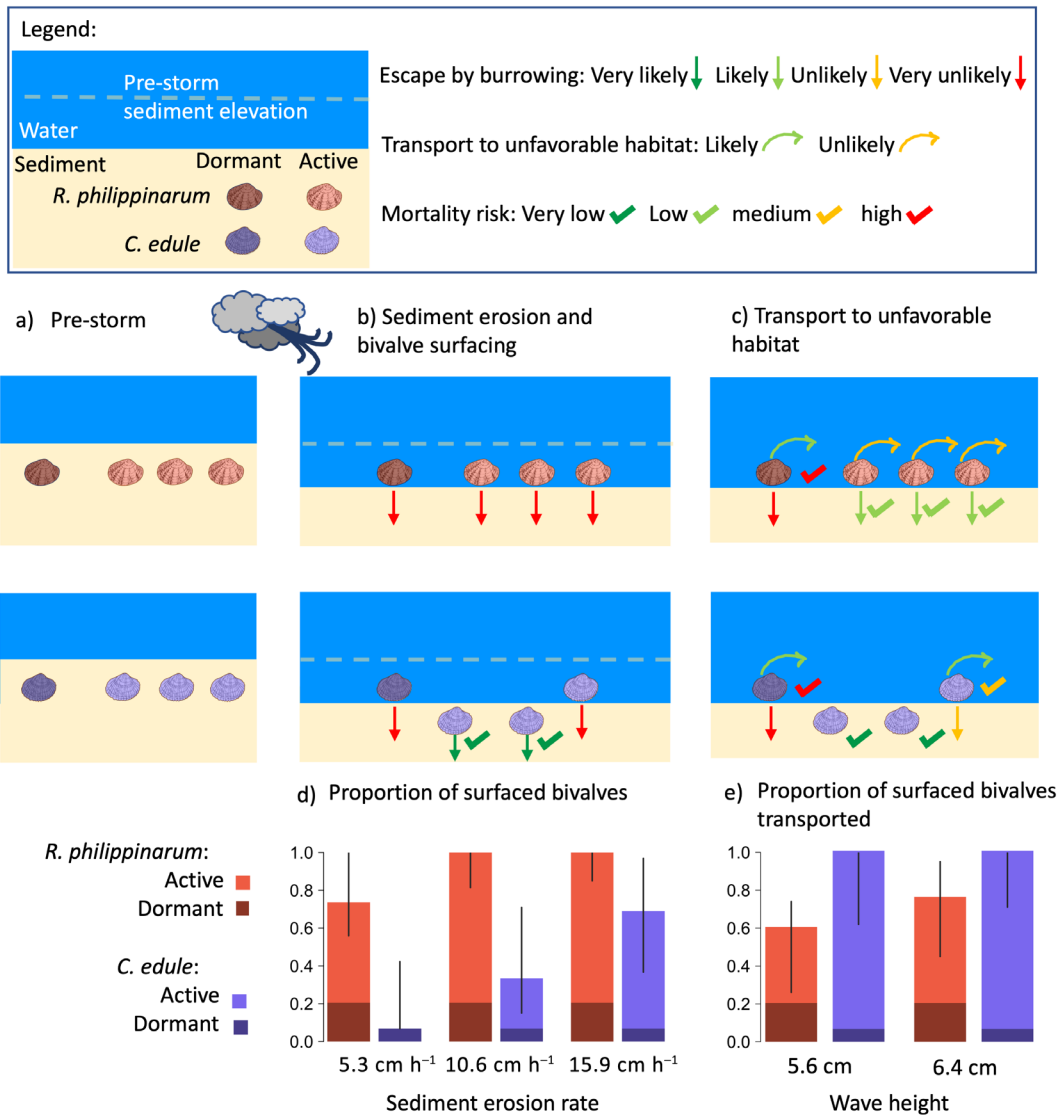


Fig. 6. Schematic overview figure showing the mortality risk vectors for (a) active and dormant *C. edule* and *R. philippinarum* during a severe storm by (b) avoiding surfacing due to sediment erosion and (c) escaping transport to unfavorable habitat due to waves, as well as the associated proportions of the experimental population that were surfaced by (d) different sediment erosion rates (5.3, 10.6, and 15.9 cm h⁻¹) and were transported by (e) different wave heights (5.6 and 6.4 cm). Please note that in (d) and (e), the experiments were performed using active bivalves; we assume that all dormant bivalves (percentages shown in (d) and (e) are derived from our observations during experiments) would be surfaced and transported as they have a reduced capacity to reburrow into the sediment. In (d) and (e), the whiskers depict the 95% confidence intervals. This figure is a schematized conceptualization of the species-specific mortality risk vectors based solely on our experiments and more research is necessary to improve our understanding of the bivalves' response to extreme sediment erosion.

example, the 2014 storm described by Zhu et al. 2019 provoked ~ 12 cm of erosion at a tidal flat in the Western Scheldt at -1.25-m NAP but produced only ~ 1 cm of erosion at - 0.25-m NAP, due to differences in the water depth during the storm. In summary, it is very difficult to predict when and where extreme erosion events with similar magnitudes as those we used in the flume would occur in the field. Nevertheless, given the upcoming increase in the frequency and magnitude of these storm events due to climate change (Stocker et al. 2014), insight into bivalves' capacity to cope with

extreme sediment erosion will help us better predict the impacts of increasingly frequent storms on the benthic community.

It is important to note that our experiments approximated extreme events where erosion occurs relatively gradually, over hours. For example, our experimental set-up is comparable to the hydrodynamic conditions during an extreme erosion event described in de Vet et al. (2020): 20 cm of erosion at an intertidal flat at the Western Scheldt occurred during a severe storm within a 3 h window, indicating that the average

erosion rate should be around 6.7 cm h^{-1} . This falls exactly between the lowest and middle erosion rates that we mimicked in the flume, but is a factor 2.4 lower than the most severe erosion rate we mimicked 15.9 cm h^{-1} . However, the comparison holds only if we assume relatively gradual and constant erosion during the storm. In reality, the peak erosion rate may occur within an hour or less. Unfortunately, there is a lack of detailed field data about the precise window in which extreme erosion occurs, due to data collection challenges from shallow water and extreme turbidity which can interfere with instrument recording during extreme conditions. The shorter the timeslot during which extreme erosion happens, the higher the chance that macrofauna may not be able to escape being surfaced and transported.

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

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

Our results revealed that the two studied species have different strategies for surviving extreme sediment erosion due to severe storm events: *C. edule* avoided surfacing and *R. philippinarum* avoided transport. Because *R. philippinarum* was far more easily surfaced than *C. edule* (Fig. 3), one may conclude that an *R. philippinarum* population would experience greater mortality from extreme storm events than a *C. edule* population. However, this is not necessarily the case.

Mortality due to storm-induced erosion is not caused by the erosion itself, but is indirectly caused by predation (Hiddink and Wolff 2002), desiccation (Kurihara 2003), and transport to unfavorable habitat (Cadée 2016). For any of these three vectors of mortality to occur, the animal must first be brought to the sediment surface (Fig. 6b,c). But, once the bivalve is brought to the surface, mortality is not an automatic outcome: a bivalve will survive provided it can avoid being transported to unfavorable habitat and can reburrow fast enough to prevent predation and desiccation.

By using our experimental results, we inferred that *C. edule* would have lower mortality due to storm-induced erosion events in the Scheldt estuary than *R. philippinarum* during storms with conditions similar to those we simulated in the 5.3 and 10.6 cm h^{-1} erosion rates, but the gap in mortality between the two species narrows in more extreme conditions, like under the 15.9 cm h^{-1} erosion rate (Fig. 6). We present our reasoning as follows: during extremes storms of a relatively moderate magnitude (5.3 cm h^{-1} of sediment erosion), no active *C. edule* will be surfaced while many active *R. philippinarum* (60% on average) will be surfaced (Fig. 6a,b). A portion of the active and surfaced *R. philippinarum* would be at risk of mortality (if 50% transported, as with a wave height of 5.6 cm (Fig. 6e), then $60\% \text{ active } R. philippinarum \text{ surfaced} \times \sim 50\% \text{ transported} = \sim 30\% \text{ total active } R. philippinarum \text{ at risk of mortality}$), whereas no active *C. edule* would be at risk for mortality because they are safely burrowed. In addition, the populations will experience mortality from the dormant portion (in our experiments, we found $\sim 20\%$ for *R. philippinarum*, $\sim 7\%$ *C. edule*; however, this percentage may be different in the field as some of the dormancy we observed could be caused by mesocosm stress), whose reduced burrowing capacity would make escape from mortality due to predation, desiccation, or transport unlikely (Fig. 6b,c). Because a much greater proportion of active *R. philippinarum* would be surfaced and experience a higher incidence of dormancy than *C. edule*, we can estimate that *R. philippinarum*'s mortality risk would be greater than *C. edule*'s due under these conditions.

On the other hand, in even more extreme conditions with a 15.9 cm h^{-1} sediment erosion rate, active *C. edule* would be surfaced, though in a smaller proportion to *R. philippinarum* (71% vs. 100% , Fig. 6b). However, out of the surfaced fraction, a higher proportion of *C. edule* would be transported than *R. philippinarum* (estimated $\sim 100\%$ vs. $\sim 70\%$ with a wave height of 6.4 cm , Fig. 6e), resulting in a more similar fraction of mortality risk for the two populations ($71\% \text{ active } C. edule \text{ surfaced} \times \sim 100\% \text{ transported} = \sim 71\% \text{ total active } C. edule \text{ at risk for mortality}$, and $100\% \text{ active } R. philippinarum \text{ surfaced} \times \sim 70\% \text{ transported} = \sim 70\% \text{ total active } R. philippinarum \text{ at risk for mortality}$). These estimates would change with additional mortality from dormant bivalves, which would almost certainly die from being surfaced. In conclusion, storms causing a sediment erosion rate of 15.9 cm h^{-1} may be equally devastating to populations of both bivalve

species, while storms of a lower erosion intensity, like 10.6 cm h^{-1} , may be more devastating for *R. philippinarum* populations than *C. edule* ones.

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

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

The relevance of specific adaptations vs. broad adaptability: an outlook

The introduced species always outperforms the native species when the changing environment favors the adaptability

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

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

Conclusion

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

Data availability statement

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

References

- Anta, J., E. Peña, J. Puertas, and L. Cea. 2013. A bedload transport equation for the *Cerastoderma edule* cockle. *J. Mar. Syst.* **111–112**: 189–195. doi:10.1016/j.jmarsys.2012.10.014
- Barry, J. 1989. Reproductive response of a marine annelid to winter storms: An analog to fire adaptation in plants? *Mar. Ecol. Prog. Ser.* **54**: 99–107. doi:10.3354/meps054099
- Bates, A. E., C. M. McKelvie, C. J. B. Sorte, S. A. Morley, N. A. R. Jones, J. A. Mondon, T. J. Bird, and G. Quinn. 2013. Geographical range, heat tolerance and invasion success in aquatic species. *Proc. Roy. Soc. B: Biol. Sci.* **280**: 20131958. doi:10.1098/rspb.2013.1958
- Beukema, J. J., R. Dekker, and J. Drent. 2017. Dynamics of a *Limecola (Macoma) balthica* population in a tidal flat area in the western Wadden Sea: Effects of declining survival and recruitment. *Helgol. Mar. Res.* **71**: 18. doi:10.1186/s10152-017-0498-7
- Bidegain, G., and J. A. Juanes. 2013. Does expansion of the introduced Manila clam *Ruditapes philippinarum* cause competitive displacement of the European native clam *Ruditapes decussatus*? *J. Exp. Mar. Biol. Ecol.* **445**: 44–52. doi:10.1016/j.jembe.2013.04.005
- Bielen, A., and others. 2016. Differences in tolerance to anthropogenic stress between invasive and native bivalves. *Sci. Total Environ.* **543**: 449–459. doi:10.1016/j.scitotenv.2015.11.049
- Bocher, P., F. Robin, J. Kojadinovic, P. Delaporte, P. Rousseau, C. Dupuy, and P. Bustamante. 2014. Trophic resource partitioning within a shorebird community feeding on intertidal mudflat habitats. *J. Sea Res.* **92**: 115–124. doi:10.1016/j.seares.2014.02.011
- Bouma, H., J. M. C. Duiker, P. P. de Vries, P. M. J. Herman, and W. J. Wolff. 2001. Spatial pattern of early recruitment of *Macoma balthica* (L.) and *Cerastoderma edule* (L.) in relation to sediment dynamics on a highly dynamic intertidal sandflat. *J. Sea Res.* **45**: 79–93. doi:10.1016/S1385-1101(01)00054-5
- Brusà, R. B., F. Cacciatore, E. Ponis, E. Molin, and E. Delaney. 2013. Clam culture in the Venice lagoon: Stock assessment of Manila clam (*Venerupis philippinarum*) populations at a nursery site and management proposals to increase clam farming sustainability. *Aquat. Living Resour.* **26**: 1–10. doi:10.1051/alr/2013042
- Cadée, G. C. 2016. Rolling cockles: Shell abrasion and repair in a living bivalve *Cerastoderma edule* L. *Ichnos* **23**: 180–188. doi:10.1080/10420940.2016.1164152
- Calderó-Pascual, M., E. de Eyto, E. Jennings, M. Dillane, M. R. Andersen, S. Kelly, H. L. Wilson, and V. McCarthy. 2020. Effects of consecutive extreme weather events on a temperate dystrophic Lake: A detailed insight into physical, chemical and biological responses. *Water* **12**: 1411. doi:10.3390/w12051411
- Cao, H., Z. Zhu, T. Balke, L. Zhang, and T. J. Bouma. 2018. Effects of sediment disturbance regimes on *Spartina* seedling establishment: Implications for salt marsh creation and restoration: Sediment dynamics affect seedling establishment. *Limnol. Oceanogr.* **63**: 647–659. doi:10.1002/lno.10657
- Cozzoli, F., M. Eelkema, T. J. Bouma, T. Ysebaert, V. Escaravage, and P. M. J. Herman. 2014. A mixed modeling approach to predict the effect of environmental modification on species distributions. *PLoS ONE* **9**: e89131. doi:10.1371/journal.pone.0089131
- Cozzoli, F., T. J. Bouma, P. Ottolander, M. S. Lluch, T. Ysebaert, and P. M. J. Herman. 2018. The combined influence of body size and density on cohesive sediment resuspension by bioturbators. *Sci. Rep.* **8**: 3831. doi:10.1038/s41598-018-22190-3
- De Backer, A., C. Van Colen, M. Vincx, and S. Degraer. 2010. The role of biophysical interactions within the ijzermonding tidal flat sediment dynamics. *Cont. Shelf Res.* **30**: 1166–1179. doi:10.1016/j.csr.2010.03.006
- Diez, J. M., and others. 2012. Will extreme climatic events facilitate biological invasions? *Front. Ecol. Environ.* **10**: 249–257. doi:10.1890/110137
- Domínguez, R., C. Olabarria, S. A. Woodin, D. S. Wetthey, L. G. Peteiro, G. Macho, and E. Vázquez. 2021a. Contrasting responsiveness of four ecologically and economically important bivalves to simulated heat waves. *Mar. Environ. Res.* **164**: 105229. doi:10.1016/j.marenvres.2020.105229
- Domínguez, R., E. Vázquez, I. M. Smallegange, S. A. Woodin, D. S. Wetthey, L. G. Peteiro, and C. Olabarria. 2021b. Predation risk increases in estuarine bivalves stressed by low salinity. *Mar. Biol.* **168**: 132. doi:10.1007/s00227-021-03942-8
- Dorai-Raj, S., 2014. Binom: Binomial confidence intervals for several parameterizations. <https://CRAN.R-project.org/package=binom>
- Fan, D., Y. Guo, P. Wang, and J. Z. Shi. 2006. Cross-shore variations in morphodynamic processes of an open-coast mudflat in the Changjiang Delta, China: With an emphasis on storm impacts. *Cont. Shelf Res.* **26**: 517–538. doi:10.1016/j.csr.2005.12.011
- Foekema, E. M., Cuperus, J., van der Weide, B. E., 2014. Risk assessment of alien species found in and around the oyster basins of Yerseke. Rapport, IMARES, Wageningen UR. <https://edepot.wur.nl/294646>
- Gray, J. S., and M. Elliott. 2009. Ecology of marine sediments: From science to management. Oxford Univ. Press. doi:10.1093/oso/9780198569015.001.0001
- Haider, F., S. Timm, T. Bruhns, M. N. Noor, and I. M. Sokolova. 2020. Effects of prolonged food limitation on energy metabolism and burrowing activity of an infaunal marine bivalve, *Mya arenaria*. *Comp. Biochem. Physiol. A Mol. Integr. Physiol.* **250**: 110780. doi:10.1016/j.cbpa.2020.110780
- Hiddink, J. G., S. A. E. Marijnissen, K. Troost, and W. J. Wolff. 2002. Predation on 0-group and older year classes of the

- bivalve *Macoma balthica*: Interaction of size selection and intertidal distribution of epibenthic predators. *J. Exp. Mar. Biol. Ecol.* **269**: 223–248. doi:[10.1016/S0022-0981\(02\)00002-3](https://doi.org/10.1016/S0022-0981(02)00002-3)
- Hiddink, J., and W. Wolff. 2002. Changes in distribution and decrease in numbers during migration of the bivalve *Macoma balthica*. *Mar. Ecol. Prog. Ser.* **233**: 117–130. doi:[10.3354/meps233117](https://doi.org/10.3354/meps233117)
- Ho, S. S., N. R. Bond, and R. M. Thompson. 2013. Does seasonal flooding give a native species an edge over a global invader? *Freshw. Biol.* **58**: 159–170. doi:[10.1111/fwb.12047](https://doi.org/10.1111/fwb.12047)
- Hu, Z., J. van Belzen, D. van der Wal, T. Balke, Z. B. Wang, M. Stive, and T. J. Bouma. 2015. Windows of opportunity for salt marsh vegetation establishment on bare tidal flats: The importance of temporal and spatial variability in hydrodynamic forcing. *J. Geophys. Res. Biogeophys.* **120**: 1450–1469. doi:[10.1002/2014JG002870](https://doi.org/10.1002/2014JG002870)
- Hu, Z., P. Yao, D. van der Wal, and T. J. Bouma. 2017. Patterns and drivers of daily bed-level dynamics on two tidal flats with contrasting wave exposure. *Sci. Rep.* **7**: 7088. doi:[10.1038/s41598-017-07515-y](https://doi.org/10.1038/s41598-017-07515-y)
- Hunt, H. L. 2004. Transport of juvenile clams: Effects of species and sediment grain size. *J. Exp. Mar. Biol. Ecol.* **312**: 271–284. doi:[10.1016/j.jembe.2004.07.010](https://doi.org/10.1016/j.jembe.2004.07.010)
- Hunt, H. L., C. A. Pilditch, R. V. Gladstone-Gallagher, and C. J. Lundquist. 2020. Spatial and temporal variation in the dispersal of clam populations on intertidal flats. *J. Exp. Mar. Biol. Ecol.* **524**: 151291. doi:[10.1016/j.jembe.2019.151291](https://doi.org/10.1016/j.jembe.2019.151291)
- Jensen, A. C., J. Humphreys, R. W. G. Caldow, C. Grisley, and P. E. J. Dyrinda. 2004. Naturalization of the Manila clam (*Tapes philippinarum*), an alien species, and establishment of a clam fishery within Poole Harbour, Dorset. *J. Mar. Biol. Ass.* **84**: 1069–1073. doi:[10.1017/S0025315404010446h](https://doi.org/10.1017/S0025315404010446h)
- Kurihara, T. 2003. Adaptations of subtropical Venus clams to predation and desiccation: Endurance of *Gafrarium tumidum* and avoidance of *Ruditapes variegatus*. *Mar. Biol.* **143**: 1117–1125. doi:[10.1007/s00227-003-1158-9](https://doi.org/10.1007/s00227-003-1158-9)
- Lake, P. S. 2003. Ecological effects of perturbation by drought in flowing water. *Freshw. Biol.* **48**: 1161–1172. doi:[10.1046/j.1365-2427.2003.01086.x](https://doi.org/10.1046/j.1365-2427.2003.01086.x)
- Le Hir, P., Y. Monbet, and F. Orvain. 2007. Sediment erodability in sediment transport modelling: Can we account for biota effects? *Cont. Shelf Res.* **27**: 1116–1142. doi:[10.1016/j.csr.2005.11.016](https://doi.org/10.1016/j.csr.2005.11.016)
- Lee, S. Y. 1996. Distribution pattern and interaction of two infaunal bivalves, *Tapes philippinarum* (Adams and Reeve) and *Anomalocardia squamosa* (Linnaeus) (Bivalvia: Veneridae). *J. Exp. Mar. Biol. Ecol.* **201**: 253–273. doi:[10.1016/0022-0981\(96\)00015-9](https://doi.org/10.1016/0022-0981(96)00015-9)
- Lenz, M., and others. 2011. Non-native marine invertebrates are more tolerant towards environmental stress than taxonomically related native species: Results from a globally replicated study. *Environ. Res.* **111**: 943–952. doi:[10.1016/j.envres.2011.05.001](https://doi.org/10.1016/j.envres.2011.05.001)
- Leprieur, F., M. A. Hickey, C. J. Arbuckle, G. P. Closs, S. Brosse, and C. R. Townsend. 2006. Hydrological disturbance benefits a native fish at the expense of an exotic fish. *J. Appl. Ecol.* **43**: 930–939. doi:[10.1111/j.1365-2664.2006.01201.x](https://doi.org/10.1111/j.1365-2664.2006.01201.x)
- Lesnoff, M., Lancelot, R., 2012. Aod: Analysis of Overdispersed data. <https://cran.r-project.org/package=aod>
- Li, B., F. Cozzoli, L. M. Soissons, T. J. Bouma, and L. Chen. 2017. Effects of bioturbation on the erodibility of cohesive versus non-cohesive sediments along a current-velocity gradient: A case study on cockles. *J. Exp. Mar. Biol. Ecol.* **496**: 84–90. doi:[10.1016/j.jembe.2017.08.002](https://doi.org/10.1016/j.jembe.2017.08.002)
- Lundquist, C. J., C. A. Pilditch, and V. J. Cummings. 2004. Behaviour controls post-settlement dispersal by the juvenile bivalves *Austrovenus stutchburyi* and *Macomona liliana*. *J. Exp. Mar. Biol. Ecol.* **306**: 51–74. doi:[10.1016/j.jembe.2003.12.020](https://doi.org/10.1016/j.jembe.2003.12.020)
- Macho, G., S. A. Woodin, D. S. Wethey, and E. Vázquez. 2016. Impacts of sublethal and lethal high temperatures on clams exploited in European fisheries. *J. Shellfish. Res.* **35**: 405–419. doi:[10.2983/035.035.0215](https://doi.org/10.2983/035.035.0215)
- Meffe, G. K. 1984. Effects of abiotic disturbance on coexistence of predator-prey fish species. *Ecology* **65**: 1525–1534. doi:[10.2307/1939132](https://doi.org/10.2307/1939132)
- Newell, R. I. E., and B. L. Bayne. 1980. Seasonal changes in the physiology, reproductive condition and carbohydrate content of the cockle *Cardium* (=Cerastoderma) *edule* (Bivalvia: Cardiidae). *Mar. Biol.* **56**: 11–19. doi:[10.1007/BF00390589](https://doi.org/10.1007/BF00390589)
- Ong, B., and S. Krishnan. 1995. Changes in the macrobenthos community of a sand flat after erosion. *Estuar. Coast. Shelf Sci.* **40**: 21–33. doi:[10.1016/0272-7714\(95\)90010-1](https://doi.org/10.1016/0272-7714(95)90010-1)
- Paphitis, D., M. B. Collins, L. A. Nash, and S. Wallbridge. 2002. Settling velocities and entrainment thresholds of biogenic sands (shell fragments) under unidirectional flow. *Sedimentology* **49**: 211–225. doi:[10.1046/j.1365-3091.2002.00446.x](https://doi.org/10.1046/j.1365-3091.2002.00446.x)
- Quinn, G. P., and M. J. Keough. 2002. Experimental design and data analysis for biologists. Cambridge Univ. Press. doi:[10.1017/CBO9780511806384](https://doi.org/10.1017/CBO9780511806384)
- R Core Team. 2020. R: A language and environment for statistical computing. R Foundation for Statistical Computing. <https://www.R-project.org/>.
- Rees, E. I. S., A. Nicholaidou, and P. Laskaridou. 1977. The effects of storms on the dynamics of shallow water benthic associations, p. 465–474. *In* Biology of benthic organisms. Elsevier. doi:[10.1016/B978-0-08-021378-1.50052-X](https://doi.org/10.1016/B978-0-08-021378-1.50052-X)
- Schneider, K. R. 2008. Heat stress in the intertidal: Comparing survival and growth of an invasive and native mussel under a variety of thermal conditions. *Biol. Bull.* **215**: 253–264. doi:[10.2307/25470709](https://doi.org/10.2307/25470709)
- Schönke, M., P. Feldens, D. Wilken, S. Papenmeier, C. Heinrich, J. S. von Deimling, P. Held, and S. Krastel. 2017. Impact of *Limacina conchilega* on seafloor microtopography

- off the Island of Sylt (German Bight, SE North Sea). *Geo-Mar. Lett.* **37**: 305–318. doi:10.1007/s00367-016-0491-1
- Shi, B., and others. 2017. Erosion and accretion on a mudflat: The importance of very shallow-water effects. *J. Geophys. Res. Oceans* **122**: 9476–9499. doi:10.1002/2016JC012316
- Shi, B., and others. 2021. Effect of typhoon-induced intertidal-flat erosion on dominant macrobenthic species (*Meretrix meretrix*). *Limnol. Oceanogr.* **66**: 4197–4209. doi:10.1002/lno.11953
- de Smit, J. C., M. Z. M. Brückner, K. I. Mesdag, M. G. Kleinhans, and T. J. Bouma. 2021. Key Bioturbator species within benthic communities determine sediment resuspension thresholds. *Front. Mar. Sci.* **8**: 726238. doi:10.3389/fmars.2021.726238
- Stocker, T. F., and others. 2014. Climate Change 2013: The physical science basis. Contribution of Working Group I to the Fifth Assessment Report of IPCC the Intergovernmental Panel on Climate Change. Cambridge Univ. Press. doi:10.1017/CBO9781107415324
- St-Onge, P., and G. Miron. 2007. Effects of current speed, shell length and type of sediment on the erosion and transport of juvenile softshell clams (*Mya arenaria*). *J. Exp. Mar. Biol. Ecol.* **349**: 12–26. doi:10.1016/j.jembe.2007.03.020
- Storey, K. B., and J. M. Storey. 1990. Metabolic rate depression and biochemical adaptation in Anaerobiosis, hibernation and estivation. *Q. Rev. Biol.* **65**: 145–174. doi:10.1086/416717
- Thieltges, D. W. 2006. Parasite induced summer mortality in the cockle *Cerastoderma edule* by the trematode *Gymnophallus choledochus*. *Hydrobiologia* **559**: 455–461. doi:10.1007/s10750-005-1345-4
- Thrush, S. F., J. E. Hewitt, M. Gibbs, C. Lundquist, and A. Norkko. 2006. Functional role of large organisms in intertidal communities: Community effects and ecosystem function. *Ecosystems* **9**: 1029–1040. doi:10.1007/s10021-005-0068-8
- Troost, K., and others, 2021. Schelpdierbestanden in de Nederlandse kustzone, Waddenzee en zoute deltawateren in 2020. Stichting Wageningen Research, Centrum voor Visserijonderzoek (CVO), IJmuiden, Netherlands. 10.18174/538895
- Vázquez, E., S. A. Woodin, D. S. Wetthey, L. G. Peteiro, and C. Olabarria. 2021. Reproduction under stress: Acute effect of low salinities and heat waves on reproductive cycle of four ecologically and commercially important bivalves. *Frontiers in Marine Science* **8**: 685282. doi:10.3389/fmars.2021.685282
- Verdelhos, T., P. G. Cardoso, M. Dolbeth, and M. A. Pardal. 2014. Recovery trends of *Scrobicularia plana* populations after restoration measures, affected by extreme climate events. *Mar. Environ. Res.* **98**: 39–48. doi:10.1016/j.marenvres.2014.03.004
- de Vet, P. L. M., B. C. van Prooijen, I. Colosimo, N. Steiner, T. Ysebaert, P. M. J. Herman, and Z. B. Wang. 2020. Variations in storm-induced bed level dynamics across intertidal flats. *Sci. Rep.* **10**: 12877. doi:10.1038/s41598-020-69444-7
- Wiesebron, L. E., N. Steiner, C. Morys, T. Ysebaert, and T. J. Bouma. 2021. Sediment bulk density effects on benthic macrofauna burrowing and bioturbation behavior. *Frontiers in Marine Science* **8**: 707785. doi:10.3389/fmars.2021.707785
- Xie, W., X. Wang, L. Guo, Q. He, S. Dou, and X. Yu. 2021. Impacts of a storm on the erosion process of a tidal wetland in the Yellow River Delta. *Catena* **205**: 105461. doi:10.1016/j.catena.2021.105461
- Yeo, R. K., and M. J. Risk. 1979. Intertidal catastrophes: Effect of storms and hurricanes on intertidal benthos of the Minas Basin, Bay of Fundy. *J. Fisheries Board Canada* **36**: 667–669. doi:10.1139/f79-096
- Zardi, G. I., K. R. Nicastro, C. D. McQuaid, M. Rius, and F. Porri. 2006. Hydrodynamic stress and habitat partitioning between indigenous (*Perna perna*) and invasive (*Mytilus galloprovincialis*) mussels: Constraints of an evolutionary strategy. *Mar. Biol.* **150**: 79–88. doi:10.1007/s00227-006-0328-y
- Zhu, Q., B. C. van Prooijen, D. C. Maan, Z. B. Wang, P. Yao, T. Dagers, and S. L. Yang. 2019. The heterogeneity of mud-flat erodibility. *Geomorphology* **345**: 106834. doi:10.1016/j.geomorph.2019.106834
- Zwarts, L., and J. Wanink. 1989. Siphon size and burying depth in deposit- and suspension-feeding benthic bivalves. *Mar. Biol.* **100**: 227–240. doi:10.1007/BF00391963

Acknowledgments

The authors would like to thank Jaco de Smit for helping in carrying out the racetrack flume experiment. This study was funded by the Buitendijkse project of Rijkswaterstaat (Netherlands Ministry of Infrastructure and Water Management) and supported by the Netherlands Organization for Scientific Research (NWO) via the project “EMERGO – Ecomorphological functioning and management of tidal flats” (850.13.020, 850.13.022, 850.13.023).

Conflict of Interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Submitted 08 February 2022

Revised 08 July 2022

Accepted 21 August 2022

Associate editor: Maitane Olabarrieta