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A biophysical metabolic approach

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Running title: A biophysical approach to bio-mediated sediment resuspension

Modelling spatial and temporal patterns in bioturbator effects on sediment resuspension: a biophysical metabolic approach

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Abstract

Tidal flats are biogeomorphic landscapes, shaped by physical forces and interaction with benthic biota. We used a metabolic approach to assess the overarching effect of bioturbators on tidal landscapes. The benthic bivalve common cockle (*Cerastoderma edule*) was used as model organism. The effect of *C. edule* on sediment resuspension was approximated as a function of the overall population metabolic rate per unit of area. We combined i) laboratory observations on how *C. edule* affect sediment resuspension along gradients of bioturbation activity, sediment cohesiveness and hydrodynamic force with ii) spatial data on the natural distribution of intertidal *C. edule* populations. This allowed us to build an integrated model of the *C. edule* effect on sediment resuspension along the tidal gradient. Owing to the temperature dependence of metabolic rate, the model also accounted for seasonal variation in bioturbators activity.

Laboratory experiments indicated that sediment resuspension is positively related to the metabolic rate of the *C. edule* population especially in cohesive sediments. Based on this observation, we predicted a clear spatial and seasonal pattern in the relative importance of *C. edule* contribution to sediment resuspension along a tidal transect. At lower elevations, our model indicates that hydrodynamics overrules biotic effects; at higher elevations, inter-tidal hydrodynamics should be too low to suspend bioturbated sediments. The influence of *C. edule* on sediment resuspension is expected to be maximal at the intermediate elevation of a mudflat, owing to the combination of moderate hydrodynamic stress and high bioturbator activity. Also, bio-mediated sediment resuspension is predicted to be particularly high in the warm season.

Research into metabolic dependency of bio-mediated sediment resuspension may help to place phenomenological observations in the broader framework of metabolic theories in ecology and to formulate general expectations on the coastal ecosystem functioning.

Introduction

Bioturbation can alter sediment dynamics (Cadée, 2001; Le Hir, et al., 2007), thereby affecting the morphology of sedimentary coastlines (Wood & Widdows, 2002; Orvain, et al., 2012; Brückner, et al., 2021), salt marsh dynamics (Bouma, et al., 2016), coastal protection services (Bouma, et al., 2014), and overall marine ecosystem functioning (Aller, 1982; Aller & Cochran, 2019). Understanding and quantifying biotic effects on sediment dynamics is crucial to the improvement of coupled bio-physical models for shallow-water environments (de Lucas Pardo, et al., 2013; Ehrnsten, et al., 2020). These models deal with large functional variability in bioturbators (Lee & Swartz., 1980; Kristensen, et al., 2012; Queirós, et al., 2013) and their heterogeneous spatial and temporal (seasonal) distribution (Gray, 1974; Herman, et al., 1999; Thrush, et al., 2003). Furthermore, the effects of bioturbation are modulated by environmental factors such as the intensity of the hydrodynamic stress and the composition of sediment (Cadée, 2001; Li, et al., 2017; Joensuu, et al., 2018; Cozzoli, et al., 2020).

The effects of benthic biota have been included in physical morphodynamic models by enhancing the parameter describing the bottom roughness, the critical erosion threshold, and the resuspension rates (Le Hir, et al., 2007). This was done mostly by using empirical relationships between bioturbators' abundance/biomass and their effect on sediment dynamics [e.g. (Wood & Widdows, 2002; Orvain, et al., 2012; Jacox, et al., 2020; Brückner, et al., 2021)]. However, recent mechanistic interpretations (Cozzoli, et al., 2018; Cozzoli, et al., 2019) suggested that macrobenthic bioturbation is mostly proportional to the bioturbators' metabolic rate, defined by the rate of biological processing of energy and material (Brown, et al., 2004a). The metabolic rate seems to be a better predictor of biogenic mixing and resuspension than abundance or biomass because of its mechanistic relationship with the intensity of the physiological activities involved in bioturbation, namely respiration, feeding and moving (Cozzoli, et al., 2019). Furthermore, the metabolic rate is a particularly useful descriptor for cross-species generalization [e.g., (Brown, et al., 2004a; Harris, et al., 2006; Martin, et al., 2013; Grady, et al., 2019)] owing to its general relationship with

individual body mass, body temperature and lifestyle (Clarke & Johnston, 1999; Gillooly, et al., 2001; Killen, et al., 2010; Beaman, et al., 2020). Therefore, the use of metabolic based models provide a promising avenue for general parameterization of the ‘pace of bioturbation’ (Ehrnsten, et al., 2020).

Some models already couple the metabolism of benthic fauna with biogeochemical processes (Ehrnsten, et al., 2020). As an example, detailed models of bioturbators energy use [i.e. Dynamic Energy Budget models, (Kooijman, 2000; van der Meer, 2006)] have been integrated into biogeochemical-hydrodynamic models of the effects of bivalves on nutrient cycles in coastal areas (Maar, et al., 2009; Grangeré, et al., 2010; Ren, et al., 2010; Saraiva, et al., 2017). However, the extensive use of accurate Dynamic Energy Budget models is hampered by their complexity (Brown, et al., 2004b; Filgueira, et al., 2011) and because they require several state variables and parameters that are difficult to derive from commonly measured rates (van der Meer, 2006).

General allometric laws can be used to simplify the upscaling of species effects on ecosystem functioning in marine soft sediments from the individual to the population level (Fang, et al., 2021). In line with this concept, we proposed a general metabolic approach to the modelling of bio-mediated sediment resuspension along a tidal transect (Figure 1). We followed the assumption that the bioturbators individual metabolic rate is mainly dependent on individual body mass and temperature (Clarke & Johnston, 1999; Gillooly, et al., 2001; Brown, et al., 2004a). This assumption provides a useful approximation of metabolic rates for exploratory investigations (del Rio, 2008). A conceptually similar approach (Kelly-Gerreyn, et al., 2014) has been used to estimate present and future biomass of benthic fauna on a global scale (Yool, et al., 2017). In line with the ‘performance’ hypothesis of a positive relationship between energy need and activity at the individual level (Daan, et al., 1990; Careau, et al., 2008), we also assumed *i*) the individual metabolic rate to be positively related to the intensity of the individual bioturbation and *ii*) the metabolic rate of a population of bioturbators to be positively related to the intensity of bioturbation per unit of area (Cozzoli, et al., 2018; Cozzoli, et al., 2019).

We re-analysed the laboratory observations on *Cerastoderma edule* (Linnaeus, 1758) published by Cozzoli, et al. (2020) using the bioturbators' metabolic rate as a general proxy of their effect on sediment resuspension (building-block 1). The relationship between *C. edule* metabolic rate and sediment resuspension was measured for different types of sediments and at different intensities of hydrodynamic stress (building-block 2). A distribution model of *C. edule* metabolic rates along a tidal transect was used to represent the natural covariance between physical and biological drivers of sediment resuspension (building-block 3). This allowed us to scale up the laboratory observations to field conditions by using a simplified scenario of tidal landscape. Such a metabolism-based relationship enabled extrapolations of how predicted temperature changes may influence bio-mediated sediment resuspension, which we investigated on a seasonal scale (building-block 4) (Fig. 1).

Building the model

Building-blocks 1 & 2: metabolic rate as a descriptor of bio-mediated sediment resuspension across physical gradients

We previously used (Cuzzoli, et al., 2020) a full factorial experimental design in mesocosm conditions to measure the amount of suspended sediment under the influence of the common cockle *C. edule*. The experimental design accounted for different homogeneously sized classes of *C. edule* specimens, ranging from 36 to 576 mg Ash Free Dry Weight of individual body mass, always building up a total biomass of 19 g AFDW m⁻². The effect of the experimental populations of *C. edule* on sediment resuspension was tested at different levels of sediment cohesiveness, with sediment silt content (*S*, %) ranging from 0 %, to 28 %. The recirculating annular flumes were used to simulate the natural dynamic changes in current velocity (*V*, cm sec⁻¹) during the tidal flooding of a sheltered tidal flat (from 5 to 30 cm s⁻¹ by steps of 5 cm s⁻¹, each step lasting 20 min). This covered most of the combinations of physical conditions and bioturbators' individual body mass as found along the transect of a sheltered tidal flat.

We previously observed that, for a similar biomass, a population of small individuals had a higher effect on sediment resuspension than a population of large individuals (Cuzzoli, et al., 2020). This was possibly because the individual metabolic and activity rates tend to increase with size as a power law with a scaling exponent lower than unity (West, et al., 1997; Kozłowski, et al., 2003; White & Seymour, 2005). As a consequence, larger individuals use a greater amount of energy overall and smaller individuals use more energy per unit of body mass (Brown, et al., 2004a). It follows that, in proportion to their body mass, smaller individuals have more intense breathing, feeding and movement activities and are thus expected to carry out more intense bioturbation (Cuzzoli, et al., 2018).

In this study, we used the empirical model of Brey (2010) to re-analyse the data set published on Cuzzoli, et al. (2020) under a metabolic perspective (Cuzzoli, et al., 2018; Cuzzoli, et

al., 2019). The Brey's model was parametrized for sedentary bivalves and a mesocosm water temperature of 18°C to estimate the standard metabolic rate (J day^{-1}) of the tested *C. edule* specimens from their body mass. Following (Allen, et al., 2005), we estimated the population Standard Metabolic Rate per unit of area (SMR_{TOT} , $\text{kJ day}^{-1} \text{m}^{-2}$) as the product of the individual metabolic rate and the spatial density (N Ind. m^{-2}) of the specimens in the laboratory flumes. This summarized the individual size and density features of the experimental populations with a single statistic (SMR_{TOT}) that can be used as a proxy for the bioturbation activity at population level (Cozzoli, et al., 2018). The variation in amount of suspended sediment per unit of area (R , g m^{-2}) across experimental treatments was modelled by multivariate regression using V , S , and SMR_{TOT} as explanatory variables:

$$R \sim V * S * SMR_{TOT} \quad (1)$$

where the operator “*” indicates use of the individual variables and their interaction terms. Detailed equations and model estimates are available as an appendix (Appendix A).

Building block 3 & 4: bio-mediated sediment resuspension along a tidal flat under the effect of temperature variation

Basic model setup: Tidal flats are characterized by a strong physical gradient along the land-channel axis (Reineck & Singh, 1980; Hu, et al., 2015). In the upper part, the bottom is submerged only during the peak phase of the tide and the hydrodynamic energy is low enough that fine sediment particles (clay $< 16 \mu\text{m}$, silt $< 63 \mu\text{m}$) can settle. Following the degrading slope towards the channel, the submersion time becomes longer and the hydrodynamic stress stronger. In these conditions, only the coarser and heavier particles (sand $< 2 \text{ mm}$) settle (Fagherazzi & Wiberg, 2009; Friedrichs, 2011; Zhou, et al., 2021). Fine sediment particles (silt, clay) exert a net attractive force between them, called cohesion (Grabowski, et al., 2011). Once the amount of fine particles reaches a certain threshold (*ca.* 10%), cohesive forces confer plasticity and “stickiness” on the whole sediment mass, making it less erodible (van Ledden, et al., 2004; Winterwerp & van Kesteren,

2004).

The exemplificative tidal flat profile simulated in this study was a slope uniformly degrading from the land (emersion frequency during an average tidal cycle $E = 100\%$) to the channel ($E = 0\%$). The variation in sediment silt content (S , %) and maximal water current velocity (V , cm sec^{-1}) along the tidal flat profile were derived from hydrodynamic model and field observations. This profile resembled the condition found in the tidal flats of a sheltered temperate coastal basin (e.g. The Oosterschelde, NL). To focus on bioturbation-mediated effects, we did not account for seasonal variation in S , E , and V . For comparison, predictions based on alternative tidal profiles (i.e. concave, convex) are shown in Appendix C (Figs. C1 and C2)..

Bioturbators activity over a tidal gradient: Bioturbators are heterogeneously distributed along the land-channel tidal transect (Gray, 1974; Herman, et al., 1999; Thrush, et al., 2003). The upper and siltier part of the tidal flat is a limiting environment for the majority of benthic organisms due to over-drying, birds predation (Zwarts, et al., 1990) and competition with vegetation (van Wesenbeeck, et al., 2007; Suykerbuyk, et al., 2012; Zhu, et al., 2016). The deeper and sandier part of the tidal flat is also unsuitable because of the lower organic content, higher mechanical stress and predation from fishes and large crustaceans (Beukema & Dekker, 2005). The bioturbators' biomass, overall population metabolism and activity generally peak in the intermediate-high part of the tidal flat (Ysebaert, et al., 2002b; Thrush, et al., 2003). The level of hydrodynamic stress and the frequency of flooding are therefore among the most important physical drivers for the distribution of benthos (Ysebaert & Herman, 2002; Ysebaert, et al., 2002b).

The integration of spatial distribution models of bioturbators based on physical drivers with models of the effect of bioturbators on sediment dynamics can account for interactions between the biological and physical drivers of sediment resuspension (Brückner, et al., 2021). However, the distribution patterns of bioturbators along tidal transects cannot be directly predicted with common average trend models because unmeasured limiting factors can interact with the (measured) system

and generate data heteroscedasticity (Cade & Noon, 2003). Logistic, (Ysebaert, et al., 2002b; Thrush, et al., 2003) or quantile regression models (Anderson, 2008; Cozzoli, et al., 2013) have proved effective in predicting the bioturbators' distribution in relation to gradients of hydrodynamic stress, salinity, frequency of inundation and sediment composition. In particular, quantile regression models focusing on the upper boundary of the distribution provide a description of ecological responses based on the law of the least limiting factor because they can be used to represent the potential response when (unmeasured) disturbance is at a local minimum (Cade & Noon, 2003; Anderson, 2008). Potential ecosystem performance is often preferred as a descriptor over realized performance because it fluctuates less in time and allow us to predict the potential effect of the investigated process/pattern (Anderson, 2008). In this study we used an upper boundary model (*i.e.*, model of the 0.95 quantile) of the metabolic rate per unit area of populations of *C. edule* in order to *i)* obtain a reliable estimate of the deterministic dependence of the bioturbation potential distribution on the key physical variables inundation frequency and hydrodynamic stress and *ii)* emphasize the estimated trends by focusing on the potential effect of bioturbators, rather than on the realized one.

Bioturbators activity over seasonal changes: Bio-mediated contribution to sediment geochemistry is known to fluctuate on seasonal basis, being higher in the warmer and more productive seasons (Zhang & Wirtz, 2017; Mestdagh, et al., 2020). This temporal variation must be considered to predict how bioturbators may contribute to the long-term morphological evolution of tidal flats (Queirós, et al., 2015). A metabolic approach may contribute to understand the effect of seasonal changes because individual metabolic rates are deterministically related to temperature (Clarke & Johnston, 1999; Gillooly, et al., 2001; Killen, et al., 2010). Once a quantitative relationship between bioturbators' metabolic rate and effects of bioturbation activity has been established, the link between temperature and metabolic rate can be used to model the potential influence of temperature on bio-mediated sediment dynamics (Cozzoli, et al., 2018; Wrede, et al., 2018). Supporting this hypothesis, increases in individual bioturbation activity with increasing

temperature have often been observed [e.g. (Kristensen, 1983; Braeckman, et al., 2010; Ouellette, et al., 2004; Baranov, et al., 2016)].

Metabolic rate distribution model: In this study, we used a subset of the benthic dataset collected by the NIOZ – Yerseke Monitor Taskforce in the Oosterschelde to model the distribution of the *C. edule* population standard metabolic rate per unit of area (SMR_{TOT} , $\text{kJ day}^{-1} \text{ m}^{-2}$) along tidal flat transects. The benthic community records were collected between 2006 and 2011 in spring, summer, and autumn. For each sampling episode, the individual standard metabolic rate (J day^{-1}) was estimated using the Brey (2010) model from the average *C. edule* individual body mass and the seasonal maximal water temperature in the Oosterschelde at the collection time: 10 °C in early spring, 20 °C in summer and 18° C for autumn (World Sea Temperature, 2020). The individual standard metabolic rate was multiplied to the population density (N of ind m^{-2}) to estimate SMR_{TOT} of the field-observed *C. edule* populations. This semi-empirical approach allowed us to integrate changes in SMR_{TOT} related to seasonal fluctuations in bioturbators' population structure with changes related to the effect of temperature on individual metabolic rates.

We used a 0.95 quantile regression model (Koenker & Hallock, 2001) to predict the upper boundary of the distribution of SMR_{TOT} along the tidal transect. Field estimates for the maximal tidal current velocity (V) and the emersion time during a tidal cycle (E) (yearly averages) were used as continuous explanatory variables and the collection season was used as a categorical explanatory variable:

$$SMR_{TOT} \sim V * E * Season \quad (2)$$

where the operator “*” indicates use of the individual variables and their interaction terms. Detailed equations and model estimates are available as an appendix (Appendix B).

Building blocks integration

The metabolic-based model of bio-mediated sediment resuspension across physical

gradients was used to predict R (Eq. 1) according to the combination of V , S , and SMR_{TOT} (Eq. 2), that characterized each point of the schematized tidal transect. We have built one scenario for purely physical sediment resuspension (*i.e.*, $SMR_{TOT}=0 \text{ kJ day}^{-1} \text{ m}^{-2}$) and one scenario for each season (spring, summer and autumn) for bio-mediated sediment resuspension. Unfortunately, the available observations were not sufficient to include a scenario for the winter season.

The current velocity profile used in the laboratory experiment mimicked the natural rises in current velocity during a tidal cycle. In our experiment we mostly observed supply-limited erosion, *i.e.*, for each current velocity step, the suspended sediment concentration reached equilibrium owing to limitation of erodible material and hydrodynamics not strong enough for mass erosion. Therefore, our conceptual model assumes that the sediment mass that can be suspended during the tidal phase is a function of the maximal hydrodynamic stress experienced, rather than to the duration of the hydrodynamic stress peak.

Our predictions were derived from laboratory observations in which the specimens were kept under a full immersion regime. However, *C. edule* living in the intertidal zone feed and move actively during the phase of immersion and active erosion of the sediment (Navarro & Widdows, 1997) while they are nearly quiescent under air exposure (Widdows & Shick, 1985). Two alternative assumptions can be made to interpret the effects of this behavioural pattern on our estimates of bio-mediated sediment resuspension along a tidal transect. The first assumption (Asm. 1) is that *C. edule* would fully compensate for low activity during the emerged phase with intense resource acquisition and breathing during the submerged phase. Thus, the amount of sediment reworking would be proportional to the overall daily metabolic requirement of the bioturbators regardless of variations in the inundation time. Consistent with Asm. 1, it has been observed that *C. edule* sharply increase their respiratory and activity rate when submerged (Widdows & Shick, 1985). However, there is no clear evidence of increased activity rate by upper intertidal individuals to compensate for the reduced inundation time available for feeding (Widdows & Shick, 1985).

Therefore, the alternative assumption (Asm. 2) is that only the fraction of the daily energy budget consumed during the submerged phase should contribute to the sediment resuspension. Asm. 2 was implemented by scaling our estimates of SMR_{TOT} distribution along the tidal transect for the fraction of flood time over the tidal cycle. While each of the two assumptions possibly exceeds in one direction or in the other, their comparison is useful to establish boundary conditions.

All analyses were performed within the free software environment *R* (R Core Team, 2019), mainly using the *quantreg* (Koenker, 2019) and *sjPlot* (Lüdecke, 2018) packages.

Results

Building-blocks 1 & 2: new insights from re-analyzing existing experimental data

The re-analysis of the data published by Cozzoli, et al. (2020) indicated that the mass of sediment suspended (R , g m⁻²) could be described as a function (Appendix A, Eq. 1) of the overall metabolic rate of the *C. edule* population (SMR_{TOT} , kJ day⁻¹ m⁻²) across variations in sediment silt content (S , %) and current velocity (V , cm sec⁻¹). In the absence of bioturbators ($SMR_{TOT}=0$ kJ day⁻¹ m⁻²), R increased with V for low values of S , while the current applied did not suspended sediment particles when the sediment column contained a high proportion of silt. In the presence of bioturbators, R increased significantly ($p < 0.001$) with SMR_{TOT} if silt was present in the sediment. Conversely, the resuspension of sandy non-cohesive sediment ($S = 0\%$) was nearly unaffected by bioturbation (Table A3, Figure 2). Although the presence *C. edule* evidently increased the amount of cohesive sediment suspended at low hydrodynamic stress, we did not observe particularly clear influences on the erosion thresholds (see also Cozzoli et al. 2020).

Building-blocks 3 & 4: Spatial and temporal trends in bio-mediated sediment resuspension

Observed spatial and seasonal distribution of bioturbators: *C. edule* were observed to be widespread in the upper part of the tidal flats, where their population was mainly composed by small individuals (Table 1). *C. edule* were more abundant and larger in the intermediate part of the tidal flat (Table 1). In the lower part of the tidal flat, *C. edule* reached a high spatial density and a large individual mass in a few sites, but this happened more rarely (Table 1). *C. edule* were on average more abundant and larger in autumn, and less abundant and smaller in spring (Table 1).

Predicted spatial and seasonal distribution of bioturbators' potential metabolic rate: The upper boundary (quantile 0.95) model (Eq. 2, Appendix B) of the *C. edule* population standard metabolic rate (SMR_{TOT} , kJ day⁻¹ m⁻²) distribution along the schematized tidal flat profile (Fig. 3A) predicted the intermediate portion of the tidal flat to have the highest potential SMR_{TOT} across all seasons (Figure 3B). Overall, the potential SMR_{TOT} was predicted to be higher in autumn due to the combination of high density, large individual body mass and still warm water temperature (Fig. 3B).

Predicted sediment resuspension in absence of bioturbation: In the upper part of the tidal flat (emersion time during a tidal cycle, $E > 75\%$), the combination of highly cohesive sediment (S between 14% and 24%) and low maximal tidal current velocity ($V < 20 \text{ cm sec}^{-1}$) meant that virtually no sediment resuspension is expected due to physical erosion (Fig. 3C). In the intermediate part of the tidal flat (E between 75% and 25%), the increasing current velocity (V between 20 and 30 cm sec^{-1}) and the decreasing sediment silt content (S between 0.5% and 14%) should lead to the resuspension of a small amount of sediment (on average 41 g m^{-2} , Fig. 3C). In the lower part of the tidal flat ($E < 25\%$) the combination of sandy, non-cohesive sediment ($S < 0.5\%$) and relatively high hydrodynamic stress ($V \geq 30 \text{ cm sec}^{-1}$) led to predict higher sediment resuspension (on average 79 g m^{-2} , Fig. 3C).

Predicted effect of bioturbators on sediment resuspension: Assuming that the entire daily energy consumption of *C. edule* contributes to sediment resuspension (Asm. 1), we predicted that the potential average increase in mass of suspended sediment in the upper tidal flat ($E > 75\%$) should be relatively low, ranging from $+ 11 \text{ g m}^{-2}$ in spring to $+ 30 \text{ g m}^{-2}$ in summer and $+ 48 \text{ g m}^{-2}$ in autumn (Fig. 3C). In the intermediate part of the tidal flat (E between 75% and 25%), *C. edule* are expected to cause a major potential average increase in sediment resuspension, ranging from $+ 51 \text{ g m}^{-2}$ in spring to $+ 114 \text{ g m}^{-2}$ in summer and $+ 174 \text{ g m}^{-2}$ in autumn (Fig. 3C). Regardless of the season, the predicted effect of *C. edule* in the lower part of the mudflat ($E < 25\%$) was low, generating an average increase in suspended sediment between $+ 11 \text{ g m}^{-2}$ (spring), $+ 20 \text{ g m}^{-2}$ (summer), and $+ 40 \text{ g m}^{-2}$ (autumn) (Fig. 3C).

Accounting for limitations in the inundation time available to bioturbate the sediment (Asm. 2), the predicted contribution of *C. edule* to sediment resuspension decreased mostly in the upper and intermediate tidal flat (respectively, average decrease of 75% and 35 % of what was predicted under Asm. 1). However, the general spatial pattern remained similar and the maximal effect of the bioturbators was always predicted in the intermediate part of tidal flat. The effect of Asm. 2 on the model prediction for the lower part of the tidal flat was negligible due to the long inundation time (Fig. 3C).

Discussion

In this study we build a model under the hypothesis that the effect of bioturbation on sediment resuspension is dependent on both biological (the overall metabolic rate of the bioturbators population) and physical variables (hydrodynamic stress and sediment cohesiveness) (Fig. 1). The common cockle *Cerastoderma edule* was used as model bioturbating species. First, we used laboratory experiments to establish a quantitative relationship between sediment resuspension and the estimated bioturbators population metabolic rate across gradients of sediment cohesiveness and hydrodynamic energy. Subsequently, we combined laboratory observations with field-collected data to model the distribution of the bioturbators' potential to increase sediment resuspension along a tidal flat gradient. The metabolic rate depends on the surrounding environmental temperature (Clarke & Johnston, 1999; Gillooly, et al., 2001; Brown, et al., 2004a), and it could thus have been possible to model the influence of seasonal changes in temperature on bio-mediated sediment dynamics. The model indicated that the potential contribution of *C. edule* to sediment resuspension could be highly variable in space and time, being particularly high in the upper-intermediate part of the tidal flats during the warmer seasons.

Building-blocks 1 & 2: relationship between population metabolism and sediment resuspension

In the absence of bioturbation and within the tested range of hydrodynamic stress, the sediment resuspension mainly depended on the sediment cohesiveness. In the absence of silt, the larger sand particles were suspended for a current flow of 15 cm sec^{-1} . The fine silt particles consolidated the sediment and increased its resistance to erosion up to a current flow of $20\text{--}25 \text{ cm sec}^{-1}$. In presence of *C. edule*, part of the energy used by the bioturbators was discharged into the sediment (Cozzoli, et al., 2019). The suspension of the non-cohesive sediment was not affected by this energy discharge, as it simply led to remixing the already loose particles. Conversely, the energy discharged on cohesive sediment disrupted the particles' cohesiveness and generated an easily erodible fluff layer (Shimeta, et al., 2002; Orvain, 2005). While cohesive non-bioturbated sediment was resistant to incipient motion, the fluff layer began to be suspended at only $5\text{--}10 \text{ cm}$

sec⁻¹ (Cozzoli, et al., 2020). The total mass of suspended cohesive sediment is linked to the thickness and extension of the bioturbated fluff layer (Orvain, 2005). Therefore, it increased as the population metabolic rate and energy discharge on the sediment increased. The relative contribution of bioturbation to cohesive sediment resuspension started to decrease when the current velocity overcame the threshold for physical erosion and continued to decrease as the current increased because even the non-bioturbated sediment was suspended (Cadée, 2001; Mermillod-Blondin, 2011).

Building-block 3: Distribution of bio-mediated sediment resuspension along a tidal transect

Excluding bioturbation (i.e. $SMR_{TOT} = 0 \text{ kJ day}^{-1} \text{ m}^{-2}$), the integrated model predicted a nearly monotonic increase in sediment resuspension at the increase of the hydrodynamic stress and at the decrease of the sediment silt content along the tidal transect. This is consistent with the expectations for sediment resuspension because of the tidal current of a sheltered tidal flat (Hu, et al., 2015; Hu, et al., 2017; Gong, et al., 2017).

In the upper and siltier part of the tidal flat, *C. edule* are expected to have a relatively high potential population metabolic rate (Asm. 1). However, only a small amount of the metabolic energy could be discharged on the sediment during the short inundation time (Asm. 2). Independently from the amount of discharged energy, the predicted contribution of *C. edule* to sediment resuspension is low because the hydrodynamic energy was so limited that only a minor portion of the disrupted sediment could be suspended.

The potential metabolic rate of *C. edule* population was predicted to be highest in the intermediate part of the tidal flat, where sediments were relatively silty and expected moderate hydrodynamic stress. This combination of favourable conditions caused that also the maximal contribution of *C. edule* to sediment resuspension was predicted in the intermediate part of the flat, even accounting for the partial limitations in the flooding time (Asm. 2). The high bio-mediated sediment resuspension predicted for the intermediate tidal flat might influence the tidal flat

morphology by triggering hydraulic and sediment dynamics affecting the upper shore as well (Wood & Widdows, 2002; Lumborg, et al., 2006; Orvain, et al., 2012; Brückner, et al., 2021).

In the lower part of the tidal flat, the relative contribution of bioturbators to sediment resuspension should remain limited regardless of the potential level of activity of *C. edule*, which could be high in autumn. Indeed, sediments were mainly non-cohesive and the high hydrodynamic force applied overwhelmed the effect of bioturbation (Cadée, 2001; Mermillod-Blondin, 2011).

Building-block 4: Seasonal trends in bio-mediated sediment resuspension

Seasonal variations in *C. edule* population abundance and individual body mass are mostly related to variation in primary production (Jung, et al., 2019) and to the life-cycle of these animals (Zwarts, 1991; Rueda, et al., 2005). This seasonal trend was intrinsically accounted by parametrizing our distribution model on field observations collected in different seasons. We applied a metabolic-based approach to further include the effects of changes in individual bioturbation activity related to changes in temperature [see (Cozzoli, et al., 2018; Wrede, et al., 2018)] and to obtain a better model of temporal variation in bio-mediated sediment resuspension. The maximum potential for the effect of the bioturbators was predicted to be located in the intermediate part of the mudflat during the whole year. In contrast, the overall quantity of suspended sediment varied greatly depending on the seasonal population metabolic rate. In line with previous studies (Braeckman, et al., 2010; Queirós, et al., 2013; Zhang & Wirtz, 2017; Mestdagh, et al., 2020), our model indicated a greater contribution to sediment dynamics during autumn owing to the combination of a higher density of individuals, large individual size, and relatively high water temperature. The spring contribution to sediment resuspension is estimated to be on average half of the autumn contribution, confirming the importance that seasonal variations can have in determining the overall contribution of biota to sediment dynamics (Queirós, et al., 2013). Although not enough field observations were available to model a winter scenario, we can hypothesize that the effect of bioturbators during winter is even lower due to the colder water temperature.

Evaluation of the approach

Our main aim was to provide a description of the potential effect of *C. edule* on sediment resuspension based on general ecological laws such as *i*) the scaling of metabolic rates with temperature and body mass as regards the estimation of the effect of bioturbators on sediment resuspension *ii*) the least limiting factor as regards the estimation of the upper boundary of the bioturbators activity distribution along the tidal gradient. Being derived from general laws, the proposed parametrization might be applicable to different hydrodynamic scenarios (Appendix C, Figs. C1 and C2) as long as the generic mechanisms of the model are validated. *C. edule* is a model organism representative of many common species of intertidal bioturbators (Cozzoli, et al., 2018; Cozzoli, et al., 2019), the effect of which can be modelled in a similar way. With some tuning in the parameters, other bio-mediated processes linked to macrozoobenthic metabolism (e.g. nutrients uptake, biorrigation, biodiffusion) might be, in principle, accounted for (Ehrnsten, et al., 2020). Owing to the general temperature dependence of metabolic rates, general metabolism-based approaches might be also suitable for broad scale climate studies (Yool, et al., 2017; Ehrnsten, et al., 2020).

Metabolic approaches have great potential for the general modelling of biophysical processes (Humphries & McCann, 2014). However, there are still major unresolved questions concerning the degree of harmony exhibited by the metabolic processes (Glazier, 2015) and there are no universally valid scaling factors in the relationships of respiration to body mass and temperature (Seibel & Drazen, 2007; Brey, 2010). Species-specific responses to external conditions [e.g. seston concentration (Navarro & Widdows, 1997), water acidification (Ong, et al., 2017), oxygen availability (Rubalcaba, et al., 2020)] may generate deviation from purely energetic expectations. Also, organisms could respond to high population densities by reducing their metabolic rate (DeLong, et al., 2014) and changing their level and/or type of activities (Duport, et al., 2006), which would cause our model to misestimate. Hence, some level of validation and phenomenological observation will always be needed to support metabolism-based predictions.

Another aspect to consider when evaluating the proposed approach is that we based our model on standard metabolic rate *i.e.* the minimum metabolic rate needed to sustain life at a specified (standard) temperature, because it is a relatively stable, measurable and predictable parameter (McNab, 1997). However, while active, animals have a higher energy consumption than their standard metabolic rate (Auer, et al., 2018). This implies that our estimates were significantly lower than the energy used during full bioturbation activity. We think this approximation is acceptable because in most organisms the average daily energy expenditure or the sustained rate of biological activity is a fairly constant multiple (typically about two to three) of the basal metabolic rate (Savage, et al., 2004). The use of models of the active metabolic rate could be considered in order to better quantify the amount of energy discharged by the bioturbators on the sediment. Also, we deliberately did not go into details on further physiological and behavioral variations that might influence the metabolism and activity of *C. edule* across different seasons, which are mainly related to gametogenesis (Iglesias & Navarro, 1991; Smaal, et al., 1997) and could be accounted for by more detailed (but less general) Dynamic Energy Budget models of *C. edule* metabolism [e.g. (Troost, et al., 2010)]. Going in this level of detail would shift the outcomes of the model, but is not expected to change the essential findings related to spatial pattern.

Mechanisms to be further investigated

Daily temperature fluctuations were not included in our study, meaning that we assumed this effect to be limited because the most of the bioturbation activity of *C. edule* occurs in the submerged phase, when the temperature is more stable (Johnson, 1965). This assumption seems reasonable given the focus of current study, but may require more focus when studying the effects of climatic variations in more detail.

By synthesizing the effect of the size-density feature of the bioturbator community by the population metabolic rate, we focused on the effect of disruption of the sediment cohesiveness. However, also other influential mechanisms exist. In particular, bioturbators may also affect sediment resuspension by modifying the bottom roughness (Anta, et al., 2013; Dairain, et al., 2020),

enhancing the fluxes of material from the water to the benthic compartment by biofiltration and biodeposition (Rakotomalala, et al., 2015; Soissons, et al., 2019) and by producing feces and pseudofeces (Widdows & Navarro, 2007). Since these phenomena occurred during our measurements, they were implicitly included in our statistical parameterization of trends in laboratory observations on bio-mediated sediment resuspension.

Our schematization is focused on sheltered sites that are dominated by tidal flow. It did not account for physical phenomena such as mass erosion due to stormy waves, which have a major impact on sediment erosion (Hu, et al., 2017). However, at a high hydrodynamic energy level the contribution of bioturbation to sediment dynamics was relatively less important (Moore, 2006; Mermillod-Blondin, 2011; Albertson & Allen, 2015), so that the inclusion of biological aspects could be overlooked (Cadée, 2001).

Conclusion

Obtaining an in-depth understanding of the complex biophysical relationships among ecological processes and ecosystem functioning has been identified as one of the current grand challenges in marine ecosystem ecology (Borja, et al., 2020). In particular, an increasing number of studies have emphasized the need to bridge the disciplines of ecology and geomorphology (Albertson & Allen, 2015; Nasermoaddeli, et al., 2018; Damveld, et al., 2020; Solan, et al., 2020). In this work we integrated different conceptual blocks to obtain a description of bio-mediated sediment resuspension *i*) rooted in the fundamental ecological theory of individual energy use and *ii*) the ability to encompass different combinations of environmental conditions, including seasonal variations . This kind of description is prognostic to develop integrated forecasts about the ecological and morphological evolution of sedimentary basins [e.g. (Brückner, et al., 2021)]. The notion that general ecological rules of metabolic scaling can be used to improve prediction about geomorphological change can extend the field of application of general ecological energy theories to the global functioning of ecosystems and the evolution of the landscape.

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Tables

Table 1: Average abundance (N of Ind. $\text{m}^{-2} \pm \text{s.e.}$, only sites in which *C. edule* was present), average individual body mass (mg AFDW $\pm \text{s.e.}$) and percentage of samples in which *C. edule* was present (%) of the field-observed *C. edule* populations by sampling season and tidal flat elevation range: Up (emersion time during a tidal cycle, $E > 75\%$), Intermediate (E between 75% and 25%) and Low ($E < 25\%$).

	Elevation	Spring	Summer	Autumn
Abundance	Up	67 $\pm$ 0	84 $\pm$ 10	78 $\pm$ 12
(N of Ind m^{-2})	Intermediate	78 $\pm$ 6	80 $\pm$ 4	111 $\pm$ 5
	Low	80 $\pm$ 13	69 $\pm$ 2	106 $\pm$ 10
Individual body mass	Up	17 $\pm$ 9	51 $\pm$ 19	63 $\pm$ 28
(mg AFDW)	Intermediate	152 $\pm$ 21	144 $\pm$ 21	224 $\pm$ 14
	Low	222 $\pm$ 146	156 $\pm$ 53	258 $\pm$ 37
Presence	Up	44	39	27
(%)	Intermediate	48	57	56
	Low	2	11	15

Figures

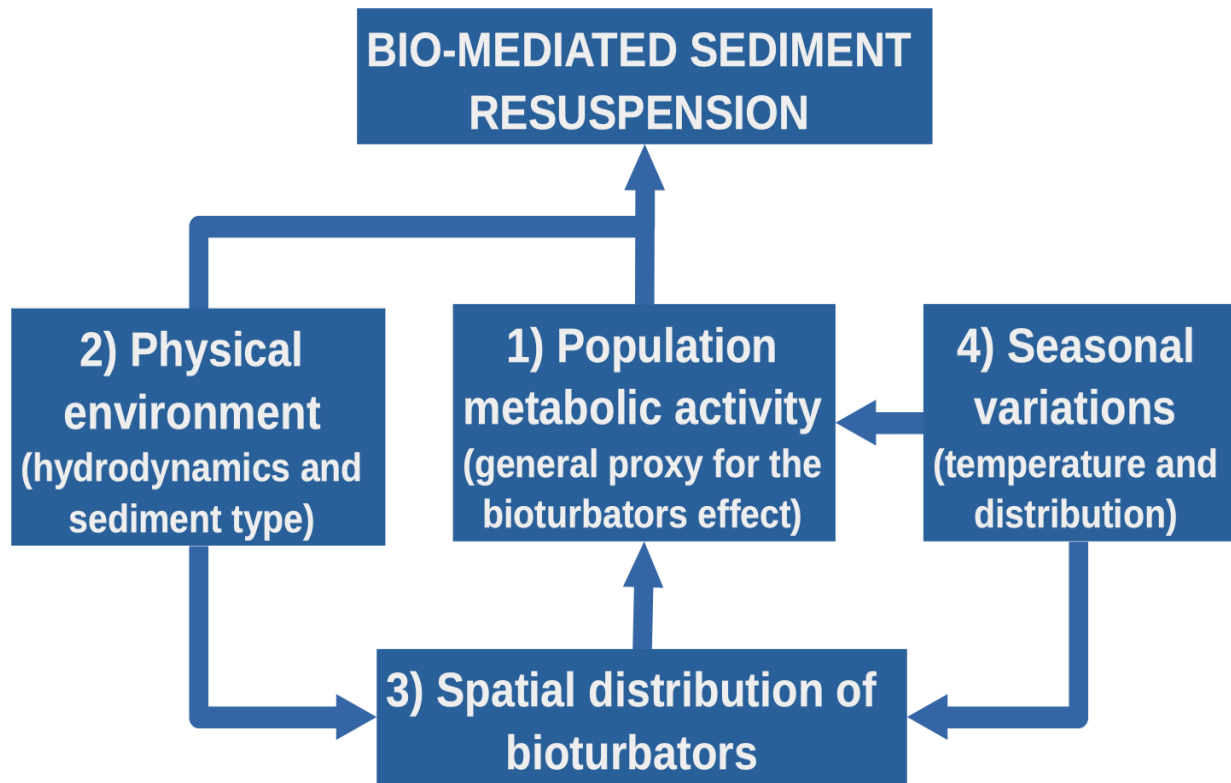


Fig. 1: Conceptual scheme. We integrated four conceptual building blocks to obtain a description of bio-mediated sediment resuspension based on a fundamental ecological descriptor as the metabolic rate (building-block 1); valid across a combination of environmental conditions (building-block 2) that are also influential for the bioturbators distribution and thereby have a realized effect (building-block 3) across seasonal variation in water temperature and population structure (building-block 4). The conceptual scheme shows the pathways considered in this study.

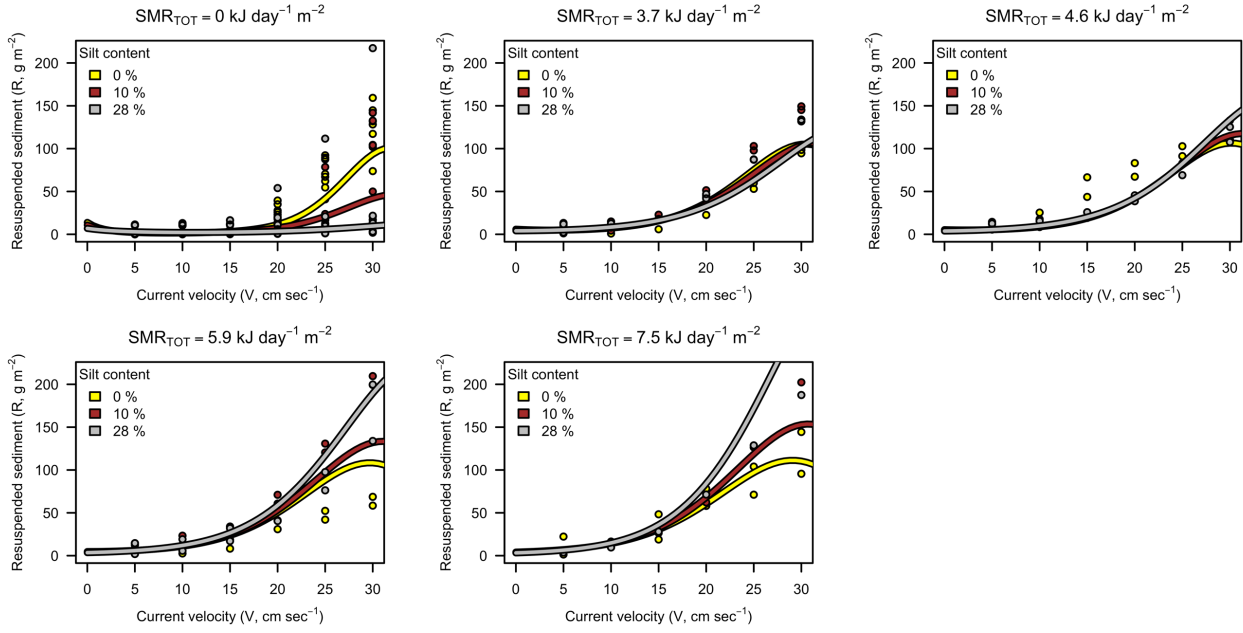


Fig. 2: Experimental results. Suspended sediment (R , g m^{-2}) for three different sediment silt contents (S , %, colored lines) and five different levels of bioturbation population metabolic rate (SMR_{TOT} , $\text{kJ day}^{-1} \text{ m}^{-2}$). Some observations (e.g. $S=10\%$ $\text{SMR}_{\text{TOT}} = 4.6 \text{ kJ day}^{-1} \text{ m}^{-2}$) were missing because of general failure of the measurement procedure. The full lines show the trends predicted by the model in Appendix A (Table A3).

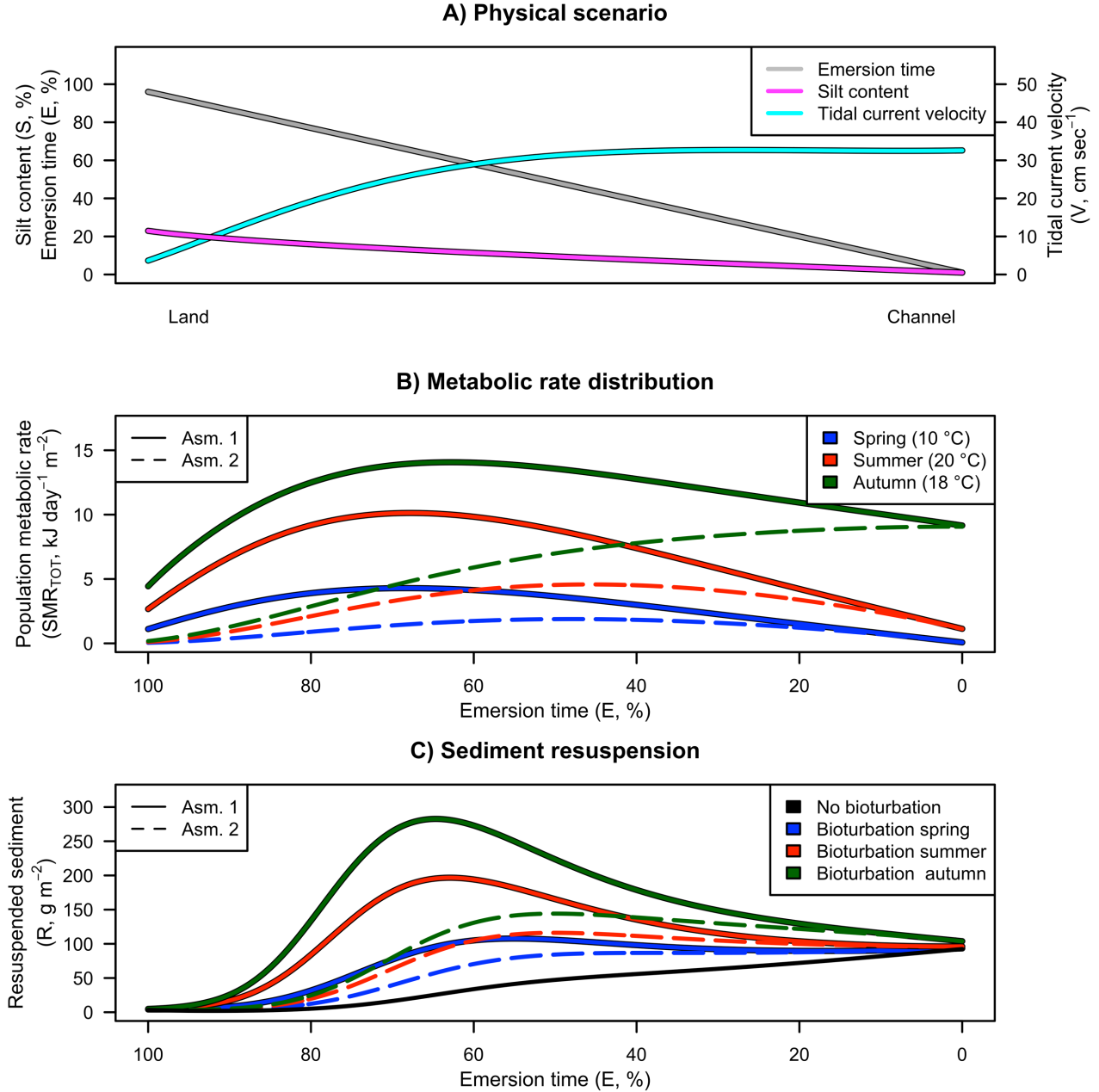


Fig. 3: A) Physical scenario. the exemplificative tidal flat profile was a slope uniformly degrading from the land (emersion frequency during an average tidal cycle $E = 100\%$) to the channel ($E = 0\%$). The variation in sediment silt content (S , %) and maximal water current velocity (V , cm sec⁻¹) along the tidal flat profile were derived from a hydrodynamic model and field observations. B) Estimated *C. edule* population potential metabolic rate (SMR_{TOT} , kJ day⁻¹ m⁻²) for spring, summer, and autumn maximal water temperature (Appendix B). Full lines indicate the overall population SMR_{TOT} (Asm. 1). Dashed lines indicate the amount of metabolic energy used during the immersion phase only (Asm. 2). C) Estimated amount of sediment suspended per tidal cycle (R , g m⁻²). Full lines indicate

the expectations for R accounting for the overall SMR_{TOT} (Asm. 1). Dashed lines indicate the expectations for R accounting for the amount of metabolic energy used during the immersion phase only (Asm. 2)