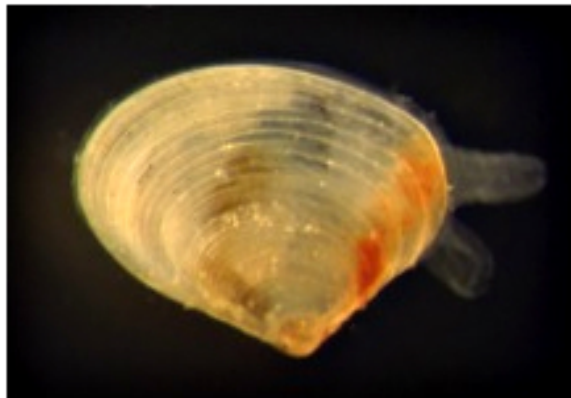# Effect of terrestrial sediment on the burial behaviour of post-settlement

Macomona liliana

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Attestation of authorship

"I hereby declare that this submission is my own work and that, to the best of my knowledge and belief, it contains no material previously published or written by another person (except where explicitly defined in the acknowledgements), nor material which to a substantial extent has been submitted for the award of any other degree or diploma of a university or other institution of higher learning."

Signed: *A.K.Hohai*   Date: 07/06/2013

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The image on the cover page is a *Macomona liliana* post-settlement juvenile with a shell length of 1.3 mm. Working with 'undersized shellfish' as one Tuapiro local put it, definitely taught me to appreciate the finer things in life, especially my husband Daniel, and two children Aydan and Caleb.

Lastly, I would not be capable of completing this thesis without the unconditional aroha of my whanau, and so my heart goes out to you all in thanks. "E ngā mana, e ngā reo, e ngā kārangaranga maha, totoro atu rā ēnei maioha, ēnei kupu whakamihi āku ki a koutou. Tena ra koutou." "To all the people, the languages, and the many callings, I extend my affectionate greetings and words of thanks to you all. Thank you all."

Abstract

Terrestrial and marine environments are connected ecosystems that are similarly vulnerable to the effects of anthropogenic stressors. Climate change and other anthropogenically-induced stressors have resulted in an increased rate of supply (mass per time per area) of terrestrial (land-derived) sediment. This sediment is exported from catchments to rivers, and subsequently, to estuarine and marine systems. Episodic events result in the catastrophic deposition of terrestrial sediment, while small-scale spatial deposition of terrestrial sediment is widespread, and frequent. One pressing issue is the effect of thin depositions of terrestrial sediment on one ecosystem function, such as recruitment of benthic fauna.

The tellinid bivalve *Macomona liliana* is an important component of estuarine and coastal benthos throughout New Zealand, representing one of the most common community dominants across marine ecosystems. Significantly, *M. liliana* is a sensitive ecological indicator of change. Post-settlement juveniles have been demonstrated to actively avoid adverse local conditions, including sediments affected by the deposition of thin terrestrial sediment. This behavioural response may be triggered by deposit-induced changes in the porewater chemistry of the deposit-underlying sediment, but not by contact of the juveniles with the terrestrial sediment.

A laboratory flume experiment was conducted to assess the effect of millimetre-thick terrestrial sediment deposits on porewater chemistry, and the burial behaviour of *M. liliana* post-settlement juveniles. Terrestrial sediment deposits impeded the diffusion of solutes across the visible sediment surface. This impedance, however, had a negligible effect on the sediment porewater chemistry as a result of resident infauna mediating the exchange of solutes between porewater and bottom water. As such, the deposition of millimetre-thick terrestrial sediment did not negatively affect the burial behaviour of post-settlement juveniles.

This study has highlighted the need for a greater understanding of the contribution of bioturbation by resident infauna to solute exchange in sediments affected by periodic deposition of terrestrial sediment. Bioturbation appears to be one of the most important variables to consider when investigating the effects of terrestrial deposits on juvenile *M. liliana* burial behaviour.

Introduction

Supply and land–ocean transfer of terrestrial sediment

Terrestrial and marine ecosystems are connected environments that are similarly vulnerable to the effects, and consequences of anthropogenic stressors. As such, an improved understanding of the linkage between these ecosystems is important for the viability of these environments in future. In New Zealand, climate change impacts have already been observed, and have been predicted to increase in future years (Kingsford, and Watson, 2011; Lundquist, Ramsay, Bell, Swales & Kerr, 2011). Climate change in combination with other anthropogenic stressors, (e.g., deforestation, catchment modification, engineered frontage and accelerated coastal development) have increased sedimentation and the area of depositional environments, and accelerated the degradation of valuable coastal habitats (Airoldi, 2003; Cummings & Funnell, 2003; Doddy et al., 2004; Edgar and Barrett, 2000; Fahey and Coker, 1992; Lohrer et al., 2004; Zhang et al., 2004).

The supply of terrestrial (land-derived) sediment is governed by climate conditions (Hsu, Kao and Jeng, 2006). Lundquist et al. (2011) have predicted that the frequency and intensity of rainfall will increase, and will consequently amplify rates of disturbance and sedimentation in estuarine and coastal ecosystems. In addition, natural perturbations and episodic events such as landslides, extreme rain events, and flooding can result in catastrophic deposition of terrestrial sediments and elevated water column turbidity in coastal marine environments, more so, in areas where steep topography supports rapid transport (Ellis et al., 2000; Norkko et al., 2002).

Bender et al. (1984) defines disturbances as either 'press' or 'pulse'. A pulse disturbance is acute, and allows an ecosystem to recover to its condition prior to the disturbance. Conversely, a press disturbance is one that is chronic, and forces an ecosystem to a different domain or set of conditions with no recovery. Understanding the difference between press and pulse disturbances in soft-sediment marine ecosystems is important because it is crucial to understanding how organisms and communities respond. A community's response to pulse and press disturbances will depend on an organisms' tolerance to stressors and on its life-history traits (Airoldi, 2000).

Griffiths and Glasby (2004) reported that the North Island of New Zealand discharges $105 \pm 9.4 \times 10^6$ tonnes of sediment per year. Sediment delivery into coastal waterways is often pulsed and correlated with storm events (Hicks et al., 2004; Wheatcroft, 2000), although frequent run off events, for example, hill slope erosion processes, are also important (Hicks et al., 2000, 2004). Fine sediment (inorganic particles with diameter <2 mm) and other materials may be transported in rivers and steams as loose particles (Owens et al., 2005), and find their way to coastal areas within minutes or hours. Here, the particles may remain in suspension for several days prior to deposition (Fahey & Coker, 1992).

The sediment of coastal catchments is discharged into and subsequently deposited in adjacent subtidal habitats, estuaries, or directly onto the continental shelf. The ecologial impacts of such deposition have been demonstrated by Cummings, Thrush, Hewitt, Norkko and Pickmere (2003), Hewitt et al. (2003), Cummings and Thrush (2004), Lohrer et al. (2006a,b), Reid et al. (2011), and Woodin, Wethey, Hewitt and Thrush (2012), (Figure 1).
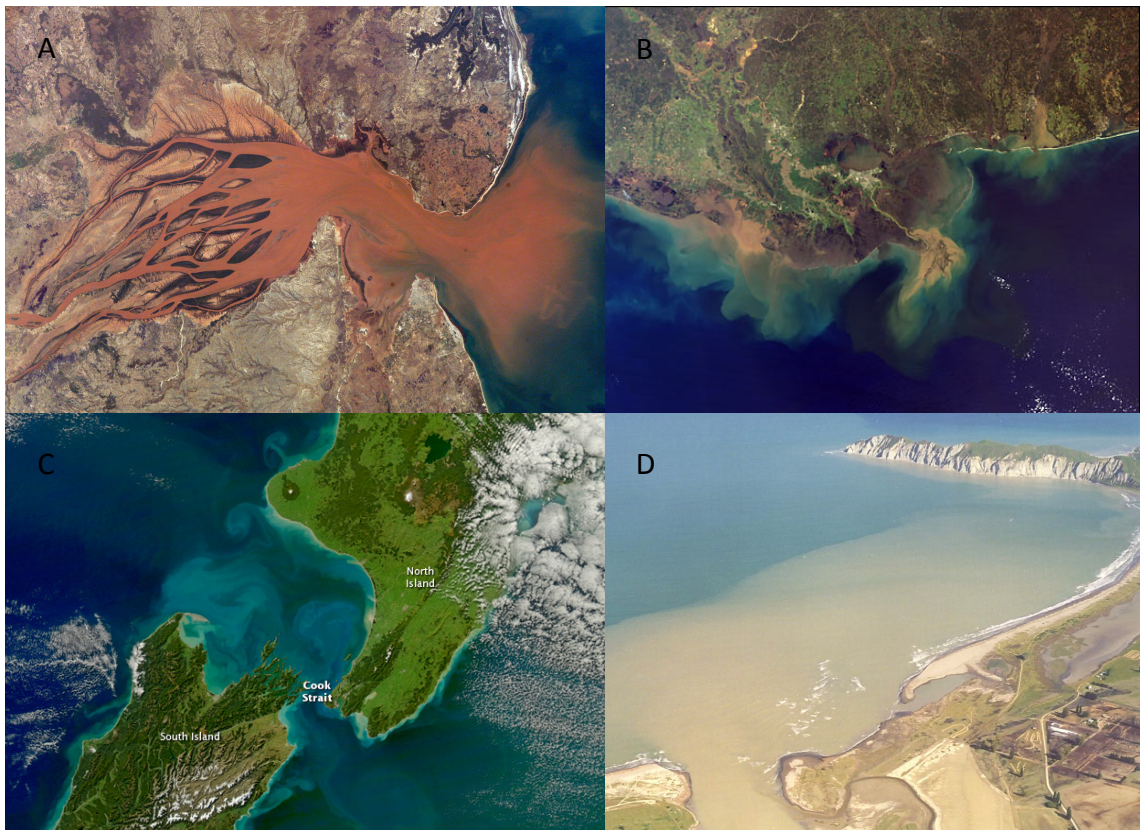
Figure 1. Satellite images (A, B, C) and an aerial photograph (D) showing sediment plumes of (A) the Betsiboka River, Madagascar (http://www.solarviews.com), (B) the Mississippi River, USA (http://visibleearth.nasa.gov), (C) Cook Straight, New Zealand (http://visibleearth.nasa.gov), and (D) the Waipaoa River, New Zealand (http://www.vims.edu).

Effect of terrestrial sediment on ecosystem functioning

While the presence of terrestrially derived sediment is natural in coastal marine habitats, the accelerated rate of sedimentation and persistence of terrestrial sediment is largely attributable to anthropogenic influences, and has been recognised as a contaminant of global concern for decades (Airoldi, 2003; Cummings et al., 2003; Cummings & Thrush, 2004; Ellis et al., 2000; Group of Experts on the Scientific Aspects of Marine environmental Protection [GESAMP], 1994). Numerous studies have reported that centimetre-thick deposits persist atop local sediments (e.g., Cummings et al., 2003; Lohrer et al., 2004; Lohrer et al., 2006b), as do finer (millimetre-scale) depositions (Woodin et al., 2012). Freshly deposited fine terrestrial material may be resuspended by waves and currents, elevating near-bed turbidity.

Suspended sediment in the water column reduces light transmission and the vision of aquatic animals (McKergow et al., 2010; Wood & Armitage, 1997). Studies have shown that suspended sediments can limit reef development (Woolfe & Larcombe, 1999; Torres & Morelock, 2002), and affect suspension feeders and primary productivity (Ellis et al., 2004). Negative effects have been demonstrated in New Zealand ecosystems, including a decline in the condition, clearance rates, and oxygen consumption of suspension feeders of the genera *Atrine, Aaptos, Styela*, (e.g., Lohrer, Hewitt & Thrush, 2006a), a decline in the condition of the mussel *Perna canaliculus*, and negative effects on the performance (growth), and physiology of the macroalga *Sargassum sinclairii*, the sponge *Tethya aurantium*, the crab *Petrolisthes elongatus*, (e.g., Steger, 2006) and the bivalves *Austrovenus stutchburyi* and *Paphies australis* (e.g., Norkko, Hewitt & Thrush, 2006).

Characteristics of terrestrial sediments

Terrestrial sediments that are deposited during catastrophic events differ from marine sediments in their physical (e.g., grain size, penetrability) and biogeochemical (e.g., microbial composition, nitrogen and phosphorus content, nutritive value to benthos) composition (Cummings et al., 2003). Terrestrial sediments contain a variety of particles, and a large proportion of these are silt and clay-sized particles (Cummings et al., 2003). Such particles are important hosts of pollutants, and only these small particles are transported in suspension and washed to sea by weak currents (Naidu,

Han, & Mowatt, 1995). Studies have shown that terrestrial sediments are enriched with organic matter, which does not necessarily represent a high-quality (i.e., nutionally important or utilisable) food source for benthic invertebrates (estimated by levels of chlorophyll *a* content and stable isotope analysis), (Cummings et al., 2003; Norkko et al., 2002). Therefore, recolonisation of the terrestrial deposits by benthic invertebrates, and, the recovery of sediments may be reduced (Cummings et al., 2003). Over time, the terrestrial sediment deposit, and the underlying marine sediment will be further modified; for example, depositions cause oxygen depletion in the sediment, and elevated concentrations of hydrogen sulfide (Norkko et al., 2002). The grain size of the ambient marine sediment is altered as a result of vertical and horizontal mixing by bioturbation and local hydrodynamics (Hewitt et al., 2003; Lohrer et al., 2004; Norkko et al., 2002), and the apparent diffusivity of terrestrial sediment deposits increases with the age (i.e., amount of weathering) (Cummings & Thrush, 2004; Cummings, Vopel & Thrush, 2009).

Terrestrial sedimentation in New Zealand aquatic environments

Several New Zealand field and laboratory studies have illustrated how the deposition of terrestrial sediment can negatively affect benthic marine ecosystems. Early studies were primarily manipulative field experiments designed to mimic episodic or press events known to occur on New Zealand sandflats, and included terrestrial deposits up to 10 cm thick (e.g., Cummings et al., 2003; Hewitt et al., 2002; Norkko et al., 2002). In contrast, more recent studies (e.g., Cummings et al., 2009; Woodin et al., 2012) have given recognition to the pressing issue of climate change and the increase in frequency and spatial distribution of thinner deposits (i.e., millimetre scale). In these studies experiments in the laboratory were combined with field experiments.

Early studies conducted in estuaries in the North Island of New Zealand similarly demonstrated that terrestrial deposits thicker than 2 cm induced hypoxia and anoxia on the sandflat, killing all fauna residents under the deposits. These experiments also documented such deposition causes long-term alteration to the habitats and communities, with little or no progressive recovery (i.e., recolonisation of the deposits) on time scales up to 20 months post deposition.

The study by Norkko et al. (2002) however, highlights that transport of surrounding ambient sediments onto the surface of the terrestrial deposits and bioturbation by macrofauna are important facilitators of macrobenthic recovery following centimetre-thick deposition of terrestrial material in marine ecosystems. There is wide recognition that catastrophic deposition of terrestrial material in intertidal habitats force benthic ecosystems to a new domain, or set of conditions, and macrobenthic recovery following such press disturbance is largely influenced by bioturbation. Further, deposition of terrestrial material in subtidal habitats also causes negative effects but the extent of the effect is a function of the stress level caused by the deposition and the tolerance of subtidal species to terrestrial sediment deposition.

Ensuing studies began to investigate the effects of millimetre-scale depositions on intertidal and subtidal habitats. For example, Lohrer et al. (2004) performed manipulative experiments in a variety of intertidal habitats in the Whitford embayment, North Island of New Zealand, to ascertain the thickness and frequency at which terrestrial sediment deposits affect the benthos. They found that depositions of terrestrial sediment 7 mm thick did not completely defaunate the sediment. Depositions as little as 3 mm, however, were sufficient to significantly alter macrobenthic community structure, that is, they found a decline in the number of individuals, taxa, and densities of nearly every common species. They also reported that repeated depositions caused cumulative negative effects.

Similar negative effects were also observed in subtidal habitats. Lohrer et al. (2006b) applied terrestrial sediment deposits (3 and 7 mm) to subtidal habitats with two contrasting community types, a coarse sand community outside the Mahurangi Harbour, North Island, New Zealand, and one located in a tidal estuary inside the harbour. Lohrer et al. found terrestrial sediment to have a greater negative effect on macrobenthic infauna of coarse sediment outside the harbour, than those accustomed to muddier sediments inside the harbour. The terrestrial sediment deposits reduced the density of community, and the number of taxa in both communities, although that in the estuary showed some sign of tolerance to the deposits, and was only altered with the thicker deposits (i.e., deposits calculated to be 7 mm thick vs. deposits calculated to be 3 mm thick). The authors mention that the deposits should have equated to layers 3 mm and 7 mm thick, however, being a subtidal habitat, the total

immersion in seawater caused the deposits to remain in a fluid, yet cohesive state, and consequently, the deposits were actually 10 mm and 20 mm respectively.

Further experiments revealed that terrestrial sediments likely affect the population and community dynamics of mobile bivalve species, dependant on the thickness and frequency of the depositions (Cummings & Thrush, 2004). Combining laboratory and field experiments, Cummings and Thrush (2004) investigated the ability of *Macomona liliana* and *Paphies australis* juveniles to burrow into surface and submerged terrestrial deposits 5 and 10 mm thick, and their subsequent ability to burrow into natural sediments. Both bivalves were placed onto the surface of terrestrial deposits over 20 h in the laboratory and their burial into the deposits recorded. The same juveniles were then exposed to natural or control sediment, and their burial into this sediment was recorded. Exposure of *M. liliana* and *P. australis* to 5 mm surface and submerged deposits decreased the burrowing rate into the sediment. Surface terrestrial sediment deposits affected juvenile burrowing more than submerged deposits, and subsequent burial into control sediment was similarly affected. Likewise, burial into surface terrestrial sediments in the field was less than burial into control sediments. The authors proposed that these responses of juvenile *M. liliana* were caused by the presence, or absence, of chemical or biogeochemical cues originating from the terrestrial sediment deposit. Further, the reduced burial of *M. liliana* and *P. australis* into control sediments following exposure to terrestrial sediments implies that terrestrial sediment deposits can have lasting negative effects on the burial behaviour of these two common bivalves.

Recent studies by Rodil et al. (2011) and Reid et al., (2011) used 5 mm thick deposits to investigate the effects of terrestrial sediment on ecosystem functioning in various sites within the Whangapoua Harbour, North Island. Reid et al. investigated whether thin terrestrial sediment deposits negatively affected connected ecosystems. They mimicked pulsed sedimentation on adjacent stream and estuarine sites in the Whangapoua Harbour to determine the effects of ~5 mm terrestrial deposits on the benthos. While Reid reported that the effects of terrestrial sediment deposits on stream sites were negligible, they reported large declines in invertebrate densities and changes in overall invertebrate community structure at estuarine sites. Similarly, Rodil et al. reported that such deposits affected macrofaunal abundance and community

composition, as well as primary productivity and photosynthetic efficiency. In accordance with literature to date, these studies demonstrate that such thin depositions have negative effects on both macrobenthic populations, and macrobenthic species assemblages, and is of great concern for coastal managers.

The negative effects of thin terrestrial sediment deposits were further stressed in a recent study by Woodin, Wethey, Hewitt and Thrush (2012). In their study, Woodin et al. (2012) investigated whether deposits of terrestrial sediment ranging from 0.06–0.8 mm altered behaviour of dominant infaunal species, which in turn affect benthic productivity. Woodin et al. assessed fluctuations in porewater pressure caused by specific hydraulic behaviours of adult *M. liliana* (i.e., burrowing, siphon relocation, feeding/respiration, pseudofeces expulsion), and oxygen flux across the sediment–water interface. They found that the terrestrial sediment increased behavioural responses associated with emigration (burrowing and relocation of the feeding area), and reduced the productivity of the microphytobenthos. The addition of terrestrial sediment increased the time an individual *M. liliana* spent burrowing and moving their inhalant siphon from 4% to 20%. Woodin et al. argue that such changes are unlikely to be sustainable, and would result in death if the individual was unable to escape the terrestrial deposit. Furthermore, they argue that such alterations in behaviour have the potential to alter the spatial distribution of the large bivalve *M. liliana*. Given the importance of organism hydraulic behaviours, which drive biogeochemical rates and surface sediment chemical signatures (Marinelli and Woodin, 2002; Wethey, Woodin, Volkenborn & Reise, 2008), seemingly small terrestrial depositions may yield shifts in community dynamics and productivity in sediments (Woodin et al. 2012).

Similar consequences, that is, a change in the structure of an entire community and alteration to ecosystem functioning can occur when thin terrestrial sediment deposits affect key processes such as recruitment (Cummings et al., 1996; Woodin et al., 1998). Recruitment is important to community structure and ecosystem functioning because it is the foundation upon which all subsequent interactions within the community take place (Woodin, Lindsay & Wethey, 1995). To better understand the effects of thin terrestrial deposits on sediment biogeochemistry and behaviour of post-settlement bivalves, Cummings, Vopel and Thrush (2009) mimicked millimetre-scale terrestrial sediment deposits (<1.7 mm) on intertidal sandflats. They investigated the changes in

the physicochemical properties of the surface sediments at a micro-scale, relevant to an individual potential colonist's site choice. They provided evidence to suggest that the deposition caused changes to the sediment porewater chemistry of the underlying marine sediment, which were then detected as chemical cues by recruits on the surface of those depositions. That is, a reduction in the supply of oxygen to the sediment, causing the end products of bacterial organic matter degradation to be exposed to juveniles in the upper few millimetres of sediment that new recruits explore. They argue that such cues provide the mechanism for the negative response of post-settlement bivalves and other macrofauna to thin terrestrial deposits observed in prior studies. Other studies in this line of research align with the hypothesis that sediment biogeochemistry affects post-settlement behaviour of juvenile recruits (e.g., Marinelli & Woodin, 2002; Marinelli & Woodin 2004; Woodin et al., 1995; Woodin et al., 1998).

Sediment biogeochemistry

Marine sediments are considered complex mixtures of organic and inorganic materials derived from marine and terrestrial sources. The processes occurring in surface marine sediments have a profound effect on the local and global cycling of many elements, thus, great effort has gone into understanding the biogeochemistry of marine sediments. Advanced understanding of the processes occurring in surficial marine sediments has developed over the past 20–30 years, and it is now well recognised that the geochemistry of marine sediments is controlled by both the composition of the material initially deposited and the chemical, biological, and physical processes that affect this material after its deposition (Berner, 1980; Burdige, 2006; Henrichs, 1992).

A significant finding that emerged over the past 20–30 years is that the oxidation (degradation) of organic matter in sediments is either the direct or indirect causative agent for many early diagenetic changes (Froelich, 1979). This finding also shed light on the role of benthic bacteria and macrofaunal involvement in diagenetic changes. Bacterial metabolism is considered the key mediator of organic matter degradation as bacterial biomass dominates in marine sediments (Burdige, 2006). The role of benthic macrofauna in organic matter degradation is also well established, and important in early diagenesis (Rhoads 1974).

Organic matter degradation occurs by an array of aerobic and anaerobic microbial processes, with a concurrent release of inorganic nutrients. Ultimately, the thermodynamic energy yield, reaction kinetics, and the physiology of the microorganisms involved govern this sequence; although, chemical reactions and sediment physical properties can also be significant agents or modifiers of diagenetic processes (Henrichs, 1991).

Jørgensen (1983) and Westrich and Berner (1988) have shown that organic matter oxidation rates increase with increasing temperature in both oxic and anoxic sediment. Essentially, large organic molecules are first fermented into small moieties, followed by complete oxidation by anaerobic respirers using a sequence of electron acceptors (e.g., Mn^{4+}, NO_3^-, Fe^{3+}, SO_4^{2-}, and CO_2; illustrated in Figure 2), (Froelich et al., 1979; Glud, 2008; Kristensen, 2000; Middleburg & Levin, 2009). Froelich et al. (1979) suggest the simplest plausible model of organic diagenesis is one in which marine organic matter having the Redfield composition, i.e., $(CH_2O)_{106}$ $(NH_3)_{16}$ (H_3PO_4), is oxidised by the oxidant yielding the greatest free energy change per mole of organic matter oxidised. When this oxidant is depleted, oxidation will proceed utilising the next highest energy producing oxidant, until either all oxidants are consumed or oxidisable organic matter is depleted. According to this sequence, a biogeochemical zonation or stratification occurs in marine sediments, which was characterised by Froelich et al. (1979).
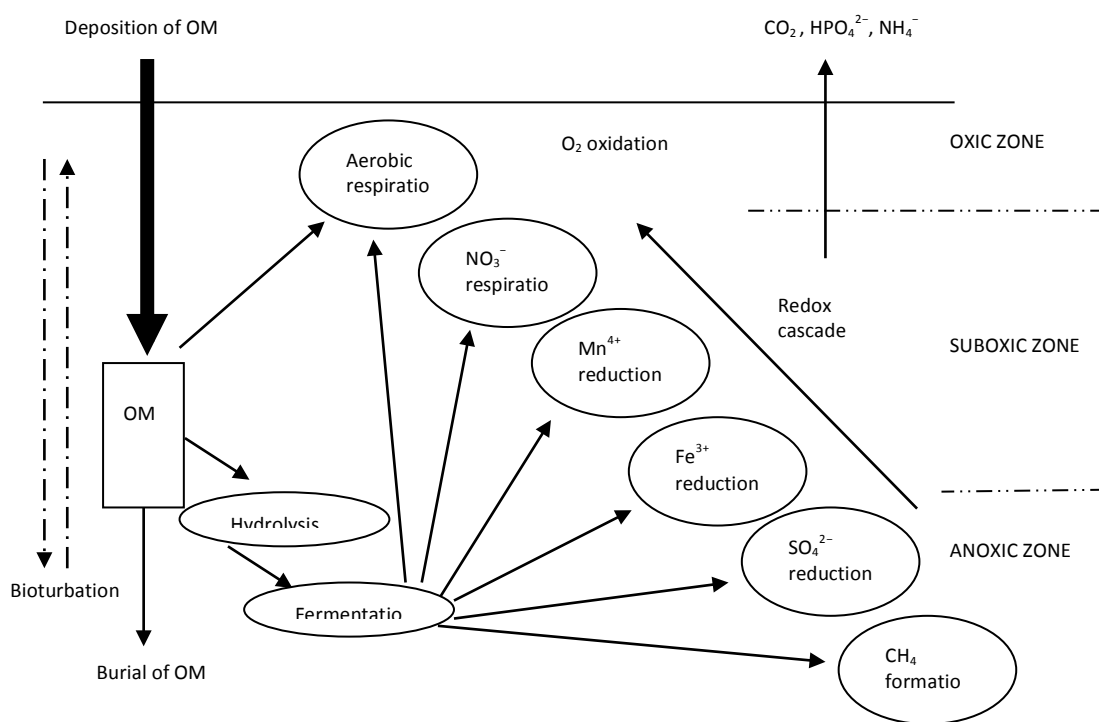
Figure 2. Conceptual model of organic matter (OM) degradation pathways, modified from Glud (2008) and Middleburg and Levin (2009). Organic matter degradation involves hydrolysis of macromolecular organic matter and fermentation into smaller compounds. These fermentation products are used by respiring microorganisms and methanogens. Oxidants are utilised sequentially, first oxygen, then nitrate, metal oxides, and sulphate. Dissolved reduced products diffuse upwards and are then oxidised: NO_3^-, nitrate; Mn^{4+}, manganese; Fe^{3+}, iron; SO_4^{2-}, Sulphate; CH_4, methane; CO_2, carbon dioxide; HPO_4^{2-}, phosphate; NH_4^-, ammonium.

Mortimer et al. (2002) suggest that the use of such zones have formed the framework for describing the early diagenesis of aquatic sediments, but they also argue that the classical scheme of biogeochemical zones is oversimplified. The classical scheme is comprised of the predicted decomposition reactions, that is, denitrification, manganese (hydr)oxide reduction, iron (hydr)oxide reduction, sulfate reduction, and methanogenesis. Numerous studies have established that oxic respiration, as the name implies, occurs in the oxic layer within the sediment, whereas denitrification and manganese and iron (hydr)oxide reduction occur in sub-oxic layers, and sulfate reduction and methanogenesis occur in the anoxic or highly reduced layers (Burdige, 2006). Kristensen (2000) has shown that the boundary between oxic and anoxic layers in marine sediments is a sharp and well-defined interface.

There is wide recognition that coastal marine sediments are reducing environments, covered only by a thin oxic layer (Glud, 2008; Kristensen, 2000). The balance between

downward transport of oxygen by molecular diffusion and advection, and oxygen consumption by aerobic respirers (e.g., bacteria, fungi, fauna), and by the reoxidation of reduced substances, determines the oxygen penetration depth in marine sediments. Mineralisation of organic matter, via the anaerobic respiration pathways, results in the formation of various reduced substances such as ammonium (NH_4^+), iron (Fe^{2+}), manganese (Mn^{2+}), hydrogen sulfide (H_2S), and methane (CH_4). Jørgensen (1982) demonstrated that these reduced substances are efficiently reoxidised within sediments because they contain a substantial amount of energy that was originally contained in the organic matter, and may occur directly or via a redox-cascade involving a series of complex abiotic and microbial catalysed redox processes.

The ammonium produced from organic nitrogen mineralisation can be oxidised aerobically by archaea, or anaerobically by bacteria, whereas dissimilatory reduction of particulate metal oxides cause the release of reduced iron and manganese in dissolved form, which are oxidised by microbes using oxygen or nitrate as electron acceptors (Middleburg & Levin, 2009). Sulfate is the second most abundant anion in seawater, and Jørgensen (1982) and Soetaert et al. (1996) have shown that sulfate reduction accounts for the majority of anaerobic mineralisation in coastal sediments. Furthermore, sulfate reduction is considered to be the most important respiration process controlling the availability of substrates such as short chain fatty acids (Froelich et al., 1979; Holmer & Kristensen, 1993). H_2S, the product of sulfate reduction, readily reacts with reactive iron to form iron sulfides (e.g., mackinawite [FeS], greigite [Fe_3S_4], and pyrite [FeS_2]), or reacts with organic matter to produce organically bound sulphur in sediments, or is reoxidised as part of the S-cycle (Middleburg & Levin, 2009). Lastly, the methane produced can be oxidised aerobically, although Boetius et al. (2000) argue that the majority is oxidised aerobically by an array of archaea and bacteria. Importantly, these secondary redox reactions account for more than 75% of oxygen consumption in coastal sediments (Glud, 2008; Jørgensen, 1982; Soetaert et al., 1996).

Estimating the sediment oxygen consumption rate from the oxygen concentration gradient in the diffusive boundary layer (i.e., the rate of diffusive oxygen uptake) is one approach used to describe oxygen dynamics in sediments (Glud, 2008; Vopel et al., 2009). Recently, Jourabchi, Van Cappellen, and Regnier (2005) have illustrated how

secondary oxidation reactions contribute towards the production of protons within the oxic zone, and thus to porewater pH. They demonstrated how pH rapidly declines to a pH minimum just below the sediment–water interface followed by a subsurface maximum in the anoxic zone as a result of ammonium, iron, manganese, sulfide, and methane reoxidation, and the reductive dissolution of metal oxides respectively. In their study Jourabchi et al. (2005) used a transport–reaction modelling approach to quantitatively predict the distributions of pH in aquatic sediments.

Berner (1980) is widely recognised for contributing to the development of transport–reaction modelling of early diagenesis, however, Wang and Van Cappellen argue that the simple analytical models in Berner (1980) are not adequate for representing the complex, multi-reaction biogeochemical dynamics. More comprehensive diagenetic models were developed to simulate the coupled and multicomponent chemical dynamics of early diagenetic systems (e.g., Berg et al., 2003; Boudreau, 1996; Canfield, 1994; Dhakar and Burdige 1996; Meysman et al., 2003; Soetaert et al., 1996; Van Cappellen & Wang 1996).

Quantifying transport processes is crucial for understanding sediment geochemical processes, and for diagenetic modelling. Diffusion and advection are important transport processes in marine sediment biogeochemistry. Different transport processes dominate in different types of marine sediment; for example, in muddy sediments diffusion represents the dominant transport process by which ions and molecules move in porewaters (Berner, 1980). In contrast, in permeable sediments, advective transport processes dominate transport of solutes. Huettel, Ziebis and Forster (1996), and Huettel, Ziebis, Forster and Luther (1998) have shown that this is particularly true where permeability exceeds 10^{-12} m^2. In muddy sediments, particles are transported by certain mechanisms, including particle sedimentation, compaction upon burial, or bioturbation.

Activities of benthic infauna are concealed from visual observation, but their effects on sediment chemical and physical properties are nevertheless apparent and have been well documented (Aller, 1980; Boudreau & Marinelli, 1994; Kristensen, 2000; Lohrer, Halliday, Thrush, Hewitt & Rodil, 2010; Rhoads, 1974; Vopel, Vopel, Thistle & Hancock, 2007). Santschi et al. (1990) define bioturbation as the combined effect of all biological activities on particle and porewater dynamics at the sediment–water interface,

whereas Sandnes et al. (2000) define bioturbation as the mechanical disturbance of benthic sediments. Shull (2009a) suggests that in the narrowest sense, bioturbation refers to the biogenic transport of particles that destroy stratigraphic signals. Shull goes on to suggest that in the broader sense, it can refer to biogenic transfer of porewater and changes in sediment physical properties due to organism activities. More recently, Kristensen et al. (2012) define bioturbation as all transport processes carried out by animals that directly or indirectly affect sediment matrices. As such, bioturbation can be divided into particle reworking and burrow ventilation, that is, the movement of particles and water. Active particle reworking involves faunal displacement and horizontal and vertical biomixing of particles, and includes burrowing, construction and maintenance of galleries, as well as ingestion and defecation of particles (Kristensen et al., 2012).

The vertical displacement of particles via unidirectional feeding is generally referred to as conveyor-belt transport, or non-local transport. That is, macrofauna live in fixed sediment burrows and move material from a fixed depth a few centimetres below the sediment surface to the surface, forming burrow mounds. Reverse conveyor-belt transport is another form of vertical displacement in which organisms feed at the sediment surface and then defecate at depth, or simply store food-rich particles at depth in burrows (Rhoads, 1974). Subductive feeding is where particles are collected at depth and deposited at the sediment surface, and interior feeding, where particles are collected and deposited within the sediment column, are also known to rework sediments (Shull, 2009a). Some organisms also ingest and egest sediment at the sediment surface, resulting in horizontal displacement of particles but limited vertical displacement (Shull, 2009a). Benthic organisms are also known to rework sediments through burrow formation. Using their burrowing apparatus, e.g., bivalve foot, polychaete proboscis, amphipod carapace, the organism creates and propagates cracks in the sediment (Dorgan, Arwade & Jumars, 2005).

Most benthic macrofauna maintain a burrow that connects to the sediment–water interface to facilitate respiration, feeding, defecation, and other metabolic processes (Shull, 2009b). Burrows exhibit a wide range of geometries, including vertical cylinders, J–, U–, or L–shaped tubes and branching networks. Macrofaunal species ventilate their burrows by use of flapping of appendages, peristalsis, thrashing body undulations, by

beating cilia, or by oscillating like pistons to meet their metabolic requirements for oxygen (Foster-Smith, 1978). These ventilation mechanisms result in intermittent burrow flushing, which exchange a portion of the fluid inside the burrow with overlying water (Shull, 2009b). This water exchange is the driving force for bioirrigation, that is, enhanced transport of porewater and associated solutes in the sediment surrounding the burrow (Kristensen et al., 2012). Aller and Yingst (1985) have shown that ventilation stimulates solute exchange between subsurface porewaters and overlying water, and therefore, redistributes dissolved reactants and products of microbial reactions. Kristensen (1984) has demonstrated that the surface area available for diffusive solute exchange, as well as the area of oxic–anoxic boundaries, is considerably increased in the presence of irrigated burrows, and Wang and Van Cappellen (1996) showed that bioirrigation reduces the build-up of iron sulfides in sediments and promotes sulfide oxidation.

Numerous approaches have been employed to quantify bioturbation, including steady-state modelling of naturally occurring radioisotope profiles, time dependent approaches using inert particulate pulse tracers, and sediment distributions of chlorophyll-*a* (e.g., Gerino et al., 1998). Microelectrodes have been used to study the effects of bioturbation on sediment biogeochemistry. The introduction of such techniques greatly advanced the understanding of processes occurring in the upper layer of marine sediments. In particular, a greater understanding of solute gradients occurring at the sediment–water interface was made possible, at high spatial (millimetre or sub-millimetre scale) and temporal (seconds) resolution, as illustrated in early studies by Revsbech and Jørgensen (1983), Revsbech and Jørgensen (1986), Cai and Reimers (1993), and more recently by Cai, Zhao and Wang (2000), Marinelli and Woodin (2002), Cummings et al. (2009), and Vopel, Wilson, Pilditch and Elwood (2009). Importantly, the detailed understanding of the transport–reaction processes that occur in the zone where new recruits and juvenile infauna explore the acceptability of the sediment surface, led to the hypothesis that sediment biogeochemistry affects recruitment decisions of newly settled and/or post-settlement juveniles.

Recruitment and porewater chemistry linkages

Recruitment is of fundamental importance to community structure because it is the foundation that all subsequent interactions within the community take place (Woodin, Lindsay & Wethey, 1995). Two processes, pre-settlement and post-settlement, determine the recruitment success of species with planktonic larvae. Adult–larvae interactions and larval supply can be considered as pre-settlement processes, while mortality, predation, active habitat selection, and emigration can be considered as post-settlement processes (Gribben & Wright, 2006). The definition of settlement varies amongst researchers. Pawlik (1992) defines settlement as the process following larval dispersal and transport, which may include reversible or irreversible contact with the substratum, exploratory behaviour, orientation, and metamorphosis. This process may occur before, during, or after contact with the substratum. Once a juvenile invertebrate has settled, it has undergone recruitment (Pawlik, 1992).

Recruitment determines the rate of addition of individuals to a given habitat (Marinelli & Woodin, 2002). The factors that guide the decision of recruits to accept or reject a site are complex and often interrelated (Marinelli & Woodin, 2002). Although the dispersal of post-settlement juvenile stages of macrobenthic invertebrates is widespread in the marine environment, the cues used by these organisms to assess substrate suitability are poorly known. Pawlik, (1992), Olafsson et al. (1994), and Cummings et al. (1996) suggest that biological interactions among existing residents on exploring residents have significant positive and negative effects on recruitment. Others have suggested biological (e.g., properties of shell material and internal biochemical mechanisms) or physical factors (e.g., sediment texture and roughness) act as cues stimulating colonisation (Turner et al., 1997; Young, 2009). Woodin and Marinelli (1998) have demonstrated a linkage between sediment biogeochemistry and recruitment, and more recently Marinelli and Woodin (2002, 2004) proposed that diagenetic transport–reaction processes that determine porewater composition drive the acceptability of sediments to new recruits. Early studies by Woodin and Marinelli (1995) provided the foundation for this argument with laboratory flume experiments, which demonstrated that juvenile recruits utilise cues associated with the disturbance of surface sediments. The authors demonstrated that surfaces that had been disturbed by a variety of events (depositional or erosional, biotic or physical) could all be

distinguished from undisturbed surfaces by the polychaetes *Nereis vexillosa* and *Arenicola cristata*, and the bivalve *Mercenaria mercenaria.*

Subsequent studies by Woodin et al. (1998) presented further evidence to suggest that ammonium concentrations, commonly observed at the surface of disturbed sediments, can be used as recruitment cues. The authors manipulated ammonium concentrations in sediments to mimic disturbed (high concentration) and undisturbed sediments (low concentration). They reported that juveniles of the polychaete *A. cristata* exposed to high ammonium concentrations exhibited behaviours consistent with rejection of the habitat, whereas juveniles of the same species readily burrowed into sediments containing ammonium concentrations typical of undisturbed surficial sediments. Additionally, Woodin et al. (1998) devised a numerical transport–reaction model to examine the influence of disturbance on surface ammonium concentrations and near-surface gradients, and examined the time course of recovery of disturbed gradients to the previously undisturbed conditions. Their model predicted that disruption of surficial sediments resulted in significant concentration changes at the sediment surface and recovery times, governed by transport–reaction processes, were in the order of minutes to hours.

Recent studies by Marinelli and Woodin (2002; 2004) further support the argument that disturbance, sediment chemistry, and recruitment decisions are linked. Marinelli and Woodin (2002) manipulated a sediment surface to mimic porewater oxygen concentrations typical of disturbed and recovering surficial sediments and determined the burial responses of the polychaete *A. cristata*, and the bivalve *M. mercenaria* into the sediment surface. In line with prior studies, undisturbed sediment was readily accepted by juveniles and characterised by high porewater oxygen concentration. Conversely, disturbed sediment was characterised by low surface and subsurface oxygen concentrations, and rejected by new recruits. Sediment that was disturbed and allowed to recover had intermediate oxygen concentrations consistent with the time scales of recovery predicted by the transport–reaction numerical model. This supports the hypothesis that sediment biogeochemistry and recruitment are linked. To further elucidate the influence of ammonium and oxygen, Marinelli and Woodin (2004) investigated the burial responses of the polychaete *Capitella* sp. 1 and the bivalve *M. mercenaria* in mud and sand environments. They predicted that (1) disturbance

(defined by low oxygen and high ammonium concentrations) can negatively affect recruitment, and (2) that the disturbance effect is more pronounced in muddy sediment. The results of their studies imply that small-scale geochemical processes affect recruitment decisions of polychaetes and bivalves.

In line with the current theory that porewater chemistry and recruitment decisions are linked, Cummings et al. (2009) demonstrated how terrestrial sediment deposition can cause (1) a disturbance of steady-state gradients in the concentration of oxygen and pH, which can decrease the penetration depth of oxygen, and lower the porewater pH, and (2) lowered burial of *M. liliana* into the sediment. The authors propose that the reduced supply of oxygen to the deposit-underlying sediment raised the position of the oxygen concentration gradient so that most of the gradient was located in the terrestrial deposit, and consequently, increased the likelihood of reduced solutes diffusing upwards and providing the negative cue and mechanism for deterred burial by juveniles at the surface of the deposit.

General biology of *Macomona liliana*

Tellinid bivalve molluscs are common and important components of estuarine and coastal benthos around the world (Roper, Pridmore, and Thrush, 1992). The wedge shell *M. liliana* (Iredale, 1915) formerly *Tellina liliana*, is an endemic tellinid bivalve that is recognised as an infaunal community dominant in intertidal embayments (Woodin et al., 2012). Adult *M. liliana* are ecosystem engineers that modify the sediment and its biogeochemical properties (Woodin et al., 2012). Numerous studies have demonstrated the significance of *M. liliana* to community structure in the intertidal sandflats of the Manukau Harbour (e.g., Cummings et al., 1993; Committo, 1995; Pridmore, Thrush, Hewitt and Roper, 1990; Thrush 1991; Thrush et al., 1997; Turner et al., 1997; Woodin et al., 2012). Others have demonstrated that *M. liliana* decrease sediment stability in the Tauranga Harbour (e.g., Lelieveld, Pilditch, and Green, 2004). *M. liliana* lives in sympatry with the venerid cockle *Austrovenus stutchburyi* (Leung and Poulin, 2008) in the mid-tide zone. For example, Lelieveld et al. (2004) reported that alongside the cockle *A. stutchburyi, M. liliana* was a dominant organism at the Tuapiro sandflats, Tauranga Harbour, and Pridmore et al. (1990) reported *M. liliana* and *A. stutchburyi* were the two most common bivalves living in

the sandflats of the Manukau Harbour. Adult *M. liliana* live 5–10 cm below the sediment surface, whereas juveniles are restricted to the top 1 cm of the sediment due to their shorter siphons (Zwarts & Wanick, 1989). Grange (1977) and Taylor (1998) suggest this species prefers well sorted fine sands, although Pridmore et al. (1990), Hewitt et al. (1996) and Cummings et al. (1997) suggest this species is less commonly found in finer sediments. Pridmore et al. (1990) also suggests that while *M. liliana* may show a preference for certain grain sizes, a narrow selectivity is not indicated.

M. liliana is a facultative deposit-feeder that uses a long inhalant siphon to ingest surface deposits and/or particles in the water column (Powell, 1979; Pridmore et al. 1991). As such, this species leaves distinct radial surface tracks (circa 1–2 cm long) on the sediment surface.

M. liliana is gonochoric (Taylor, 1988), and the findings of Taylor (1988) support the hypothesis that exogenous factors control sex differentiation in this species. Taylor (1998) found that sexual maturity occurs in individuals' with a shell length ≥22 mm. The reproductive cycle of *M. liliana* includes a ripe stage, a spawning stage, and a spent stage (Taylor, 1998). The timing of the reproductive cycle is associated with seasonal changes in environmental variables, including temperature, salinity, and seasonal production of phytoplankton and benthic microalgae (Taylor, 1988). Both Taylor (1998) and Roper et al. (1992) reported asynchronous spawning that is protracted on a Manukau mid-tide sandflat. Under laboratory conditions, Taylor (1998) was able to induce spawning of adult *M. liliana* by temperature shock treatment and addition of gametes. Taylor also attempted to induce spawning by chemical stimulation (i.e., injection of potassium chloride and sodium hydroxide), however, this method had no effect.

Recruitment of this species has been well studied on the Manukau sandflats. The structure of the local Manukau sandflat population is strongly influenced by the presence of small (<5 mm shell length) individuals (Roper et al., 1992). For high-energy environments in the Manukau sandflat, recruitment patterns are linked to physical transport processes, post-settlement migration, and high numbers of *Boccardia syrtis* tube-mats (Taylor, 1998). Larval supply and active habitat selection by settling larvae are postulated by Taylor (1998) to influence population structure in sheltered environments. Juvenile *M. liliana* typically grow 2–3 mm in the first year (Roper et al.,

1992) and are considered adults once their shell length reaches ≥20 mm. This species is known to reach sizes of up to 60 mm (Powell, 1979), and densities of juveniles can reach up to ~10^3 m^{-2} (Ahrens et al., 2002). Furthermore, decreasing *M. liliana* density may increase sediment stability up to 200% (Lelieveld et al., 2004).

M. liliana is considered a highly mobile bivalve (Turner et al., 1997; Norkko et al., 2001). Schneider, Walters, Thrush and Dayton (1997) reported that the speed of active lateral movement by adults can reach circa 10 cm day^{-1}. Juveniles disperse along the sediment surface as bedload, or in the water column with the assistance of byssus threads (e.g., Cummings et al., 1993; Cummings et a., 1995; Lundquist et al., 2004; Petuha, Lundquist & Pilditch, 2006), and can reach a speed of 10 m day^{-1} (Cummings et al. 1993). A recent study by Petuha et al. (2006) predicted that juveniles can travel up to 80 m day^{-1} in the bedload, and circa 3 km day^{-1} by drifting in the water column. According to their model calculations, Petuha et al. reported that a continuously drifting juvenile travelling unidirectionally could disperse across the Manukau Harbour (22 km) in 7 spring tidal cycles. Short-term byssus drifting and long-term bedload transport are most likely to occur in the field, but the effect of many biological and physical factors on juvenile dispersal remains poorly understood.

Both juvenile and adult *M. liliana* have well documented behavioural responses that have resulted in their recognition as sensitive indicators of change, namely burial, crawling, and drifting. Woodin et al. (2012) reported that adult *M. liliana* exhibit behaviours that can be detected by fluctuations in porewater pressure waveforms, for example, burrowing, siphon relocation, pseudofeces expulsion, and defecation. Previous laboratory and field experiments indicated that *M. liliana* have several other behaviours, including emergence and drifting in the water column (e.g., Cummings et al., 1993; Cummings et al., 1995; Lundquist et al., 2004; Pridmore et al., 1991; Turner et al., 1997). By either emerging from the sediment or burrowing into the sediment, *M. liliana* can increase or decrease the likelihood of transport. Juvenile *M. liliana* emerge from the sediment surface and may either crawl along the sediment surface or initiate drifting behaviour to avoid adverse conditions. Roper and Hickey (1994) and Roper, Nipper, Hickey, Martin and Weatherhead (1995) have shown that juveniles crawl from copper- chlordane- and zinc-dosed sediments to adjacent clean control sediments.

Burial, crawling, and drifting behaviour of *Macomona liliana*

Burial (or burrowing) behaviour of macrofauna constitutes an intrinsic part of their basic living activities and is as fundamental as foraging and breeding (Sassa, Watabe, Yang & Kuwae, 2011). Active burrowing in sediment-dwelling bivalves requires a widened gape of the valves and extension of the foot (Romano, Sarà, Salvo, Bishop, Mazzola & Widdows, 2011). Active burrowing by *M. liliana* over a period of time, that is, the burial rate, is used to assess the species' acceptability or intolerance to various environmental conditions. Burial rate is measured by adding a known quantity of bivalves onto a sediment surface and counting the number of individuals that have not burrowed into the sediment after a period of time. Roper and Hickey (1994) found that juveniles decided to accept or reject a substrate in the first 10 minutes of contact with the substrate. This was adopted in studies designed to assess the acceptability of polychaete (*Boccardia syrtis*) tube-mat dominated substrates (Cummings et al., 1996), terrestrial deposit-disturbed sediments (Cummings and Thrush, 2004; Cummings et al., 2009), contaminated sediments (Roper and Hickey, 1994; Roper et al., 1995), and as a measure of the sensitivity of juvenile *M. liliana* to UV-photoactivated fluoranthene (Ahrens et al., 2002). In the latter study, failure to rebury into control sediments following exposure to fluoranthene concentrations was considered as being indicative of a moribund condition, as juveniles would be unlikely to survive under natural conditions if lying motionless on the sediment surface for a prolonged time (Ahrens et al., 2002). In the field, however, juveniles can actively disperse from the sediment surface, or be transported passively, and the likelihood of remaining on the sediment surface for a prolonged time is therefore largely influenced by their behaviour, and/or local hydrodynamics.

Following burial, juveniles may return to the sediment surface (emergence). This behaviour has been well described in Cummings et al. (1993) for *M. liliana*, and is indicative of a bivalve's desire to avoid the sediment conditions. Studies have observed emergence behaviour from *M. liliana* when they have been offered 'burnt sand', 'defaunated natural sediment', and 'glass beads' (e.g., Cummings et al., 1993; Lundquist et al., 2004). It has also been suggested that emergence behaviour in bivalves may be triggered by 'favourisation', a parasite induced mechanism that modifies the behaviour of the bivalves to allow for parasitic transmission to end hosts

(Desclaux, Montaudouin & Bachelet, 2002). Trematode metacercariae infection has been documented in *M. liliana* (Leung and Poulin, 2008), however, the effect on emergence behaviour has not been studied to date.

Traditionally, the dispersal of larvae via bedload transport was considered the dominant mechanism for the distribution of many bivalves, however, the significance of drifting (also referred to as floating) by post-settlement juvenile *M. liliana* is also recognised as an important dispersal mechanism (Cummings et al., 1993; Cummings et al., 1995; Lundquist et al., 2004). Norkko et al. (2001) and Petuha et al. (2006) have shown that drifting is an important process that determines spatial and temporal patterns of *M. liliana* distributions in soft sediments. The ability to drift allows juveniles to avoid adverse locations, such as contaminated sediments, and then repopulate those same locations when the sediments are no longer contaminated (e.g., Pridmore et al., 1991). This ability not only increases the potential for survival, but also aids the resilience of this species in dynamic environments where anthropogenic influences are common.

To initiate drifting, *M. liliana* secretes a thin hyaline (also referred to as byssus) thread. This thread increases the viscous drag exerted on the bivalve, enabling it to be lifted from the sediment surface and be transported in the water column by relatively weak currents (Sigurdsson, Titman, and Davies, 1976; Sorlin, 1988; Cummings et al., 1993). The phenomenon of drifting via byssus threads is documented in >23 bivalve species, including 5 Tellinacea (Sigurdsson et al., 1976; Cummings et al., 1993). Through a series of laboratory experiments, Sorlin (1988) was able to induce a drifting response in the tellinid bivalve *Macoma balthica* by external stimuli (i.e., temperature and current). In this study, temperature was the synchronising stimulus. Sorlin reported that thermal treatment elicited displacement in the sediment only, whereas moving water resulted in displacement in the sediment and subsequent drifting or floating behaviour. Although water current may induce floating in the laboratory, it is unlikely that *M. balthica* bivalves would always respond in that way in a natural environment (Sorlin, 1988).

Similarly, Cummings et al. (1993) induced drifting in post-settlement juvenile *M. liliana* under laboratory conditions. Cummings et al. found no evidence of a seasonal component in the drifting of *M. liliana.* They did observe that juveniles quickly

burrowed into native 'burnt sand', but readily emerged, and subsequently drifted, when a current was provided. This response, however, could not be replicated in natural sediment, and it was proposed that when conditions are favourable, there is no reason for juveniles to move away.

Lundquist et al. (2004) emphasized that *M. liliana* actively influence post-settlement transport in response to both substrate type and flow regime, and found that juveniles were more likely to disperse with higher flow. Thread production is the likely mechanism adopted for drifting by *M. liliana*, and branched and unbranched threads have been documented in drifting juveniles (Cummings et al., 1993)*.*

Hypothesis

Considering the following evidence: (1) most biologically and chemically active sediments are characterised by steep solute gradients in the upper layers that organisms inhabit and new recruits explore, (2) disturbances of surficial sediments impose a change in surface chemistry that juveniles may detect as they explore the sediment surface, and (3) thin (1–2 mm) terrestrial sediment deposits disturb the sediment porewater chemistry and negatively affect the burial of post-settlement juveniles of the bivalve *M. liliana*, the purpose of this thesis is to further elucidate the linkage between sediment porewater chemistry and burial behaviour of *M. liliana* by testing the hypothesis that:

Juvenile bivalves that reject sediment onto which terrestrial sediment has been deposited do so not from the contact of the juvenile bivalve with the terrestrial sediment deposit, but from a change in the redox chemistry of the deposit-underlying marine sediment. Information about such change is transmitted through the deposit to the bivalves on the surface of the deposit in the form of reduced solutes. If so, then I expect terrestrial sediment deposited onto less diagenetically active sediment (i.e., sediment with lower rates of organic matter degradation) to affect burial less than deposits onto diagenetically active sediment (i.e., sediment with higher rates of organic matter degradation). Specifically, the null hypothesis is:

There will be no difference in burial behaviour of *M. liliana* post-settlement juveniles placed on the surface of terrestrial sediment deposited over natural intertidal sediment versus over intertidal sediment depleted of organic matter.

Material and methods

I conducted a series of experiments in a recirculating seawater flume over May and June 2011 to investigate the effects of terrestrial sediment deposits on the burial behaviour of *Macomona liliana* post-settlement juveniles, and on sediment porewater chemistry. Cores of two types of sediment were used in this series, intact natural intertidal sediment (hereafter, intertidal), and intertidal sediment from which organic matter was removed by combustion (hereafter, depleted). The intertidal sediment was heterogeneous (due to bioturbation) and diagenetically active. The depleted sediment was homogeneous (due to the absence of organic particles and infauna) and less diagenetically active.

In each of five replicate flume experiments (hereafter, experimental runs) the surfaces of four sediment cores were exposed to flowing seawater: one core of intertidal sediment (C), one core of depleted sediment (D), and one core of each sediment type treated with surface deposits of terrestrial sediment (CTS and DTS). Post-settlement juvenile *M. liliana* were added to these surfaces and their subsequent burial behaviour was observed during the 10 min immediately following their placement on the sediment surface, and up to 4 h later. Differences between the sediment core porewater chemistry were investigated by measuring vertical profiles of porewater oxygen concentration, pH, and oxidation–reduction potential (hereafter, redox) before addition of *M. liliana*. Because only one flume was available, the experimental runs were conducted consecutively. Each experimental run lasted two days.

Sampling sites

I obtained terrestrial sediment from a landslide at Hahei Beach, Coromandel, North Island (Figure 3). Intertidal sediment and post-settlement juveniles of *M. liliana* were collected concurrently from the Tauranga Harbour on the first day of each experimental run. Tauranga Harbour is a large tidal inlet on the northeast coast of the North Island, New Zealand. The sampling site was located at a sheltered mid-intertidal sandflat 80 m east of Tuapiro Channel in the northern basin of the harbour (37° 29.394′ S, 175°, 57.108′ E; Figure 4). Here, *M. liliana* and *Austrovenus stutchburyi* are the dominant macrofaunal species (Lundquist et al., 2004).
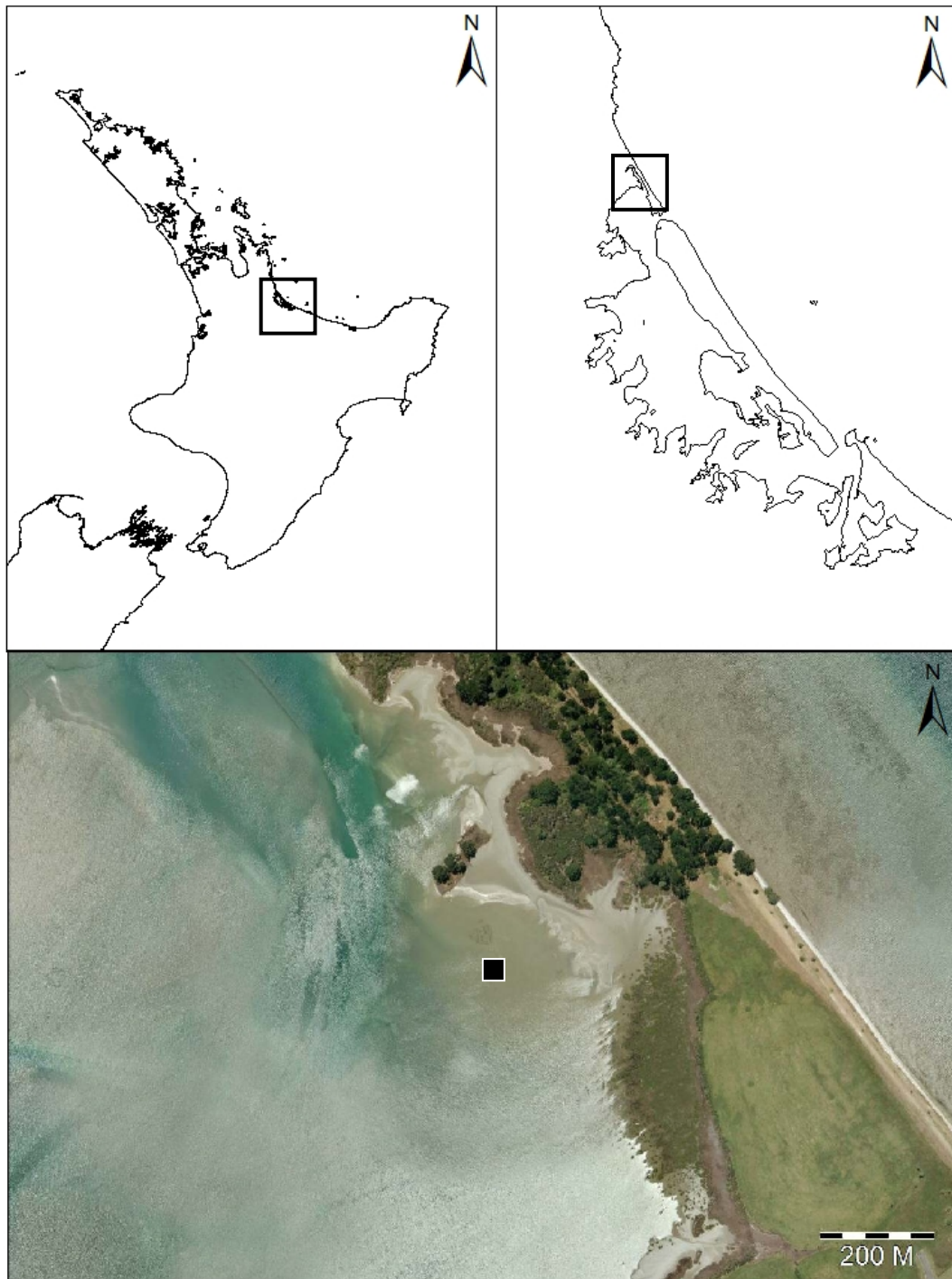
Figure 3. Map of region and location of the terrestrial sediment source. Satellite image showing the northern end of Hahei Beach, Coromandel Peninsula (http://www.tcdc.govt.nz/Our-Services/Maps-Geographical-data-GIS/). The black marker indicates the location of the landslide.
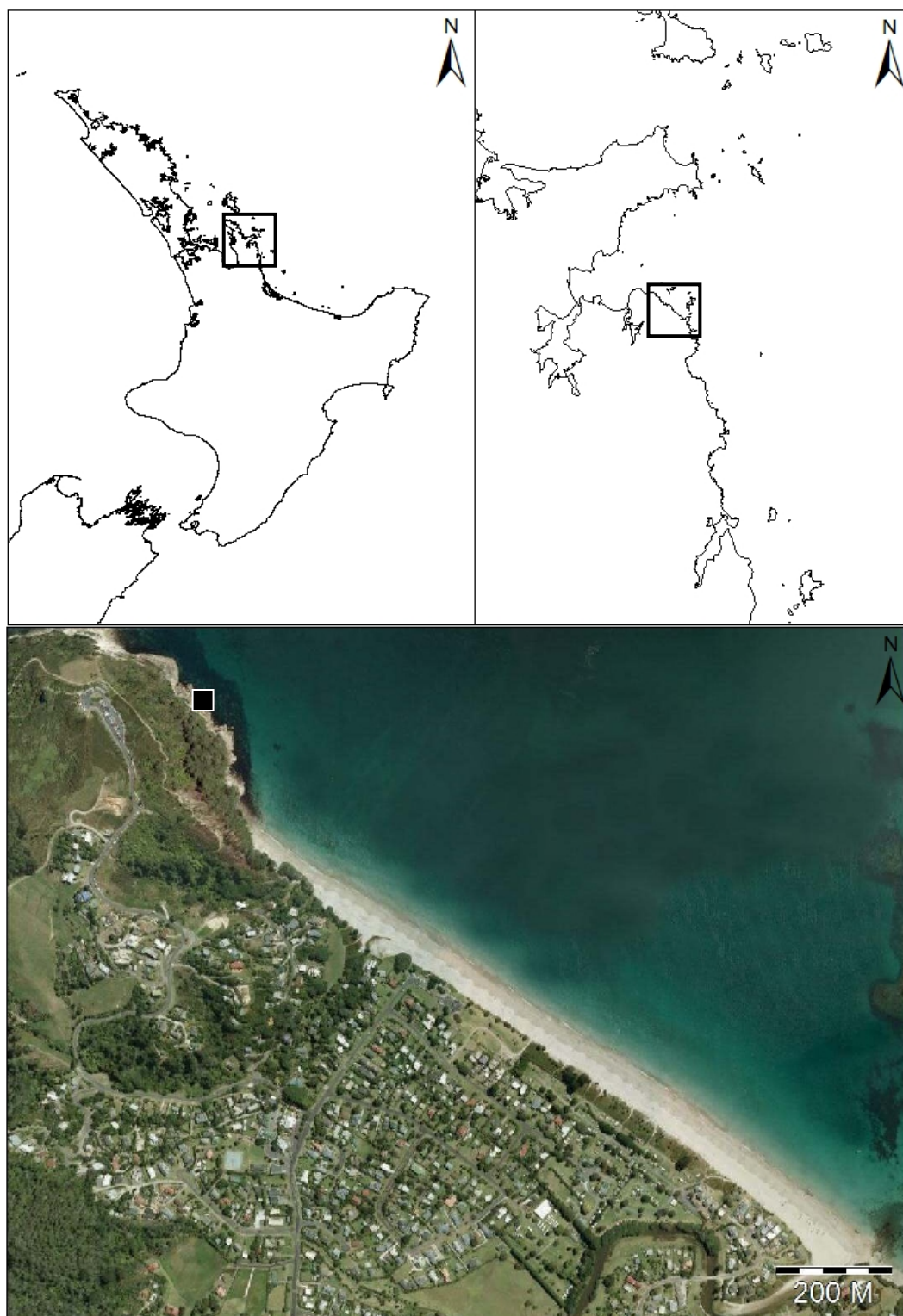
Figure 4. Map of the region and location of the study site. Satellite image showing the Tuapiro sandflats at the northern basin of the Tauranga harbour (http://map.westernbay.govt.nz/ivy/ivyq.html). The black marker indicates the location of the randomised sediment sampling.

Intertidal sediment

I collected six cores of intertidal sediment on the first morning of each experimental run between one hour before and one hour after the time of low tide with acrylic tubes (inner diameter = 5.3 cm, length = 30 cm). One tube at a time was inserted into the sediment at each of six locations previously defined by Cartesian co-ordinates. These co-ordinates were generated randomly for each run, in units expressed as footsteps from a fixed point on the sandflat (Figure 4). The tubes were inserted ~10 cm into the sediment and a stopper placed at the bottom of each tube to enclose the sediment core. The tubes were then transported on ice to the laboratory within 2 h of collection. Of the six sediment cores, the two least disturbed (i.e., no large cockles or crabs present on sediment surface) were inserted into the flume. One sediment core was frozen, and later used to analyse sediment water content, organic matter content and grain size distribution. The remaining three sediment cores were discarded.

Bivalves

Individuals of *M. liliana* were collected at the same location as the cores of intertidal sediment. The surface of the sediment (top 2 cm) was scraped with a small plastic shovel and washed through a 500-μm mesh with seawater. The retained material was then placed into seawater filled bags and transported on ice to the laboratory within 2 h. In the laboratory, juvenile *M. liliana* were transferred into aerated artificial seawater and measured with a stereomicroscope (× 40 magnification). Lined graph paper was used to measure their shell length; only individuals with 1–2 mm shell length were selected. For each experimental run, 80 individuals were randomly selected from those of the desired size, and photographed with graph paper in the background as a scale reference. Of these, 20 individuals were then held in each of four containers filled with aerated, artificial seawater for use within 24 h.

Depleted sediment

Dry intertidal sediments of different particles sizes (≤500 μm) were obtained from the Waikato Aquatic Laboratory and combined to achieve a grain size distribution similar to that of the intertidal sediment (i.e., 500 μm; 250 μm; 125 μm; and <63 μm comprised of ~10%, ~65%, ~20%, and ~5% respectively). The combined sediment was then combusted in a muffle furnace at 450°C for 6 h to remove organic matter and stored in sealed containers. This sediment was then added to acrylic tubes filled with

artificial seawater so that the volume of sediment added was approximately equal to that of the intertidal sediment cores.

Terrestrial sediment

Approximately 100 g of terrestrial sediment was suspended in 100 mL artificial seawater on the first day of each run. This suspension was poured through a 250-μm mesh to remove large particles and then added to the flume to make a terrestrial sediment deposit. One PVC tube (inner diameter = 6.5 cm) was placed directly above each core to confine the suspension to the flume seawater directly above the sediment core, and prevent terrestrial sediment deposition on to the bottom of the flume and the neighbouring sediment cores. The opening of this tube was protruding 5 cm above the water surface. Preliminary trials showed that addition of 15 mL of terrestrial sediment suspension to the seawater inside a PVC tube resulted in a 1–2 mm thick deposit on the surface of the sediment core. This deposit remained intact when the flow speed of the flume seawater was 2.41 cm s^{-1}. An additional 10 mL of suspension from each run was stored in a sealed container to quantify particle size distribution.

Experimental setup

Seawater flume

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 flume. 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 (541 cm downstream from the flume entrance) allowed the insertion of tubes containing the sediment cores. These holes were distributed along a line perpendicular to the raceway and spread over a considerable proportion of the flume width (confined to the central 33 cm in the cross stream direction). To account for possible cross-stream variations in flow speed, the position of each of the four core treatments was rotated across experimental runs (Table 1; Figure 5).

Table 1. Positions of each sediment core in the working section of the flume during each experimental run. CTS, intertidal sediment with a 1–2 mm surface terrestrial deposit; DTS, depleted sediment with a 1–2 mm surface terrestrial deposit; C, intertidal sediment; D, depleted sediment.

	Core position			
Run	1	2	3	4
1	CTS	DTS	C	D
2	D	CTS	DTS	C
3	C	D	CTS	DTS
4	DTS	C	D	CTS
5	CTS	DTS	C	D
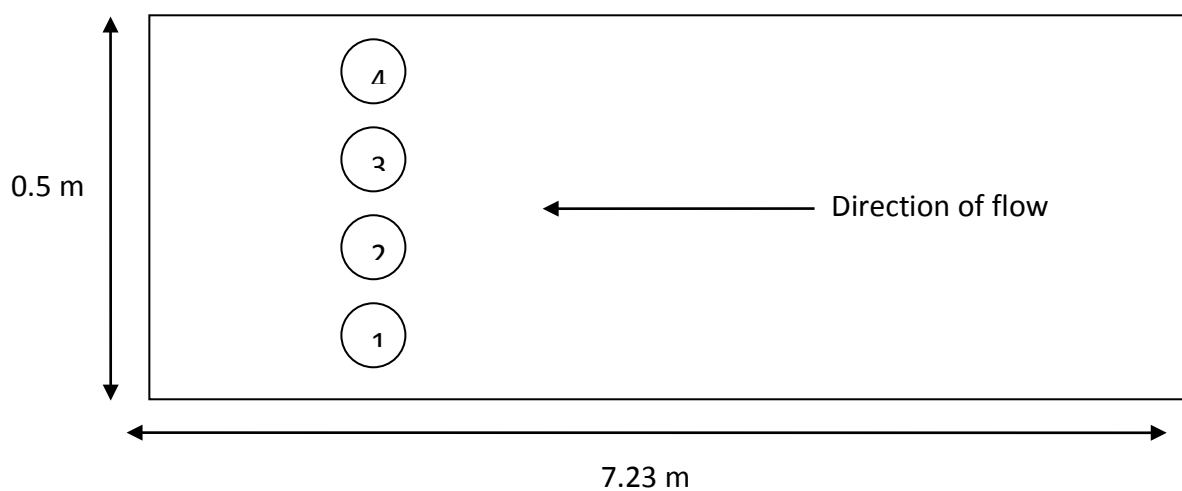
Figure 5. Aerial view of the core positions 1, 2, 3, and 4 in a recirculating flume (not drawn to scale).

Sediment-filled tubes were inserted into the flume so that the rims of the tubes were flush with the flume floor. Tubes were held in place with nylon collars fitted with internal O-rings and secured to the underside of the flume. Weighted petri dishes were placed over each hole while the flume was being filled with seawater to avoid disturbance of the surface of the sediment core inside the tube.

Once the flume was filled to 19 cm, the sediment cores inside the four tubes were raised with a precision extruder so that their surfaces were flush with the flume floor. The surfaces of those two cores that required a terrestrial surface deposit (Table 1) were then lowered by ~1 mm. A PVC tube was placed over each sediment core, and then terrestrial sediment was added to the seawater inside two PVC tubes as described above to create a deposit on the surface of two cores. The suspended sediment particles were allowed to settle for 30 min. For the remaining two cores, seawater was poured through the PVC tubes instead of the terrestrial sediment suspension. After 30 min, all PVC tubes were carefully removed and a multiparameter sonde was submerged downstream of the working section. The free stream flow was adjusted to 2.41 cm s^{-1} (impeller speed of 2 Hz) and the flume was left running overnight to allow reestablishment of porewater solute gradients, which were potentially disturbed during collection, transportation, and handling of the sediment cores. Experiments were conducted at ambient temperature, and fluorescent lights fitted above the working section of the flume supplied photosynthetically active radiation between the hours of 8 am and 6 pm.

Experimental sequence

Each experimental run was carried out over two days following the same sequence of handling steps. On Day 1 juvenile *M. liliana* and intertidal sediment were sampled as described above. The sediment-filled tubes were inserted into the flume and the flume was filled with seawater. The correct sized bivalves were then obtained from the bagged material, photographed, and transferred into holding containers. Terrestrial sediment suspensions were added to the surfaces of cores to create surface deposits. The multiparameter sonde was calibrated and programmed to record data over the duration of the experimental run, and inserted into the flume. In the morning of Day 2, two pH, two redox, and five oxygen vertical porewater microprofiles (Table 2) were measured in each of the sediment cores within the flume. Following these

measurements, 20 live juvenile *M. liliana* were added to the seawater flume, approximately 2 cm upstream of each of the four sediment cores, and allowed to drift with the flow onto the sediment surface. One digital photograph was taken every minute for 10 min starting immediately after their introduction to the surfaces of the sediment cores. Thereafter, one digital photograph was taken every hour until completion of the experiment.

Table 2. Date of sediment collection and parameter measured in each of the preliminary runs A and B, and in each of the five experimental runs. *n* = the number of replicate measurements in each sediment core. O$_2$, dissolved oxygen; Eh, redox potential, A, preliminary run A; B, preliminary run B.

Run	Date	Parameter	*n*
A	17 May 2011	O$_2$	5
B	19 May 2011	O$_2$	5
1	24 May 2011	Eh	2
2	26 May 2011	O$_2$	5
3	31 May 2011	Eh	2
4	2 June 2011	pH	2
5	10 June 2011	pH	2

Measurements and observations

Flume seawater

To characterise the variation in seawater flow and boundary-layer dynamics, flow velocity measurements were made with a Sontek 10 MHz Acoustic Doppler Velocimeter (ADV) at the flume bed surface (integrating 0–18 mm of the ADV sample volume above the flume floor) over 10 min at a sampling frequency of 4 Hz. In addition, vertical profile velocity measurements were made above the centre of each core at heights ranging from 0.25 cm to 8 cm (at 0.5 cm intervals).

A YSI multiparameter 6600V2-4 sonde was used to measure temperature (°C), salinity (‰), and dissolved oxygen content (% saturation) of the flume seawater. The sonde also recorded the intensity of the photosynthetically active radiation (PAR) with a LI-192 Underwater Quantum Sensor (LI-COR) submerged in the flume seawater, facing upward. Ecowatch for Windows software was used to program the sonde to measure once per second over the duration of each run. All sensors were calibrated following YSI instructions (see www.ysi.com). Although the experiment constituted of five replicate runs, an additional two preliminary replicate runs were conducted (herein referred to as preliminary run A and preliminary run B) and are included in the analysis of seawater properties (Table 2).

Sediment porewater

Vertical microprofiles of sediment porewater oxygen concentration, pH, and redox were measured using Unisense microelectrodes. Profiles of porewater oxygen concentration were measured because oxygen is physiologically important to organisms and has strong concentration gradients in surficial sediments (Glud, 2008). Seawater pH was measured because of its status as a master variable, and linkage to all major biogeochemical reaction processes in sediments (Jourabchi et al., 2005). Measurement of redox was included to locate the chemocline, i.e., the transition between oxidising and reducing sediments.

All profiles were measured at a resolution of 0.1 mm normal to the sediment surface, beginning in the flowing seawater above the diffusive boundary layer (~2 mm above the sediment surface) to a maximum depth of 5.5 mm. To measure a profile, one microelectrode was mounted on a motorised micromanipulator that was attached to a

stand. The stand was suspended from an acrylic beam across the roof of the flume, so that the microelectrodes were aligned to measure profiles in each of the sediment cores within the flume (Table 2).

The software Profix (Unisense) was used to control the stepwise movement of the micromanipulator via a motor controller, and record the data from the microelectrodes. The microelectrodes were calibrated once a day, before commencement of a measurement series, at the experimental temperature following the instructions of the manufacturer (see www.unisense.com).

Data analyses

Digital photographs

The shell length of *M. liliana* was measured with analySIS Life Science Research (analySIS LS Research) image analysis software. Each image was calibrated against the graph paper scale and individuals were measured to the nearest 0.01 mm. Shell lengths were pooled in to 0.01 mm size classes and a histogram was produced to assess size distribution.

Individuals remaining on the sediment surface after 10 min, 1, 2, 3, and 4, h were counted using the digital photographs. Crawling traces, if any, were measured to the nearest 0.01 mm. These images were calibrated using the known length of the acrylic tube inner diameter as a scale reference.

Sediment

Terrestrial sediment deposit

The visual appearance of the deposits was described by surface colour and roughness, and the presence or absence of macrofaunal burrows or traces. The particle size distribution of the deposit was measured with a Malvern Mastersizer–2000 (Malvern Instruments Ltd). The deposit thickness was identified by a distinct change in the slope of the oxygen microprofiles. This change occurs because of differences in the diffusivity of the deposit and underlying 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$_2$ concentration gradient in the DBL and the constant O$_2$ concentration of the overlying mixed seawater.

Intertidal and Depleted sediment

The visual appearance of sediment surface was described as above. Analyses of sediment particle size, water content, and organic matter content were carried out on the homogenised top 5 cm of the sediments cores. Water content was determined by weight loss after drying at 80°C for 24 h. Organic matter content, measured as loss on ignition, was determined by combusting dried sediment in a muffle furnace at 450°C for 6 h. For both procedures, sediment was allowed to cool in a desiccator for 30 min and weighed to the nearest 0.1 mg.

The sediment grain size distribution was determined by wet sieving the homogenized sediment using 7 mesh sizes (63 µm; 125 µm; 250 µm; 500 µm; 1.0 mm; 2.0 mm; 4.0 mm). The weight of the sediment was calculated following Giere (1993), whereby total dry weight of sample minus dry weight of sieved fractions equals dry weight of the sediment that was lost through the finest sieve, that is, 63 µm. The phi scale: $\phi = -\log^2$ (grain size, mm) was used represent grain size when calculating granulometric indices. A cumulative frequency curve was created for intertidal and depleted sediment to calculate the Median particle diameter, Md = (ϕ16 + ϕ50 + ϕ84)/3, the lower (Q$_1$ = ϕ25) and upper quartiles (Q$_3$ = ϕ75), the inclusive Sorting Coefficient, QD$_1$ = (ϕ84 − ϕ16)/4 + (ϕ95 − ϕ5)/6.6, and the inclusive Graphic skewness, SK$_1$ = (ϕ16 + ϕ84 − 2ϕ50)/2(ϕ84 − ϕ16).

Oxygenation

The profiles across the diffusive boundary layer were used to estimate the rate of the diffusive O$_2$ uptake (DOU) following Jørgensen and Revsbech (1985) and Rasmussen and Jørgensen (1992). The oxygen penetration depth (OPD) was measured from the deposit–sediment interface (CTS and DTS), or from the sediment–water interface (C and D).

Statistics

The probability of bivalves remaining on the sediment surface after 10 min (called 'p') was predicted because juvenile *M. liliana* initiate burrowing in the first 10 min of their placement (Roper et al., 1994). Ordinary least squares were inapplicable, because p is required to lie between 0 and 1. Therefore a logistic model (general linear model, binomial family) was used because a proportion from count data was being estimated (R.K.S. Hankin, personal communication, April 5, 2011). Because independent Bernoulli trials (i.e., experiment with two outcomes, buried, not buried) were summed, binomial distribution was used.

Analysis of images revealed that although 20 bivalves were added to the surface of each sediment core, several individuals could not be accounted for immediately following their placement in 5 instances. If so, it was assumed they either landed on the floor of the flume outside of the sediment core, or remained in the pipette. Therefore, the statistic used was the number of animals remaining on the surface after ten minutes (n = 18–20). To retain all trials whatever the value of n, generalised linear modelling was used to weight the data with respect to n; larger values of n constituted more statistically informative experiments. The experiment included four positions across the width of the flume ('pos' = 1, 2, 3, 4).

The analyses revealed that core position affected 'p', with a p-value of $0.0122 \times 3 = 0.0366$, showing that fluid mechanical environmental variability is likely to be an important factor. In this study, the core position within the flume was viewed 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. These trials revealed that the appropriate regressors were intertidal and depleted sediment ('lower_org') and the presence or absence of a terrestrial sediment deposit ('upper_terrig'). The statistical software R was used to conduct all statistical analyses. See Appendix Tab 1 for a statistical analysis summary.

Results

This chapter presents characteristics of seawater and sediment properties, and findings from the behavioural observation.

Flume environment: seawater

Sonde data are presented for preliminary runs A and B, run 1, 2, 3, and 4. Photosynthetically active radiation and temperature varied over the course of the day. Temperature in the flume varied between 16.6 and 18.3°C, and the photosynthetically active radiation varied between 3.3 and 22.1 µmol quanta m^{-2}s^{-1}. The salinity of the flume seawater was 32‰, and dissolved oxygen varied between 90 and 94% saturation (Table 3).

The mean flow velocity of the flume seawater was 1.68 cm s^{-1}. Time-series measurements revealed variation in this velocity across the width of the flume. The velocity of the flow was highest above core 1 and gradually decreased across the width of the flume so that the lowest velocity was experienced above core 4. Similarly, vertical profile velocity measurements revealed variation in flow velocity across the width of the flume. The variation revealed from vertical measurements, however, was not consistent with time-series measurements. Instead, the velocity of the seawater above cores 2 and 3 had a slightly higher velocity than cores 1 and 4 (Table 4).

Table 3. Flume seawater properties (temperature, irradiance, salinity, and dissolved oxygen) for preliminary runs A and B, and runs 1, 2, 3, and 4. Averages are given ± 1 S.D. PAR, photosynthetically active radiation; DO, dissolved oxygen; A, preliminary run A; B, preliminary run B.

	Temperature (° C)		PAR	Salinity	DO
Run	Min	Max	(μmol quanta m^{-2}s^{-1})	(‰)	(% saturation)
A	17.6	18.5	11.8±8.0	32.2±0.05	90.6±1.1
B	16.2	17.6	11.6±6.6	32.6±0.02	92.0±0.6
1	16.9	18.4	8.5±6.6	32.7±0.01	92.5±0.6
2	18.9	20.0	9.5±6.7	32.8±0.02	93.7±0.5
3	16.6	18.3	7.4±6.1	32.9±0.07	90.3±0.7
4	16.9	18.1	5.3±4.4	32.7±0.07	92.5±1.1

Table 4. Flume seawater flow velocity above the centre of each core in vertical profile and time series measurements when the impeller speed is 2 Hz. Free-stream flow (u) refers to the mean of all vertical velocity measurements made above each core, and 0.76 cm above the sediment core respectively. Core positions are confined to the central 33 cm in the cross stream direction of the flume.

	Free-stream flow velocity (cm s^{-1})			
	Core 1	Core 2	Core 3	Core 4
Vertical profiles	2.06	2.11	2.12	2.06
Time series	1.93	1.82	1.55	1.43

Flume environment: sediment

Surface structure and colour

The topography of the brown surface of the intertidal sediment was heterogeneous. Macrofaunal burrows and patches of green films, presumably made by microphytes, were observed (Figure 6A).

The surface of the terrestrial sediment deposit over intertidal sediment was orange, smooth, and free of disturbance immediately after its deposition. In as little as 30 min, however, small openings of polychaete burrows appeared. On the following day, 4 hours after placement of the juveniles, the density of burrow openings (average diameter, 0.5–0.8 mm) ranged from 37 to 123 openings per core. Up to four green patches (5 mm longest axis) and 32 siphons were present and black, excavated sediment had buried small (up to 3 cm^2) patches of the deposit (Figure 6B).

In contrast to intertidal sediment, the surface of depleted sediment was homogeneous, smooth, flat, red-brown, and devoid of macrofauna and green films (Figure 6C). The absence of infauna resulted in a smooth flat surface of the terrestrial sediment deposit when the deposit was applied. Traces of buried *Macomona liliana* crawling at the surface of the deposit-underlying depleted sediment were observed during the experiment, which modified the surface of the terrestrial sediment deposit so it was no longer a flat surface. In contrast to intertidal sediment with a terrestrial sediment deposit, there was no reworking of the deposit in depleted sediment with a terrestrial sediment deposit by infauna. That is, there was no horizontal and vertical mixing of particles (e.g., construction and maintenance of galleries, ingestion and defecation of particles) although there was minor reworking of the deposit by the juvenile *M. liliana* displacing the particles (e.g., burrowing and crawling traces), (Figure 6D).
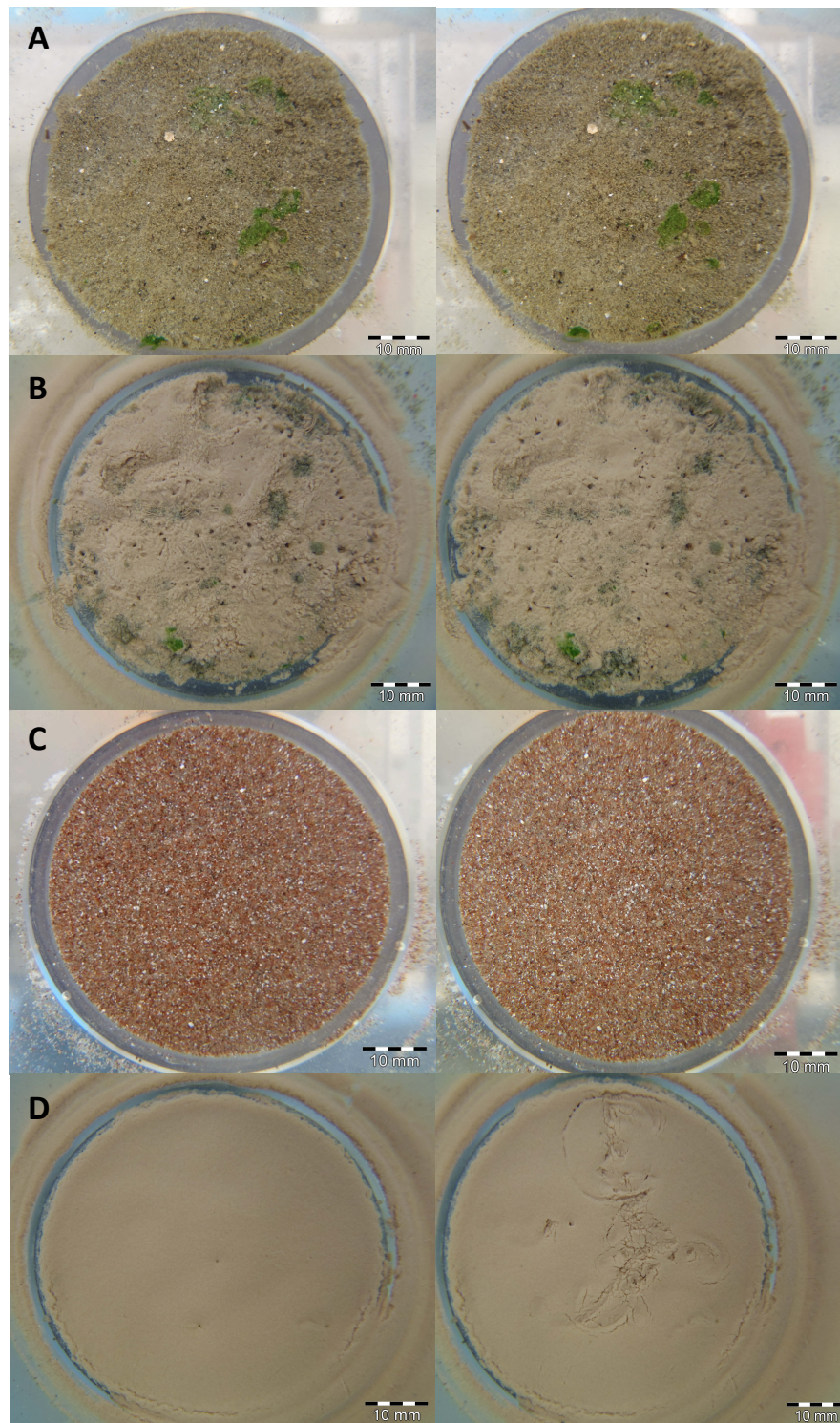
Figure 6. Images showing the surface, structure, and colour of each sediment core. *Left panel,* prior to addition of juvenile *M. liliana*; *Right panel,* at the completion of the experiment. (A) Intertidal sediment; (B) intertidal sediment with a 1–2 mm terrestrial sediment deposit; (C) depleted sediment; (D) depleted sediment with a terrestrial sediment deposit.

Granulometry

Intertidal and depleted sediment

Intertidal sediment was comprised of poorly sorted fine and very fine sand, whereas depleted sediment was comprised of moderately sorted medium sand (Figures 7–8). The median particle diameter of intertidal sediment was 144 µm with a lower and upper quartile of 218 and 88 µm respectively, whereas the median particle diameter of depleted sediment was 330 µm with a lower and upper quartile of 435 and 268 µm respectively (Table 5). Mud (<63 µm), water, and organic matter contents were higher in intertidal sediment (13.4%, 27.1%, and 2.2% respectively) than depleted sediment (2.4%, 19.4% and 0.4% respectively) (Table 5).

Terrestrial sediment suspension

Terrestrial sediment was well to moderately well sorted. Median particle diameter, lower quartiles, and upper quartile of the particles applied in runs 1 to 5 were similar in each experimental run. Median particle diameter ranged from 87 to 98 µm, and lower and upper quartiles ranged from 112 to 136 µm and 74 to 77 µm respectively. Mud content was variable, and ranged from 41 to 53% (Table 5). Water content and organic content were not determined.
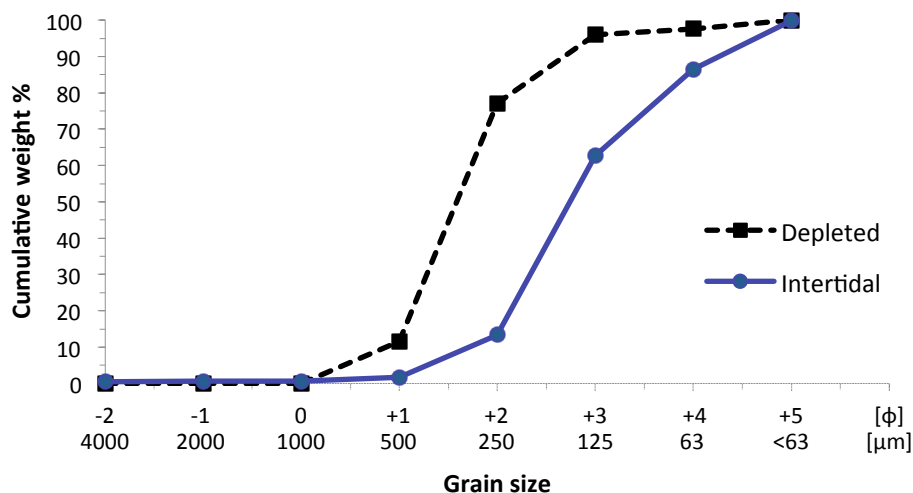
Figure 7. Granulometric curves of intertidal sediment and depleted sediment. Solid circles, intertidal sediment; solid squares, depleted sediment.
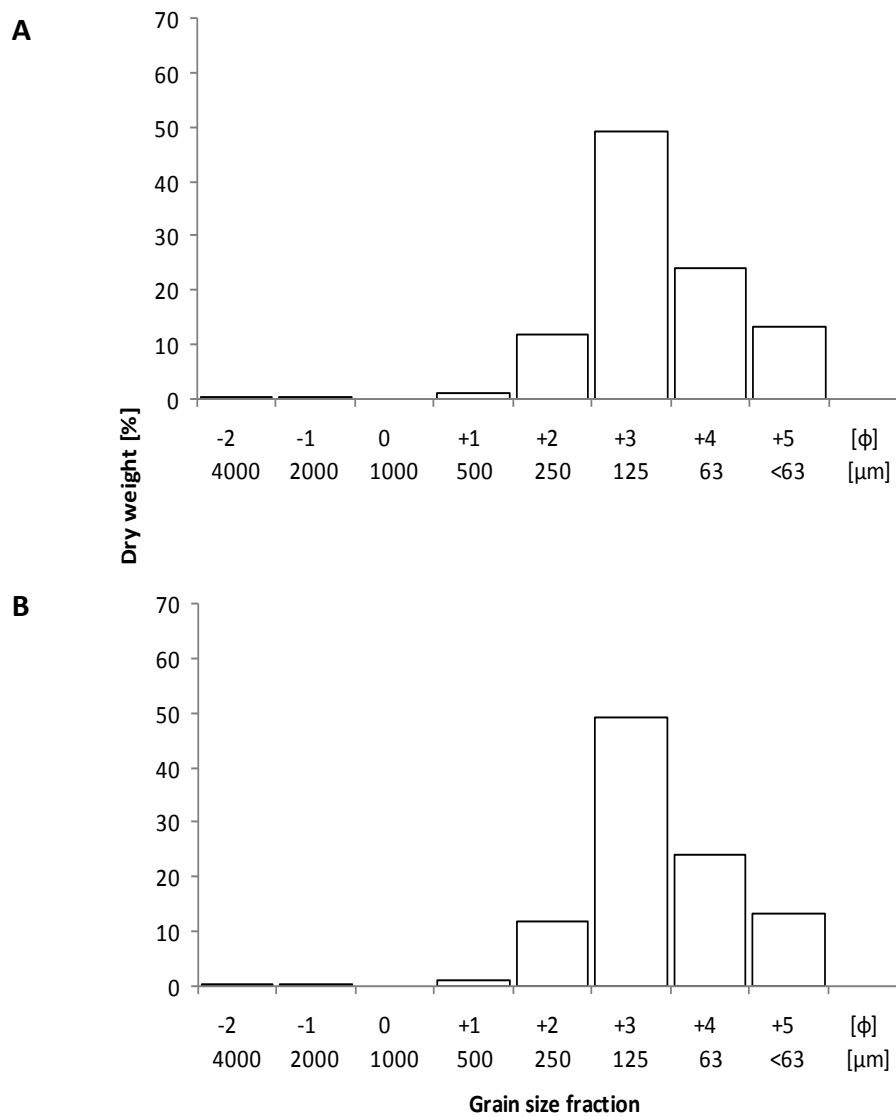
Figure 8. Sediment grain size fractions for (A) intertidal and (B) depleted sediment. Fractions are 2000–4000 μm (very fine gravel); 1000–2000 μm (very coarse sand); 500–1000 μm (coarse sand); 250–500 μm (medium sand); 125–250 μm (fine sand); 63–125 μm (very fine sand); <63 μm (mud).

Table 5. Characteristic granulometric indices for intertidal, depleted, and terrestrial sediment. Cores of intertidal sediment and depleted sediment from each run were pooled, and samples of terrestrial sediment from each run were analysed separately for each run. The indices are given in the phi scale and in the metric scale for the median, lower, and upper quartiles.

Granulometric index	Intertidal sediment	Depleted sediment	Terrestrial sediment				
			Run 1	Run 2	Run 3	Run 4	Run 5
Median (μm)	144	330	98	87	98	87	95
Lower Quartile Q_1 (μm)	218	435	136	114	134	112	125
Upper Quartile Q_3 (μm)	88	268	77	74	77	74	76
Inclusive Sorting Coefficient QD_1	2.00 poorly sorted	0.70 moderately sorted	0.55 moderately well sorted	0.43 well sorted	0.55 moderately well sorted	0.41 well sorted	0.52 moderately well sorted
Inclusive Graphic skewness SK_1	0.111	0.115	-0.107	-0.116	-0.105	-0.119	-0.111

Porewater solutes

The addition of millimetre-scale terrestrial sediment deposits modified the distribution of solutes in the porewater of intertidal and depleted sediment. The deposits ranged in thickness from 1 to 2.4 mm (Table 6). Results are presented as per parameter. See Appendix Tab 2 for a complete summary of all microelectrode measurements.

Table 6. Thickness of terrestrial sediment deposit applied to the surfaces of intertidal sediment and depleted sediment in preliminary runs A and B, and runs 2, 4, 5. CTS, intertidal sediment with a terrestrial deposit; DTS, depleted sediment with a terrestrial deposit. Averages are given ± 1 S.D. The dash indicates that the terrestrial sediment thickness could not be determined.

Run	Deposit thickness (mm)	
	CTS	DTS
A	1.84 ± 0.09	-
B	1.74 ± 0.05	-
2	1.90 ± 0.12	2.4 ± 0.20
4	1.00*	1.20*
5	1.20*	1.50*

* Average and S.D. not determined

Table 7. Porewater chemistry measurements in intertidal sediment (C) intertidal sediment with a terrestrial sediment deposit (CTS) depleted sediment and (D) depleted sediment with a terrestrial sediment deposit. $[O_2]_{sur}$: oxygen concentration at the sediment surface; DOU: rate of diffusive oxygen uptake, OPD: oxygen penetration depth; pH_{bw}: pH of the flume bottom seawater; pH_{min}: pH minimum; $pH_{mindepth}$: depth in the sediment porewater where the pH minimum occurs; ΔpH: magnitude of change in pH from the sediment surface; Eh_{sur}: redox potential at the sediment surface; Eh_{min}: lowest redox potential in the sediment porewater. Vertical profiles were measured to a maximum depth of 5.5 mm in the sediment porewater of each sediment core.

Sediment	$[O_2]_{sur}$ (%)	DOU ($\mu mol\ m^{-2}\ h^{-1}$)	OPD (mm)	pH_{bw}	pH_{min}	$pH_{mindepth}$ (mm)	ΔpH	Eh_{sur} (mV)	Eh_{min} (mV)
C	61	1273 ± 130	1.06 ± 0.09	7.9	7.2	~1.8	0.7	219	-136
	76	898 ± 140	1.40 ± 0.31	7.9	7.4	~1.0	0.5	117	-243
	68	812 ± 75	1.24 ± 0.05						
CTS	85	645 ± 90	0.76	7.9	7.1	1.5–2.5	0.8	212	-53
	81	599 ± 63	0.86	7.9	7.3	3.0–3.5	0.6	109	-109
	87	732 ± 120	0.84						
D	101	18 ± 4	>5.5	7.8	7.6	~2.0	0.2	205	168
		16 ± 7		7.9	7.6	1.4–2.4	0.3	105	86
		28 ± 15							
DTS	100	69 ± 8	>5.5	7.8	7.4	~2.9	0.4	210	106
		46 ± 16		7.8	7.5	~4.6	0.3	197	103
		63 ± 10							

Oxygen

Microprofiling measurements in intertidal sediment revealed that the O_2 concentration decreased toward the surface of the sediment from 100% saturation to between 61 and 76% saturation. The rate of the diffusive O_2 uptake ranged from 812 to 1273 $\mu mol\ m^{-2}\ h^{-1}$, and the average O_2 penetration depth ranged from 1.06 ± 0.09 to 1.40 ± 0.31 mm (Table 7; Figures 9–11). The effective diffusive boundary layers ranged in thickness from 0.4 to 0.7 mm (Table 7).

In contrast to intertidal sediment, the oxygen concentration in depleted sediment was high at the sediment surface and oxygen penetrated to a depth exceeding 5.5 mm. The rate of the diffusive O_2 uptake ranged from 16 to 28 $\mu mol\ m^{-2}\ h^{-1}$ (Table 7; Figures 9–11). The thickness of the diffusive boundary layer ranged from 0.3 to 0.7 mm (Table 7).

Terrestrial sediment had a mild effect on the distribution of oxygen in both intertidal and depleted sediment. The shape of the O_2 profile measured across the terrestrial deposit and the underlying intertidal sediment was similar to that of intertidal sediment. The porewater of intertidal sediment below the terrestrial deposit, however, contained less O_2. The diffusive oxygen uptake across the sediment–water interface was lower, that is, the drop in the O_2 saturation in the diffusive boundary layer was less steep, and the saturation at the deposit-underlying sediment surface was lower (Figures 9–11). The O_2 saturation decreased from 100% to between 81 and 87% saturation at the sediment surface, and accordingly, the rate of the diffusive O_2 uptake was lower, ranging from 599 to 732 $\mu mol\ m^{-2}\ h^{-1}$. The O_2 penetration into the deposit-underlying sediment was lowered slightly, compared with that of intertidal sediment, ranging from 0.7 to 0.9 mm. The difference between O_2 penetration depth (ΔOPD) between intertidal sediment and intertidal sediment with a terrestrial sediment deposit ranged from 0.3–0.5 mm (Table 7). The diffusive boundary layer thickness ranged from 0.3 to 0.9 mm (Table 7).

The general shape of the oxygen profile in depleted sediment with a terrestrial sediment deposit was very similar to that in depleted sediment. The oxygenation of the porewater was slightly less than that of depleted sediment (maximally by 2%). Likewise, the OPD exceeded 5.5 mm (Table 7; Figures 9–11). The diffusive boundary layer thickness ranged from 0.3 ± 0.05 mm to 0.6 ± 0.12 mm (Table 7).
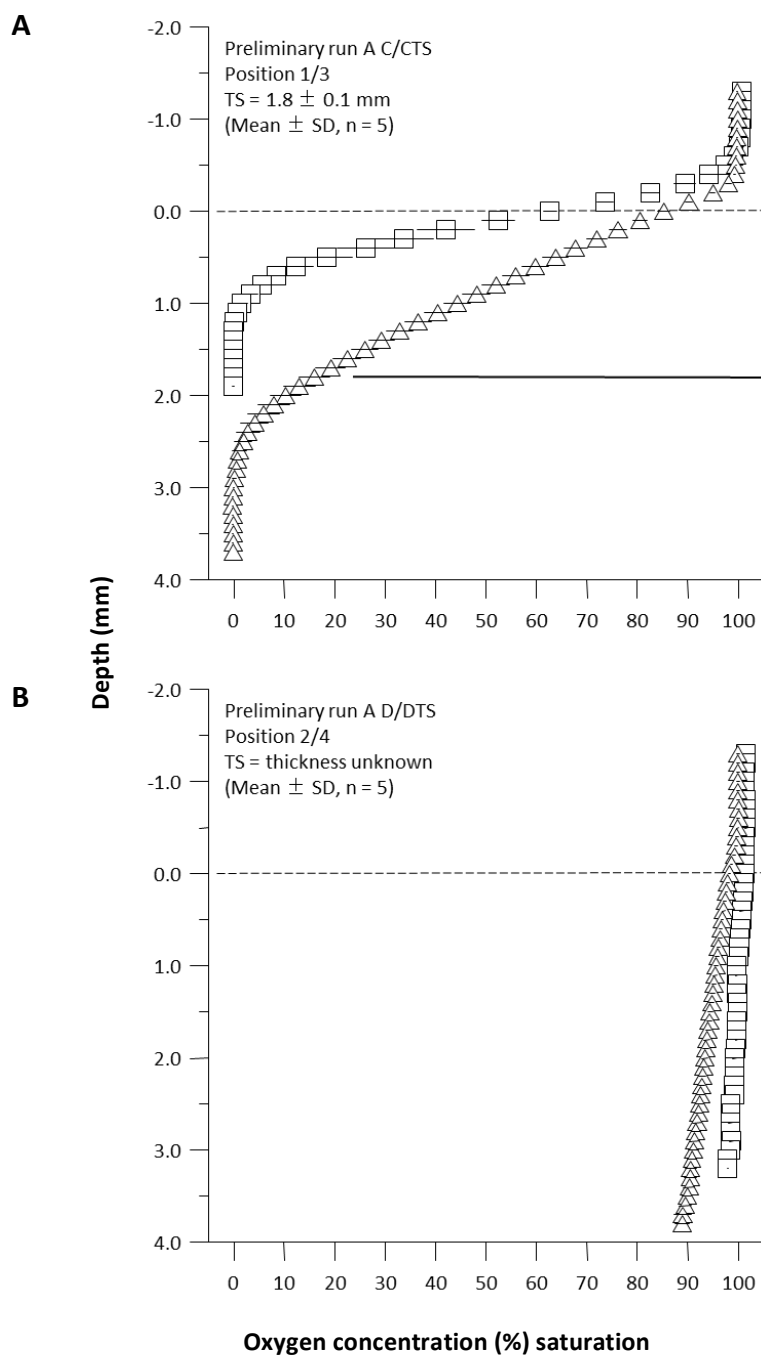
Figure 9. Porewater oxygen concentration microprofiles (mean ± S.D., *n* = 5) in intertidal (A) and depleted (B) sediment measured in preliminary run A. Squares: untreated sediment; triangles: surface covered with a 1–2 mm thick layer of terrestrial sediment; the dashed lines indicate the surfaces of the untreated intertidal sediment and the solid lines indicate the surface of the deposit-underlying sediment.
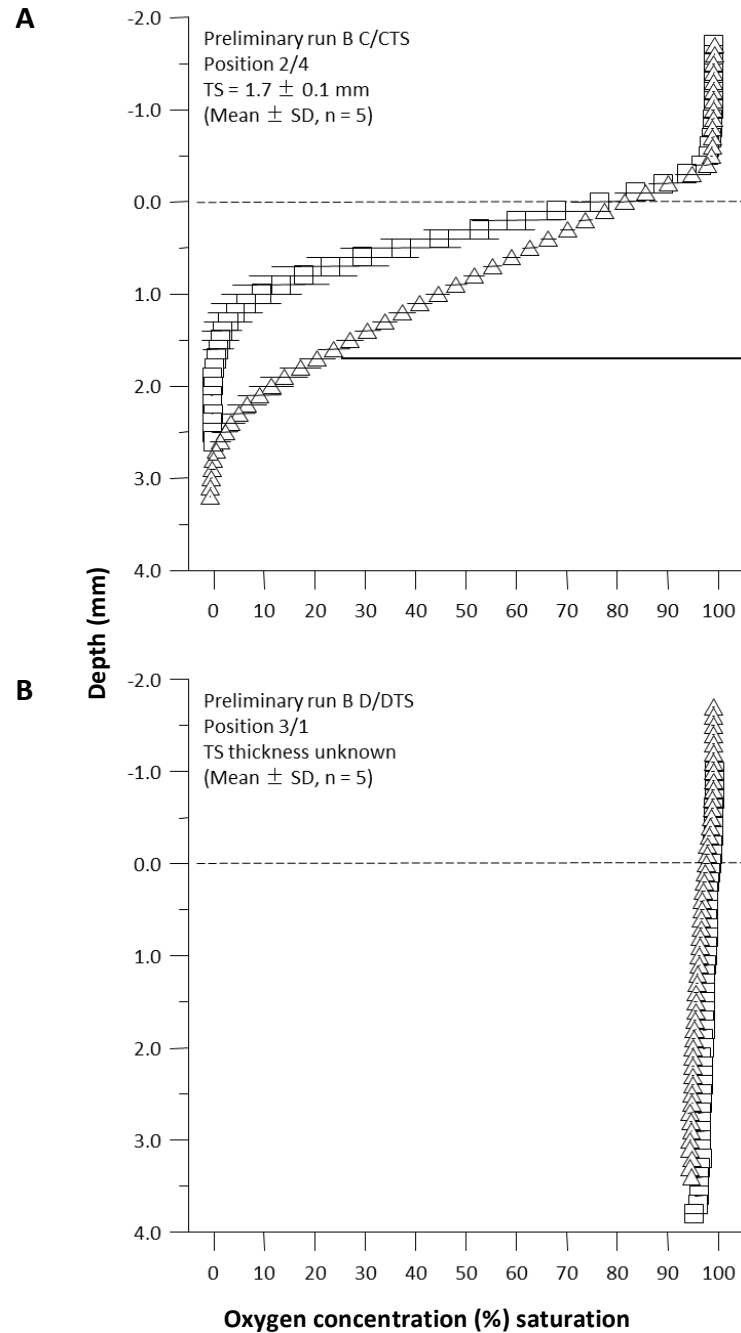
Figure 10. Porewater oxygen concentration microprofiles (mean ± S.D., *n* = 5) in intertidal (A) and depleted (B) sediment measured in preliminary run B. Squares: untreated sediment; triangles: surface covered with a 1–2 mm thick layer of terrestrial sediment (TS); the dashed lines indicate the surfaces of the untreated intertidal sediment and the solid lines indicate the surface of the deposit-underlying sediment (A). The thickness of the TS is unknown in B.
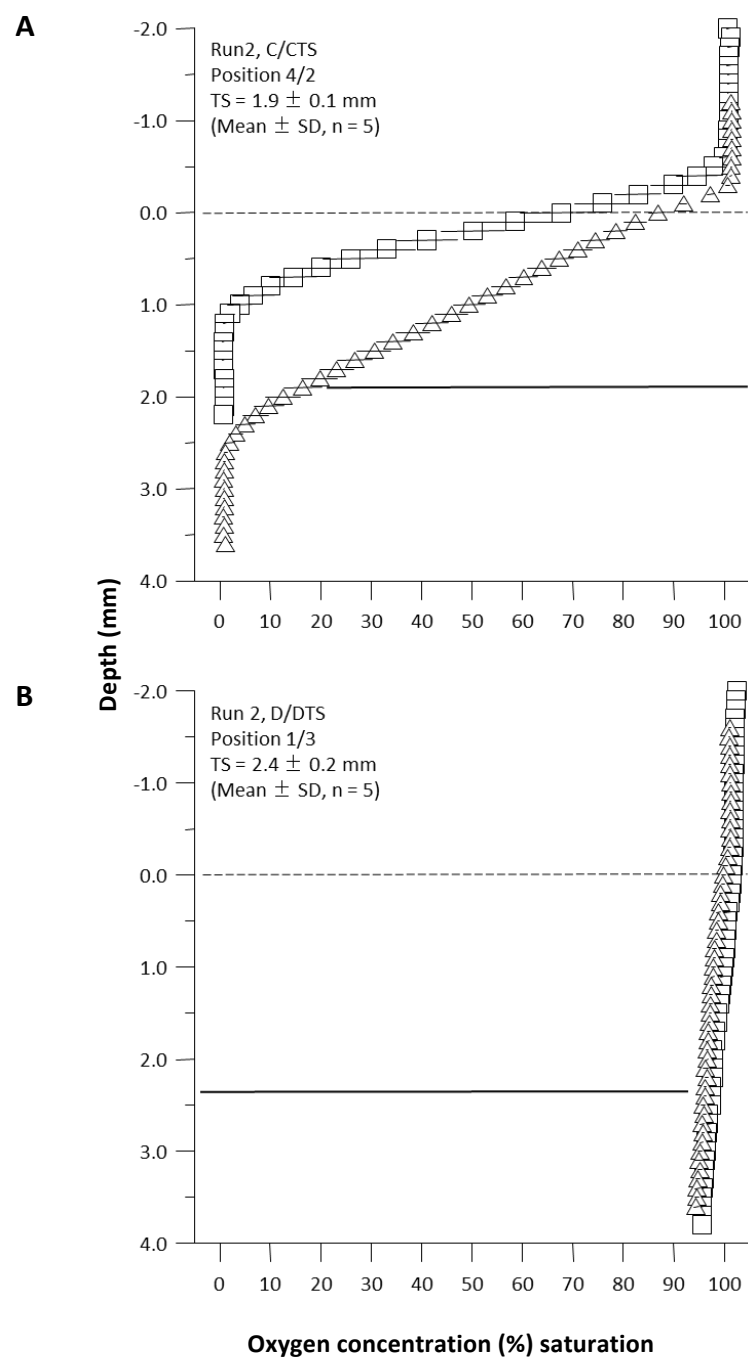
Figure 11. Porewater oxygen concentration microprofiles (mean ± S.D., *n* = 5) in intertidal (A) and depleted (B) sediment measured in run 2. Squares: untreated sediment; triangles: surface covered with a 1–2 mm thick layer of terrestrial sediment (TS); the dashed lines indicate the surfaces of the untreated intertidal sediment and the solid lines indicate the surface of the deposit-underlying sediment.

pH

The pH of the flume seawater (pH_{bw}) ranged between 7.8 and 7.9. The sediment surface pH (pH_{sur}) was 7.6. All the sediment profiles exhibited similar general features; a sharp decrease to a minimum (pH_{min}) just below the sediment–water interface, an increase with depth to a subsurface maximum (pH_{max}), followed by a pH that remains constant or decreases slightly with depth. The pH_{min} in intertidal sediment ranged between 7.2 and 7.4 and occurred at depths between ~1.0 and ~1.8 mm. The porewater pH_{max} ranged between 7.2 and 7.5 and occurred at depths between ~2 and 3 mm (Table 7; Figures 12–13).

In contrast to intertidal sediment, the features that shape the pH profiles in depleted sediment are less pronounced. The pH declined to a minimum at depths between ~1.3 and ~2.4 mm, followed by an increase to a maximum at ~3.5 mm depth. The decrease in pH was not as sharp (pH_{min}= 7.6), and below the pH maximum (pH_{max} = 7.7) the pH did not remain constant but decreased with depth. Further, ΔpH was less compared to intertidal sediment (Table 7; Figures 12–13).

The effect of a terrestrial sediment deposit on pH did not differ between intertidal and depleted sediments. The general trend in pH decreased to a minimum, followed by an increase with depth, which then remained constant, was observed for both sediment types when a terrestrial deposit was applied. The decline in pH to the minimum, however, was not as sharp as the decline to the minimum observed in intertidal and depleted sediment, and the pH_{min} was more pronounced (Figures 12–13).

Consequently, ΔpH was greater compared to intertidal and depleted sediment (Table 7). Intertidal sediment with a terrestrial deposit had a pH_{min} range of 7.1 to 7.3 and occurred in the sediment porewater at a depth similar to that seen in intertidal sediment (relative to the deposit–sediment interface), (Table 7; Figures 12–13). The pH_{min} in depleted sediment with a terrestrial deposit ranged from 7.4 to 7.5, and likewise, occurred in the sediment porewater at a depth similar to that seen in depleted sediment (Table 7; Figures 12–13).
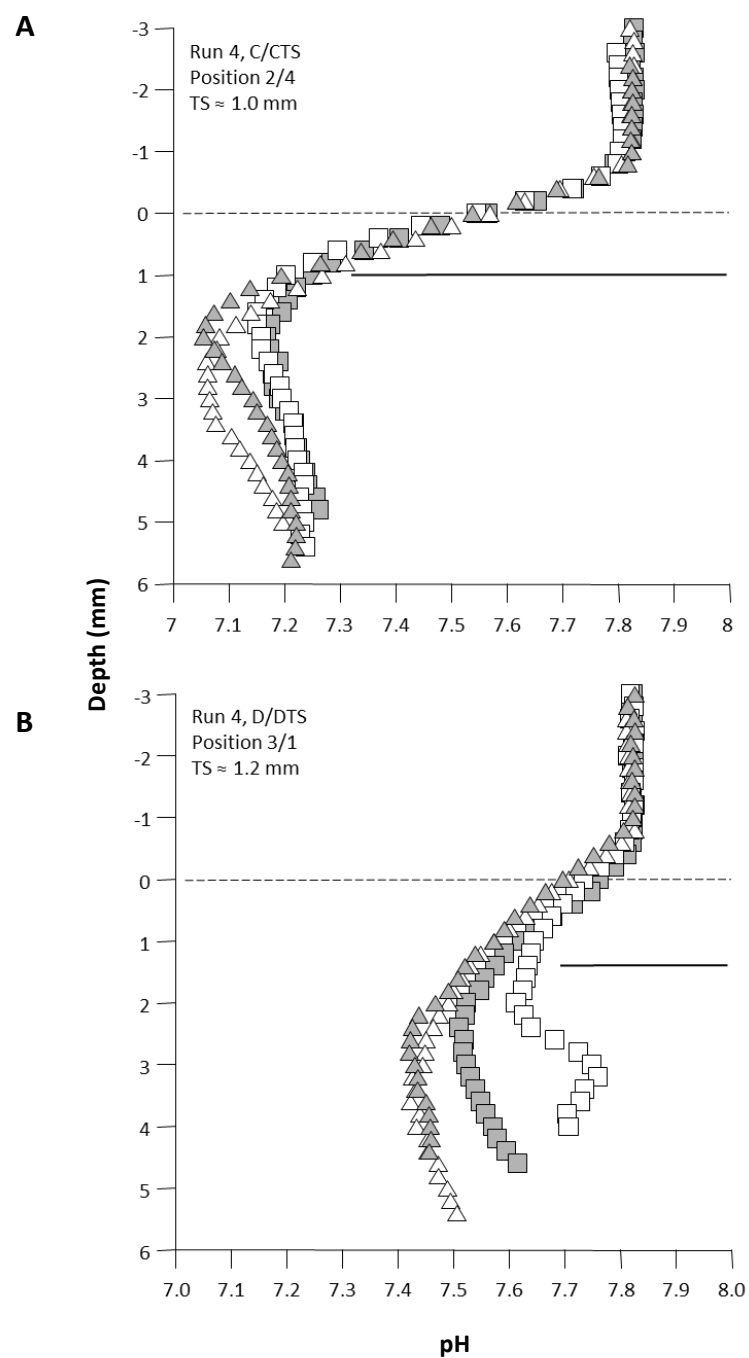
Figure 12. Porewater microprofiles of pH concentration in intertidal (A) and depleted (B) sediment measured in run 4. Squares: untreated sediment; *triangles*: surface covered with a 1–2 mm thick layer of terrestrial sediment; grey shading: replicate measurements. The dashed lines indicate the surfaces of the untreated intertidal sediment and the solid lines indicate the surface of the deposit-underlying sediment.

A
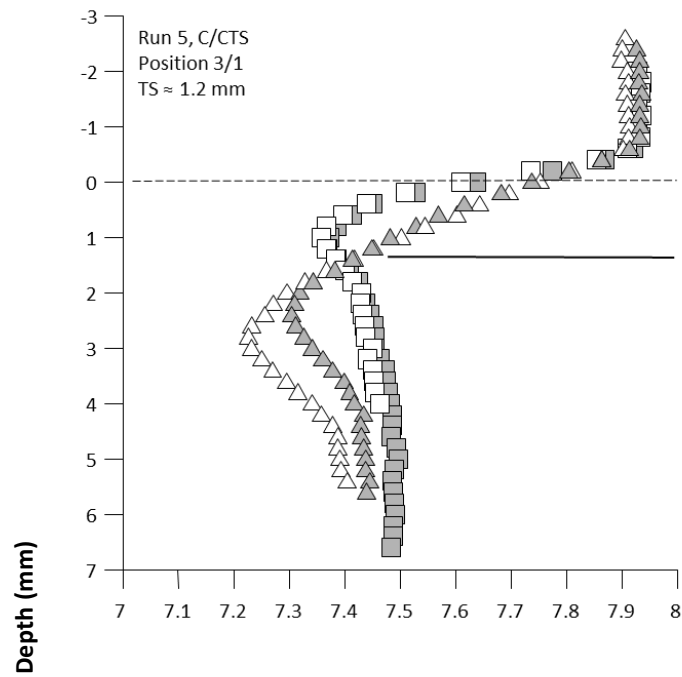
B
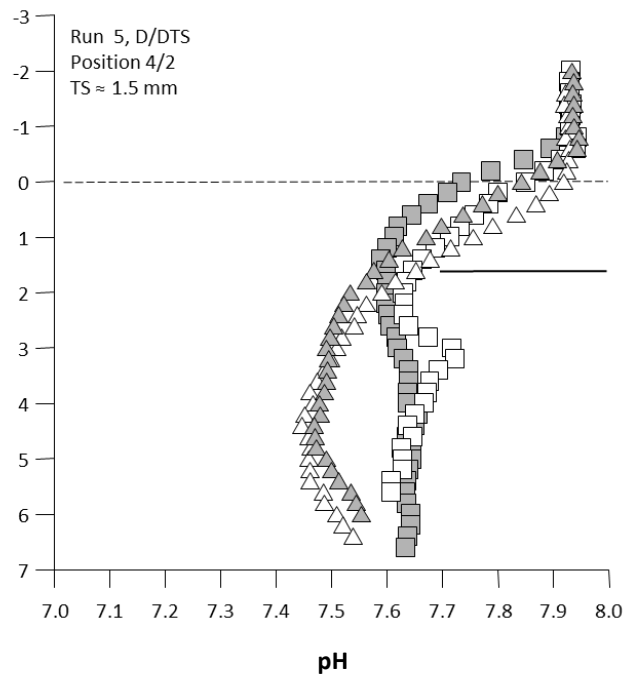
Figure 13. Porewater pH concentration microprofiles in intertidal (A) and depleted (B) sediment measured in run 5. Squares: untreated sediment surface; triangles: surface covered with a 1–2 mm thick layer of terrestrial sediment; grey shading: replicate measurements. The dashed lines indicate the surfaces of the untreated intertidal sediment and the solid lines indicate the surface of the deposit-underlying sediment.

Redox

Redox profiles revealed that the chemocline, that is, the sharp change in the sediment porewater from oxidising to reducing conditions, occurred from 2 to 4 mm depth (Table 7; Figures 14–15). In contrast to intertidal sediment, there was no shift from oxidising to reducing conditions in the sediment porewater of depleted sediment. Rather, the redox potentials remained positive to a depth of 5.5 mm, the maximum depth measured (Table 7; Figures 14–15).

The redox profiles indicated that when a terrestrial sediment deposit was present, the depth of the chemocline moved down approximately the same as the deposit thickness. That is, it stayed at the same depth in the original sediment. The vertical shift in redox was consistent with the thickness of terrestrial deposits that were applied to treated sediments. The depth of the chemocline ranged between 1.5 and 4.5 mm (Table 7). Like depleted sediment, there was no shift from oxidising to reducing conditions in the sediment porewater of depleted sediment with a terrestrial deposit, accordingly, the redox potentials remained positive (Table 7; Figures 14–15).
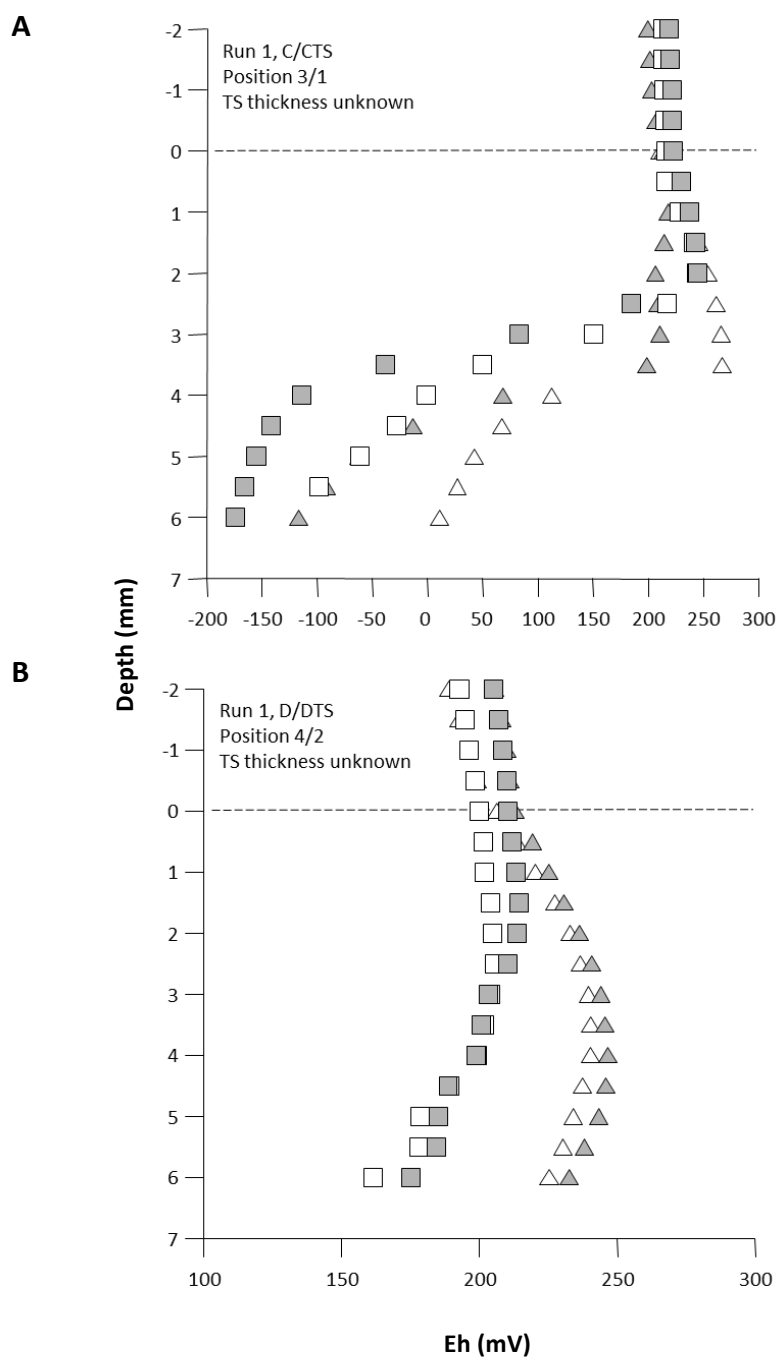
Figure 14. Porewater redox microprofiles in intertidal (A) and depleted (B) sediment measured in run 1. Squares: untreated sediment surface; triangles: surface covered with a 1–2 mm thick layer of terrestrial sediment; grey shading: replicate measurements. The dashed lines indicate the surfaces of the sediment. The thickness of the terrestrial sediment deposit (TS) is unknown in A and B.
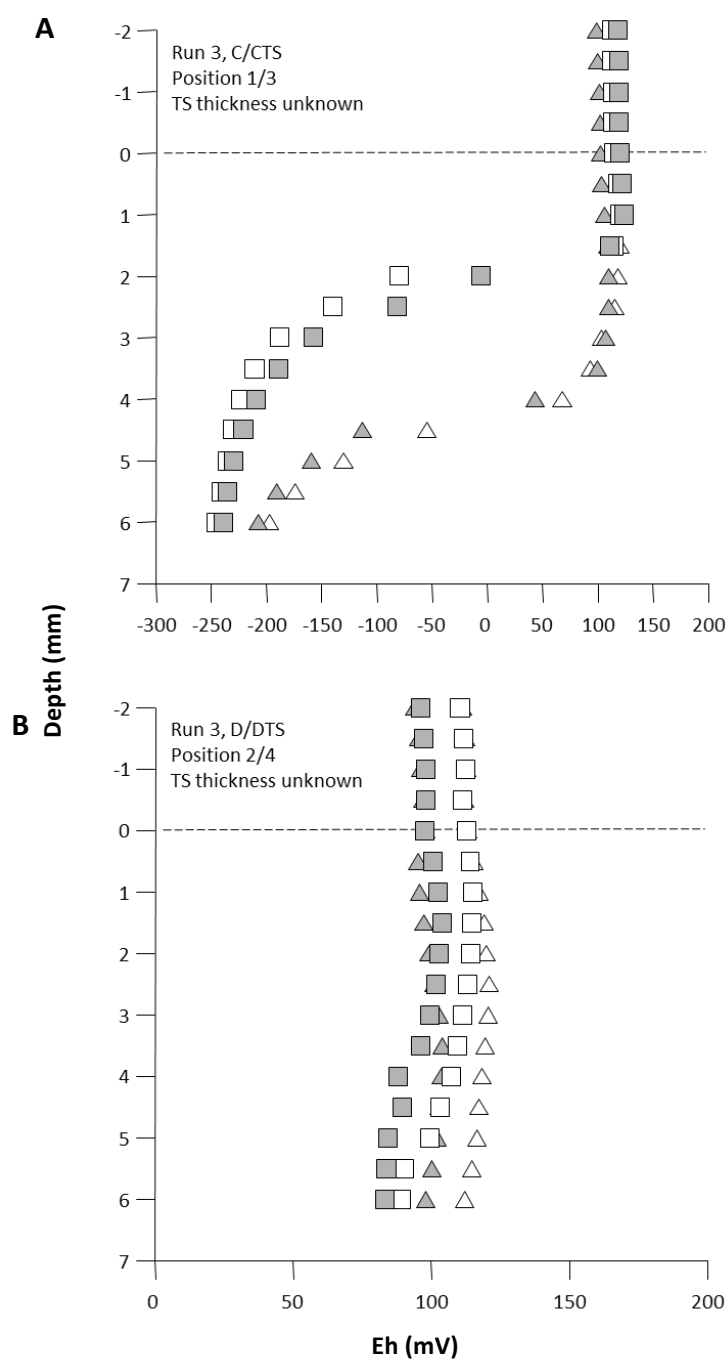
Figure 15. Porewater redox microprofiles in intertidal (A) and depleted (B) sediment measured in run 3. Squares: untreated sediment surface; triangles: surface covered with a 1–2 mm thick layer of terrestrial sediment; grey shading: replicate measurements. The dashed lines indicate the surfaces of the sediment. The thickness of the terrestrial sediment deposit (TS) is unknown in A and B.

Macomona liliana size distribution

The average shell length of individuals used in this experiment was 1.6 ± 0.2 mm (n =
400), and individuals were representative of post-settlement recruits under 1 year old
(Roper et al., 1992). The smallest and largest shell lengths recorded were 1.1 and 2.3
mm. There were 20 individuals ranging between 2.0 to 2.3 mm, larger than the
maximum desired shell length (Figure 16). See Appendix Tab 3 for actual size
distributions in each core, in each run.
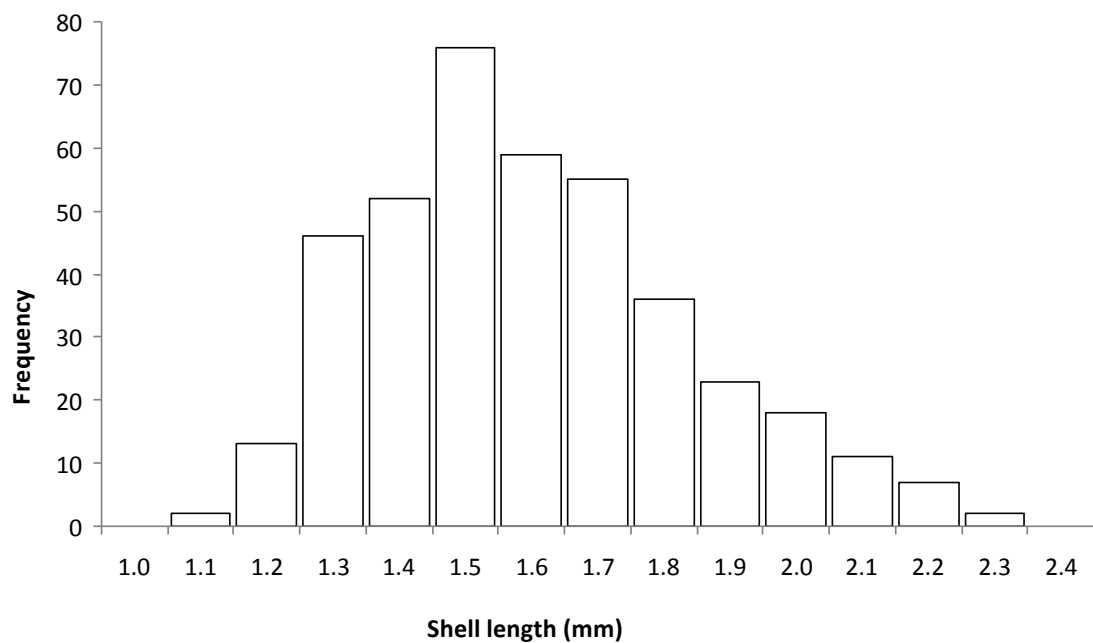
Figure 16. *Macomona liliana*. **Size frequency of the 400 individuals used throughout the experiment.**

Effect of treatment on *Macomona liliana* burial behaviour

Logistic regression analyses revealed a significant difference in the burial behaviour of *M. liliana* post-settlement juveniles placed onto the surfaces of terrestrial sediment deposits with underlying intertidal and depleted sediment treatments. Intertidal sediment increased the probability of juveniles burying into the sediment irrespectively of treatment (C and CTS; p = 0.010245), and contrary to expectation, a terrestrial sediment deposit also increased the probability of juveniles burying into the sediment (CTS and DTS; p = 0.00765), (Figure 17).
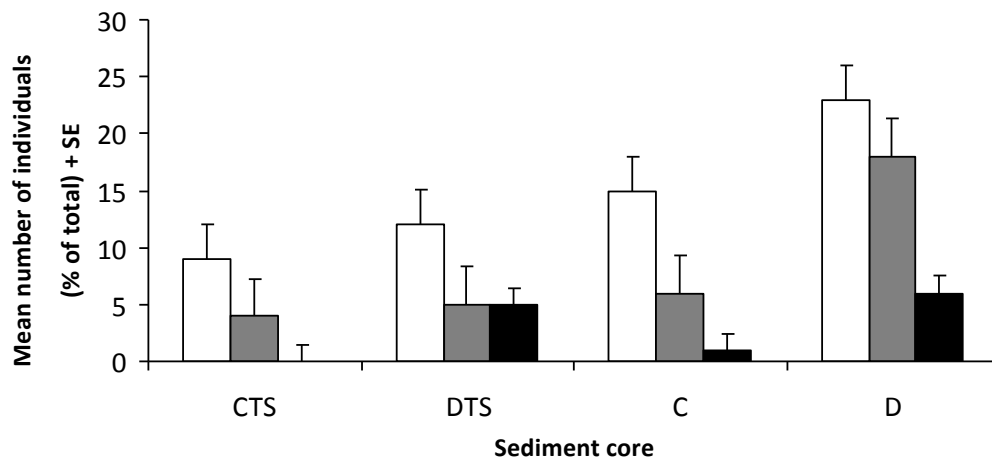
Figure 17. *Macomona liliana.* **Percentage of total juveniles that remained on the sediment surface in each sediment core at 3 min, 10 min, and 4 h after their placement in the flume. Twenty individuals were added to each sediment core in each of five replicate runs. White bars, 3 min; grey bars, 10 min; black bars, 4 h.**

Macomona liliana behavioural responses

Burial and post burial behaviours (Figure 18) were classed into the following categories (a summary of all behaviours is given in Table 8):

Buries immediately: From the starting condition (i.e., resting on one valve where it landed on the sediment surface), the foot digs into the sediment anterior end first, with the apex-siphonal end protruding from the sediment. The bivalve continues to bury deeper in the sediment so the siphonal end is no longer protruding, and the bivalve is completely buried within 3 min.

> Initial burial of juveniles was high and was the most common behavioural response observed. Once placed onto the surfaces of the sediment cores, the majority of bivalves (>60%) had buried within the first 3 min in all sediments (Figure 17).

No movement: Bivalve remains in the starting position for the duration of the experiment (4 h).

> Over longer durations, bivalves did not bury into depleted sediments (D and DTS) compared to intertidal sediments (C and CTS). Only 6 individuals (1.5% of 400) remained in the starting position (i.e., lying on one valve) throughout the duration of the experiment. Of these, 5 exhibited this response on the surface of the DTS core and the remaining individual on the surface of intertidal sediment. Interestingly, these responses occurred when the corresponding sediment core was in either position 1 or 4.

No movement, and then buries: Bivalve remains in the starting position for a period longer than 3 min, but not exceeding 10 min, followed by the foot digging into the sediment anterior end first, with the apex-siphonal end protruding from the sediment. The bivalve continues to bury deeper in the sediment so the siphonal end is no longer visible, and the bivalve is completely buried within 10 min.

> Delayed burial was exhibited in 21 individuals (5.3% of 400). Of these, 4% were classed in this category. This delayed burial response was observed in all sediment cores, but at a higher frequency in those treated with a terrestrial sediment deposit, compared to those without (12 individuals versus 4 individuals).

No movement, crawls, and then buries: Bivalve remains in the starting condition for a period longer than 3 min, but not exceeding 10 min. Bivalve orientates itself so the apex is uppermost, with the anterior end in front and siphonal end behind. Using the foot, the bivalve crawls along the sediment surface, anterior end first. The foot digs into the sediment anterior end first, with the apex-siphonal end protruding from the sediment. The bivalve continues to bury deeper in the sediment so the siphonal end is no longer visible, and the bivalve is completely buried within 10 min.

> Delayed burial, which included 'exploratory behaviour' (i.e., crawling on the sediment surface), was exhibited by 5 individuals (1.3%). This response was observed only in intertidal sediments (C, CTS). In contrast to 'delayed burial' this response occurred at a higher frequency in sediments without a terrestrial sediment deposit.

Post-burial behaviours were noted, and classed in to the following categories:

Avoidance by crawling: Following burial, the bivalve is assumed to be orientated so the apex is uppermost, with the anterior end in front and siphonal end behind. Using the foot, the bivalve crawls along the deposit-underlying sediment surface. 'Crawling traces' are evident on the surface of the terrestrial sediment deposit.

> This response was detectable only in depleted sediments (D, DTS) and was evident in DTS from 'crawling traces' imprinted in the deposit. Although bivalves may have exhibited this behaviour in intertidal sediments (C, CTS) this could not be confirmed. Crawling on the deposit–underlying sediment surface was detected in all runs in DTS cores, and crawling just below the sediment surface was detected in all D cores. Crawling was observed to last up to 4 h. Crawling traces were up to 45 mm long (Figure 6).

Emergence: Following burial, the bivalve appears at the surface, anterior end foremost, with valves slightly open and the foot brought close to the gape. The animal moves upward out of the sediment until only its siphonal end remains embedded. Whilst in this position, the foot is protruded and moves in and out and slides up and down the shell and valves open and close several times. The animal then completely emerges from the sediment and topples over, coming to rest on one valve (as described in Cummings et al., 1993).

This response was observed only in those sediments comprised of depleted sediment and was coupled with 'exploratory behaviour'. Bivalves would emerge from the sediment and remain with the siphonal end embedded, so that they were orientated in a vertical or upright position. Whilst in this position, the foot would protrude from the shell and move in and out and slide up and down the shell. This lasted for seconds up to several minutes, before toppling over onto one valve. Bivalves would either remain on one valve or 'explore' the sediment by crawling a distance on the surface. Once in a different locale bivalves would become orientated in the vertical position again. This behavioural pattern was repeated until the bivalve reburied or left the core via drifting. Emergence and exploratory behaviour was observed over the duration of the experiment (4 h).

Drifting: Usually following emergence behaviour, or from the starting condition, bivalve skids across the sediment surface in the direction of the water flow, becoming orientated with the apex of the shell facing in to the flow.

Like all post-burial responses, drifting was only observed in depleted sediment. Only 1% of juveniles, that is, 4 individuals drifted from the sediment. This occurred in runs 4, and 5. Drifting did not occur during the initial 10 min, but thereafter.
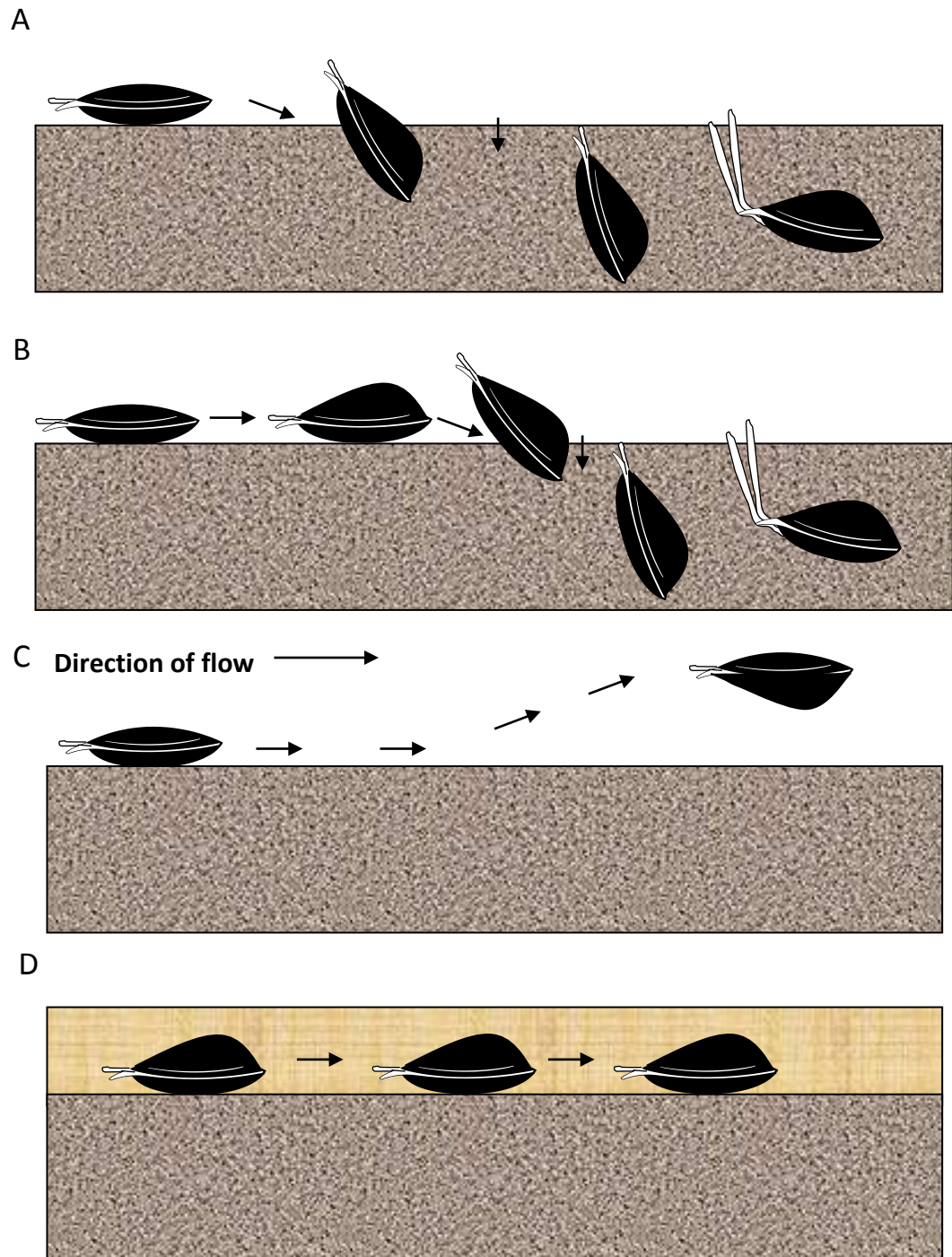
Figure 18. *Macomona liliana.* **Illustration showing the burial behaviours: (A) Buries immediately where they land; no movement and then buries (B) no movement, crawls and then buries; and the post-burial behaviours: (C) drifting behaviour (D) avoidance by crawling.**

Table 8. *Macomona liliana.* **Observed behavioural responses for each treatment. Closed parentheses, percent of total that exhibited the behavioural response and the run in which the behavioural response was observed; closed brackets, core position. CTS, intertidal sediment with a 1–2 mm surface terrestrial deposit; DTS, depleted sediment with a 1–2 mm surface terrestrial deposit; C, intertidal sediment; D, depleted sediment.**

Sediment	Burial behaviour				Post-burial behaviour		
	Buries immediately where they land	No movement	No movement, then buries	No movement, crawls, then buries	Emergence behaviour	Drifting behaviour	Crawling under sediment
CTS	Yes (all runs) [1, 2, 3, 4]	No	Yes (1.5%, runs 2, 3, 4,& 5) [1, 2, 3, 4]	Yes (<1%, run 4) [4]	No	No	No
DTS	Yes (all runs) [1, 2, 3, 4]	Yes (1.3%, run 3 & 4) [4, 1]	Yes (1.5%, runs 1,2, & 3) [2, 3, 4]	No	No	No	Yes (all runs) [1, 2, 3, 4]
C	Yes (all runs) [1, 2, 3, 4]	Yes (<1%, run 3) [1]	Yes (<1%, run 1 & 2) [3, 4]	Yes (1%, run 1 & 4) [2, 3]	No	No	No
D	Yes (all runs) [1, 2, 3, 4]	No	Yes (<1 %, run 1 & 4) [3, 4]	No	Yes (3.8%, all runs) [1, 2, 3, 4]	Yes (1%, run 2, 4, 5) [1,3, 4]	Yes (all runs) [1, 2, 3, 4]

Discussion

The design of this study was influenced by the evidence presented by Cummings et al. (2009) that showed a link between sediment geochemistry and the behaviour of post-settlement juvenile bivalves. In light of this evidence, this study had the following expectations: (1) Terrestrial sediment would negatively affect burial behaviour of post-settlement juveniles when deposited onto intertidal sediment, (2) terrestrial sediment would affect burial behaviour of post-settlement juveniles less when deposited onto sediment depleted of organic matter, and (3) the difference in burial behaviour between (1) and (2) was caused by differences in the oxidation–reduction (redox) chemistry of the deposit-underlying sediment.

Terrestrial sediment deposits did not negatively affect the burial behaviour of post-settlement juveniles when deposited onto the surfaces of intertidal and organic matter depleted sediment (herein, depleted sediment), contrary to similar work by Cummings et al. (2009). Rather, a terrestrial sediment deposit increased the probability of juveniles burying into the sediment, irrespective of the type of deposit-underlying sediment. Juvenile bivalves were more likely to bury into intertidal sediment than depleted sediment, irrespective of whether it had a terrestrial deposit or not. The results of this study showed a statistically significant difference in the burial behaviour of *Macomona liliana* post-settlement juveniles if placed on the surface of terrestrial sediment deposited over natural intertidal sediment compared to terrestrial sediment deposited over depleted intertidal sediment.

Effect of terrestrial sediment deposition on porewater chemistry

The steep solute gradients in the upper layers of sediment may provide information to recruits about the sediment organic matter content and resultant sediment–seawater solute exchange (Marinelli & Woodin, 2002). In this study, oxygen, pH, and redox potential were measured to characterise the porewater chemistry of sediments with differing diagenetic activity and quantify the intertidal sediment's chemical response to the deposition of terrestrial sediment. Analysis of the oxygen, pH and redox profiles revealed that thin (1–2 mm) terrestrial deposits have a minor effect on the sediment porewater chemistry. The deposits impeded the exchange of solutes between the

underlying sediment and the overlying seawater. This impedance resulted in minor changes in the depth distribution of dissolved oxygen and pH. That is, the oxygen penetration depth was reduced in the deposit-underlying intertidal sediment maximally by 0.5 mm (Table 7).

Sediment oxygenation

The oxygen concentration was always highest in the water column where eddy diffusion and turbulent flow mix solutes, and lowest in the sediment. The oxygen concentration declined approaching the sediment–water interface within the diffusive boundary layer. In this layer, surface friction retards the flow and flow speed is predominantly determined by viscous forces. At the sediment–water interface the velocity approaches zero. In the diffusive boundary layer, eddy diffusion becomes insignificant relative to molecular diffusion; therefore, molecular diffusion becomes the principle mechanism for mass transport (Glud, 2008; Santschi et al., 1983). Oxygen consumption processes, such as aerobic respiration from the degradation of organic matter and the reoxidation of products from this degradation, cause a sharp drop in the porewater oxygen concentration (Fenchel and Jørgensen, 1977; Glud, 2008). This consumption limits the penetration of oxygen so that the oxic–anoxic boundary occurs at a depth ~1 mm (Table 7). Such oxygen penetration depth is characteristic of productive, shallow, coastal waters, whereas permeable sandy and deep sea sediments usually have an oxygen penetration depth with cm or dm scales (Glud, 2008; Kristensen, 2000).

When a terrestrial sediment deposit was applied to intertidal sediment, the overall oxygen penetration depth increased (i.e., from the surface of the terrestrial sediment deposit into the underlying intertidal sediment). The oxygen penetration depth in the deposit-underlying sediment, however, was not greatly altered (Table 7).

Low oxygen consumption of the depleted sediment caused high porewater oxygen concentration in this sediment; this consumption may be explained by the absence of organic matter. Consequently, the low oxygen consumption resulted in the oxic–anoxic boundary occurring deeper than 5.5 millimetres in the sediment.

Distribution of pH

Porewater pH profiles exhibit distinct features that can be related to bottom water chemistry, solid sediment composition, and redox reactions associated with the degradation of organic matter (Jourabchi et al., 2005). The redox profiles of the intertidal sediment used in this study was similar to typical coastal marine sediments. The pH decreased sharply just below the sediment surface (pH_{min}) followed by a subsurface maximum (pH_{max}) in the anoxic zone (Figures 12–13). In sediments, oxic mineralisation and the reoxidation of reduced compounds (ammonium, Fe^{2+}, Mn^{2+}, S^{2-}, and CH_4) decrease the pH, causing a sharp drop below the sediment surface (Boudreau, 1991; Jourabchi et al., 2005; Revsbech et al., 1983). A subsequent increase in pH with depth is attributed to the reductive dissolution of iron and manganese (hydr)oxides coupled to organic matter and sulfide oxidation (Jourabchi et al., 2005; Reimers et al., 1996; Van Cappellen and Wang, 1996). At a certain depth the pH starts to decrease again as a result of sulfate reduction and, to a lesser extent, iron sulfide precipitation in the anoxic zone, which causes the subsurface maximum, characteristic of aquatic sediments (Jourabchi et al., 2005; Figures 12–13).

Intertidal sediment with a terrestrial sediment deposit also exhibited these distinct features. The impedance of molecular diffusion, however, caused a pH decrease 2–3 mm deep in the sediment porewater. This accentuated the local minimum (Figures 12–13), which is also shown in pH profiles by Cummings et al., (2009) and affirms the inference that the deposits impede the exchange of hydrogen ions between underlying sediment and bottom seawater. Comparably, pH profiles in depleted sediment exhibited the same trend observed in intertidal sediment, except that the pH_{min} and pH_{max} are not as prominent. This may be due to the reduced cycling or absence of Fe and Mn. The distinction of these features was further reduced in the presence of a terrestrial deposit.

Redox potential

The redox potential is a measure of the tendency of a chemical species to acquire electrons and thereby be reduced. The transition from oxidising to reducing conditions in the intertidal sediment occurred below the oxygen penetration depth, approximately 1 mm (Figures 14–15). The redox potential of the suboxic sediment layer may be kept positive (oxidising conditions) by the input of oxygen by

bioturbation and the presence of oxidised iron and manganese compounds (Kristensen, 2000). When a terrestrial sediment deposit was applied to intertidal sediment, the transition from oxidising to reducing conditions was not greatly altered. This supports the earlier observation that the oxygen penetration depth into the deposit-underlying intertidal sediment was not greatly altered (Table 7).

Effect of terrestrial sediment deposition on burial behaviour of *Macomona liliana*

The addition of terrestrial sediment deposits did not negatively affect the behaviour of post-settlement juveniles, contrary to the study by Cummings et al. (2009). The juveniles preferred sediments with a terrestrial deposit over sediments without a terrestrial deposit, and intertidal sediments over depleted sediments. In particular, burial into sediments with a terrestrial deposit was favoured in the short term (first few minutes), whereas in the long term (>4 hours), intertidal sediments were preferred over depleted sediments (Figure 18).

The negligible effect of terrestrial sediment deposition on the porewater chemistry of intertidal and depleted sediment explains why the terrestrial sediment deposit did not cause a negative effect on the burial behaviour of juveniles in this study. It was assumed that the addition of a thin layer of terrestrial sediment to the surface of intertidal sediment would create sediment conditions similar to that in the study by Cummings et al. (2009), and a negative effect on burial behaviour would be observed. That is, I expected a reduction in the oxygen penetration depth and a reduction in the number of juveniles burying into intertidal sediment after a surface deposit of terrestrial sediment was applied. I assumed that the absence of organic matter would ensure the absence of negative cues associated with the degradation of organic matter and so bivalve burial behaviour would be affected less when terrestrial sediment was deposited on depleted sediment.

The application of terrestrial sediment had a mild effect on the sediment porewater chemistry and the data show that these changes were not sufficient to cause a negative effect on burial behaviour. The macrofauna in the intertidal sediment may have kept the sediment oxygenated, and so negative cues were also absent, and no negative effect on burial behaviour was observed. The rapid burial into intertidal and

depleted sediments, underlying terrestrial sediment deposits, indicate that thin terrestrial sediment deposits do not negatively affect the burial behaviour of post-settlement juvenile bivalves into these sediments.

Sediment preferences

Although burial into the two sediment types was initially rapid, there were significant differences in the burial rate of *M. liliana* between sediment core treatments (see above). Tallqvist (2001) suggests that burial in sediment-dwelling bivalves is affected by biotic and abiotic factors, such as predator presence, oxygen deficiency, and sediment characteristics. Considering that the bivalves were collected from the intertidal sediment, and therefore adapted to this environment, it is not surprising that this type of sediment was preferential over depleted sediments. Further, the differences in grain size distribution between intertidal and depleted cannot be ruled out from having influenced burial by the bivalves.

Despite the sediment being well oxygenated, rejection of depleted sediment can be emphasised by emergence, drifting, and avoidance behaviour, which was observed in depleted sediment only (Table 8).

Although the grain size distribution in depleted sediment differed slightly from that in intertidal sediment (330 and 144 μm respectively) and so may have caused differences in behaviour of juveniles, the most likely cause for emergence, drifting and avoidance behaviour was the lack of organic matter as it aligns with prior studies, which have observed rejection of native 'burnt' and defaunated sand by *M. liliana*. For example, Cummings et al. (1993) used native sediment, that was sieved and combusted to induce byssus drifting in juvenile *M. liliana*. That is, sediment that was collected from the same location as the juvenile *M. liliana* induced drifting behaviour when it was depleted of organic matter by combustion in agreement with this study. Similarly, Lundquist et al. (2004) compared the behaviour of juvenile *M. liliana* placed onto the surface of native defaunated sediment and glass beads with the same size distribution to examine the effect of organic content on dispersal, independent of grain size; likewise, they observed byssus drifting. Further, benthic deposit-feeding population densities are characteristically correlated with sedimentary organic content and/or microbial biomass or abundance (Levington, 1979), and the absence of a fecal-rich sediment surface could also be the reason for rejection of depleted sediment. For

example, Crassle, Snelgrove and Butman (1992) have shown that the bivalve *Mulinia lateralis* prefers organically rich mud over abiotic glass beads in both flowing and still water.

The findings from this study affirm that combusted or defaunated sediments are unfavourable, and are sufficient to induce emergence, and subsequent dispersal behaviour (Table 8; Figure 6). Although the terrestrial sediment deposit does not affect burial, it may affect the post-settlement juveniles' ability to disperse by trapping the bivalves beneath the deposit.

Reduced end-products from the degradation of organic matter may serve as important cues for recruits, and if these compounds do not accumulate, the cues may not be present. Juveniles appear to be unable to detect such chemical cues from the depleted sediment underlying a terrestrial deposit. This was apparent by their rapid burial into depleted sediment with a terrestrial deposit. An initial response of crawling or avoidance by horizontal movement may not have been possible due to the high content of mud (silt and clay) particles, and therefore bivalves decided to move vertically.

Bioturbation context

The finding that there was no significant effect of thin terrestrial sediment deposits on sediment porewater chemistry and on the burial behaviour of *M. liliana* post-settlement juveniles in this study is contrary to the effect reported by Cummings et al. (2009). Importantly, the reduction in oxygen penetration depth in this study was not as pronounced as that observed by Cummings et al. (2009) when a similar terrestrial sediment deposit was applied (1.0–2.4 mm in this study versus 0.5–1.7 mm in Cummings et al). In contrast to Cummings et al. (2009), this study used intact sediment cores to represent natural diagenetically active coastal sediments. In doing so, the physical, biological, and chemical processes that are found in coastal sediments were present, including macrofauna and their associated structures and activities. Consequently, negative cues associated with the microbial degradation of organic matter that possibly deter bivalves from burrowing into the sediment may have been absent. The subsurface supply of oxygen to the sediment by macrofauna and their associated activities and structures in the intertidal sediment possibly buffered or

compensated for the addition of terrestrial sediment. This is one explanation as to why both sediment porewater distribution of oxygen and pH, and burial behaviour, were not negatively affected.

The ventilation of burrow structures is assumed to be the principle mechanism responsible for the subsurface supply of oxygen to the sediment. Predominantly burrow clearing occurred shortly after the deposit was applied onto the surface. This was evident by the numerous tiny holes on the surface 30 min following application of terrestrial sediment. Other macrofaunal activities, such as surface deposit feeding were observed after 12 h.

One particularly important factor that has been shown to control diagenetic reactions is the pumping of seawater through burrows and mixing of porewater with bottom seawater during burrow construction and feeding. Aller and Aller (1988) suggest that by enhancing solute exchange between overlying water and pore fluids, irrigation supplies dissolved minerals, oxygen, and sulfate from the water column, alters the spatial and temporal distribution of reactions, and lowers concentrations of reduced end-products of the microbial degradation of organic matter. Mermillod-Blondin, Rosenberg, François-Carcaillet, Norling and Mauclaire (2004) found that the bioirrigation activites of the amphipod *Corophium volutator* and the polychaete *Nereis diversicolor* doubled the solute exchange between the water and the sediment.

The differences between the findings in this study and that of Cummings et al. (2009) may be due to Cummings et al. excluding infauna by sieving, freezing, and washing the sediment before introducing juvenile *M. liliana*. Freezing is a common method of preserving and killing macrofauna in sediments, however, this defaunation method has also been shown to significantly alter biogeochemical properties of the sediment (Tollhurst, Chapman, Underwood & Cruz, 2012), and can cause a release of intracellular nutrients to the porewater due to cell breakage, referred to as freeze-lysable inorganic nutrients. For example, García-Robeldo, Corzo, Papaspyrou, Jiménez-Arias and Villahermosa (2010) have demonstrated that freezing increases the porewater content of inorganic nutrients NO_2^-, NO_3^-, NH_4^+, and PO_4^{3-}. The reoxidation of these substances via chemolithotrophic reactions, e.g., nitrification, can affect the sediment oxygen uptake (Burdige, 2006).

The sediment environment Cummings et al. (2009) presented to post-settlement juvenile *M. liliana* was devoid of macrofauna and therefore the sediment was supplied with oxygen exclusively by diffusion across the deposit, not as a result of bioturbation. Such conditions can be thought of as being analogous to those that occur following a large deposition of terrestrial sediment. Carbon enrichment stimulates anaerobic respiration, which results in a high oxygen demand. This was reflected in the higher average rate of diffusive oxygen uptake in control sediments used by Cummings et al. (2009) (1605 µmol m^{-2} h^{-1}) compared to the control sediments in this study (994 µmol m^{-2} h^{-1}).

Differences between the study by Cummings et al. (2009) and this study, suggest that the effects of the terrestrial sediment on burial is likely to be context-specific. The effect of the terrestrial deposit will differ depending on whether it is applied to the surfaces of intact intertidal sediment or defaunated intertidal sediment. For defaunated sediment, the terrestrial deposit will affect the only mechanisms for the sediment supply with oxygen, that is, the diffusive transport of oxygen across the sediment surface. For bioturbated intact sediment, however, the sediment will receive oxygen across the subsurface burrow linings, a transport route that is not affected by the terrestrial deposit. That is, the difference in the effect of terrestrial deposits is caused by differences between intact and defaunated sediments in the relative contribution of surface versus subsurface uptake of oxygen to the overall uptake.

A negative effect on burial from the deposition of terrestrial sediment may eventually occur in intact intertidal sediments once the contribution of bioturbation by benthic macrofauna to the overall oxygen supply via porewater bioirrigation, as well as the physical destruction of the deposit via particle reworking, is insufficient to prevent the accumulation of reduced end products of organic matter degradation in the porewater. If the contribution of the two mechanisms decreases then diffusion across the visible sediment surface becomes the dominating transport route. This diffusion is affected by the thickness, and the diffusivity of the terrestrial deposit. For example, thicker deposits cause a greater impedance of solute exchange, and weathering of the deposit increases the diffusivity (Cummings et al., 2009), decreasing impedance. If a terrestrial sediment deposit increases in thickness over time due to frequent sedimentation, and is not eroded by water currents, then the macrofauna will

eventually be killed, and the effect of the deposit on diffusive oxygen supply through the visible sediment surface will dominate.

Based on the evidence discussed above I suggest that terrestrial deposits 1–2 mm thick will have a negligible effect on the burial behaviour of *M. liliana* into the intertidal sediments of the Tuapiro Sandflats, Tauranga Harbour, and on the deposit-underlying sediment porewater chemistry, given that (1) benthic macrofauna are present, (2) the sediment is not recovering from any large scale disturbances prior to the deposition, and (3) the deposit of terrestrial sediment is the result of a single event.

Potential influence of flow

Flow velocity profiles and time series measurements were measured in the seawater above each core position and from 0.25 cm to 8 cm above the sediment surface in each core position. The data revealed differences between core positions in flow velocity, which most likely resulted from wall effects (Table 4 & Appendix Tab 4). Previous detailed mapping of the flume by Lundquist et al., (2004) revealed a variation in flow conditions across the width of the same flume, because of wall effects. The fastest flows were slightly to the right of centre (above core position 2). A more recent study by Vopel et al., (2009) in the same flume revealed that the flow varied by <10% at each core position. Slightly higher flow speeds were recorded for the inner core positions compared to the outer cores, in agreement the wall effects observed in the former study.

Interestingly, the behavioural responses analysis of *M. liliana* indicated that the variation in flow speed may have affected their burial behaviour. Although the number of individuals that did not bury into the sediment was not significant, these individuals remained on the sediment surface only on cores exposed to lower flow velocity (Table 8). An important question in respect to burial is does lower flow velocity affect burial behaviour? In coastal intertidal environments the current velocity changes constantly, and is a characteristic feature of the intertidal environment. How such variations could potentially influence juvenile *M. liliana* burial behaviour is yet to be demonstrated.

In this study only 1% of juvenile bivalves drifted off the sediment surface into the water column. Drifting was observed in inner and outer cores (Table 8). Previous laboratory studies have shown that higher flow velocities can promote dispersal. For

example, Lundquist et al., (2004) has shown that flow speed is an important variable affecting dispersal fates for both *M. liliana* and *Austrovenus stutchburyi*, and Petuha et al., (2006) have shown that live juvenile transport via bedload transport and byssus drifting increases with increasing flow. The importance of flow speed on burial, however, has yet to be confirmed.

The interaction of moving water with bivalves is important, especially for species that are capable of drifting. In still water conditions, *M. liliana* are incapable of actively dispersing from the sediment (either as bedload, or drifting in the water column) and Cummings et al., (1993; 1995) found that behavioural responses are limited to burrowing into the sediment or remaining on the sediment surface. For near-surface-dwelling juvenile bivalves, movement with sediment is inevitable when hydrodynamic forces are sufficient to create moving sediment ripples (Roegnar et al., 1995). Therefore, once bivalves emerge from the sediment they will inevitably be transported, either with sediment bedload or via drifting in the water column, when there are high flow velocities.

Dame (2011) suggests that deposit-feeding bivalves require slow flow to allow the accumulation of deposited seston as a food source. Lopez and Levington (1987) suggest that small grain sizes and slow current flow correlate with higher densities of benthic algae, so one could expect the opposite response, and expect higher burial in lower flow environments. Although the design of this experiment does not allow for meaningful interpretation of the lower burial of *M. liliana* into cores with slower flow above the core, the fact that slow flow may be detectable by juvenile bivalves, and possibly contribute towards the cues used by bivalves to influence their decision to bury into sediment is very interesting and calls for further investigation.

Appraisal of methodology

The use of laboratory flumes in benthic ecological research has been demonstrated by numerous studies, and was fundamental to the nature of this study. Despite the flow being unidirectional and of low velocity, it was important to mimic realistic diffusive boundary layer thickness because solute exchange between sediment and bottom seawater is a function of these conditions. The diffusive boundary layer achieved in this study (0.3 mm to 0.9 mm) was similar to typical environmental conditions. In the

field, however, the diffusive boundary layer changes constantly because the flow velocity oscillates due to wind waves. Furthermore, conducting the experiment under flowing conditions, as opposed to under still water conditions enabled the observation of behavioural responses in *M. liliana* that only occur in the presence of a flow (i.e., crawling and drifting).

During the preliminary experimental runs, the speed of the impeller in the flume was adjusted to increase the speed of the seawater flow in the flume to identify the maximum speed that could be used, without eroding the terrestrial sediment deposit. At higher speeds, small particles were entrained but the deposit remained intact, and at a very high speed the terrestrial layer was severely eroded. The speed of the seawater in the flume (2.41 cm s^{-1}) was similar to the speed that occurs where *M. liliana* are found (e.g., Green, Black & Amos, 1997; Lundquist et al., 2004; Petuha et al., 2006). Future studies using a wave tank, where more realistic flow conditions can be simulated, may reveal if the deposition of terrestrial sediment affects the behaviour of juveniles under conditions of faster and oscillating flows.

The flume also allowed access for measurement of porewater gradients with microelectrodes. Fine scale measurements of oxygen and pH concentration and redox potential provided a detailed understanding of the effects of thin terrestrial sediment deposits on the distribution of porewater solutes. One limitation of microprofile measurements is that they measure the distribution of porewater solutes in one very small (~20 μm) location only, and small changes in faunal activity can cause large differences in the microprofiles.

The ability to collect intact intertidal sediment using flume-specific acrylic tubes, and subsequently insert these sediment cores intact into the flume allowed the natural chemical and biological structure of the cores to be retained with minimal disturbance. The inclusion of intact natural sediment, as opposed to using sediment that has been washed and sieved, revealed that bioturbation plays an important role with respect to the effects of terrestrial sediment deposits on solute distribution and juvenile *M. liliana* burial behaviour. Using pre-sieved washed intertidal sediment from the laboratory as my depleted sediment caused slight differences in the grain size distribution between intertidal and depleted sediment. These differences are unlikely to have caused any differences in the burial behaviour of *M. liliana*, but it would have

been more appropriate to have collected fresh intertidal sediment from the Tuapiro sandflat, and subsequently washed and sieved the fresh sediment.

Furthermore, the flume allowed manipulation of treatments (i.e., the addition of terrestrial sediment) and offered the opportunity to make detailed observations of post-settlement juvenile *M. liliana* burial behaviour that would be difficult to achieve in the field. Making detailed observations of juvenile *M. liliana* burial behaviour was limited to the digital images captured every 1 min for the initial 10 min following their placement, and analysing the burial behaviour of juveniles into the sediment would be easier if a combination of video and still images were captured. Staining the bivalves may also make analysis easier. For example, other laboratory and field experiments (e.g., Cummings & Thrush, 2004; Lundquist et al., 2004; Norkko et al., 2001; Petuha et al., 2006) have stained bivalves using fluorescein (100 mg L^{-1}) for 3 h, or marked bivalves with non-toxic spray paint or a permanent marker pen and found no negative effect of these staining methods on bivalve behaviour.

Given that the effect of millimetre-scale terrestrial sediment deposition is likely to be context-specific, it would be beneficial to conduct a similar laboratory flume experiment to investigate how the relative contribution of diffusion across the diffusive boundary layer of the visible sediment surface, and across subsurface burrow linings to the overall sediment oxygen supply changes with the structure and density of the resident macrofaunal community. For example, this study could be conducted using intact intertidal sediment from a location where *M. liliana* and burrow constructing macrofauna can be found, and by defaunating the same sediment and altering the structure and density of bioturbating macrofauna in the sediment. By adding known quantities of tube dwellers into the sediment, one could control the amount of bioturbation within the sediment, and thus, the amount of oxygen and dissolved reactants supplied across the tube linings. By controlling the relative contribution of the subsurface supply of oxygen, it is possible to establish the thickness of terrestrial sediment at, which the effect of the deposit on diffusive oxygen supply through the visible sediment surface will dominate.

Conclusions

The current paradigm concerning terrestrial sediment deposition suggests that even millimetre-scale deposits can affect the burial behaviour of an important endemic tellinid bivalve and thus cause detrimental effects to marine ecosystem functioning. Contrastingly, this study demonstrates that thin terrestrial sediment deposits may not deter burial of post-settlement juvenile bivalves of the species *Macomona liliana.*

Comparing the results of this study with a study by Cummings et al. (2009) suggests that the effect of millimetre-scale terrestrial deposits on the burial behaviour of these bivalves may be context-specific. That is, the effect that the terrestrial deposit will have on the burial behaviour of juvenile *M. liliana* will depend on other factors such as bioturbation by resident macrobenthic infauna. Periodic disturbance of surface sediment is a natural feature of marine environments, and the deposition of thin terrestrial sediment is one example of such disturbance. The presence of resident infauna and their role in shaping the porewater chemistry must be considered when asking the question whether disturbances by terrestrial sediment deposits will affect recruitment decisions of juvenile *M. liliana*.

The deposit will impede solute diffusion across the visible sediment surface but this impedance may not be important because the exchange of solutes between porewater and bottom water may be largely mediated by the infauna. As long as infauna inhabits the sediment, terrestrial sediment deposits may not have a significant effect.

This study has highlighted the need for a greater understanding of the effect of bioturbation on solute exchange. Bioturbation appears to be one of the most important variables to consider when investigating the effects of terrestrial deposits on juvenile *M. liliana* burial behaviour.

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Appendices

Appendix 1

Statistical analysis summary of generalized liner modeling using ('lower_org') and ('upper_terrig') as regressors.

summary(glm ((m10/m0) ~ lower_org,family=binomial,weight=m0,data=a))

Call:

glm(formula = (m10/m0) ~ lower_org, family = binomial, data = a, weights = m0)

Deviance Residuals:

   Min   1Q Median   3Q   Max

-2.2284 -1.4473 -0.4924   0.9766   2.3025

Coefficients:

        Estimate Std. Error z value Pr(>|z|)

(Intercept)   -2.0236   0.2219 -9.121   <2e-16 ***

lower_orgTRUE -0.8996   0.3932 -2.288   0.0221 *

Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

(Dispersion parameter for binomial family taken to be 1)

   Null deviance: 48.464 on 19 degrees of freedom

Residual deviance: 42.804 on 18 degrees of freedom

AIC: 79.009

Number of Fisher Scoring iterations: 5

Appendix 2

Analysis summary of microelectrode measurements in preliminary runs A and B, and in each of the five experimental runs. *n* = the number of replicate measurements in each sediment core. CP, core position; P, parameter; DBL, diffusive boundary layer; SD, standard deviation; pH_{min} , pH minimum; pH_{max}, pH maximum; Eh, redox potential at the sediment surface; Eh, redox potential minimum; O_{2sur}, oxygen percent saturation at the sediment surface; OPD, oxygen penetration depth.

					DBL		Clay	
Run	CP	Treat	n	P	(mm)	SD	(mm)	SD
A	3	CTS	5	ox	0.3	0.00	1.84	0.09
B	4	CTS	5	ox	0.4	0.00	1.74	0.05
1	1	CTS	2	Eh	-	-	-	-
2	2	CTS	5	ox	0.3	0.00	1.90	0.12
3	3	CTS	2	Eh	-	-	-	-
4	4	CTS	2	pH	0.8	-	1.00	-
5	1	CTS	2	pH	0.9	-	1.20	-
A	4	ITS	5	ox	0.38	0.04	-	-
B	1	ITS	5	ox	0.6	0.12	-	-
1	2	ITS	2	Eh	-	-	-	-
2	3	ITS	5	ox	0.3	0.05	2.40	0.20
3	4	ITS	2	Eh	-	-	-	-
4	1	ITS	2	pH	0.9	-	1.20	-
5	2	ITS	2	pH	0.6	-	1.50	-
A	1	C	5	ox	0.4	0.05	-	-
B	2	C	5	ox	0.4	0.00	-	-
1	3	C	2	Eh	-	-	-	-
2	4	C	5	ox	0.5	0.08	-	-
3	1	C	2	Eh	-	-	-	-
4	2	C	2	pH	0.7	-	-	-
5	3	C	2	pH	0.6	-	-	-
A	2	I	4	ox	0.3	0.00	-	-
B	3	I	5	ox	0.4	0.09	-	-
1	4	I	2	Eh	-	-	-	-
2	1	I	5	ox	0.5	0.08	-	-
3	2	I	2	Eh	-	-	-	-
4	3	I	2	pH	0.7	-	-	-
5	4	I	2	pH	0.7	-	-	-

			pH$_{min}$	pH$_{max}$	Eh$_{sur}$	Eh$_{min}$	O$_{2sur}$		OPD	
Run	CP	Treat			(mV)	(mV)	(% sat)	SD	(mm)	SD
A	3	CTS	-	-	-	-	85	1.2	2.60	0.21
B	4	CTS	-	-	-	-	81	1.1	2.60	0.19
1	1	CTS	-	-	212	-53	-	-	-	-
2	2	CTS	-	-	-	-	87	1.8	2.74	0.11
3	3	CTS	-	-	109	-203	-	-	-	-
4	4	CTS	7.1	7.6	-	-	-	-	-	-
5	1	CTS	7.3	7.4	-	-	-	-	-	-
A	4	ITS	-	-	-	-	98	0.3	-	-
B	1	ITS	-	-	-	-	98	0.5		
1	2	ITS	-	-	210	197	-	-	-	-
2	3	ITS	-	-	-	-	100	0.4	>5.5	-
3	4	ITS	-	-	106	103	-	-	-	-
4	1	ITS	7.4	7.7	-	-	-	-	-	-
5	2	ITS	7.5	7.6	-	-	-	-	-	-
A	1	C	-	-	-	-	61	1.5	1.06	0.09
B	2	C	-	-	-	-	76	5.5	1.40	0.31
1	3	C	-	-	219	-136	-	-	-	-
2	4	C	-	-	-	-	68	8.2	1.24	0.05
3	1	C	-	-	117	-243	-	-	-	-
4	2	C	7.2	7.6	-	-	-	-	-	-
5	3	C	7.4	7.6	-	-	-	-	-	-
A	2	I	-	-	-	-	101	0.6	-	-
B	3	I	-	-	-	-	99	0.4	-	-
1	4	I	-	-	205	168	-	-	-	-
2	1	I	-	-	-	-	101	0.3	>5.5	-
3	2	I	-	-	105	86	-	-	-	-
4	3	I	7.6	7.7	-	-	-	-	-	-
5	4	I	7.6	7.8	-	-	-	-	-	-

Appendix 3

Macomona liliana. Size distribution (shell length measured in millimetres) of post-settlement juveniles used in each experimental run.

	Run 1		
Core 1	Core 2	Core 3	Core 4
1.63	1.37	1.39	1.61
1.67	1.52	1.64	1.56
1.43	1.78	1.7	1.14
1.27	1.62	1.49	1.48
1.56	1.13	1.41	1.27
1.40	1.88	1.7	1.1
1.89	1.52	1.75	1.36
1.53	1.61	1.46	1.15
1.70	1.42	1.49	1.21
1.66	1.86	2.16	1.39
1.30	1.61	1.38	1.89
1.30	1.62	1.74	1.57
1.41	1.81	1.43	1.54
1.70	1.58	1.4	1.2
1.65	1.23	1.51	1.76
1.48	2.04	1.78	1.3
2.13	1.43	1.58	1.42
1.74	1.47	1.44	2.04
1.66	1.62	1.55	1.5
2.04	1.52	1.98	1.25

Run 2			
Core 1	Core 2	Core 3	Core 4
1.49	1.43	1.63	1.42
1.51	1.32	1.28	1.47
1.39	1.40	1.68	1.58
2.17	1.33	1.42	1.48
1.36	1.30	1.30	1.31
1.54	1.43	1.21	1.57
1.52	1.21	1.84	1.77
1.38	1.49	1.46	1.41
1.33	1.38	1.31	1.59
1.37	1.72	1.35	1.42
1.60	1.49	1.33	1.51
1.90	1.42	1.30	1.62
1.63	1.31	1.41	1.45
1.39	2.00	1.31	1.39
1.47	1.72	1.35	1.54
1.40	1.60	1.29	1.67
1.84	1.56	1.26	1.81
1.36	1.47	1.33	1.89
1.42	1.66	1.62	1.82
1.54	1.47	1.48	1.45
Core 1	Core 2	Core 3	Core 4

	Run 3		
Core 1	Core 2	Core 3	Core 4
1.15	1.50	1.22	1.37
1.67	1.50	1.72	1.30
1.43	2.17	1.82	1.29
1.12	2.27	1.82	1.63
1.36	1.63	1.74	1.23
1.43	1.77	1.71	1.16
1.20	1.27	1.72	1.28
1.23	1.44	1.89	1.30
1.60	1.42	1.43	1.13
1.55	2.12	1.62	1.55
1.88	1.29	1.59	1.45
1.59	1.70	1.62	1.38
2.06	1.24	1.97	1.45
1.96	1.93	1.77	1.80
1.27	2.20	1.50	1.27
1.67	1.77	1.62	1.61
1.07	1.93	1.89	1.45
1.34	1.66	1.45	1.51
1.41	1.19	1.62	1.31
1.60	1.46	1.58	1.26
Core 1	Core 2	Core 3	Core 4

	Run 4		
Core 1	Core 2	Core 3	Core 4
1.20	1.65	1.60	1.48
1.47	1.68	1.63	1.46
1.58	1.64	1.26	1.58
1.47	1.57	1.30	1.33
1.35	1.84	1.47	1.25
1.85	1.30	1.51	1.76
1.75	1.38	1.43	1.80
1.92	1.67	2.21	1.35
1.37	1.66	1.35	1.64
1.51	1.34	1.43	1.53
1.43	1.47	1.57	1.42
1.52	2.03	1.73	1.91
1.74	1.54	1.56	1.38
2.17	1.58	1.36	1.32
1.59	1.57	1.38	1.51
1.70	1.59	1.40	1.30
1.46	1.79	1.34	1.65
1.22	1.43	1.57	1.26
1.29	1.5	1.33	1.83
1.79	1.73	2.10	1.21

Core 1	Core 2	Core 3	Core 4

	Run 5		
Core 1	Core 2	Core 3	Core 4
1.73	1.43	1.32	1.70
1.43	1.32	1.60	1.98
1.29	1.55	1.42	1.54
1.33	1.81	1.37	1.76
1.67	1.73	1.30	1.79
1.58	1.44	1.79	1.50
1.50	2.10	1.71	1.94
1.42	2.06	1.94	1.93
1.68	1.26	1.70	1.63
1.69	1.69	1.54	1.86
1.52	1.98	1.70	1.63
1.48	2.02	1.26	1.52
2.05	1.29	1.28	1.77
1.42	2.00	1.60	1.38
1.75	1.12	1.46	1.83
1.47	1.5	1.26	1.96
1.99	1.51	1.97	1.61
2.00	1.75	1.78	1.60
1.49	1.61	1.88	1.18
1.63	2.02	1.78	1.29

Core 1	Core 2	Core 3	Core 4

Appendix 4.

Flume seawater free-stream flow velocity for each core position at each height interval above the flume floor in vertical profile measurements when the impeller speed is 2 Hz.

Height	Core position			
	1	2	3	4
8.00	2.19	2.33	2.29	2.21
7.50	2.24	2.25	2.33	2.19
7.00	2.25	2.21	2.25	2.14
6.50	2.20	2.20	2.26	2.21
6.00	2.22	2.21	2.24	2.29
5.50	2.18	2.25	2.27	2.05
5.00	2.29	2.24	2.25	2.19
4.75	2.16	2.23	2.28	2.03
4.50	2.17	2.13	2.27	2.16
4.25	2.08	2.35	2.21	2.20
4.00	2.20	2.32	2.32	2.02
3.75	2.07	2.24	2.27	2.10
3.50	1.90	2.16	2.26	1.97
3.25	1.86	2.12	2.01	2.09
3.00	2.00	2.20	2.05	2.18
2.75	1.87	2.14	2.07	2.11
2.50	2.00	2.30	1.94	1.94
2.25	2.23	2.23	2.23	2.01
2.00	1.93	2.06	2.28	2.08
1.75	2.00	1.95	1.99	1.96
1.50	2.10	2.07	1.85	2.00
1.25	1.94	1.75	1.80	1.94
1.00	1.75	1.85	1.68	1.88
0.75	1.97	1.66	2.10	1.74
0.50	1.96	1.80	1.78	2.01
0.25	1.77	1.83	1.67	1.79