Sediment microtopography predicts localised benthic ecosystem functioning and the effect of species interactions

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ABSTRACT: Soft-sediment ecosystems play a crucial role in marine environments, yet understanding the relationships between species composition and ecosystem functioning remains challenging. We investigated the potential of sediment microtopography as a predictor of ecosystem functioning in soft-sediment environments. We conducted controlled laboratory experiments focusing on the activity and microtopography generated by 2 co-occurring and functionally important species: the tellinid bivalve *Macomona liliana* and the maldanid polychaete *Macroclymenella stewartensis*. Custom-built, flow-through, gas-tight tanks were utilized to quantify sediment microtopography and assess benthic fluxes and porewater nutrient concentrations. Rugosity explained between 35 and 61% of the variability in oxygen, ammonium and nitrate + nitrite fluxes and was positively correlated with the variability of deep porewater ammonium concentrations. As a first step to validating direct links between microtopography and biophysical drivers of ecosystem processes, we highlight the potential to advance biodiversity—ecosystem function relationships for seafloor habitats. Broader investigation of the potential of microtopography as a surrogate for ecosystem functioning will lay the groundwork for novel approaches to predict and characterize changes in these vital coastal environments and inform management strategies.

KEY WORDS: Microtopography · Biogeochemistry · Benthic fluxes · Nutrients · Bioturbation

1. INTRODUCTION

Soft-sediment ecosystems play a vital role in marine environments, contributing to nutrient cycling, habitat provision and overall ecosystem resilience. However, the relationships between species composition and ecosystem functioning in these environments remains challenging (Godbold et al. 2011). The presence of multiple species and the complex interactions among them and their local environment often lead to emergent outcomes in terms of ecosystem processes (Michener et al. 2001, Snelgrove et al. 2014). Most soft-sediment habitats exhibit features visible at the sediment—water interface (e.g. tubes, burrows and mounds) that reflect the presence and activity of resident species (Azhar et al. 2022, Schenone et al. 2022).

The resulting microscale variations (ranging from millimetres to a few centimetres, hereafter termed microtopography), often appearing as a mosaic of depressions and elevations, represent the visual outcome and the tangible signatures of bioturbation and its interaction with the physical processes that take place in and above the sediment over time (Huettel & Gust 1992, Passarelli et al. 2012).

The effects of bioturbation reverberate throughout the sediment, shaping its physical and chemical properties. As burrowing organisms traverse the sediment layers, they create channels and burrows that serve as conduits for the exchange of nutrients, oxygen and organic matter (Volkenborn et al. 2007, Kristensen et al. 2012). These bioengineered structures create transient oxic and anoxic micro-environments, enhancing

conditions that promote biogeochemical reactions and microbial activity. As a result, nutrient and carbon cycling, remineralization of organic matter and denitrification are among the biogeochemical processes that are intensified and driven by these complex interactions between bioturbators, the sediment and the overlying water (Mermillod-Blondin et al. 2004, Lessin et al. 2018).

To date, studies exploring the linkages between microtopography and ecosystem functioning have been limited. Biogenic microtopographic structures have been shown to influence sediment stability by increasing the thickness of the benthic boundary layer, lowering bed roughness and increasing the surface area available for microphytobenthos (Paterson & Black 1999, Aller 2001, Woodin et al. 2010, Passarelli et al. 2012, Volkenborn et al. 2012, Paterson et al. 2018). The interaction of the near-bed flows with microscale topography and biogenic structure was also linked to increased phytoplankton deposition and flux of particulate organic matter toward the bed (Eckman 1990, Pilditch et al. 1997, Huettel & Rusch 2000). These notions underscore the need for comprehensive investigations that not only validate the role of microtopography in mediating ecological functions but also evaluate whether it could offer an improved basis for predicting ecosystem responses to environmental changes. Given the range of sediment types and communities that exist on the seafloor, improvement is likely to result from using microtopographic variation as a surrogate for biodiversity and ecosystem function that, once validated, can be rapidly collected at multiple sites to encompass natural heterogeneity and generate ecologically meaningful maps and time-series.

In this context, controlled laboratory experiments are valuable tools that allow us to isolate and study the relationship between variables. As a first step, such experiments provide a controlled environment in which it is possible to test hypotheses, quantify the creation of microtopographical structures of individual species and link it to their capacity to alter sediment biogeochemical fluxes. In this study, we address the potential of sediment microtopography as a predictor of ecosystem functioning and biogeochemical processes in soft-sediment environments. We focused on the activity and microtopography generated by 2 co-occurring and functionally important species that differentially influence a variety of sedimentary rates and processes: the tellinid bivalve *Macomona liliana*, a facultative deposit feeder and bio-irrigator, and the maldanid polychaete *Macroclymenella stewartensis*, a head-down conveyor-belt feeder (Schenone et al. 2019, Schenone & Thrush 2020).

2. MATERIALS AND METHODS

2.1. Experimental design

Custom-built, flow-through, gas-tight tanks were constructed for this experiment. The tanks consisted of PVC sides (internal size: $30 \times 30 \times 4$ cm) held together by large screw bolts with o-ring seals. One side of the tank had evenly spaced holes to allow the insertion of rhizons (www.rhizosphere.com, pore size: 0.2 µm, filter length: 2.5 cm, Seeberg-Elverfeldt et al. 2005) for porewater extraction (Fig. 1). Water inflow was provided via a peristaltic pump (flow rate: 10 ml min^{-1}) through tubing positioned ~5 cm above the sediment surface. The outflow tube was positioned at the top of the tank.

Sediments from Whangateau Harbour, New Zealand (36° 18′ 41.5″ S, 174° 46′ 26.3″ E), were collected using PVC cores. On return to the lab, sediment cores were sliced at 0–2, 2–5, 5–8, 8–11, 11–14, 14–17 and 17–19 cm, and each layer was separately wet-sieved (500 µm) to remove macrofauna and homogenise the sediment, then left to settle overnight. Once all of the sediment had deposited, the overlying water was siphoned out and the sediment was layered in the tank to reestablish the sediment profile. To minimise bubble formation and facilitate sediment settling, the tank contained sufficient seawater to cover the sediment when each sediment layer was added. Once filled with sediment, the tank was left to stabilise for 24 h before animals were introduced.

Four treatments were used in this experiment: sediment with 2 specimens of *Macroclymenella stewartensis* (MS), sediment with 2 specimens of *Macomona liliana* (ML), sediment with 1 individual of each species (MSML) and control sediment with no macrofauna (C). Each treatment was replicated 3 times.

2.2. Flow-through incubations

To isolate the influence of benthic macrofauna on sediment processes and avoid any confounding effect of photosynthesis, each tank was incubated in a dark, temperature-controlled room (20°C). A continuous flow of filtered (200 µm) seawater was passed over the sediment surface using a peristaltic pump. Before incubation, each tank was allowed to pre-equilibrate in the dark for 5 d after the addition of the animals to allow the sediments to reach steady state (Eyre et al. 2002, Scott et al. 2008).

During the incubation, water samples were collected for analysis of dissolved nutrients and dissolved oxy-
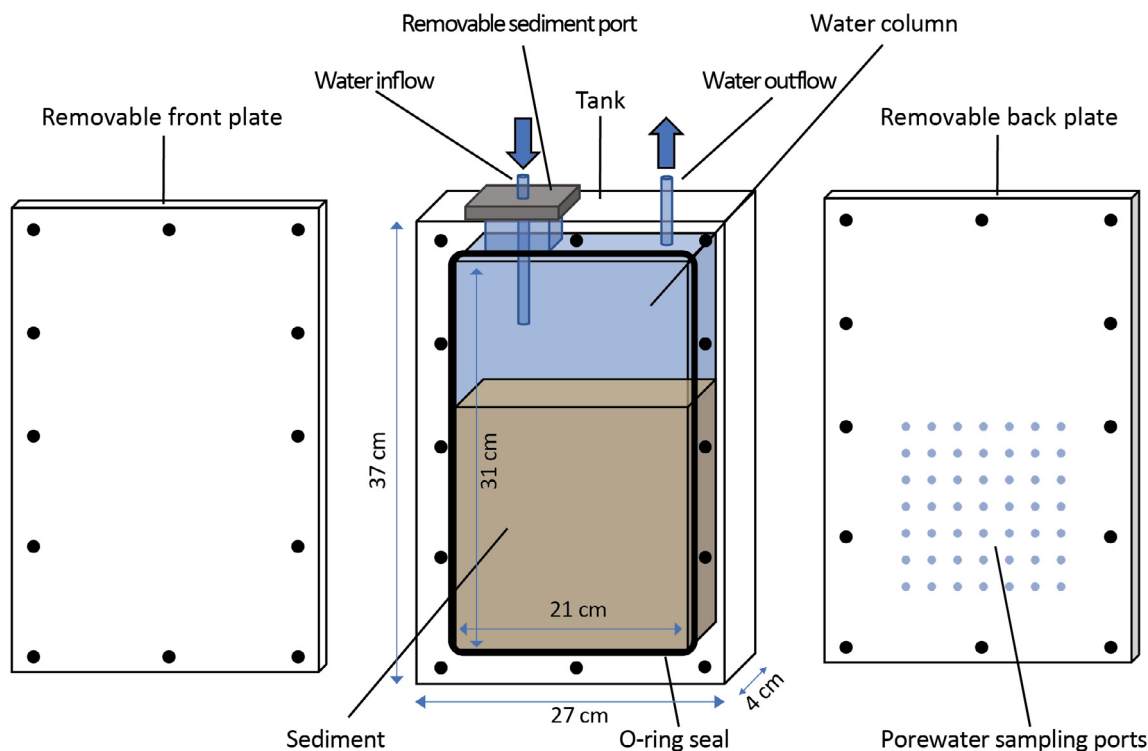
Fig. 1. Custom-built, flow-through, gas-tight incubation tank and porewater extraction setup

gen (O_2). Starting 1.5 h after the beginning of the incubation, 5 water samples were taken of the inflow and outflow at 1.5 h intervals over a 6 h period. O_2 was measured from the outflow water, allowing it to feed into a 50 ml Falcon tube and immediately measuring it with a Firesting O_2 meter (FSO2-4; PyroScience). Water samples for dissolved nutrients were taken by collecting outflow water into 15 ml acid-washed centrifuge tubes, and frozen at −20°C until analysis. After each sampling event, porewater samples (0.5 ml each) were extracted from the rhizons at depths of 1 and 3.5 cm and collected into a single porewater nitrite + nitrate (NO_x) sample. At the end of each incubation, porewater samples were collected from 20 rhizons distributed across the width of the tank and down to a sediment depth of 8 cm (Fig. 1) to obtain a 2D profile of porewater ammonium (NH_4^+) concentrations. Porewater samples were stored frozen at −20°C until analysis.

2.3. Nutrient analysis

Seawater nutrient samples were analysed for nitrate + nitrite, phosphate (PO_4^{3-}) and ammonium on a Latchet QuickChem 8500 Flow Injection Analysis System (FIA, Hach) using colourimetric analysis (Hansen & Koroleff 1999) at Portobello Marine Labo-

ratory (University of Otago, New Zealand). The detection limit was 0.07 µmol l^{-1} for NO_x^- and NH_4^+, and 0.03 µmol l^{-1} for PO_4^{3-}. The precision was ±0.7% for NO_x^-, ±0.31% for NH_4^+ and ±1.2% for PO_4^{3-}. Porewater nitrate (NO_3^-) and nitrite (NO_2^-) concentrations were determined manually in small (300 µl) sample volumes according to García-Robledo et al. (2014). The detection limit was 0.1 and 0.7 µmol l^{-1} for nitrite and nitrate, respectively. The precision was ±2.8 and ±1.3% for nitrite and nitrate, respectively. Porewater ammonium and phosphate concentrations were determined at the Leigh Marine Laboratory (University of Auckland) using a Latchet QuickChem 8500 FIA and colourimetric analysis (Hansen & Koroleff 1999). The detection limit for NH_4^+ and PO_4^{3-} was 0.09 and 0.01 µmol l^{-1}, respectively. The precision was ±2.0% for NH_4^+ and ±0.8% for PO_4^{3-}. Porewater nitrate concentrations were below the detection limit, and phosphate concentrations from both seawater and porewater were close to the detection limit and thus excluded from data analysis.

2.4. Flux calculations and porewater ammonium pools

Benthic fluxes were calculated using the equation ($C_{out} − C_{in}$) × F/A, where C represents the concentra-

tion of any analyte, C_{out} and C_{in} are the outflow and inflow concentration (μM), respectively, F is the peristaltic pump flow rate (0.6 l h^{-1}), and A is the surface area of the tanks (0.008 m^2). Fluxes per treatment replicate were calculated as the mean of the fluxes of the 5 sampling timepoints across the 6 h incubation. The mean shallow (0−5 cm) and deep (5−10 cm) porewater NH$_4^+$ concentrations were calculated as the mean of the samples extracted from the first 2 and the last 2 rows of rhizons, respectively. The spatial variability in shallow and deep porewater NH$_4^+$ concentrations was then calculated as their standard deviation.

2.5. Sediment microtopography

During the incubations, the tanks were photographed using a Nikon D610 camera placed perpendicular to the tank, at a distance of 40 cm. The photos where then analysed using the image-processing program ImageJ version 1.53t (Schneider et al. 2012). Surface rugosity was calculated using the equation: $R = S_D/L_D$, where R is the rugosity, S_D is the surface distance measured with a segmented line, and L_D is the linear distance measured with a straight line.

2.6. Statistical analysis

To determine whether the different species treatments created different levels of surface microtopography, we used a 1-way ANOVA and a Tukey's post hoc test. Data were checked for normality (Shapiro-Wilk test) and homogeneity of variance (Levene's test) and no transformations were necessary. Permutational multivariate analysis of variance (PERMANOVA) was used to examine the effects of the species treatment (categorical) and rugosity (continuous) on benthic fluxes and determine if either of the 2 factors was associated with significant differences in the rate of benthic fluxes. The interaction between species treatment and rugosity was tested and removed from the model when not significant. To avoid overfitting given the small sample size, linear regression was used to investigate the relationship between microtopography and sediment oxygen demand (SOD), ammonium (NH$_4^+$) and nitrite + nitrate (NO$_x^-$) fluxes and porewater ammonium and nitrite. Finally, the relationship between microtopography and the spatial variability of shallow and deep porewater ammonium was assessed through linear regression. All statistical analyses were performed in R version 4.3.1 (R Core Team 2021).

3. RESULTS

3.1. Microtopography

Sediment rugosity was significantly different between treatments (1-way ANOVA, $F_{3,8} = 5.024$, p = 0.03). In particular, *Macroclymenella stewartensis* (MS) generated the highest levels of rugosity, while *Macomona liliana* (ML) and the combined treatment (MSML) created intermediate levels of rugosity (Fig. 2). All species treatments were significantly different from the control treatment (C). *M. liliana* was significantly different from the *M. stewartensis* treatment (Tukey's pairwise comparison test, p = 0.042), but neither the *M. liliana* nor the *M. stewartensis* treatments differed statistically from the combined treatment.

3.2. Benthic fluxes

Looking at the relationship between rugosity and ecosystem functions, we observed significant positive relationships between sediment rugosity and SOD ($F_{1,10} = 15.13$, $R^2 = 0.60$, p = 0.007) and NO$_x^-$ influx ($F_{1,10} = 12.45$, $R^2 = 0.61$, p = 0.008) (Fig. 3). A positive relationship was also apparent for NH$_4^+$ efflux ($F_{1,10} = 5.29$, $R^2 = 0.35$, p = 0.054), although the model explained less variability than for the other functions and was marginally non-significant.

The mechanisms underpinning these relationships were further explored by separating the effect of rugosity and species composition using PERMANOVA. The results indicated that while rugosity was a significant factor in explaining differences in SOD, NH$_4^+$ and NO$_x^-$ fluxes, the identity of the test species was not significantly correlated to any ecosystem function (Table 1).
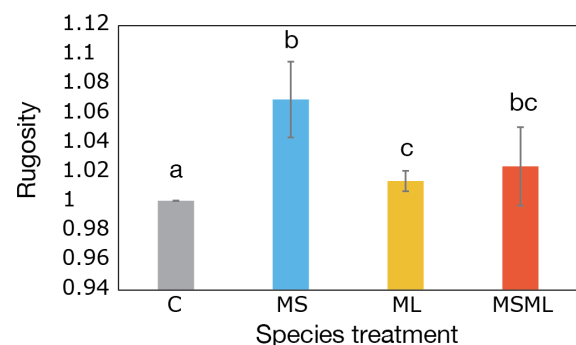

Fig. 2. Mean surface rugosity (±SE). Species treatments: C, control; MS, *Macroclymenella stewartensis*; ML, *Macomona liliana*; MSML, combined *M. stewartensis* and *M. liliana*. Lowercase letters above the bars represent statistical groupings (α = 0.05)
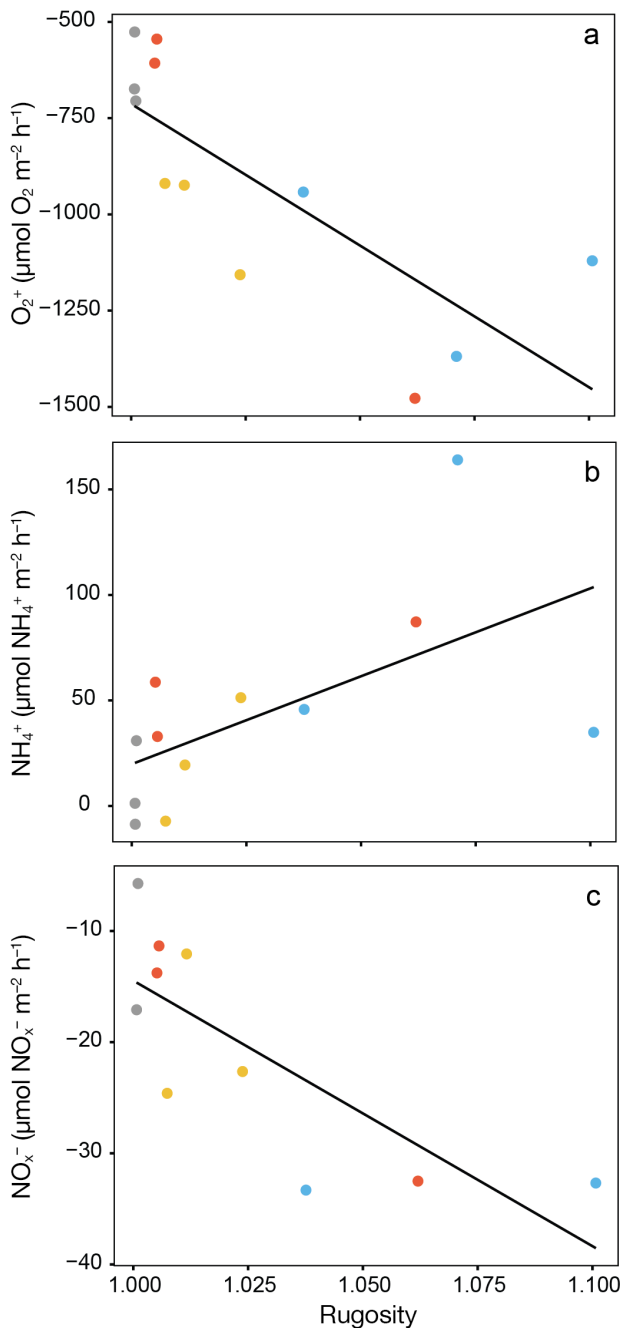
Fig. 3. Relationship between surface rugosity and (a) sediment oxygen consumption, (b) ammonium efflux and (c) NO_x^- influx. Grey = control; blue = *Macroclymenella stewartensis*; yellow = *Macomona liliana*; red = combined *M. stewartensis* and *M. liliana*. Black lines represent the fitted regressions

Table 1. Results of permutational multivariate analyses of variance to study the effects of the species (categorical) and rugosity (continuous) on benthic fluxes. Significance: **p < 0.01, *p < 0.05, ·p < 0.1

Factor	df	MS	*F* model	p (perm)
O$_2$				
Rugosity	1	667739	17.1978	0.006**
Treatment	3	56550	1.4565	0.303
Residuals	7	38827		
Total	11			
NH$_4$$^+$				
Rugosity	1	8559	4.4414	0.055·
Treatment	3	893	0.4633	0.735
Residuals	7	1927		
Total	11			
NO$_X$$^-$				
Rugosity	1	552.82	9.4006	0.024*
Treatment	3	20.44	0.3476	0.785
Residuals	5	58.81		
Total	9			

ysis of the variability of porewater ammonium showed that rugosity was significantly positively correlated with the variability of deep porewater ammonium pools ($t = 2.83$, p = 0.018, Fig. 4). In particular, surface rugosity explained 44% of the variability in deep porewater ammonium. Sediment rugosity was also significantly positively correlated with the concentration of porewater NO_2^- in the surface sediment ($F_{1,8} = 10.95$, $R^2 = 0.58$, p = 0.011, Fig. 5).

4. DISCUSSION

Ecosystem functioning in soft-sediment ecosystems is the result of complex interactions between biotic and abiotic factors (Gammal et al. 2019). Therefore, establishing direct links between the presence and absence of species and predicting the delivery and rate of ecological functions is often challenging. Surface microtopography is an indicator of the activity of infaunal and epifaunal organisms, their functional traits, their biotic interactions and their interactions with the environment. It may not work equally in all sediment types (e.g. well sorted, wave-swept sand), but we argue that some information on biodiversity and ecosystem function will be carried by biogenic microtopography. The degree to which this is true will require broader experimentation and field verification. Nevertheless, this study shows the great potential of microtopography as an easily measurable habitat property that offers valuable clues on underlying processes and functions.
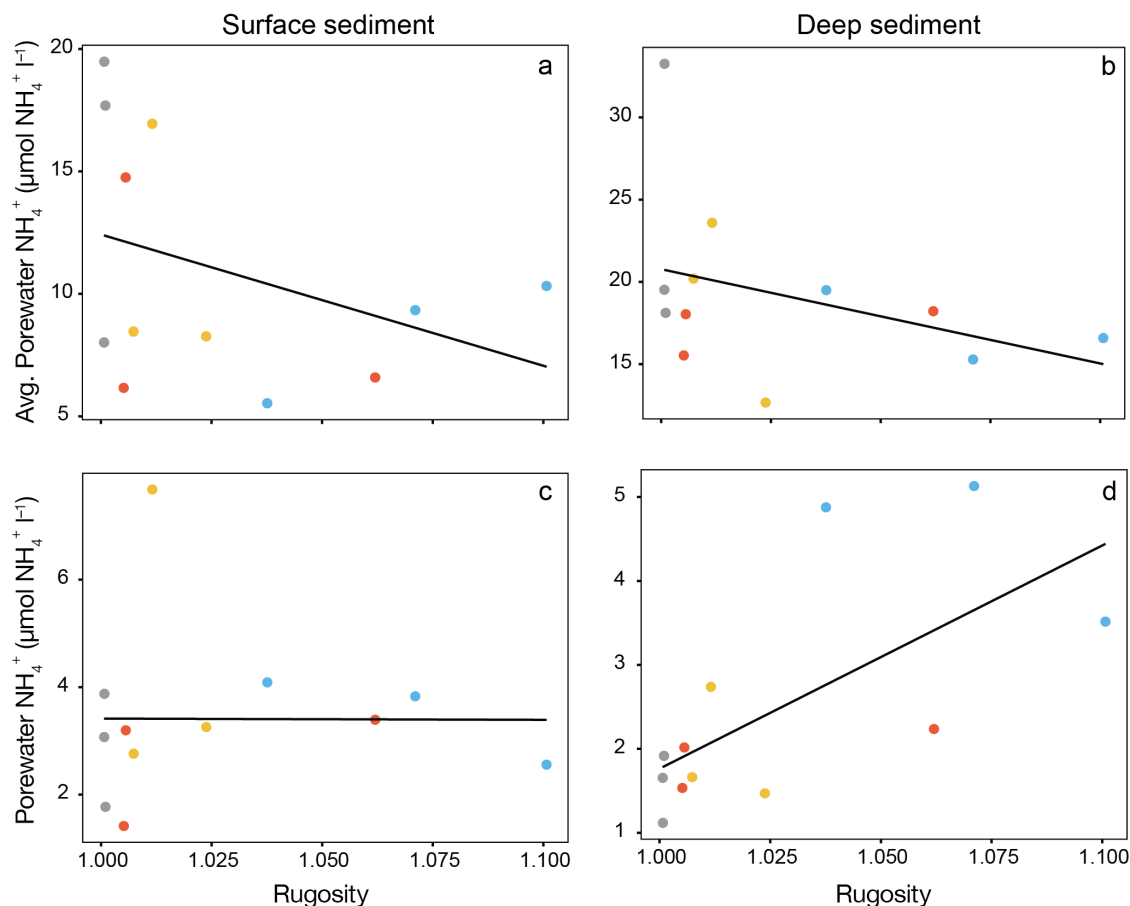
3.3. Porewater nutrients

No significant relationship was detected between microtopography and either shallow or deep porewater ammonium concentrations. However, the anal-

Fig. 4. Relationship between surface rugosity and (a) shallow and (b) deep porewater NH_4^+ mean concentrations, and between surface rugosity and (c) shallow and (d) deep porewater NH_4^+ variability. Grey = control; blue = *Macroclymenella stewartensis*; yellow = *Macomona liliana*; red = combined *M. stewartensis* and *M. liliana*. Black lines represent the fitted regressions

Through controlled laboratory experiments and species composition manipulations, we showed clear connections between surface microtopography and sediment biogeochemical processes. Specifically, we explored the relationship between microtopography and oxygen and nutrient fluxes and porewater pools and whether either species composition or sediment microtopography was associated with significant differences in the rate of benthic fluxes. Biogenic microtopography is the result of the activity of the small organisms that live in the sediment and carries the signature of their functionality. The differences in rugosity levels can be explained by the different behaviours of our target species. *Macroclymenella stewartensis* is an upward conveyor-belt feeder that creates sediment mounds surrounding the opening of its tube. This has a more pronounced effect on surface microtopography than the facultative deposit feeder *Macomona liliana*, which feeds on the surface through a long inhalant siphon leaving bird-footprint-like feeding traces. Previous studies showed that their different behaviours lead to different levels of stimulation

of benthic biogeochemical fluxes and that their interaction is synergistic rather than additive, with *M. liliana* appearing to mask the effect of *M. stewartensis* (Schenone et al. 2019, Schenone & Thrush 2020). This
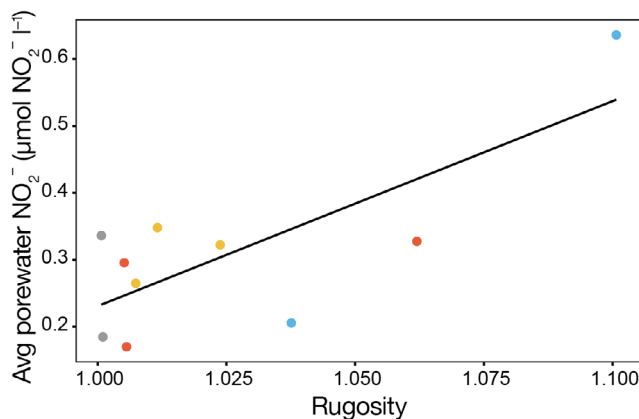

Fig. 5. Relationship between surface rugosity and porewater NO_2^- concentrations. Grey = control; blue = *Macroclymenella stewartensis*; yellow = *Macomona liliana*; red = combined *M. stewartensis* and *M. liliana*. Black line represents the fitted regression

is consistent with our findings on the relationship between the biogenic microtopography these animals create and their influence on benthic fluxes. Interestingly, the signature of their synergistic interaction was also detectable in the way these organisms affected the sediment surface, with *M. liliana* decreasing the overall rugosity created by *M. stewartensis*. Similarly, the greater bioturbation potential of the maldanid polychaete, which had a more pronounced effect on surface rugosity, led to greater spatial variability of porewater nutrients in deeper sediments compared to the effect of the tellinid bivalve, with deep (~5—10 cm) variability levels even higher than those observed in shallow (~0—5 cm) sediments. Once again, a synergistic interaction was observed, with the bivalve partially masking the effect of the polychaete.

Soft-sediment ecosystems simultaneously provide many functions. While biogeochemistry is only a part of this complex multifunctionality, it is likely to respond to sediment microtopography. Here, we focused on sediment oxygen consumption and processes associated with nitrogen cycling. Previous studies already identified biogenic structures and microtopography as important components of sediment biogeochemical fluxes (Ziebis et al. 1996, Passarelli et al. 2012, Huettel et al. 2014). The presence of surface features of key bioturbators has been shown to be a powerful indicator of benthic fluxes, more so than the species densities and community composition in intertidal sandflats (Schenone & Thrush 2020, Schenone et al. 2022). However, the link between features and the organisms that create them can be elusive and difficult to unveil, especially in subtidal, species-rich habitats. Thus, overall measurements of sediment structure could be more practical and useful in these systems to predict and characterize ecosystem functioning. Huettel & Gust (1992) investigated the contribution of biogenic sediment microtopography, termed bioroughness (e.g. burrow excavations, feeding traces and faecal pellets) on interfacial solute fluxes in permeable beds and demonstrated that simulated bioroughness elements increased advective porewater flows. Similarly, other studies showed that the presence of epifaunal species, such as mussels, and the creation of structures on the sediment surface alters the properties of the benthic boundary layer, generating pressure differences that drive advective porewater flow (Ziebis et al. 1996, Van Duren et al. 2006, Moulin et al. 2007). These studies highlight the fact that in natural systems, rugosity features interact with hydrodynamics and therefore may be even more important descriptors of sediment biogeochemistry and ecosystem functioning than our

findings would suggest. Our work extends and complements previous research on microtopography showing that it is not only an element playing a role in the magnitude and direction of the biogeochemical processes that take place at and below the sediment surface, but also a powerful indicator of ecosystem functioning. The scale over which rugosity was measured in this study was limited to a linear distance of 20 cm. This was sufficient to capture the microtopographical features created by our study species. However, in natural systems, microtopography is the result of complex interactions among multiple species and environmental factors, and detecting clear relationships between multiple processes can be challenging. Moreover, this study was limited to 2 species and their combination in a controlled laboratory environment, with limited replication, and caution must be used when extrapolating the results beyond its scope, to real-world ecosystems. Natural sediments contain a multitude of species whose interactions with each other and the environment drive ecosystem functioning. Thus, considering more diverse assemblages and how the resulting complexity affects microtopography and its link to functioning will be crucial to make generalizations on the use of microtopography.

Despite the subtle variation in surface rugosity observed (between 1.0007 and 1.1007, corresponding to a variation on the vertical axis from a few mm to ~2.5 cm), the differences between treatments and the relationships between rugosity and ecosystem functions were clear and highly significant. The fluxes of oxygen, ammonium and combined nitrite + nitrate exhibited strong associations with microtopography. Similarly, porewater nitrite concentrations and the spatial variability of porewater ammonium were significantly correlated with sediment rugosity. This suggests that increased levels of biogeochemical processes, induced by high levels of bioturbation, result in higher surface microtopographical complexity (Fig. 6). In this experiment, surface complexity was exclusively a result of macrofaunal bioturbation. Bioturbation increases oxygen penetration and heterogeneity in the sediment; thus, we observed an increase in oxygen drawdown and ammonia efflux at the sediment—water interface (Mermillod-Blondin et al. 2004, Pischedda et al. 2008, Fanjul et al. 2011). Bioturbation and the consequent increased sediment heterogeneity also explains the high variability in porewater ammonia concentrations, and the presence of a positive relationship between surface microtopography and deep (5—10 cm) rather than shallow (0—5 cm) sediment porewater ammonium is consistent with the lower reactivity of deeper sediment compared to surface sediment.
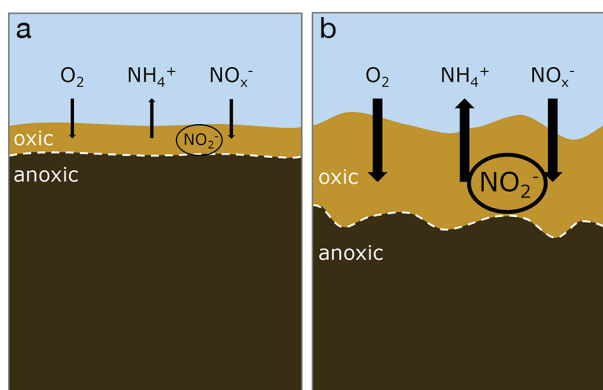
Fig. 6. Simplified soft-sediment ecosystem in a scenario of (a) low bioturbation-induced surface microtopography and (b) high bioturbation-induced surface microtopography. The sizes of the arrows and circles are proportional to the magnitude of solute fluxes and concentrations, respectively

The increase in oxic—anoxic interfaces due to bioturbation could also increase the activity of denitrifying bacteria, which would explain the increase in the influx of NO_x^- from the water with increasing rugosity (Kristensen et al. 2011, Fulweiler et al. 2013, Stief 2013). Similarly, a well-oxygenated surface layer caused by the bioturbation activities of *M. stewartensis* and *M. liliana* can stimulate ammonium oxidation to nitrite (the first step of nitrification) (Mayer et al. 1995, Pelegrí & Blackburn 1995, Satoh et al. 2007), which may have been a driver behind the positive correlation between rugosity and surface sediment porewater nitrite concentrations. The intricate interplay of species interactions and ecological functions in soft-sediment ecosystems demands innovative approaches that transcend the limitations of traditional methods. Sediment microtopography holds the potential to bridge this gap by providing insights into the physical and biological underpinnings of ecosystem processes. The strength of the relationships observed and the consistency of our findings across multiple biogeochemical processes support the extension of our results beyond our study and the use of microtopography as an indicator of sediment ecological functions. We anticipate that our findings will have implications for both ecological theory and management strategies, ultimately advancing our ability to promptly detect and manage changes in these vital coastal environments.

Future research should explore these relationships with different functional groups to incorporate the influences of diverse species assemblages and environmental fluctuations. Different animals have different functionalities and therefore may affect sediment functioning in different ways. In addition, individuals of the same species can change their behaviour and

functional performance over time (Piersma & van Gils 2011, de Juan et al. 2022), or their behaviour can be impacted by contaminants (You et al. 2023). Thus, in addition to looking at the overall small-scale rugosity, researchers could study whether these different functionalities leave different signatures on different aspects of sediment microtopography, and if we can use these properties to predict functioning in complex habitats with multiple species. Moreover, attributes of microtopography that result from faster, instantaneous activities of benthic organisms could better predict fast sediment processes that happen over smaller temporal scales. This could lead to novel rapid and ecologically insightful characterizations of benthic habitats and could drive the upscaling of ecological measurements that are more tractable at small scales (Schenone et al. 2023).

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