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Terrigenous deposits in coastal marine habitats: influences on sediment geochemistry and behaviour of post-settlement bivalves

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ABSTRACT: Dispersal of post-settlement juvenile macrofauna is widespread in the marine environment, yet the cues used by these organisms to assess substrate suitability are poorly known. We investigated how deposition of fine terrestrial sediments (TS, 0.5 to 1.7 mm thick) affects both the solute concentrations at the sediment–water boundary and the burrowing behaviour of juvenile tellinid bivalves *Macomona liliana*. To elucidate previously observed gradual reduction in the strength of macrofaunal responses with increasing age of deposits, the effect of TS weathered in the field for 0, 7 and 14 d, and the influence of surface and buried TS layers, were also investigated. Burrowing was significantly reduced in 0 and 7 d old surface TS compared with controls, but there was no effect of buried deposits on *M. liliana* burrowing, irrespective of sediment age. Microelectrode measurements showed that thin surface TS layers reduced the supply of O_2 to the underlying sediment, raising the position of the vertical [O_2] and pH gradients so that most of the gradient was located in the TS layer itself, rather than deeper in the sediment below it. Consequently, the likelihood of juveniles that are active in the near-surface layers being exposed to upward diffusing end products of microbial decomposition was increased. These results suggest a mechanism for the observed negative response of post-settlement *M. liliana* (and other macrofauna) to TS deposits associated with sedimentation events, and an avenue for further research into potential geochemical cues (especially pH and associated geochemical species).

KEY WORDS: Soft sediment · Terrestrial deposits · Settlement cues · *Macomona liliana* · pH · O_2 · Diffusivity · Diffusive oxygen uptake · Microprofiles

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INTRODUCTION

Dispersal of post-settlement juvenile stages of macrobenthic invertebrates is frequent and widespread in the marine environment (Beukema & Vlas 1989, Gunther 1992, Commito et al. 1995), and is important in the regulation and organisation of benthic populations and communities (Dayton et al. 1994, Norkko et al. 2001). In environments such as estuaries, which have a high proportion of direct developing species (Stocks 2002), dispersal of post-settlement life stages is especially important in the maintenance of population connectivity and persistence. In soft-sediment systems, such dispersal can occur both passively, in association with sediment bedload transport (Emerson & Grant 1991, Commito et al. 1995), and actively (e.g. Sigurdsson et al. 1976, Butman 1987). Upon arrival at a potential settlement site, individuals will encounter a sediment surface and make a decision concerning its acceptability; juveniles that accept the substrate will bury into the sediment, while those that reject the substrate will not. The cues used by post-settlement organisms to make settlement decisions are poorly known. For soft-sediment macrofauna, experimental

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work has demonstrated responses to chemicals associated with other fauna (Woodin 1985, Woodin et al. 1993), sediment food quality (Nilsson et al. 2000, Stocks & Grassle 2001), and the presence of other fauna (Cummings et al. 1996, Olivier et al. 1996, Dahms et al. 2004).

Marinelli & Woodin (2004) suggest that the acceptability of sediments to new colonists is influenced by transport and reaction processes that determine gradients in the concentrations of porewater solutes. The reaction processes within the sediment cause the production or consumption of solutes via either biologically mediated (e.g. photosynthesis of microphytes and bacterial mineralization of organic matter) or abiotic means (e.g. mineral dissolution, Jørgensen & Boudreau 2001). Transport processes such as diffusion and advection displace solutes within the sediment and through the sediment–water interface. Disturbance of the sediment–water interface can result in short- and long-term modifications of such gradients, thus potentially affecting colonisation of the sediment. Larvae and juveniles of some species can differentiate between disturbed and undisturbed surface (top few mm) sediments in response to short-term (min to h) changes in gradients of porewater O_2 and ammonium (Woodin et al. 1995, Woodin 1998, Marinelli & Woodin 2002, 2004). Periodic/recurring short-term changes in porewater solute gradients may result from, for example sediment disruptions by the activity of animals, or by wind-waves (Vopel et al. 2007). In contrast, disturbances that involve changes in the solid phase of the sediment can modify solute gradients at the sediment–water interface more persistently (Williamson et al. 1999, Glud et al. 2007).

An example of a persistent and large-scale disturbance is the deposition of terrigenous sediments in coastal environments (e.g. Milliman & Meade 1983, Thrush et al. 2004). Terrigenous sediments are often supplied to coastal habitats during discrete rainfall events, as suspended matter via waterways, and/or directly as a result of landslides. Thick (>2 cm) terrestrial sediment (TS) deposits require significant exposure to wind and waves, or remobilization by crabs during their burrowing activities to become dispersed (Norkko et al. 2002). Thinner layers (3 to 10 mm) remain visually obvious on sandflats even 10 d after their deposition (Lohrer et al. 2004). Layer thickness decreases over time due to gradual erosion, and/or mixing with ambient sand washed in from the surrounding sandflat. Moreover, the properties of the deposits change over time, with coarse sand and chlorophyll *a* levels increasing and organic content decreasing (Norkko et al. 2002, Cummings et al. 2003, Lohrer et al. 2004). Thus, it is obvious how TS that are deposited atop marine sediments may alter sedimentary transport and reaction processes and, consequently, any associated geochemical signals.

Field experiments have shown that deposition of thick (>2 cm) TS layers often results in mass mortality of resident infauna, and that recovery is very slow (i.e. years; Norkko et al. 2002, Cummings et al. 2003). Thinner deposits (1 to 20 mm) also negatively affect macrofaunal communities, causing declines in densities of common species, and in total numbers of taxa and individuals (Thrush et al. 2003, Lohrer et al. 2004). Furthermore, post-settlement bivalves exposed to TS deposits exhibit reduced burrowing rates and dispersal abilities, suggesting that settlement on such deposits can have a lasting effect, even if an individual is able to find a more suitable habitat at a later date (Cummings & Thrush 2004). These observations may partially be explained by modification of porewater solute transport and reaction processes by the TS deposits.

This paper describes a laboratory experiment designed to mimic the effects of thin (<1.7 mm) deposits of TS on sandflats in order to understand the resulting biogeochemical changes, and to better interpret the observed responses of post-settlement bivalve colonists. Changes in the physicochemical properties of the surface sediments were investigated at a micro-scale, relevant to an individual potential colonist's site choice. We used surface and buried deposits of fresh and weathered TS to account for the 2 *in situ* observations mentioned above: (1) over time, TS deposits may remain intact on the surface of the sediment or become gradually buried as they get covered by surrounding sediment transported as bedload (Norkko et al. 2002, Lohrer et al. 2004); and (2) the physicochemical properties of TS change with increasing length of exposure to the environment ('age'; see Cummings et al. 2003, Lohrer et al. 2004).

We chose post-settlement juveniles of the tellinid bivalve *Macomona liliana* (Iredale, 1915) as the study organism. *M. liliana* are common in New Zealand benthic communities, and are highly mobile post-settlement dispersers (e.g. Norkko et al. 2001). O_2 was measured because of its role in multiple metabolic processes and its strong influence on the gradients of other redox-active porewater solutes (Jørgensen & Boudreau 2001). pH was studied as it is considered a master variable that is linked to all major biogeochemical reaction processes in sediments (Jourabchi et al. 2005). Furthermore, pH influences the toxicity of several chemical species (e.g. H_2S, NH_3; Ben-Yaakov 1973, Boudreau & Canfield 1988, Bagarinao 1992), shell formation (e.g. Green et al. 2004, Gazeau et al. 2007) and likely also the physiological condition of benthic organisms (Kleypas et al. 2006), particularly the early life history stages. Concentration gradients of solutes at the sediment–water interface result from

their production and consumption, and the impedance by the sediment of their diffusive transport. To characterise the latter variable, we measured the apparent diffusivity of the TS deposits.

MATERIALS AND METHODS

Experimental design. To investigate the effects of TS deposits on the burrowing behaviour of *Macomona liliana* juveniles, and on porewater gradients in O_2 concentration (hereafter [O_2]) and pH, a series of experiments was conducted in low-flow aquaria in a constant temperature laboratory. We measured changes in the microprofiles of O_2 and pH in response to TS deposits, and the burial responses of juvenile bivalves into the same sediments. We chose 3 sediment treatments: surface TS deposits (TS-surface), buried TS deposits (TS-buried), and natural surface sediments obtained from the site where the juvenile *Macomona liliana* were collected (control sediment, C). The first 2 treatments were designed to reflect the fact that TS deposits may remain intact on the surface of the sandflat (TS-surface) or may become buried by ambient sediment moving with bedload (TS-buried). The TS-surface treatment consisted of 3 cm of control sediment, which was covered by a thin (<1.7 mm) layer of TS. The TS-buried treatment consisted of 3 cm of control sediment, which was covered by a thin layer of TS and a ~1 mm thick layer of control sediment. The control sediment treatment consisted of 3 cm of sediment only. To investigate the responses of *Macomona liliana* juveniles to deposits of TS that were weathered for different periods, 3 separate experiments were conducted using TS that mimicked new deposits (0 d old, run A), or had been aged in the field by deposition onto an intertidal sandflat for 7 d (run B) or 14 d (run C). The different TS ages are hereafter referred to as 0 d TS, 7 d TS and 14 d TS. Four replicates were used per treatment per run.

Sediments and bivalves. TS was obtained from the catchment above Mahurangi Harbour, on the east coast of the northern North Island, New Zealand. This is typical of the TS which is washed into New Zealand's North Island estuaries and harbours during storms/heavy rain events. The 'source plot' of TS was established at mid-tide level on the Wairoa Island sandflat at Manukau Harbour, Auckland, in the following way: TS was mixed with seawater (50:50 seawater:sediment) and deposited into a 2 m diameter area on the sandflat to a depth of 5 cm. The 7 and 14 d TS were collected from this source plot at the beginning of their respective runs, 7 and 14 d later, respectively. The 0 d TS was an identical mix that had not been deposited on the sandflat. The TS was predominantly comprised of fine sand in all runs (78 to 80% of volume), with a significant portion of silt (8 to 15%; Table 1). The 7 d TS (run B) contained slightly more medium sand, and less silt than the 0 or the 14 d TS (i.e. 3.5 to 4.5% differences; Table 1). Control sediment and juveniles of *Macomona liliana* were collected from the Wairoa Island sandflat at the beginning of each run. The control sediment was sieved (0.5 mm mesh) and frozen to defaunate it, and then thawed and thoroughly washed with seawater. This sediment was predominantly comprised of medium, coarse and fine sand (Table 1).

Juvenile *Macomona liliana* were collected by sieving surface sandflat Wairoa Island sediments in seawater (0.5 mm mesh); the material retained on the sieve was returned to the laboratory and individuals <3 mm (shell length) were sorted under a stereomicroscope. The bivalves were kept in filtered, aerated seawater under the same temperature and light regime as the experiments conducted (see below), and were used in the experiments within 3 d of collection.

Setup. Experiments were conducted in rectangular aquaria ($78 \times 9 \times 10$ cm; 522 cm^2 working surface area), with recirculating seawater, under constant temperature and 24 h dim light. Seawater flow in the working area of the aquaria was ~2 cm s^{-1}. A bilge pump (Johnson 32-1015-01) pumped seawater into each aquarium from separate 15 l reservoirs through a silicon tube. To dissipate turbulence generated by the in-flowing water, a baffle and a straw array were inserted at 10 and 13 cm, respectively, from the upstream end of each aquarium. The baffle consisted of a plate with numer-

Table 1. Grain size composition (% volume) of the terrestrial (TS) and control sediments used during the experiments. Composition was determined using a Galai particle analyser (Galai Cis-100; Galai Productions). Classifications follow the Wentworth scale

TS / sediment	Clay (<3.9 µm)	Silt (3.9–62.5 µm)	Fine sand (62.5–500 µm)	Medium sand (250–500 µm)	Coarse sand (500–2000 µm)	Gravel/shell hash (>2000 µm)
0 d TS (run A)	0.24	12.90	80.24	3.42	2.24	0.96
7 d TS (run B)	0.15	8.55	79.86	7.06	3.98	0.40
14 d TS (run C)	0.29	15.10	78.33	2.61	2.77	0.91
Control sediment	0.00	0.56	20.20	37.14	32.91	9.20

ous small holes (0.5 cm diameter), and the straw array (7 cm high × 7 cm long) was comprised of 0.5 cm diameter straws. Water travelled past the baffle, through the straw array, over the sediment, and then left the aquaria by gravity through a horizontal row of holes along the upper edge of the aquaria end walls. Water depth in the aquaria was ~9 cm. Seawater temperature and conductivity were monitored in one aquarium throughout the experiments, using a PortaMess 913 (Knick) and a conductivity sensor (SE204, Knick), respectively. The temperature of the seawater was 14.5 ± 0.2°C, and the conductivity was 41.7 ± 0.5 mS (means ± SDs, n = 9).

Protocol. Sediment was added to each of 4 aquaria to a depth of 3 cm, and the aquaria were filled with seawater, which was then kept aerated using aquarium pumps. After 6 to 8 h, the aerators were removed, flow was initiated, and a TS suspension was added to those aquaria requiring a TS treatment. To do so, aliquots of 40 cm^3 of TS were mixed with seawater to make the sediment liquid enough to pour. This mixture was then slowly added to the aquaria upstream of the baffles and straw arrays. The TS gradually and evenly settled on the surface of the sediment over time. The aquaria were then left overnight (14 h). This resulted in TS-surface deposits ranging from 0.5 to 1.7 mm thick over the experiment (derived from microelectrode measurements; see below; Table 2). The next morning, the flow was stopped, seawater in the aquaria and reservoirs was changed (taking care not to disturb the TS deposits), and the flows were reinstated. A thin layer of control sediment was then added to the surfaces of the sediment in those aquaria requiring a TS-buried treatment: aliquots of 40 cm^3 of sediment were mixed with seawater and added at the water surfaces along the length of the working area of the aquaria, allowing the sediment to settle through the water columns to the aquarium floors. It was not possible to add this heavier sediment to the aquaria using the same methodology as that used to add the TS suspensions. Our rationale for adding the TS to the flumes in this way was based on our observations of how this occurs in the field situation. TS commonly enters an estuary in suspension after being mixed with seawater, and settles on the seafloor once tides/currents have subsided (Cummings et al. 2003).

Table 2. Thickness (mm) of the terrestrial sediment (TS) layer of replicate TS-surface treatments

Run (TS age)	1	2	3	4	Mean ± SD
A (0 d)	1.0	0.8	1.1	1.7	1.15 ± 0.39
B (7 d)	0.8	1.5	1.4	0.6	1.08 ± 0.44
C (14 d)	1.1	0.5	1.0	1.1	0.93 ± 0.29

One hour later, 50 *Macomona liliana* juveniles were added to each aquarium by introducing them just below the water surface using a pipette and allowing them to drift to the sediment surface. Due to the time required to measure microprofiles of porewater solute concentrations, microelectrode measurements could be made in only 4 aquaria on a single day; thus, 1 to 2 replicates of each of the 3 treatments were run each day, and each run was completed over 3 d.

Preliminary measurements. To estimate the incubation time needed to establish 'steady state' conditions in the TS treatments, time series of [O_2], pH and apparent H_2 diffusivity were simultaneously measured over a period of 80 min starting at 6 min before the addition of a 0 d TS suspension to one aquarium containing 3 cm of control sediment. Three sensors were positioned at 0.1 to 0.2 mm above the surface of the control sediment: a needle-type, fiber-optic O_2 microsensor (Precision Sensing; tip diameter <0.05 mm, 90% response time <0.5 s), a pH microelectrode (Unisense; tip diameter: 0.05 mm) and a diffusivity microelectrode (Unisense; tip diameter: 0.1 mm; Revsbech et al. 1998). In addition to the time-series measurements, one vertical O_2 profile and one pH profile were measured before and 2 h after the addition of the TS suspension.

Behavioural observations of *Macomona liliana*. To determine the burrowing response of post-settlement *Macomona liliana* juveniles to the treatments, the number of individuals that remained on the sediment surface (i.e. had not buried) after 1, 2 and 4 h was recorded. Once they had buried, it was evident from movement traces on the sediment surface that the juveniles were crawling below the sediment surface; this was noted in all treatments.

Microprofiles. One [O_2] profile, one pH profile, and 2 profiles of apparent H_2 diffusivity were measured, normal to the sediment surface and across the sediment–water interface, in each replicate aquarium at a resolution of 0.1 mm. O_2 was measured with a Clark-type microelectrode, with an internal reference and a guard cathode (tip diameter: 0.05 mm, stirring sensitivity <1%, 90% response time <1 s) (Revsbech 1989). pH and the apparent H_2 diffusivity [the product of sediment porosity (ϕ) and the effective H_2 diffusion coefficient (D_S)] were measured as described above. Measurement of the apparent H_2 diffusivity was based on the diffusion of H_2 from an internal sensor reservoir, through an internal diffusion barrier positioned within the sensor tip, and out into the surrounding porewater of the sediment (Revsbech et al. 1998). The [H_2] at the tip of the sensor was then a function of the apparent diffusivity in the medium. The internal reservoir was continuously flushed with H_2 at a constant flow rate.

To measure profiles, one O_2 and one apparent diffusivity microelectrode were mounted on a motorized

micromanipulator that was attached to a stand. The 2 electrodes were positioned at the sediment surface, and were arranged in a line perpendicular to the direction of seawater flow. The tips were aligned with each other using the seawater surface as a reference. After one profile was completed with each microelectrode, the O_2 microelectrode was replaced with a pH microelectrode, the tip of the pH microelectrode was aligned with the tip of the apparent diffusivity microelectrode as described above, and one profile was again measured with each electrode. The PC Windows program Profix (Unisense) controlled the stepwise movement of the micromanipulator via a motor controller, and read the data automatically from the microsensor amplifiers via an A/D converter (ADC-101, Pico Technology) connected to the parallel port of a laptop PC.

All microelectrodes were calibrated once a day at the experimental temperature. The apparent diffusivity microelectrode was calibrated by measuring the electrode current in 2 media of known diffusivity: 0.04–0.06 mm glass beads and the overlying static seawater. The reference value for the diffusivity of H_2 in static seawater was calculated from the diffusivity of O_2 (Broecker & Peng 1974) corrected for temperature according to Yuan-Hui & Gregory (1974). The apparent diffusivity in glass beads was taken from Revsbech et al. (1998). The O_2 microelectrode and the fiber-optic microsensor were calibrated in 100% air-saturated seawater and in seawater that had been deoxygenated with sodium sulfite. Standard buffers were used to calibrate the pH microelectrode.

Data analysis. The relative positions of the surfaces of the control sediment and the upper and lower boundary of the surface deposit of TS along a vertical scale were identified by distinct changes in the slope of the $[O_2]$ profiles. Such changes resulted from differences in the solute diffusivity in free seawater and in the 2 types of sediment. The top of the diffusive boundary layer (DBL) (i.e. the boundary between the free-flowing water and the diffusive boundary layer) was determined as the intersection between the extrapolated linear $[O_2]$ gradient in the DBL and the constant $[O_2]$ of the overlying mixed seawater (Jørgensen & Des Marais 1990).

The average apparent diffusivities (ΔD_S) of the control sediment and the surface and subsurface TS deposits were estimated by averaging data points along the profiles through the deposits or control sediment. To account for the spatial resolution of the diffusivity microelectrode, data points measured within 0.2 mm of the interfaces between seawater, control sediment and TSwere excluded from this calculation (for details, see Revsbech et al. 1998).

The O_2 consumptions of the sediment treatments were estimated in 2 ways, i.e. using both the measured porewater $[O_2]$ profiles and the profiles measured across the DBL above the sediment surface. The profiles across the DBL were used to estimate the rate of the diffusive O_2 uptake (DOU) following Jørgensen & Revsbech (1985) and Rasmussen & Jørgensen (1992). The sediment $[O_2]$ profiles were used to model the depth-integrated O_2 consumption rates (R) and a depth profile of the O_2 consumption following Berg et al. (1998). To do so, measured diffusivities of the 2 different sediment types (terrestrial and control sediment) and the depths of their interfaces were required. O_2 profiles measured in the TS-buried treatment did not allow detection of this interface. Consequently, no depth-integrated O_2 consumption and no O_2 consumption profiles were computed, i.e. the O_2 consumption of the TS-buried treatment was calculated only from $[O_2]$ profiles in the DBL.

The significance of the differences in apparent diffusivity, bottom water pH and the change in porewater pH (ΔpH) among treatments (i.e. control, TS-surface, TS-buried) were assessed separately for each run using ANOVA (PROC GLM, SAS Institute 1999). Differences among treatments in the numbers of *Macomona liliana* individuals that did not burrow over time (i.e. 1, 2 and 4 h after addition) were also tested separately for each run using repeated measures ANOVA (PROC GLM, SAS Institute 1999). When time × treatment interaction terms were significant, the analyses were conducted separately for each time. Actual differences between treatments were determined using Tukey's tests. Prior to the ANOVAs, the normality and homogeneity of variances of the data were assessed using Shapiro-Wilks and F-max tests, respectively, and data were rank transformed if required. To determine whether the effect of the TS-surface treatment on the DOU differed with 'age' of the TS, the change in DOU versus the thickness of the deposit was plotted separately for each TS age/run, and the slope of the linear regression through each set of data points was calculated. The significance of the differences in slopes among runs was assessed using ANCOVA (PROC GLM, SAS).

RESULTS

Preliminary measurements

Measurements of $[O_2]$ made in one aquarium prior to the addition of TS revealed an effective DBL thickness of ~0.4 mm (Fig. 1A, hollow circles). O_2 penetrated the sediment down to 0.9 mm, and the pH declined from 8.02 in the bottom water, to a minimum of 7.47 in the sediment porewater at 0.6 mm depth (Fig. 1B). Addition of 0 d TS to this aquarium resulted

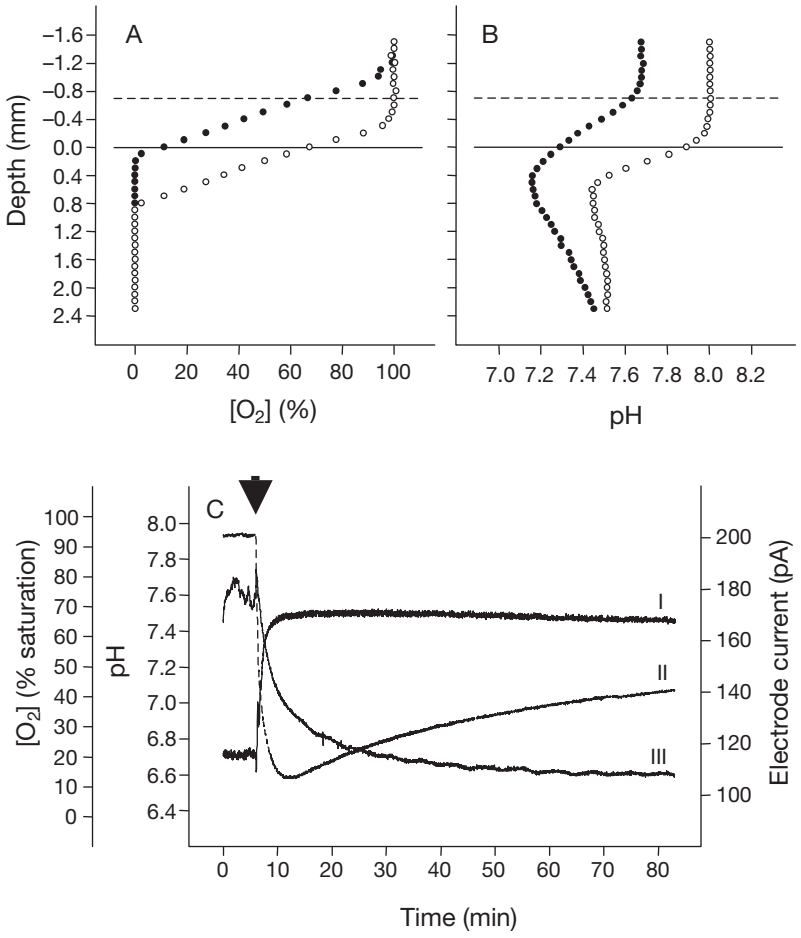

Fig. 1. Vertical profiles of (A) $[O_2]$ and (B) pH recorded 10 min before (○) and 2 h after (●) a 40 cm^3 0 d terrestrial sediment (TS) suspension was added to an aquarium containing control sediment. The TS–seawater interface (– – –) is located 0.7 mm above the original sediment surface (——). (C) Simultaneous time-series measurements of $[O_2]$ (curve III), pH (curve II), and H_2 diffusion (curve I) in the diffusive boundary layer 0.1 to 0.2 mm above the sediment surface. The TS suspension was added to the aquarium 6 min after the recording began (arrow)

in an elevation of the sediment surface by 0.7 mm. Consequently, the tips of the microelectrodes that were initially positioned in the DBL at 0.1 to 0.2 mm above the sediment surface became buried in the deposit as sedimentation progressed. The signal of the H_2 electrode was initially low, but had increased to a high and constant value (Fig. 1C) by only ~10 min after TS addition, indicating a rapid initial deposition and no subsequent gradual compaction of the surface layer. $[O_2]$ decreased from ~75 to 37% saturation within 5 min of TS addition, and continued to decrease slowly as the TS layer built up (Fig. 1C). In contrast, the pH decreased from 7.94 to a minimum of 6.58 within 5 min and increased slowly thereafter (Fig. 1C). Two hours after TS addition, the O_2 penetration depth measured from the surface of the TS layer was 1.0 mm (Fig. 1A, solid circles). As the surficial TS deposit was 0.7 mm thick, O_2 had penetrated only 0.3 mm into the underlying control sediment. Also after 2 h, the pH of the bottom water and the minimum pH in the sediment porewater had decreased by ~0.3 (Fig. 1B).

Apparent gas diffusivities

The average apparent diffusivities of the control sediments were similar in all runs (0.62×10^{-5} to 0.64×10^{-5} cm^2 s^{-1}; Table 3). Diffusivities of the surface TS deposit ranged from 1.07×10^{-5} to 1.19×10^{-5} cm^2 s^{-1} throughout the experiment, and were significantly higher than those of the control sediment in all runs (Table 4). Inspection of the microprofiles of apparent diffusivity measured in the TS-buried treatment revealed no distinct changes in H_2 diffusivity along the profile through the surface layer of the control sediment, the TS deposit, and the underlying sediment, but rather a gradual increase in diffusivity with depth. The particles of the control sediment partially sank into the surface deposit of TS so that the uppermost sediment was comprised of particles of control sediment mixed with TS. To estimate the diffusivity of this mixed layer, we averaged data points along the profiles down to the depth at which the apparent diffusivity approached that of the control sediment. These estimates were slightly higher (0.66×10^{-5} to 0.72×10^{-5} cm^2 s^{-1}), but were significantly different from those of the control treatment only in run B (Table 4).

O_2 penetration, DOU, *R* and O_2 consumption profiles

O_2 penetration depth

The average O_2 penetration depth, calculated over all 12 replicates for each treatment, was lowest in the control sediment treatment (0.70 ± 0.13 mm) and highest in the TS-surface treatment (1.35 ± 0.28 mm). In the TS-buried treatment, O_2 penetrated down to 0.90 ± 0.16 mm.

Table 3. Apparent diffusivity (ϕD_S) of control sediment (control, 0.3 to 5 mm depth), surface terrestrial sediment (TS) deposit (TS-surface), and buried TS deposit (TS-buried, 0.3 to 1.3 mm depth); average pH of the bottom seawater in runs and treatments (n = 4); and magnitude of drop in pH (ΔpH) along a vertical profile measured from a position above the diffusive boundary layer to 4 mm deep in the control sediment. Values are means ± SDs

Treatment	ϕD_S ($\times 10^{-5}$ cm^2 s^{-1})	Bottom seawater pH	Pore seawater ΔpH
Run A (0 d)			
Control	0.64 ± 0.06	7.62 ± 0.04	0.59 ± 0.01
TS-buried	0.72 ± 0.16	7.62 ± 0.10	0.67 ± 0.06
TS-surface	1.07 ± 0.04	7.49 ± 0.04	0.74 ± 0.06
Run B (7 d)			
Control	0.62 ± 0.02	7.69 ± 0.07	0.77 ± 0.02
TS-buried	0.68 ± 0.01	7.59 ± 0.06	0.91 ± 0.10
TS-surface	1.16 ± 0.03	7.66 ± 0.10	0.85 ± 0.10
Run C (14 d)			
Control	0.64 ± 0.03	7.65 ± 0.03	0.73 ± 0.05
TS-buried	0.66 ± 0.07	7.63 ± 0.05	0.71 ± 0.08
TS-surface	1.19 ± 0.04	7.67 ± 0.05	0.72 ± 0.07

DOU and *R*

The average DOU of the control sediment (DOU_C), estimated from the slopes of the average $[O_2]$ profiles in the DBL of runs A to C, was 1605 µmol m^{-2} h^{-1} (Table 5). The average DOU of the TS-surface treatment (DOU_{surf}) was similar (1501 µmol m^{-2} h^{-1}), while that of the TS-buried treatments (DOU_{sub}) was lower (1176 µmol m^{-2} h^{-1}). Modeling of the 12 porewater $[O_2]$ profiles measured in the control and the TS-surface treatments revealed average depth-integrated *R* that were ~20 and ~50% lower than the respective averages for DOU. The relationship between the change in *R* and the thickness of the TS-surface deposit revealed by linear regression showed that a surface layer of 0 d TS (run A) reduced the total depth-integrated O_2 consumption of the sediment (incl. the TS-surface deposit) by 643 µmol m^{-2} h^{-1} mm^{-1} relative to control sediments, whereas 7 and 14 d old TS-surface deposits reduced *R* by only 397 and 487 µmol m^{-2} h^{-1} mm^{-1}, respectively (Table 6; p = 0.0055, ANCOVA).

Table 4. Results of ANOVA to investigate differences in apparent diffusivity, bottom water pH, and change in pore seawater pH among treatments of a particular run. Multiple comparisons: Duncan's tests; TS-surface: surface terrestrial sediment, TS-buried: buried terrestrial sediment, and C: control sediment treatments. Trt: treatment; ns: not significantly different (p > 0.05)

Run (TS age)		Pr > *F*	*F*-value	MS	SS	df	Multiple comparisons
Apparent diffusivity (ϕD_S)							
A (0 d)	Trt	0.0094	9.78	30.38	60.75	2	TS-surface > TS-buried, C
	Error			3.11	21.75	7	
B (7 d)	Trt	<0.0001	41.14	64.00	128.00	2	TS-surface > TS-buried > C
	Error			1.56	14.00	9	
C (14 d)	Trt	0.0056	9.74	48.56	97.13	2	TS-surface > TS-buried, C
	Error		44.88	4.99		9	
Bottom water pH							
A (0 d)	Trt	0.0390	4.75	0.02	0.043	2	C, TS-buried > TS-surface
	Error			0.00	0.04	9	
B (7 d)	Trt	0.3093	1.36	0.01	0.02	2	ns
	Error			0.05	0.01	8	
C (14 d)	Trt	0.4809	0.80	0.00	0.00	2	ns
	Error			0.00	0.02	9	
Change in pore seawater pH (ΔpH)							
A (0 d)	Trt	0.0064	9.34	0.02	0.05	2	TS-surface, TS-buried > C
	Error			0.00	0.02	9	
B (7 d)	Trt	0.1529	2.40	0.02	0.03	2	ns
	Error			0.01	0.06	8	
C (14 d)	Trt	0.9280	0.08	0.00	0.00	2	ns
	Error			0.00	0.04	8	

Table 5. Diffusive oxygen uptake (DOU ± SD, µmol m^{-2} h^{-1}) and/or depth-integrated O_2 consumption (*R* ± SD, µmol m^{-2} h^{-1}) of control sediment (DOU-control, *R*-control), TS-surface treatments (DOU-surface, *R*-surface), and TS-buried treatments (DOU-buried). DOU was calculated from the $[O_2]$ gradient in the diffusive boundary layer. *R* was estimated from porewater $[O_2]$ profiles

Run (TS age)	DOU-control	*R*-control	DOU-surface	*R*-surface	DOU-buried
A (0 d) (n = 4)	1613 ± 318	1365 ± 93	1630 ± 481	739 ± 180	954 ± 148
B (7 d) (n = 4)	1619 ± 549	1062 ± 254	1324 ± 402	854 ± 166	1465 ± 124
C (14 d) (n = 4)	1564 ± 429	1369 ± 667	1548 ± 529	793 ± 169	1108 ± 336
Overall (n = 12)	1605 ± 401	1292 ± 388	1501 ± 449	796 ± 156	1176 ± 302

Table 6. Reduction in depth-integrated O_2 consumption (ΔR-surface) caused by a 1 mm thick surface terrestrial sediment (TS) deposit relative to the control sediment, and the contributions of the surface TS deposit and the underlying sediment to the total depth-integrated O_2 consumption (R-surface, mean ± SD, n = 4). Values for ΔR-surface were derived using the slope of the linear regression of measurements from surface TS and control sediment treatments

Run (TS age)	ΔR-surface (μmol m^{-2} h^{-1} mm^{-1})	R^2	R-surface (μmol m^{-2} h^{-1}) Surface TS deposit	Underlying control sediment
A (0 d)	643	0.974	137 ± 90	467 ± 160
B (7 d)	397	0.978	252 ± 88	602 ± 105
C (14 d)	487	0.940	121 ± 119	672 ± 210

O_2 consumption profile

In the control sediment, O_2 consumption was highest just beneath the sediment–water interface (Fig. 2). In contrast, O_2 consumption peaked at the boundary between the oxic and the anoxic layer in the TS-surface treatments (see Fig. 3 for example profiles). Depending on the thickness of the surface TS deposit, this boundary was positioned near the surface of the deposit-underlying sediment or at some depth in this sediment. The average depth-integrated O_2 consumption of the sediment underlying a TS-surface deposit increased with age of the TS (Table 6). The depth-integrated O_2 consumption of the TS-surface layer itself was highest in the 7 d TS (run B) and lowest in the 14 d TS (run C, Table 6). The O_2 profiles measured in the TS_{sub} treatment (Fig. 4) did not allow detection of the interfaces between the 2 sediment types, terrestrial sediment and control sediment.

pH

The pH of the aquarium bottom water was very similar in all treatments and runs (i.e. average pH_{bw} >7.59), although it was slightly lower in the 0 d TS-surface treatment than in the remaining treatments of run A (average: 7.49, Table 3; p = 0.0390, Table 4). Table 3 shows the magnitude of change in pH (ΔpH) across the DBL to 4 mm deep in the underlying control sediment per treatment per run. In the control sediment treatments, pH decreased by maximally 0.59 ± 0.01 in run A, 0.77 ± 0.02 in run B, and 0.73 ± 0.05 in run C. Significant differences in ΔpH between treatments were detected only in run A, where the magnitude of the decrease was larger in the TS-surface and TS-buried treatments than in the control treatment (Table 3; p =

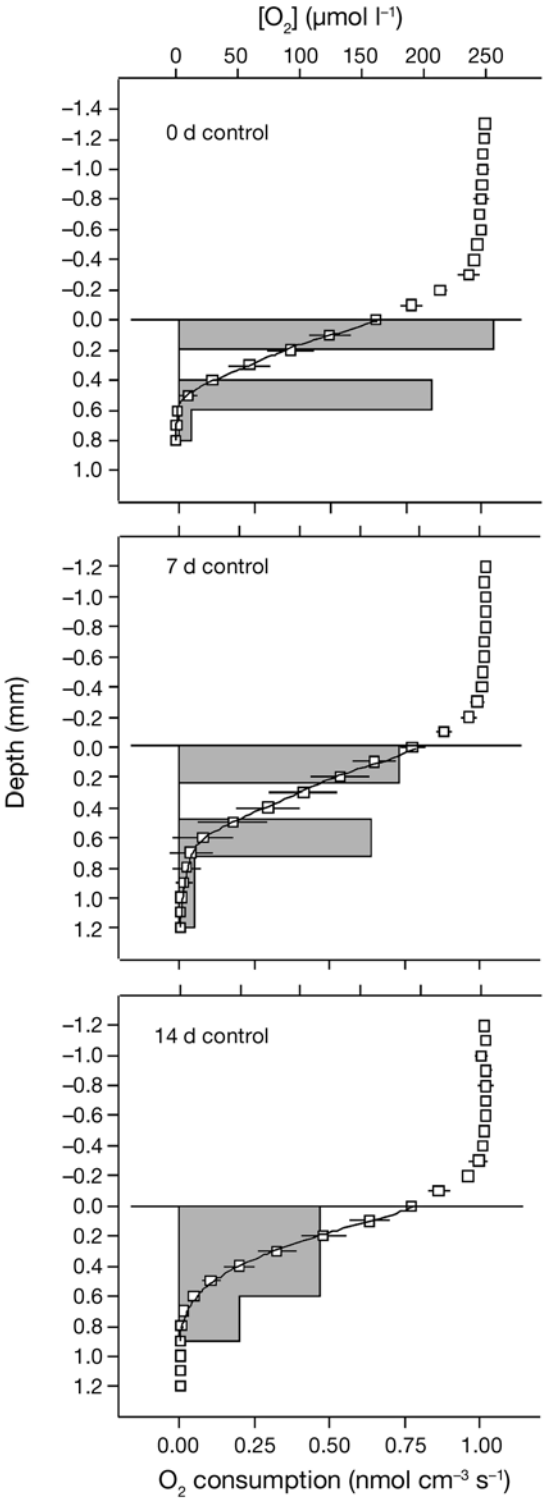

Fig. 2. Examples of vertical $[O_2]$ (□) and O_2 consumption (bars) profiles through the sediment–water interface of the control treatment (means ± SD, n = 4) for each experimental run. O_2 consumption profiles and fits (R^2 > 0.9991) were modeled as described by Berg et al. (1998). (——) Sediment surface. Concentrations are given per volume of porewater, but consumption rates are given per volume of sediment

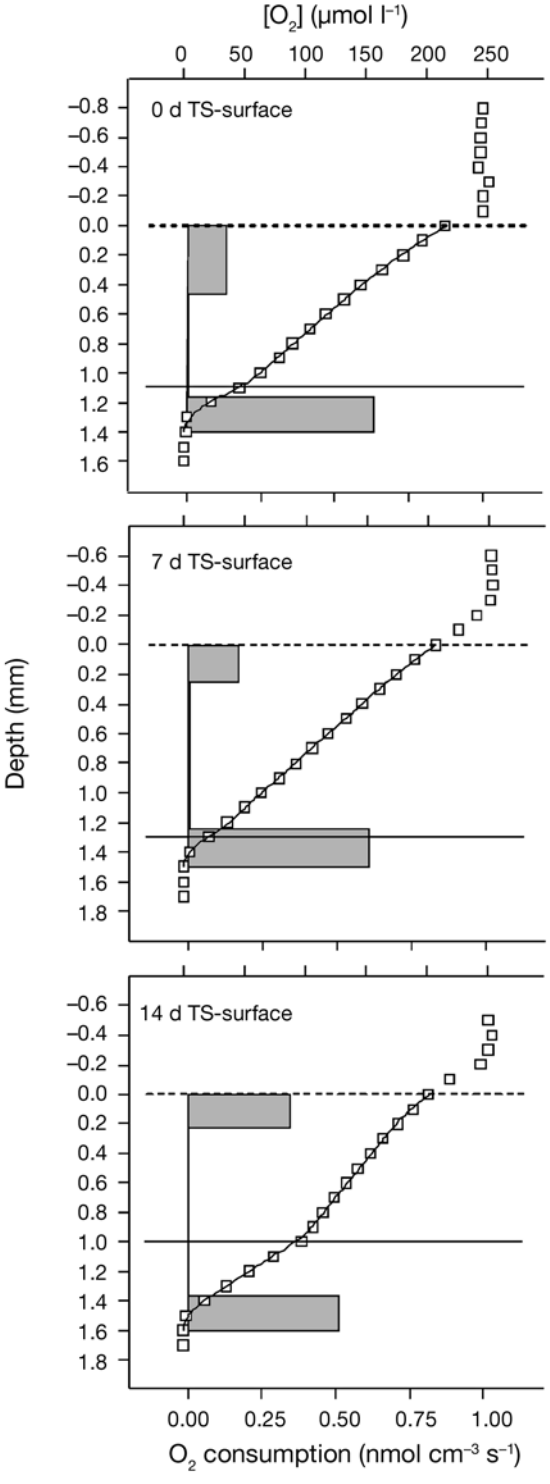

Fig. 3. Examples of vertical $[O_2]$ (□) and O_2 consumption (bars) profiles through the sediment–water interface of the TS-surface treatment for each experimental run. O_2 consumption profiles and fits ($R^2 > 0.9991$) were modeled as described by Berg et al. (1998). (——) Interface between the TS-surface deposit and the underlying sediment, (------) TS surface. Concentrations are given per volume of porewater, but consumption rates are given per volume of sediment

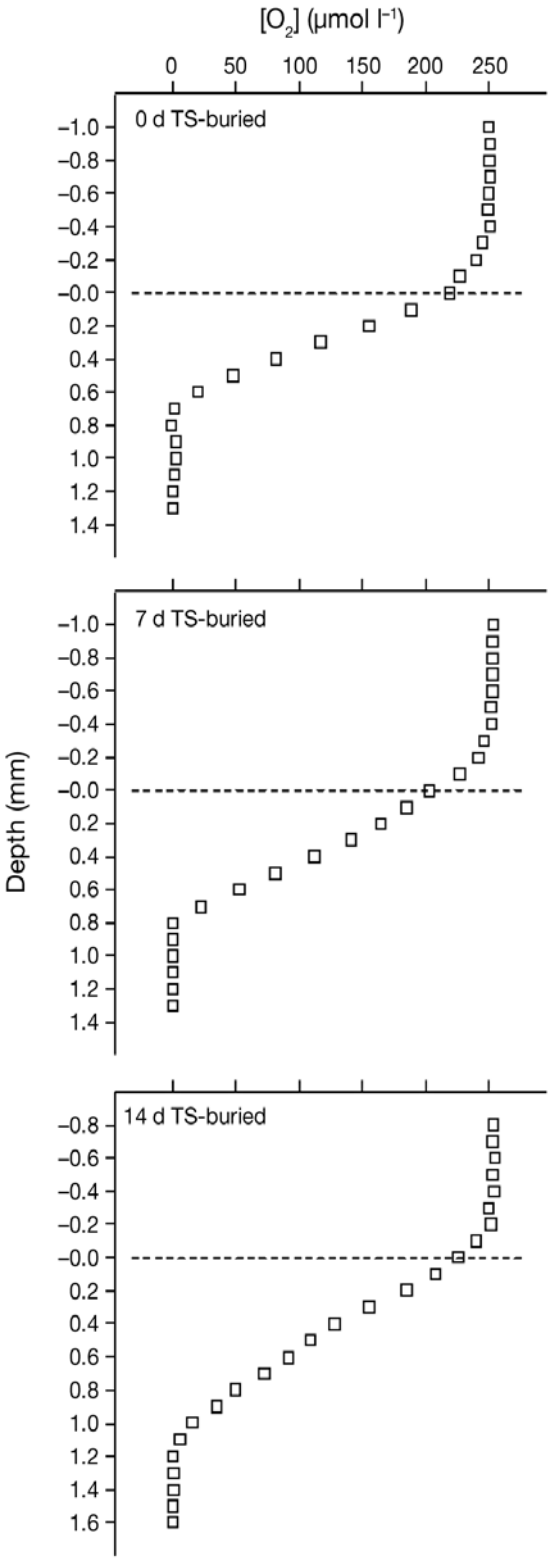

Fig. 4. Examples of vertical $[O_2]$ profiles (□) through the sediment–water interface of the TS-buried treatment for each experimental run. (- - - -) Surface of the TS-buried treatment. Concentrations are given per volume of porewater

0.0064, Table 4). In the TS-surface treatment, the pH shift (ΔpH_{surf-C}) decreased with increasing TS age (i.e. 0.15 ± 0.05, 0.09 ± 0.08, and −0.03 ± 0.10 in runs A to C, respectively) (Table 3). In the TS-buried treatment, the pH shift (ΔpH_{sub-C}) was highest in run B and lowest in run C (i.e. 0.08 ± 0.06, 0.13 ± 0.08, and 0.02 ± 0.02 in runs A to C, respectively). Interestingly, the pH shift in the TS-surface treatment was highly correlated with apparent diffusivity (i.e. R = −0.891); such a strong correlation was not observed in the TS-buried treatment (i.e. R = 0.376).

Behaviour of *Macomona liliana*

Burial of *Macomona liliana* juveniles was high throughout the experiment irrespective of treatment (>70%; Fig. 5). However, significant negative effects of surface TS deposits were detected in runs A and B (Table 7). Significantly fewer individuals had buried in the TS-surface than in the control treatments 1, 2 and 4 h after their addition to the aquaria with 0 and 7 d TS-surface sediments (Table 7). For the 0 d TS-surface treatment, these differences equate to an average of 6 to 7 more individuals (or 10.5 to 13.5% of the total number added; Fig. 5) that had not buried into the sediment. For the 7 d TS-surface treatment, this difference was slightly higher, at 6 to 10 ind. (11.6 to 20% of those added). Although the burrowing response of *Macomona* in the TS-buried treatments was always intermediate between that in the TS-surface and control treatments (Fig. 5), there was no statistically significant effect of the TS-buried treatment of any age on burrowing (Table 7). Similarly, no burrowing differences were detected between any of the treatments of run C (Fig. 5, Table 7).

DISCUSSION

This study has demonstrated that millimeter-thin surface deposits of terrigenous sediments affect both the chemistry of the sediment–water interface and the

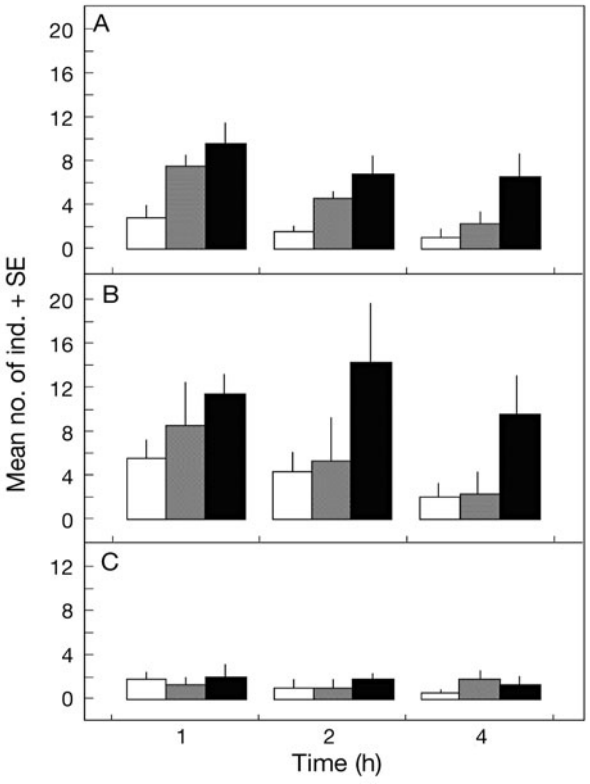

Fig. 5. *Macomona liliana*. Number of juveniles that had not burrowed in each treatment [0 d TS (run A), 7 d TS (run B), and 14 d TS (run C)] at 1, 2 and 4 h after their addition to the aquaria. Fifty individuals were added to each aquarium. White bars: control sediment treatment; grey bars: buried TS treatment; black bars: surface TS treatment

Table 7. Results of repeated measures ANOVA to investigate the effects of treatments/runs on *Macomona liliana* burrowing. Multiple comparisons: Tukey's tests; TS-s: surface terrestrial sediment, TS-b: buried terrestrial sediment, and C: control sediment treatments. Trt: treatment; ns: not significantly different ($p > 0.05$)

Run (TS age)	Time	Pr > *F*	*F*-value	MS	SS	df	Multiple comparisons
A (0 d)	Trt	0.0002	20.30	332.53	997.58	3	
	Time × Trt	0.0003	7.93	14.03	84.18	6	
	Error (Time)			1.77	31.83	18	
	1 h	<0.0001	26.89	205.42	616.25	3	TS-s, TS-b > TS-b, C
	2 h	0.0003	20.04	90.75	272.25	3	TS-s, TS-b > TS-b, C
	4 h	0.0058	8.31	64.42	193.25	3	TS-s, TS-b > TS-b, C
B (7 d)	Trt	0.0242	5.49	495.47	1486.42	3	TS-s, TS-b > TS-b, C
	Time × Trt	0.0558	2.65	18.22	109.33	6	
	Error (Time)			6.88	110.00	16	
C (14 d)	Trt	0.0233	5.21	22.92	68.75	3	ns
	Time × Trt	0.3267	1.25	0.92	5.50	6	
	Error (Time)			0.73	13.17	18	

burrowing of post-settlement juvenile bivalves. Our measurements of changes in surface and near-surface porewater chemistry (diffusivity, O_2 and pH) were investigated at the micro-scale, i.e. at and near the sediment–water interface — a scale likely to be important to a potential small, post-settlement colonist. In combination, these results provide (1) a mechanistic understanding of the observed negative responses of soft-sediment macrofauna to sedimentation events (Cummings et al. 2003, Cummings & Thrush 2004, Lohrer et al. 2004), and (2) some insight into the potential cues used by post-settlement juvenile bivalves to determine the suitability of a habitat for settlement.

The main effect of surface TS deposits was a change (decrease) in the penetration depth of O_2 (measured from the deposit–sediment interface to the depth of the anoxic sediment), and in the porewater O_2 concentrations and pH (Tables 3 & 6). Supply of O_2 to the sediment underlying the TS deposit is essential for the oxidation of reduced end products of mineralisation in the sediment column, and prevents these reduced end products from diffusing upward towards the surface sediments where the juveniles are active. Oxygen consumption in control sediments was partly due to oxic respiration (microbial decomposition of organic matter using oxygen as the electron acceptor) and oxidation of reduced end products of anaerobic decomposition of organic matter (e.g. sulfides, Mn^{2+}). The latter processes cause maximum O_2 consumption and minimum pH near the oxic–anoxic boundary. Addition of a surface TS deposit decreased the penetration depth of O_2 so that the oxic–anoxic boundary (the zone where reduced solutes are oxidized) shifted upwards, closer to the surface of the sediment. Thus, the likelihood of infauna residing in near-surface sediments being exposed to upward diffusing end products of microbial decomposition was increased. pH was also lowered due to oxidation of reduced solutes diffusing from below. A negative correlation was observed between the apparent diffusivity of the TS-surface deposit and O_2 consumption in the deposit-underlying sediment. A similar correlation between the rate at which TS-surface deposits reduced the total (deposit + underlying sediment) O_2 consumption and the TS-surface diffusivity was not observed (Table 6, ΔR), indicating that the O_2 consumption zone had simply shifted.

The supply of O_2 to the deposit-underlying control sediment is affected by the diffusivity of the TS deposit. Weathering of TS increased its diffusivity (Table 3); consequently, the O_2 consumption of the underlying sediment also increased (Table 6). Both the O_2 consumption of sediment underlying the TS-surface (Table 6) and the diffusivity of the TS-surface deposit (Table 3) increased with TS age (correlations were 0.984 and 0.961, respectively). The greater diffusivity might have resulted in higher diffusion of O_2 from the bottom water down into the sediment, and presumably, also of reduced solutes (e.g. sulfides, Mn^{2+}) from sediment porewater up into the bottom water. As TS diffusivity increased, the oxic–anoxic boundary might have shifted downwards into the sediment where other reactions (e.g. calcite dissolution and sulfide oxidation by $Fe(OH)_3$) could have buffered against proton production processes.

Surface and buried deposits of fresh and weathered TS were incorporated into this experiment because (1) over time, surface TS deposits may become gradually buried as they get covered by ambient sediment transported as bedload (Norkko et al. 2002), and (2) there is a positive correlation between macrofaunal colonisation and the length of time the TS remains on the sandflat (see Cummings et al. 2003, Lohrer et al. 2004). As expected, burrowing by *Macomona liliana* juveniles into surface TS deposits was significantly reduced (Fig. 5, Table 7), and the strength of this response was influenced by the age of the deposits. Fewer juveniles burrowed into the 0 and 7 d TS-surface treatments compared with the control sediment treatments, but burial was not affected by the oldest (14 d) TS-surface treatment (Table 7, Fig. 5).

While the bivalves were clearly negatively affected by surface TS treatments relative to controls, the response to these very thin deposits was not as strong as that observed in previous experiments involving 5 to 10 mm TS layers, which also demonstrated reduced burrowing into treatments with buried (5 mm thick) TS deposits (Cummings & Thrush 2004). In this experiment, *Macomona liliana* burrowing was not affected by TS-buried treatments of any age (Table 7). This difference is not surprising given that the chemical responses detected here are likely to be magnified in thicker deposits.

We expected that the effect of surface TS deposits on juvenile *Macomona liliana* burrowing would be strongest in the 0 d TS-surface treatment and weaken with TS weathering. While more individuals burrowed in the most weathered (14 d) TS, we noted that burial was lower in the 7 d TS relative to the 0 d TS treatment (Fig. 5). Due to our experimental design, it is not appropriate to statistically test for differences in burial at different TS ages. As expected, the reduction in O_2 consumption, R (i.e. ΔR-surface), caused by a 1 mm thick TS-surface deposit relative to control sediment was greatest when fresh (0 d) TS was applied, because these deposits had the lowest diffusivity (Table 6). Unexpectedly, however, the weakest reduction in R was caused by the 7 d TS rather than the 14 d TS deposits (Table 6). The relatively high R in these treatments (i.e. relatively low ΔR) may be due to a higher O_2 consumption in the 7 d TS-surface deposit (Table 6).

This could have resulted from, e.g. a higher organic content in the 7 d TS, which would in turn elevate carbon oxidation, and/or enhance oxidation of reduced inorganic species (e.g. H_2S, Mn^{2+}, Fe^{2+}) diffusing upwards from the underlying sediment. A potentially higher flux of reduced species from the sediment into the 7 d TS-surface deposit was in fact indicated by the higher ΔpH of the control sediment underlying the 7 d TS-surface layer compared to that underlying the 0 d or 14 d TS-surface treatments (Table 3). Unfortunately, however, organic content was not measured so this inference cannot be confirmed.

Studies by Woodin et al. (1995), Woodin (1998) and Marinelli & Woodin (2002, 2004) found correlations between short-term changes in concentrations of porewater oxygen and ammonium in response to small-scale disturbance, and burrowing response of post-settlement bivalves and polychaetes. The results of our study provide further evidence of the link between sediment chemistry and post-settlement behaviour, and point to the importance of pH in reflecting this response. For example, the toxicity of sulphide to aerobic organisms increases with decreasing pH (see Vismann 1996, and references therein). Lower pH has also been shown to decrease porewater [CO_3^{2-}], resulting in carbonate undersaturation and mortality of juvenile *Mercenaria mercenaria* (0.2 to 1 mm) due to shell dissolution over day timescales (Green et al. 2004). The differences in ΔpH in these experiments relate to the pH at >1 mm depth; for an individual to respond to such differences requires the transfer of a chemical signal to the surface of the sediment, or detection via sensors in some part of the bivalve (e.g. foot) below the sediment surface. No pre-burrowing substrate 'testing' (e.g. use of the foot to probe the substrate) by juvenile *Macomona liliana* was observed in these experiments, nor was there any attempt to initiate dispersal (sensu Cummings et al. 1993). Rather, they either remained stationary on the sediment surface, or buried.

The design of our laboratory experiments involved simplification of the environment actually experienced by post-settlement juvenile bivalves on an intertidal sandflat. Firstly, defaunated sandflat sediments were used, so the effect of activities of other animals (e.g. burrowing and feeding by polychaetes) that would likely disrupt the sediment layers, and thus influence the solute gradients in the sediment–water interface, was not considered. Secondly, the experiments were conducted in low velocity flow that was steady and unidirectional, which are conditions far removed from those in the more turbulent, dynamic sandflat. However, the responses to the TS treatments used in the experiment may still be applicable in a more realistic environment. Traces of experimental deposits of 1 mm thick TS remained after 10 d on a sandflat (Lohrer et al. 2004). Irrespective of their persistence time in the field, even relatively short-term exposure to TS (<1 d) is long enough to negatively affect infauna (Cummings & Thrush 2004). Compared to previous experiments using thicker layers of TS, the magnitudes of the effects on bivalve burrowing noted in our experiments are low (maximum non-burial rates of 20%). However, these differences are likely to be significant at the population level, and will be magnified if organisms are exposed to repeated disturbance by frequent, albeit small, TS depositions.

In conclusion, our study has shown how millimeter-thin deposits of terrigenous sediments can affect the chemistry of the sediment–water interface and the burrowing of post-settlement juvenile bivalves. The results suggest that further investigations on pH and associated geochemical species may be useful in elucidating cues used by post-settlement bivalves, and indeed by other macrofauna, in determining habitat suitability.

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