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Thin terrestrial sediment deposits on intertidal sandflats: effects on pore water solutes and juvenile bivalve burial behaviour

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Abstract

Changes in land use and climate increase the supply of terrestrial sediment (hereafter, TS) to coastal waters worldwide but the effects of these sediments on benthic ecosystem functioning are not well known. Past experiments with defaunated, intertidal sediment suggested a link between the de-oxygenation of sediments underlying a thin (mm) layer of TS and reduced burial rates of juvenile macrofaunal recruits. We examined this link predicting that surficial TS deposits will still negatively affect burial when applied to sediments that are initially well oxygenated due to bioturbation (C) or depleted of organic matter (D). We observed the behaviour of post-settlement juveniles of the tellinid bivalve *Macomona liliana* on the surface of four treatments; C, D, and the same sediments to which we added a thin layer of TS (CTS, DTS). Pore water analyses confirmed that the diffusive impedance of the 1.7–1.9 mm TS deposit decreased the oxygenation of the underlying intertidal sediment (CTS) but not that of the depleted sediment (DTS). Unexpectedly, (1) the application of a TS deposit significantly increased but not decreased the probability of burial, irrespectively of treatment, and (2) juveniles more likely buried into C than into D. We attribute the failure to document a negative effect of TS on the recruits' burial to the activity of the resident macroinfauna (CTS) or the absence of organic matter (DTS). Our results underline the important role of the resident macrofauna in mediating the stress response of benthic ecosystems.

1 Introduction

Changes in land use, a rising sea level, and extreme rainfall events increase the supply of terrestrial sediment (hereafter, TS) to coastal habitats, either as suspended particles via waterways or directly from landslides (Milliman and Meade, 1983; Thrush et al., 2004). The suspended TS eventually settles forming a deposit on the surface of the soft-sediment seafloor. This deposit – until reworked by benthic fauna or resuspended by flow – alters functions of the sedimentary ecosystem. It affects benthic organic carbon decomposition and production by: impeding the sediment–seawater exchange of reactive solutes (Cummings et al., 2009), altering the behaviour of benthic species and associated solute reaction dynamics (Cummings et al., 2009; Woodin et al., 2012) or, depending on the scale of the deposit, the composition of the benthic species assemblage (Thrush et al., 2003).

For centimetre-thick TS deposits, experiments in New Zealand estuaries have documented changes in benthic faunal assemblages due to migration, mortality, and recruitment failure (Norkko et al., 2002; Cummings et al., 2003; Lohrer et al., 2004). More commonly, TS deposits form thin, millimetre thick layers but these can still modify the sedimentary ecosystem by negatively affecting the burial behaviour of juvenile recruits and the sediment uptake and release of dissolved O_2 and hydrogen ions (Cummings et al., 2009). The effect of thin TS deposits on the distribution of pore water solutes in underlying sediment will be a function of macrofaunal activity, which is influenced by how the layer formed. For example, compare these two scenarios: suspended TS may form a thin deposit on the surface of coastal sediment already colonised by burrowing macrofauna. Such deposit will impede the diffusive solute exchange across the visible sediment surface, but it may not affect solute exchange across subsurface linings of macrofaunal burrows. In contrast, a centimetre thick deposit will defaunate the sediment and over time, tidal currents and waves may erode it down to a thin millimetre-thick layer. In such a case, the deposit covers the entire sediment–seawater exchange surface and so affects all solute exchange.

For the latter scenario (i.e. thin TS layer deposited on defaunated sediment), Cummings et al. (2009) suggest a link between the TS-induced decrease in the oxygenation of the underlying sediment and reduced burial of post-settlement juvenile recruits of the tellinid bivalve *Macomona liliana* (Iredale, 1915). Their results supported the hypothesis that benthic solute transport and reaction processes affect the behaviour of recruits (see also Woodin et al., 1995; Woodin 1998; Marinelli and Woodin 2002, 2004), specifically, that recruits at the surface of the deposit probe reduced products of the microbial decomposition of organic matter to assess the suitability of the underlying sediment.

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If juvenile recruits reject the TS deposit in response to a cue caused by a deposit-induced decrease in the oxygenation of the underlying sediment, but not in response to contact with TS, then this behaviour should be a function of the sediments' reactivity and resident macrofauna. Less reactive sediment (less organic matter) should cause less rejection than reactive sediment (more organic matter) if TS deposits of identical diffusive properties cover both sediments. Similarly, TS deposits over reactive sediment with burrowing macrofauna should have a lesser effect on burial behaviour than deposits over reactive defaunated sediment.

Here we extend the study by Cummings et al. (2009) testing whether TS deposits negatively affect burial of juvenile recruits (i) in the presence of macroinfauna and (ii) in the absence organic matter in the underlying sediment. To do so, we observed the behaviour of post-settlement juvenile *M. liliana*, the bivalve species used by Cummings et al. (2009) on the surface of TS deposited over (i) undisturbed, bioturbated intertidal sediment and (ii) intertidal sediment from which we removed dead and living organic matter by combustion (hereafter, depleted sediment). Assuming that the juveniles are responding to underlying pore water solute concentrations and not the TS deposit directly (sensu Cummings et al., 2009), we predicted that burial into bare depleted sediment and depleted sediment to which a layer of TS was added would not differ because the TS layer does not build up reduced solutes in the underlying sediment. Similarly, we also predict that burial into bioturbated sediment and bioturbated sediment to which a TS layer was added would not differ because the resident macrofauna oxygenates the sediment enough to offset TS induced accumulation of reduced solutes. If direct contact with TS is the driver then in both sediments (bioturbated and depleted) the TS treatments should have a lower burial rate.

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2 Material and methods

2.1 Experimental design

We conducted five replicate experiments (hereafter, Runs) in a recirculating seawater flume to investigate how deposits of TS on the surface of two types of intertidal sediment affect pore water solute concentrations and the burial behaviour of post-settlement juvenile *M. liliana*. Because only one flume was available, we conducted the Runs consecutively in May and June 2011; each Run lasted two days (Table 1).

On the first day of each Run, we inserted two cores of each sediment type into the flume, intact natural intertidal sediment (hereafter, intertidal), and intertidal sediment from which living and dead organic matter was removed by combustion (hereafter, depleted). We covered the surface of one core of each sediment type with a thin layer of TS. That is, each Run tested four sediment treatments: intertidal sediment (C), depleted sediment (D), TS over intertidal sediment (CTS) and TS over depleted sediment (DTS, Table 1, Fig. 1).

On the second day of each Run, after an 18 h acclimation of the sediment below unidirectional flume flow (free stream flow velocity $\sim 2.4\,\mathrm{cm\,s^{-1}}$), we recorded either five O_2 (Run 1, 2, 3), two oxidation–reduction potential (Eh, Run 4), or two pH (Run 5) microprofiles in each sediment core (Table 1). After profiling, we stopped the flume flow and released twenty post-settlement juvenile individuals of *M. liliana* from one pipette placed above each of four sediment cores so that they drifted onto the sediment surface. We initiated the flow and observed their burial behaviour over the following 4 h.

2.2 Sediments and bivalves

We collected intertidal sediment and post-settlement juvenile *M. liliana* concurrently from Tauranga Harbour, a large tidal inlet on the northeast coast of the North Island, New Zealand. The collection took place at a sheltered mid-intertidal sandflat 80 m east of Tuapiro Channel in the northern basin of the harbour (37°29′29″ S, 17°56′51″ E)

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on the first morning of each Run within one hour either side of low tide. Fine sands (median grain diameter ~ 120–170 µm) with a low (~ 4–8 %) silt/clay (< 63 µm) content characterise sediments at the collection site. The clam *Austrovenus stutchburyi* and *M. liliana* dominate macrofaunal biomass but numerically the most important taxa are polychaetes (~ 34 per 0.01 m^2) followed by bivalves (~ 13 per 0.01 m^2) and amphipods (~ 10 per 0.01 m^2) (Lelieveld et al., 2004, Pratt et al., 2013).

To collect juvenile *M. liliana*, we washed surface sediment with seawater on 0.5-mm mesh and placed all retained material into one seawater-filled bag. In the laboratory, we sorted this material under a dissecting microscope placing 20 post-settlement juvenile *M. liliana* in each of four containers filled with aerated, artificial seawater. Their shell length was 1.6 ± 0.2 mm (mean ± 1SD, $n = 400$, max = 2.3 mm, min = 1.1 mm).

To collect intertidal sediment, we inserted one acrylic tube (inner diameter = 5.3 cm) ~ 10 cm into the sandflat at each of six sites randomly defined with Cartesian coordinates within a 10-m diameter area. Stoppers placed at the bottom and the top of each tube enclosed the sediment core. Of these six sediment cores, we inserted two into the flume and froze one for later analyses of sediment water content, organic matter content, and grain size distribution. To make cores of organic-matter depleted sediment, intertidal sediment was combusted in a muffle furnace at 450° C for 6 h to remove organic carbon, and then added to acrylic tubes filled with artificial seawater.

We obtained TS from a landslide at Hahei Beach, Coromandel, and suspended about 100 g of this sediment in 100 mL artificial seawater on the first day of each run. We poured this suspension through a 250-µm mesh to remove large particles and then used 15 mL to create a 1–2 mm thick deposit on the surface of each of two cores in the flume. Ten millilitres was used for particle size analyses.

We measured particle size, water content, and organic matter content of the homogenised top 5 cm of the intertidal sediment following Giere (1993). This sediment was comprised of poorly sorted fine and very fine sand (median particle diameter, 114 µm). Depleted sediment was moderately sorted medium sand (median particle diameter, 330 µm). Mud (< 63 µm), water, and organic matter contents were higher

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in intertidal sediment (13.4, 27.1, and 2.2 %, respectively) than in depleted sediment (2.4, 19.4 and 0.4 %, respectively). The median diameter of the well or moderately well sorted particles in the TS suspension, determined with a Malvern Mastersizer-2000, ranged from 87 to 98 µm. The mud content of this sediment ranged from 41 to 53 %.

2.3 Seawater flume environment

The flume consists of a 7.23 m long, 50 cm wide, and 50 cm deep acrylic channel with a 40-cm diameter return pipe that runs beneath the channel. An impeller in the descending arm of the return pipe regulates flow speed via a variable-speed AC motor. Four holes in the floor of the working section (550 cm downstream from the flume entrance) allowed the insertion of tubes containing the sediment cores. These holes were evenly spaced along a line perpendicular to the raceway and confined to the central 33 cm in the cross-stream direction.

We inserted the sediment-filled tubes into the flume through its bottom plate and then filled the flume with artificial seawater to 19 cm. Thereafter, we raised the sediment inside the four tubes with a precision extruder so that their surfaces were flush with the flume floor. We then lowered the surfaces of those two cores that required a surface deposit of TS (Table 1) by ~ 1–2 mm and applied the deposit.

To apply a deposit of TS, we placed one PVC tube (inner diameter = 6.5 cm) above each sediment core in the flume. The PVC tubes confined the suspension of TS to the seawater directly above the sediment core, and prevented deposition on to the bottom of the flume and the neighbouring sediment cores. We added the suspension to the seawater inside the two PVC tubes above the receiving cores and waited 30 min for particles to settle. For the remaining two cores, seawater was added to the PVC tubes instead of the TS suspension. All PVC tubes were then carefully removed, the flow was started (free stream velocity = 2.41 cm s^{-1}) and the flume was left running overnight.

Flume seawater temperature, salinity, and oxygen content, measured with YSI 6600V2–4 multiparameter sonde submerged downstream of the flume working section, ranged from 17 to 2 °C, 32.7 to 32.9, and 90 to 94 % saturation. The intensity

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of the photosynthetically active radiation incident from the ceiling lights of the laboratory was 22 µmol photons $m^{-2}\ s^{-1}$ (LI-192 Underwater Quantum Sensor, LI-COR). The ceiling lights were off from 20:00 to 07:00 h.

Four 10-min time series measurements with a Sontek 10 MHz acoustic Doppler Velocimeter revealed that the flow velocity of the seawater in the boundary layer (0–18 mm) above flume bottom was highest in core position 1 (1.9 $cm\ s^{-1}$) and gradually decreased towards core position 4 (1.4 $cm\ s^{-1}$). To account for this variation, we rotated the position of each of the four core treatments across Runs (Table 1).

2.4 Pore water profiling

We measured vertical microprofiles of pore water O_2 concentration, pH and Eh with Unisense hard- and software at a resolution of 0.1 mm (O_2), 0.2 (pH) and 0.5 mm (Eh) normal to the sediment surface from a position in the flowing seawater above the diffusive boundary layer (~ 2 mm above the sediment surface) to a maximum depth of 5.5 mm. We calibrated the Unisense microelectrodes once a day before commencement of a measurement series following the instructions of the manufacturer (see www.unisense.com).

2.5 Bivalve behaviour and surface activity

To record the burial behaviour of juvenile *M. liliana*, we took one digital underwater photograph of the surface of each sediment core per minute for the first 10 min starting immediately after their placement. Thereafter, we took one photograph every hour until completion of the experiment. We used the digital photographs to count juveniles on the sediment surface 1, 10, and 240 min after their placement and to observe their behaviour. The photographs of the CTS treatment revealed counts and diameter of polychaete burrow openings, siphons, microphyte patches, and patches of black, subsurface sediment.

Based on the photographs, we quantified the following behaviours:

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Immediate burial – the juvenile rested on one valve; the foot dug into the sediment anterior end first, so that the apex-siphonal end of the shell was protruding from the sediment. It continued to bury deeper so that the siphonal end was no longer protruding and completely buried within 3 min. *Delayed burial* – the juvenile rested on one valve for > 3 min before it buried as described above within 10 min. *Delayed search and burial* – the juvenile rested on one valve for > 3 min before it orientated itself so that its apex was uppermost, with its anterior end in front and siphonal end behind. Using the foot, the juvenile crawled along the sediment surface, anterior end first. Its foot dug into the sediment anterior end first, with the apex-siphonal end protruding from the sediment. The juvenile completed burial within 10 min. *Emergence* (see Cummings et al., 1993) – after complete burial, the juvenile resurfaced, anterior end foremost, with its valves slightly open and the foot brought close to the gape. The juvenile then moved upward until only its siphonal end remained embedded, toppled over, coming to rest on one valve. *Drift* – some juveniles that had buried into depleted sediment emerged to first crawl a distance on the sediment surface, stop, and then position their shells vertically. The juveniles then toppled onto one valve and skidded downstream with the apex of the shell facing upstream and left the core surface via byssus drifting. *Subsurface search* – traces indicated that the juvenile crawled below the surfaces of the TS deposit.

2.6 Data analyses

Two distinct changes in the slope of the O_2 microprofiles indicated the position of the upper and lower boundaries of the TS deposits. These changes resulted from differences in O_2 diffusivity between the deposit and the underlying sediment and overlying seawater. We estimated the sediment diffusive O_2 uptake across the visible sediment surface (hereafter, DOU) from the slope of the O_2 concentration gradient in the diffusive boundary layer and the diffusion coefficient for O_2.

Consistent with Roper and Hickey (1994), Cummings et al. (1996), and Cummings and Thrush (2004), we used the number of juveniles remaining on the sediment surface 10 min after their placement as a measure of the sediment acceptability. To predict the probability of juveniles to remain on the sediment surface after 10 min, we used a logistic model (generalized linear model, binomial family, software R). To retain all trials whatever the value of n ($n = 18$–20), the data were weighted with respect to n; larger values of n constituted more statistically informative experiments. We viewed minor variation in flow velocity across the flume as a proxy for fluid mechanical environmental variability caused by variations in tidal flow velocity, turbulent intensity, etc.; this was done by considering results from each position as part of a statistical ensemble. With this assumption, different combinations of regressors were trialled. The trial revealed that the appropriate regressors were sediment type (intertidal and depleted) and the presence or absence of a TS deposit.

3 Results

3.1 Sediment surface structure and colour

The brown surface of intertidal sediment showed millimetre-scale topography (C in Fig. 1). The orange surface of the TS overlying this sediment was smooth and free of disturbance immediately after its deposition. In as little as 30 min, however, small openings of polychaete burrows (average diameter, 0.5–0.8 mm), siphons, traces, and patches of green microphytes (longest axis 15 mm) appeared (Fig. 1, Table 2). On the following day, 4 h after placement of the juveniles, we counted 37 to 123 burrow openings per core. Up to four green patches (5 mm longest axis) and 32 siphons were present and black, excavated sediment had buried small (3 cm^2) patches of the deposit.

In contrast to intertidal sediment, the red-brown surface of depleted sediment was homogeneous and flat (D in Fig. 1) and the orange surface of the TS deposit overlying this sediment remained smooth and flat until the juveniles were placed (DTS in Fig. 1).

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3.2 Pore water chemistry

3.2.1 Oxygenation

On average, O_2 penetrated intertidal sediment across the visible sediment surface 1.1 to 1.4 mm (Table 3; example profiles in Fig. 2). For all three runs, application of a TS deposit (1.7–1.9 mm thick) decreased this penetration to 0.8 or 0.9 mm. In contrast, the pore waters of TS-treated and bare depleted sediments contained dissolved O_2 to at least 5 mm depth, the maximum depth measured.

The average DOU of the intertidal sediment ranged from 826–1161 µmol m^{-2} h^{-1} (Table 3). Application of TS decreased this range to 591–695 µmol m^{-2} h^{-1}. In contrast, deposition of TS onto the surface of depleted sediment had the opposite effect on DOU. For all three Runs, the mean DOU of the depleted sediment, ranging from 16–28 µmol m^{-2} h^{-1}, was lower than that of TS-covered depleted sediment (46–71 µmol m^{-2} h^{-1}). We attribute this difference to the O_2 consumption of the TS deposit (< 55 µmol O_2 m^{-2} h^{-1}).

3.2.2 pH and Eh

All pore water pH profiles (with one exception) share common features: a steep decrease in pH to a minimum at some depth below the sediment surface followed by a brief increase and, in some profiles, stable pH at depth (Fig. 2). Depositing TS over intertidal sediment decreased the subsurface pH minimum; however, it did not change the depth of this minimum measured from the surface of the intertidal sediment. We observed a similar trend in the pH profiles of the depleted sediment, which showed less pronounced subsurface peaks at greater depths and higher pH at depths.

Inspection of our Eh profiles revealed a transition from oxidising to reducing pore water at 2–4 mm depth of the intertidal sediment (Fig. 2). The depth of this transition measured from the surface of the TS deposit increased by the thickness of the deposit.

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The Eh profiles in the depleted sediment indicated that the sediment was oxidised to the maximum depth measured.

3.3 Macomona liliana

In five instances, of the 20 post-settlement juveniles released in the bottom seawater, we counted only 18 or 19 individuals on the sediment surface immediately following their release. The missing juveniles either landed on the floor of the flume outside of the sediment core, or remained in the pipette and so excluded themselves from statistical analyses.

Burial of *M. liliana* juveniles was rapid throughout the experiment irrespective of treatment (Fig. 3). On average more than 70 (C, CTS, DTS) and 60 % (D) of the juveniles buried within the first minute. After three minutes, more than 77 (C, CTS, DTS) and 60 % (D) had buried (Immediate burial, Table 4). The bulk of the remaining individuals exhibited delayed burial so that by the end of 10 min more than 80 (C, CTS, DTS) and 90 % (D) had entered the sediment. We observed delayed search and burial only in treatments C and CTS.

Logistic regression analyses of those juvenile counts taken 10 min after start of the experiment revealed that application of a TS deposit did not decrease but significantly increased the probability of burial of juvenile *M. liliana* ($p < 0.01$). Furthermore, the probability of burial into intertidal sediment was significantly higher than that into depleted sediment irrespective of treatment (one-sided p-value of 0.01025). Because juvenile counts after four hours included individuals that had emerged from the sediment and excluded individuals that had drifted away from the sediment (D only, Table 4), we did not attempt any logistic regression analysis at this time interval.

Post-burial behaviours occurred more frequently in D and DTS treatments. Specifically D treatments exhibited emergence and drift (19 individuals). In treatments C and DTS, respectively, one and five individuals did not move after placement over the course of the experiment. Interestingly, we observed subsurface search, which is, crawling below the TS deposit, in depleted sediment (DTS and D) but not in intertidal

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sediment (C, CTS) confirming that juveniles preferred intertidal sediment over depleted sediment (Table 4).

4 Discussion

Cummings et al. (2009) demonstrated that millimetre-thin deposits of TS over defaunated intertidal sediment negatively affect the burial of post-settlement juvenile *Macomona liliana* and suggested that the juveniles are responding to reduced solute concentrations in the deposit underlying sediment but not to the TS deposit directly. Following this hypothesis, we predicted that burial into bare organic-matter depleted sediment (D) and depleted sediment to which a layer of TS was added (DTS) would not differ because the TS layer does not build up reduced solutes in the underlying sediment. Similarly, we also predicted that burial into intact, bioturbated sediment (C) and bioturbated sediment to which a TS layer was added (CTS) would not differ because the resident macrofauna oxygenates the sediment enough to offset TS induced accumulation of reduced solutes. To test these predictions, we deposited TS over both sediment types and failed to demonstrate a negative effect of TS on juvenile burial. In fact, we observed the opposite effect; deposition of TS significantly increased the probability of juvenile burial.

Put in the context of the above study by Cummings et al. (2009), our results suggest that the effect of thin TS deposits on burial behaviour of juvenile *M. liliana* is a function of the sediment disturbance history. Centimetre-thick depositions killing the resident macroinfauna (Norkko et al., 2002; Cummings et al., 2003) increase the sediment O_2 demand while decreasing the size of the surface area for the diffusive sediment–seawater exchange of O_2 and the contribution of burrow irrigation and particle displacement to this exchange. Even a thin TS deposit left atop sediment conditioned by such event may expose the juvenile recruits on its surface to reduced solutes and so alter their behaviour. The sediments used in our study, however, were either biotur-

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bated (C, CTS) or depleted of organic matter (D, DTS), and therefore, did not cause the negative effect on burial observed in Cummings et al. (2009).

Although burrow irrigation must have been stopped during application of the TS, the numerous holes in the deposit that appeared shortly after this application suggest that polychaetes quickly re-established the seawater flow through their burrow and associated subsurface solute exchange. Depending on the spacing of burrows and the diffusive properties of their walls, such solute exchange can effectively control diagenetic reactions and pore water solute concentrations in the upper sediment layer (Aller & Aller, 1998). In addition to burrow irrigation, *M. liliana* recruits moving horizontally at the boundary of the TS deposit and underlying sediment started to rework the TS deposit – an effect also observed by Cummings et al. (2009). Eventually this activity and the activity of resident macrofaunal community will work the fine particles of the TS deposit into the upper sediment layer and so diminish its effect on the sediment–seawater solute exchange.

Consistent with Cummings et al. (2009), our TS deposits modified the pore water concentrations of O_2 and hydrogen ions because they increased the diffusive distance between solute source and sink. For O_2, diffusing from the overlying seawater into the sediment, the diffusive impedance of the TS deposit caused significantly lower OPD and lower DOU (Table 3, Fig. 2). Cummings et al. (2009), reported similar effects but because their sediment exhibited a higher reactivity and a smaller area of the solute exchange surface, they observed much more pronounced decreases in OPD. Their defaunated intertidal sediment consumed on average 40 % more O_2 than the sediment used in our study (~ 1600 versus ~ 970 µmol O_2 m^{-2} h^{-1}) and O_2 penetrated this sediment only ~ 0.7 mm versus ~ 1.2 mm in our study (Table 3).

The irrigation of numerous polychaete burrows in our TS deposit-covered sediment may have prevented accumulation of reduced products of the anaerobic microbial decomposition of organic matter and so reduced the O_2 demand of the re-oxidation of these products at the oxic–anoxic boundary. In the two studies we compare here, the deposition of TS unlikely altered the contribution to the overall diffusive O_2 uptake of

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this re-oxidation but decreased that of the aerobic microbial decomposition of organic matter in a significantly smaller volume of oxygenated sediment. Explaining the rejection of the substrate by juvenile *M. liliana*, Cummings et al. (2009), suggested that the reduced depth of the oxic–anoxic boundary increased the chance of juveniles to encounter reduced pore water solutes. In our study, however, the relatively high OPD and low DOU indicate a lower pore water content of reduced solutes, apparently sufficiently low not to trigger substrate rejection.

Our pH measurements indicate that TS deposits acidify the pore water of the underlying intertidal sediment. Such decrease in the concentration of hydrogen ions may affect recruitment because it can lower the saturation of the sediment with respect to calcite and/or aragonite and so cause dissolution mortality of shell-bearing newly settled invertebrates (Green et al., 1998, 2004, 2009). Cummings et al. (2009), already demonstrated one immediate effect on pore water pH: the TS particles form a deposit of low pH that by diffusion of hydrogen ions lowers the pH of the underlying intertidal sediment. Over time (minutes to hours), the diffusive release of hydrogen ions from the TS deposit removes the concentration gradient until the pH of the deposit reaches that of the overlying bottom seawater (see Fig. 1c in Cummings et al., 2009). Our measurement 18 hours after the deposition confirmed a second mechanism that acidifies the porewater of the TS deposit underlying intertidal sediment. The TS deposit impedes the diffusion of hydrogen ions from their source in the underlying intertidal sediment – marked by a characteristic concentration peak (Fig. 2, see Jourabchi et al., 2005) – into the bottom seawater and so increases pore water concentrations, that is, it further lowers the pore water pH. The 1.5 mm thick deposit applied in Cummings et al. (2009) lowered the subsurface pH minimum by 0.15 units; the slightly thicker deposit (1.7–1.9 mm) used in our study had a lesser effect, 0.09 units. These differences may have resulted from differences in the diffusivity of the TS deposit, the depth of the pH minimum, and/or the rate of the subsurface hydrogen ion production. In contrast to the effect demonstrated earlier by Cummings et al. (2009), this effect will last as long as the TS deposit remains intact on the surface of the sediment. Regardless of which

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direction hydrogen ions diffuse across the deposit–sediment boundary, over time, the particle reworking activity of the resident macroinfauna and turbulent flow in the bottom seawater will mediate any effect of a single thin-layer deposition event on pore water pH. The role of repeated TS deposition and resuspension, however, is less predictable but subject of on-going studies.

We demonstrated that our juvenile recruits favoured intact intertidal sediment over depleted sediment. Our pore water measurements confirmed the low reactivity of the latter sediment (Fig. 2), suggesting that factors other than contact with reduced pore water solutes may affect burial. The small difference in the particle size distribution of depleted and intertidal sediment may certainly have caused differences in behaviour but many other potential factors exist. For example, recruits may favour or avoid the presence of other fauna (Cummings et al., 1996; Olivier et al., 1996; Dahms et al., 2004), chemicals associated with other fauna (Woodin 1985; Woodin et al., 1993), or certain food qualities (Nilsson et al., 2000; Stocks and Grassle, 2001). Interestingly, the three modes of post-burial behaviour – emergence, drift, and subsurface crawling – were observed only in the treatments that used depleted sediment. This observation aligns with prior studies, which demonstrated rejection of native "burnt" and defaunated sand by *M. liliana* (e.g., Cummings et al., 1993; Lundquist et al., 2004) and that the juvenile dislike sediments from which organic matter has been removed. The differences in post-burial behaviour between TS-covered (DTS) and bare depleted sediment (D, Table 4) warrant further study to clarify if, in fact, the presence of a surface layer of TS changes the bivalves' perception of their biogeophysical environment.

In summary, we failed to replicate the negative effects on burial of post-settlement juvenile *M. liliana* observed by Cummings et al. (2009) using intact bioturbated or organic-matter depleted sediment. We conclude that the effect of millimetre-thin TS deposits on the burial behaviour of *M. liliana* is context-specific, perhaps a function of the disturbance history, that is, the structure of the resident macrofaunal community and its ability to control a large share of the overall sediment–seawater solute exchange. This

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ability will certainly have limits that future studies may explore to understand thresholds in the responds of intertidal sandflat ecosystems to the deposition of TS.

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Table 1. Date of sediment collection in 2011, type and number of pore water microprofiles measured in each core, maximum and minimum flume seawater temperature during the Runs and allocation of sediment core treatments to each of the four core positions.

Run	Date	Profiles (n)	Temp. (°C) Max	Min	Core position (no. of juveniles) 1	2	3	4
1	24 May	O_2 (5)	18.4	16.9	CTS	DTS	C	D
2	26 May	O_2 (5)	20.0	18.9	D	CTS	DTS	C
3	31 May	O_2 (5)	18.3	16.6	C	D	CTS	DTS
4	2 June	Eh (2)	18.2	16.9	DTS	C	D	CTS
5	10 June	pH (2)	–	–	CTS	DTS	C	D

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Table 2. Number and diameter (Mean ± 1 SD, mm) of burrow openings, number of siphons and green and black patches showing at the surface of a TS deposit overlying intertidal sediment (CTS) four hours after application of the deposit.

	Experimental run				
	1	2	3	4	5
Burrow openings	68	75	64	37	123
Average diameter	0.66 ± 0.33	0.51 ± 0.23	0.52 ± 0.26	0.46 ± 0.23	0.75 ± 0.37
Minimum diameter	0.19	0.15	0.08	0.16	0.15
Maximum diameter	1.68	1.21	1.46	1.27	1.63
Siphons	0	32	0	12	0
Green patches	2	3	4	3	0
Black patches	4	11	8	6	1

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Table 3. Average diffusive O_2 uptake (DOU, mean ± 1 SD, $n = 5$) across the visible sediment surface and O_2 penetration depth (OPD, mean ± 1 SD) in bare intertidal (C) and depleted (D) sediments and deposit-underlying intertidal (CTS) and depleted (DTS) sediments. For CTS and DTS, OPD is the distances from the sediment–deposit to the oxic–anoxic boundary. The oxic–anoxic boundary in D and DTS was below 5 mm depth, the maximum depth measured.

Run	Treatment	DOU ($\mu mol\, m^{-2}\, h^{-1}$)	OPD (mm)
1	C	1161 ± 274	1.1 ± 0.1
	CTS	649 ± 78	0.8 ± 0.2
2	C	826 ± 201	1.4 ± 0.3
	CTS	591 ± 58	0.9 ± 0.2
3	C	935 ± 283	1.2 ± 0.1
	CTS	695 ± 133	0.8 ± 0.2
1	D	18 ± 4	> 5 –
	DTS	71 ± 7	> 5 –
2	D	16 ± 7	> 5 –
	DTS	46 ± 16	> 5 –
3	D	28 ± 15	> 5 –
	DTS	63 ± 10	> 5 –

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Table 4. Macomona liliana. Behavioural response of post-settlement juveniles placed onto the surfaces of TS-treated and bare intertidal (CTS, C) and depleted (DTS, D) sediment. Data represent the number of individuals that exhibited the behaviour, a dash indicates that a behaviour was not observed.

Response	C	CTS	D	DTS
Burial				
Immediate burial	90	91	76	87
Delayed burial	3	6	1	6
Delayed search and burial	4	1	–	–
Post-burial				
Emergence	–	–	15	–
Drift	–	–	4	–
Subsurface search	–	–	22	4
No movement	1	–	–	5

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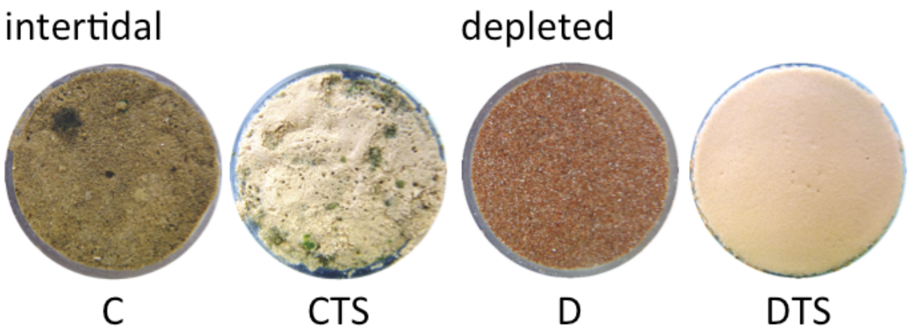

Fig. 1. Surface photographs of four sediment core treatments after 18 h: (C) intact intertidal sediment, (CTS) intertidal sediment covered with TS, (D) organic-matter depleted sediment, and (DTS) depleted sediment covered with TS. Core diameter = 5 cm.

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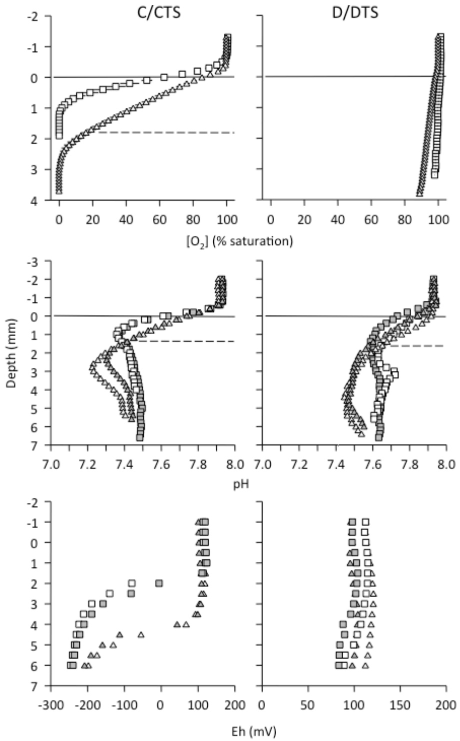

Fig. 2. Example mean pore water O_2 concentration microprofiles (mean ± 1 SD, $n = 5$) and microprofiles of pH and oxidation–reduction potential in intact intertidal (C/CTS, left panel) and organic-matter depleted intertidal sediment (D/DTS, right panel). Squares: untreated sediment surface; triangles: surface covered with a 1–2 mm thick layer of TS. The solid lines indicate the sediment–water interface and the dashed line the boundary between the TS deposit underlying intertidal sediment. Open and grey symbols represent replicate profiles. C, untreated intertidal sediment; CTS, intertidal sediment covered with TS; and DTS, organic-matter depleted sediment covered with TS.

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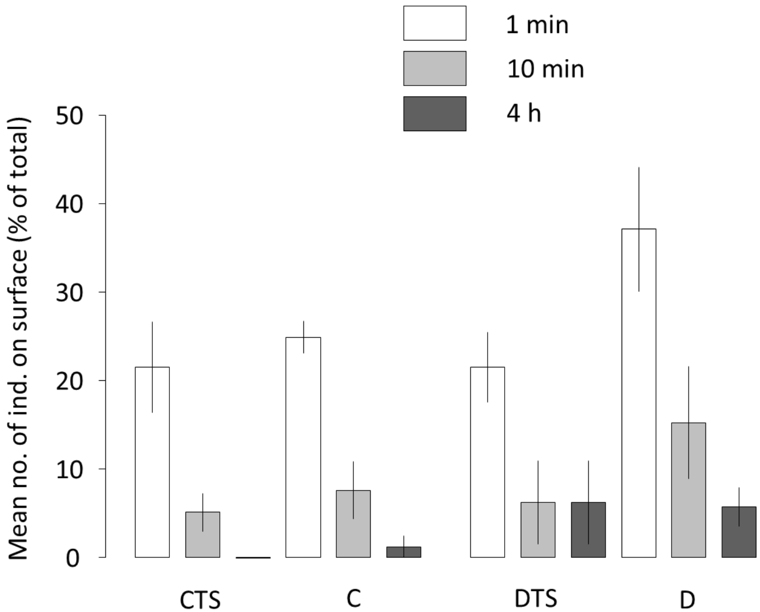

Fig. 3. Macomona liliana. Average number of post-settlement juveniles (mean ± 1 SD, $n = 5$) remaining on the sediment surface after 1 min, 10 min and 4 h after placement expressed as a percentage of the total initially added (18–20 individuals). C, untreated intertidal sediment; CTS, intertidal sediment covered with TS; and DTS, organic-matter depleted sediment covered with TS.

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