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# **The context-specific roles of a bioturbating crab (*Austrohelice crassa*) on ecosystem functioning**

A thesis submitted in fulfilment of  
the requirements for the degree of

**Doctor of Philosophy**

in

**Biological Sciences**

at

**The University of Waikato**

by

**Hazel R. Needham**



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The University of Waikato

2011

For my parents

Ray and Carol



*Austrohelice crassa*  
(Dana, 1851)

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# Abstract

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Bioturbating macrofauna can have major effects on their physical, biological and biogeochemical surroundings, altering ecosystem functioning. *Austrohelice crassa* (herein *Austrohelice*) is a burrow building estuarine crab endemic to New Zealand. The abundant and widespread nature of this species infers that its effects on sediment processes are likely to be significant. This thesis explores *Austrohelice*'s impact on ecosystem functioning quantifying both density and habitat induced differences in sediment reworking rates, solute and particle fluxes. The underpinning mechanisms by which changes are mediated are also examined.

I hypothesised that organism behaviour, sediment type and interactions between both factors have the potential to mediate changes to ecosystem functioning. Sediment reworking rates were calculated from four parameters: burrow and crab density, burrow morphology, burrow permanency and burrow maintenance, measured across a sedimentary gradient. Burrows were over 18 times more stable in mud than sand equating to over an order of magnitude reduction in sediment reworking rates, shifting the primary bioturbational role from burrow builder in mud to sediment mixer (bulldozer) in sand. Burrow decay rates, combined with differences in burrow and crab densities, were primarily responsible for changes in reworking rates among sediment types.

An *in situ* density manipulation experiment was conducted in a non-cohesive sand and a cohesive muddy-sand to test the hypothesis that the functional plasticity of *Austrohelice* among sediment types would be reflected in measures of solute

exchange; a proxy for ecosystem functioning. In both habitats, *Austrohelice* regulated nutrient cycling, creating strong density driven effects on solute exchanges. Increasing crab density enhanced sediment O<sub>2</sub> demand and the flux of NH<sub>4</sub><sup>+</sup> from the sediment, indicating much of the response was physiologically driven. Despite lowering microphyte standing stock through deposit feeding, *Austrohelice* also increased benthic primary production per unit of chlorophyll *a*. Important context-specific differences were also revealed, most notably for NH<sub>4</sub><sup>+</sup> fluxes, which were higher where burrows and their associated microbial communities were most stable.

Laboratory based flume experiments were conducted to test if increasing burrow density amplified sediment erodibility and if the different reworking rates (and hence functionality) between sediment types, would affect sediment stability. Context-specific effects on particle fluxes associated with burrow density were observed among sediment types. Increasing burrow density reduced erodibility in cohesive mud, whereas in non-cohesive sand erosion rates were unimodal, being greatest at low burrow densities. Increased trapping of bedload material alongside a reduction in flow velocity due to surficial pellets was attributed to the reduction in the mass of sediment eroded in sand at high burrow densities. In mud, the linear decrease in erodibility associated with increased burrow density was attributed to crab activity at low tide whereby high concentrations of fine particles (silt-clay) are sluiced from burrows, creating both a smoothing and consolidating effect on the sediment surface.

This thesis highlights the value of assessing organism characteristics and behaviour alongside organism density to identify the mechanisms which govern

ecosystem level processes among habitats. Integration of such information in to functional group studies and sediment dynamic models will broaden conceptual frameworks and avoid oversimplification of highly complex organism-sediment interactions.

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## Preface

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The main body of this thesis comprises three research based chapters (Chapters 2-4). Chapters 2 and 3 have been published in internationally renowned scientific peer reviewed journals. I assumed the responsibility of fieldwork programmes, laboratory and data analysis and for writing this thesis. Except where explicitly referenced, the material in this thesis was produced from my own ideas and work under the supervision of Conrad Pilditch, Andrew Lohrer and Simon Thrush.

Chapter 2 has been published by the journal *Marine Ecology Progress Series* Volume 414: 179-193 (2010), under the title “Habitat dependence in the functional traits of *Austrohelice crassa*, a key bioturbating species” by H. R Needham, C.A Pilditch, A.M. Lohrer and S.F. Thrush.

Chapter 3 has been published by the journal *Ecosystems* Volume 14, issue 7: 1096- 1109 (2011), under the title “Context-specific bioturbation mediates changes to ecosystem functioning” by H. R Needham, C.A Pilditch, A.M. Lohrer and S.F. Thrush.

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# Chapter 1

## General introduction

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### **1.1 Introduction**

The importance of certain species in the regulation of diversity, energy flow and ecosystem processes is a well known phenomenon in ecology. Bioturbating organisms alter the physical environment in which they live through their activities and movement. In soft sediment systems, this biologically mediated modification of the benthos increases habitat heterogeneity (Levin and Paine 1974) and influences processes such as sediment transport, carbon trapping, primary production and nutrient recycling (Lohrer et al. 2004, 2010, Mermillod-Blondin and Rosenberg 2006, Thrush et al. 2006, Le Hir et al. 2007). Bioturbators therefore play an important role in the regulation and maintenance of ecosystem functioning and the consequent goods and services derived from the systems in which they live (Beaumont et al. 2007, 2008).

#### **1.1.1 Burrow building fauna**

Burrow building bioturbators create a heterogeneous three dimensional matrix through the benthos extending the sediment-water interface. These pathways have been likened to veins and arteries in that burrows aid the transport of particles, nutrients, oxygen and metabolites through the sediment system (Reise 2002). The physical act of burrowing, increases sediment permeability (Ridd 1996) and porewater flux, alters surface topography and translocates material between reaction

zones, enhancing remineralisation rates (Aller and Dodge 1974, Meadows and Meadows 1991). Burrows increase the surface area over which solute exchange can occur and provide extensive habitat for microbial communities which exert strong control over biogeochemical processes and create gradients of exchange. Burrow ventilation, which can occur both passively and actively, is closely coupled to bioturbation as bioturbation subducts labile material and ventilation speeds up reaction rates through increased oxygenation (D'Andrea 2002, Pillay and Branch 2011 and references therein). These processes alter the pathways and magnitude of solute fluxes, enhancing benthic-pelagic coupling (Nielsen et al. 2004). Therefore the activities of bioturbators far exceed abiotic transport processes such as the molecular diffusion of solutes or organic matter burial through sedimentation.

Despite the influence of bioturbators on soft sediments being introduced as a concept by Darwin, our current understanding of the causal mechanisms behind the observable effects of bioturbation are still limited (Meysman et al. 2006). This is because organism-sediment interactions are often highly complex and non-linear, with numerous feedbacks between the two. Processes do not necessarily occur at one spatial scale and likely differ in magnitude as a function of sediment type (Hewitt et al. 2007). Therefore drawing generalities and inferences can be fraught with problems (Thrush et al. 2000).

As organism traits are increasingly used to group species in order to predict and model changes to ecosystem functioning (Bonsdorff and Pearson 1999, Bremner et al. 2006, Suding et al. 2008), it is ever more pertinent that we strive to understand the underpinning mechanisms by which organism-sediment interactions occur and how interactions differ as a function of sediment properties and organism density.

Development of assessment tools for ecosystem-based monitoring and management is becoming increasingly important as global anthropogenic pressures on natural environments continue to grow and management focus shifts to address issues of loss of function and concomitant ecosystem services (Christensen et al. 1996, Thrush and Dayton 2010). Empirical studies which address the mechanism by which an organism facilitates change to ecosystem processes are therefore invaluable for advancing conceptual frameworks and development of accurate predictive tools for monitoring and management.

In New Zealand, the endemic surface deposit feeding burrow building grapsid crab *Austrohelice crassa* (herein *Austrohelice*), comprise a significant component of the estuarine benthos in the mid to high intertidal zone (McClay 1988). *Austrohelice* is a relatively small species (< 26mm carapace width), often present in high densities (up to 462 m<sup>-2</sup>, Jones and Simons 1983). When first creating a burrow, crabs are observed to thrust the propodi and dactyli of the last 3 pairs of legs in the sediment pulling out lumps of substrate. The hole is then widened by a rocking motion of the carapace. Once the initial depression is made, the chelipeds are used to deepen the hole, removing sediment by pushing or rolling particles clear of the burrow aperture (Thompson 1930). Although field observations addressing the peak activity periods of *Austrohelice* have been contradictory, it is generally acknowledged that as the tide recedes, most crabs emerge to clear away burrow debris (Beer 1959, Fielder and Jones 1978, Williams 1985). This is done by creating discrete pellets which are rolled out of the burrow entrance or by pushing cohesive sediment against folded chelae (McClay 1988). *Austrohelice* is a territorial species; therefore feeding is conducted indiscriminately close to each burrow entrance. Pseudofaecal pellets

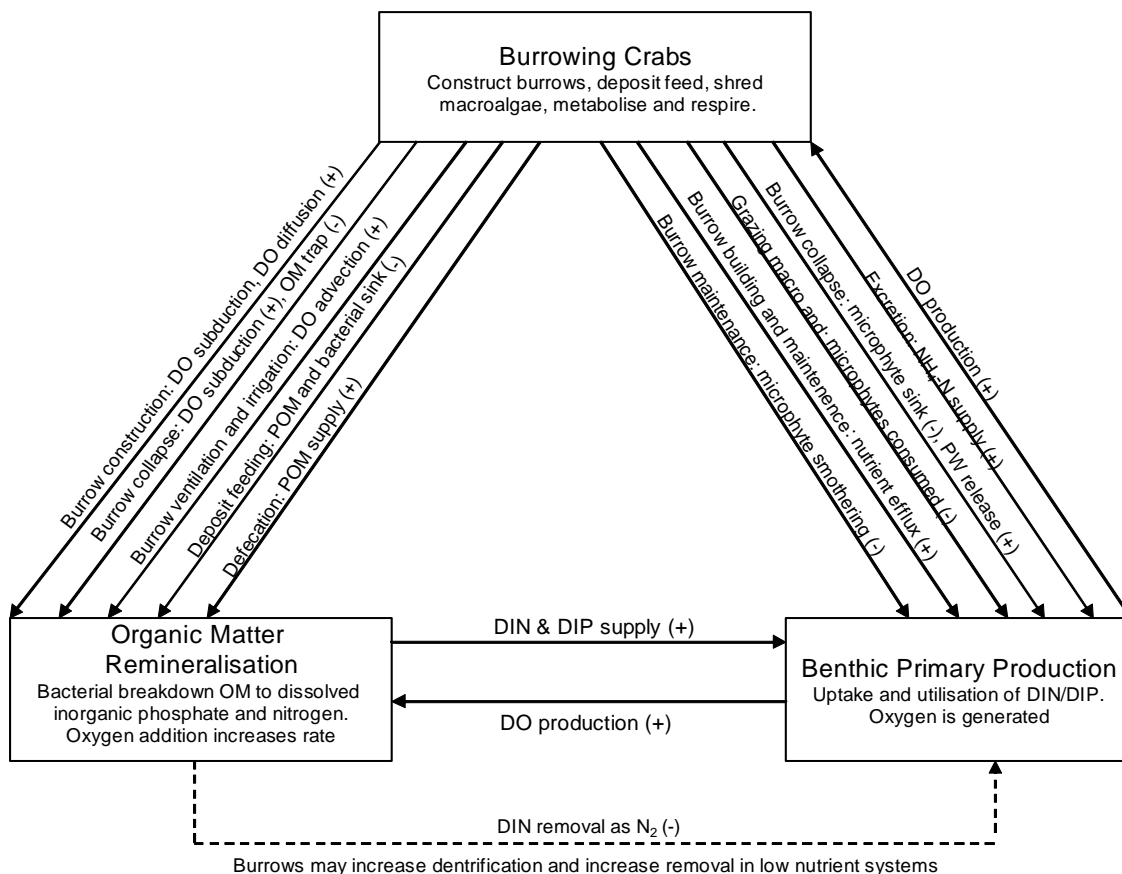
created during feeding are distinct from those created during burrow excavation due to their smaller size and often lighter colouration.

Due to *Austrohelice*'s ubiquitous nature among sediment types, their biological traits and often high densities, it is likely that this species will be a significant contributor to ecosystem functioning. However, few studies to date have aimed to directly assess *Austrohelice*'s impact on ecosystem processes (Morrisey et al. 1999) despite their high resilience to, and remediation of, anthropogenic impacts (Gibbs et al. 2001, Thrush et al. 2003). Although this species has been somewhat overlooked in published literature to date, other similar crab species have been extensively studied (Botto et al. 2005, Gutiérrez et al. 2006, Escapa et al. 2007, Fanjul et al. 2007, Kristensen 2008). Therefore some of the complex organism sediment interactions can be hypothesised due to an *a priori* understanding of how local scale interactions may impact on ecosystem processes (Figure 1.1). Consideration of this 'interconnectedness' is essential if key mechanisms are to be developed and utilised as predictive tools (Levin et al. 2001).

### **1.1.2 Key interactions between burrowing crabs and their environment**

Shallow intertidal systems are highly productive and responsible for recycling upwards of 80% of the nutrients made available for primary production in coastal areas (Rowe et al. 1975, Nixon 1981, Jensen et al. 1990). As a burrow building surface deposit feeder, the impact of *Austrohelice* on microphyte populations and subsequent benthic productivity is likely to be significant (Figure 1.1). *Austrohelice* consume detrital material excreting the waste product ammonia, which is a preferential source of nitrogen utilised by benthic microphytes and bacteria. However, microphytobenthos likely comprise a significant portion of *Austrohelice*'s

diet, reducing their overall biomass. For example, the soldier crab *Mictyris longicarpus* reduced sediment chlorophyll *a* by 77% which in turn reduced benthic primary production by 71% (Webb and Eyre 2004). The physical act of building a burrow may further reduce productivity by relocating microphytes to deeper sediment layers, or by reducing light penetration through increased erosion and turbidity.



**Figure 1.1.** Schematic of the key interactions between burrowing crabs, organic matter recycling and benthic primary producers in a generalised benthic system. Positive (+) interactions include supply and facilitation, whilst negative interactions (-) are those which are inhibitory or act as sinks. Strengths of such interactions are not inferred. DO: dissolved oxygen, POM: particulate organic matter, DIN: dissolved inorganic nitrogen, DIP: dissolved inorganic phosphorous, PW: pore water. Adapted from Lohrer et al. 2004.

The physical presence of burrow structures also has direct influence over solute exchanges by increasing the sediment-water interface over which geochemical processes occur, and provides habitat for differing microbial communities. Nitrogen is one of the most limiting nutrients for phytoplankton production in coastal areas (Ryther and Dunstan 1971). By constructing burrows, nitrifying bacteria may be stimulated by the co-occurrence of both oxygen and ammonium (Aller 1982). *Neohelice granulata* (previously *Chasmagnathus granulata*) a burrowing crab in SW Atlantic estuaries, has been shown to positively influence the nitrogen levels in sediments, in turn, enriching benthic primary producers (Botto et al. 2005). However, deep portions of burrows may present reducing conditions where nitrification can also be reversed; a process known as 'nitrate reduction' (Nishio et al. 1982).

Denitrification, the transformation of nitrate back to dinitrogen gas ( $N_2$ ), can alter the net gain or loss of nitrogen from a system. For example, Nielsen et al. (2004) demonstrated that high densities of a burrow building worm *Nereis diversicolor* accounted for 50-77% of bulk sediment nitrification but also 58-82% of nitrate reduction in mudflat sediments. Close coupling of these two processes has also been indirectly observed in crab burrows and may be dependent on burrow morphology and depth (Botto et al. 2005). However, the structure and complexity of burrows may be controlled by extrinsic factors, primarily sediment grain-size. Morrissey et al. (1999) found *Austrohelice* burrows in muddy sediment to be larger (by a factor of up to 14.8) and more complex, though not always deeper, than in sand. Burrows were also present in higher densities in mud and represented 14% of the surrounding sediment volume which reduced to 2.4% in sand. Differences in

burrow morphology due to changes in sediment properties or organism density are therefore likely to influence the strength and patterns of solute flux in a given area.

As well as acting as conduits for solute fluxes, the flux of particulate matter may also be greatly affected by the presence of burrows. Particles are moved deeper in to the sediment than would occur by physical processes alone, entrapping organic material (depicted as a negative interaction in Figure 1.1) and modifying remineralisation rates. *Neohelice granulata* can increase sediment surface area by 3-7 times (Katz 1980, Iribarne et al. 1997) exhuming  $4.8 \text{ mg m}^{-2} \text{ d}^{-1}$  of readily labile carbon (Gutierrez et al. 2008). However, material trapped in burrows is more labile than that returned to the surface, resulting in a net sink for carbon in saltmarshes. Such relationships highlight the need to address organism behaviour alongside processes such as sediment deposition.

Burrow construction is known to alter sediment permeability and structure as both the sediment matrix and interstitial pore waters are mixed in the building process (Nowell and Jumars 1984, Ridd 1996, Botto and Iribarne 2000, Escapa 2008). The formation of water filled burrows often results in a reduction of bulk shear strength, bulk density (particularly in cohesive sediments) and erosion thresholds, but increases permeability and erosion potential, particularly where burrow densities are high (Grabowski et al. and references therein 2011). Conversely, crab burrows may also trap and retain particulate matter in estuarine systems. For example, *Neohelice granulata* traps  $> 100 \text{ g dry weight d}^{-1}$  of sediment in its burrows (Botto and Iribarne 2000). Sediment particles may also be biogenically sorted by crabs during the feeding process, further disturbing the sediment surface and increasing both water content and penetrability (Tamaki et al 1992, Botto and Iribarne 2000). Not

only are sediments stripped of surface binding microphytes, but pelletised material can increase bed roughness, altering flow velocities and bed shear stresses, potentially destabilising sediments (Botto and Iribarne 2000, Widdows and Brinsley 2002).

Destabilisation of the sediment matrix through burrow collapse may alter the diagenic pathways and processes in estuarine sediments and increase the flux of nutrients from interstitial pores to the overlying water column. Sediment stability is likely to be influenced by the density of burrow structures and the inherent sediment properties surrounding them. Populations of *Uca pugnax* have been documented as excavating 120-160 cm<sup>3</sup> sediment m<sup>-2</sup> d<sup>-1</sup>, which continually mixed the upper 8-15 cm of sediment (McCraith et al. 2003), whereas *Neohelice granulata* and *Uca uruguayensis* have documented sediment reworking rates of 2235 g m<sup>-2</sup> d<sup>-1</sup> and 679 g m<sup>-2</sup> d<sup>-1</sup> respectively due to differences in behaviour and sediment type (Botto and Iribarne 2000). Frequent burrow collapse is most likely to occur where cohesive properties (silt-clay) are low. However, as the numbers of studies which have quantitatively assessed erosion potential in burrowed sediments are few to date, the capacity for individual species to influence sediment dynamics is still poorly understood and highly debated.

The degree to which burrow builders influence ecosystem processes and reaction rates has previously shown density dependent effects (Aller 1980, 1983, Kristensen 1984, 1985, Wethey et al. 2008, Widdows 2009). Even the most ubiquitous macrobenthic species show some habitat preferences which contribute to changes in density across environmental gradients (Ysebaert and Herman 2002, Thrush et al. 2003a). Increasing organism density will increase the interactions between

individuals due to their proximity to one another, which may have both positive and negative effects on ecosystem processes. For instance, surface deposit feeders will exert greater grazing intensity when present in high densities, potentially altering the direction and degree of sediment-water solute exchange and sediment stability through their impact on microphytobenthic populations (Marinelli 1992). Competition for resources may also alter behavioural responses in such mobile fauna, influencing sediment particle and nutrient fluxes. Greater physical proximity of burrow structures may amplify solute exchange as the diffusion distances between burrows are shorter (Aller and Aller 1998, Gilbert et al. 2003), but could also increase sediment erosion potential (Widdows et al. 2009). Greater availability of metabolic products such as ammonium can stimulate microbial metabolism (Henriksen et al. 1983, Kristensen 1985), but increased macrofaunal density also results in greater sediment oxygen demands (Sandwell et al. 2009). Hence, changes in organism density can exert strong control over ecosystem processes and should be considered in experimental design (Widdicombe and Austen 1998, Lohrer et al. 2004, D'Andrea and DeWitt 2009).

It is apparent, from the interactions discussed above, that organism behaviour and density have a key involvement in many ecological processes and the degree to which ecosystem functions are maintained. This thesis aims to quantify and compare the density driven effects of *Austrohelice* on ecosystem processes among sediment types and examine the underpinning mechanisms that mediate change.

## 1.2 Thesis Organisation

The main body of this thesis is comprised of three experimental and observational studies of *Austrohelice crassa* and its influence on ecosystem functioning among differing sediment environments. Chapter 2 examines the context-specific nature of *Austrohelice* burrowing behaviour and consequent sediment reworking rates across a sediment gradient. Chapters 3 and 4 quantify the density driven effects of *Austrohelice* and their burrow structures on ecosystem processes, namely solute fluxes (Chapter 3) and particle fluxes (Chapter 4) in both a cohesive muddy sediment and a non-cohesive, sand. A summary of the aims and objectives of each research chapter follow.

- **Chapter 2**

I conducted interlinking field observations and measurements to determine how crab density, burrow density, burrow morphology, burrow permanency and burrow maintenance altered as a function of sediment type. These measures were then used to parameterise a simple sediment reworking model to determine sediment mixing rates in three key habitats and elucidate the primary bioturbational role of *Austrohelice* in these sediments.

- **Chapter 3**

I carried out *in situ* crab density manipulations using caged sediment plots to quantify the degree to which *Austrohelice* influences nutrient cycling rates and pathways (a proxy for ecosystem functioning) in both cohesive and non-cohesive sediments using benthic flux chambers. Changes in flux rates between sediment types were assessed to establish if context-specific differences in burrowing

behaviour (Chapter 2) were attributable to the observed flux patterns. Interactions between *Austrohelice* and the microbial communities in each sediment type were determined by conducting flux chamber incubations in both daylight and at night. Extensive measures and sampling of environmental variables were carried out to further examine the interactions between organism and environment among sediment types.

- **Chapter 4**

I quantified how both the presence of *Austrohelice* burrows and their density affected sediment stability and erosion rates in a laboratory based annular flume study. Particle fluxes in both a non-cohesive sand and a cohesive mud were assessed at burrow densities appropriate to those sediment types, as well as in areas without burrows. Intact sediment cores containing naturally constructed *Austrohelice* burrows collected from the field were used to mimic the natural conditions as much as possible. The aim was to relate the observed differences in particle fluxes in each sediment type back to the underpinning context-specific nature of *Austrohelice* bioturbation as discussed in Chapter 2, as well as examining the ways in which observed patterns may influence ecosystem functioning.

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## Chapter 2

# Habitat dependence in the functional traits of *Austrohelice crassa*, a key burrowing species

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### **2.1 Introduction**

Soft sediment environments are the most common habitats on the planet (Snelgrove 1999). Intertidal areas form only a small percentage of these environments, but offer a heterogeneous matrix of sedimentary and hydrodynamic conditions for macrofauna. Many macrofaunal species display some degree of habitat selectivity due to their lifestyle or trophic mode and patterns of organism distribution differ across sediment gradients (Levinton and Kelaher 2004). The activity and behaviour of some macrofaunal species can have disproportionate effects on their environment, relative to their body size, by influencing processes such as sediment transport, carbon trapping, primary production and nutrient regeneration, which are often measured as indicators of ecosystem functioning (Widdicombe and Austen 1998, Lohrer et al. 2004, Webb and Eyre 2004, Thrush et al. 2006). Organism morphology and behaviour have been used to group species according to their functional traits to infer impacts on ecosystem processes (Tilman 2000, Hewitt et al. 2008). However, habitat mediated differences in functioning of an individual species have not been considered in the application of functional trait analyses.

Bioturbating macrofauna (i.e. species that alter their sedimentary environment through their movement) often play a key role in ecosystem functioning (Mullan Crain and Bertness 2006 and references therein) and are commonly categorised as either bulldozers or burrow builders. Bulldozers perpetually move through the sediment matrix below the surface disturbing the top few centimetres of sediment. Organisms that perform this mode of bioturbation (for example, heart urchins) alter the sediment matrix through increased oxygen penetration and as sediment is destabilised through their movement, organic matter is subducted stimulating remineralisation and porewater release (Osinga et al. 1997, Hollertz and Duchene 2001, Lohrer et al. 2004). In contrast, burrow builders create structures in which they live more or less permanently or use as a refuge from predation and environmental stress. Burrow building fauna primarily mediate change to the sediment environment through the extension of the sediment-water interface, increasing the area available for oxidative exchange to take place. Burrows increase microorganism habitat and enable translocation of particles to different reaction zones through non-local mixing and sediment trapping, altering remineralisation rates (Aller and Yingst 1978, Kristensen et al. 1985, Botto and Iribarne 2000)

Grouping organisms according to their functional traits enables predictions of their broad-scale influences on ecosystem functioning. Methods for evaluating ecological functioning such as trophic group, biological trait and functional group analysis are evolving as ecosystem based management tools (Roth and Wilson 1998, Bonsdorff and Pearson 1999, Bremner et al. 2006). These approaches are supported by natural history information and data from small-scale studies investigating the influence of bioturbators on ecosystem rates and processes.

However, such studies are often conducted without exploring the underpinning mechanisms by which the observed changes were mediated. For instance, although many studies have linked patterns in nutrient exchange to the density of burrowing organisms, alterations in species behaviour or burrow structure created by their increased proximity to one another are not often addressed (D'Andrea and DeWitt 2009). Similarly, with bulldozing macrofauna, many studies have linked changes in rates and processes to their presence, but have not quantified sediment reworking rates to support their findings (Lohrer et al. 2005). Organism behaviour, sediment type and interactions between both factors have the potential to mediate changes to ecosystem functioning.

Many Crustacea, including several burrowing crab species have proven to be functionally important in intertidal habitats (Lee 1998, Kostka et al. 2002, McCraith et al. 2003, Botto et al. 2005, Gutierrez et al. 2006, Fanjul et al. 2008, Kristensen 2008 and references therein). The impact of these crabs on ecosystem functioning is likely to be related to their density, activity, burrow morphology and permanency (i.e., the rate at which burrows collapse and are rebuilt); factors that are likely to vary among species and sediment type. While variations in crab density and burrow morphology with sediment type and shore position have been well documented (Takeda and Kurihara 1987, Lim and Diong 2003, Mouton and Felder 1996, Iribarne et al. 1997, Morrissey et al. 1999, Breitfuss 2003, Salgado Kent and McGuinness 2006), sediment reworking rates have rarely been quantified (Katz 1980, Gardner et al. 1987, Wolfrath 1992, Botto and Iribarne 2000, McCraith et al. 2003). Measurements of sediment reworking are important when defining bioturbatory activity of an organism in its environmental context. Whilst a burrower's bioirrigation capacity is suggested by the increase in

sediment-water interface created through burrow building, if burrow collapse rate is high, the overriding functional significance of the species may be mediated through increased sediment turnover. For example, McCraith et al. (2003) demonstrated that the rate of fiddler crab burrow turnover was linked to marsh plant root density resulting in differences in sediment mixing rates. Studies that acknowledge differences in behaviour or bioturbation rates within a species across differing sediment types and physical conditions, have only recently become more common (Biles et al. 2003, Escapa et al. 2008, Sassa and Watabe 2008).

Here I assessed the functional role of a burrow building, surface deposit feeding, grapsid crab *Austrohelice crassa* (c.f *Helice crassa*, Dana 1852, herein referred to as *Austrohelice*); a ubiquitous component of New Zealand's estuaries. These highly mobile organisms which grow up to 2.3 cm carapace width (CW) are often found in high densities (up to 462 m<sup>-2</sup>, Jones and Simons 1983), in the mid to high shore region. They inhabit a wide spectrum of sediment types from silt to coarse sand with reported burrow depths of up to 60 cm (Nye 1977, Morrissey et al. 1999). Despite being recognised as important bioturbators in many New Zealand estuaries, sediment reworking rates have not been quantified in previous studies (Morrissey et al. 1999, Williamson et al. 1999, Gibbs et al. 2001, Norkko et al. 2002). As grapsids do not secrete reactive mucous or reinforce their burrows like burrowing shrimp (Nickell and Atkinson 1995, Kristensen and Kostka 2005), differences in burrow permanency and morphology (a proxy for burrow wall surface area), are likely to occur with changes in sediment grain size. If burrow permanency is distinctly different in cohesive or non-cohesive sediments, this will alter the frequency that a crab re-builds its burrow; in turn altering the rate at which sediment is mixed. Similarly, if burrow morphology varies as a function of

sediment type, differences in burrow wall surface area among habitats may drive changes in ecosystem processes such as nutrient exchange. By assessing the differences in burrowing behaviour and sediment reworking capacity of *Austrohelice* I aimed to elucidate its primary bioturbational role across habitats.

To quantify possible shifts in *Austrohelice* contribution to ecosystem functioning through bioturbation, I constructed and parameterised a simple sediment reworking model in different habitats types. Specifically, as a function of sediment type (cohesive mud to fine sand), I determined four terms to calculate sediment mixing rates 1) burrow and crab density 2) burrow morphology and depth related changes in the surface area and volume of these structures, 3) burrow permanency, and 4) sediment excavation rates during burrow maintenance. Burrow permanency provided the dynamic element of this model. Similar to Gardner et al.'s (1987) regeneration model, my assumption was that a new burrow was built for each one infilled. Burrow morphology measurements not only quantified the amount of sediment excavated during burrow formation, but also enabled calculation of the increase in sediment-water interface, allowing the primary bioturbatory function of *Austrohelice* in each sediment environment to be determined.

## ***2.2 Methodology***

Four interlinking observational studies were conducted to determine the terms required to calculate sediment reworking rates in three differing sediment environments (Figure 2.1); fine sand (PE2), muddy sand (PA4) and mud (PA1). Burrow permanency observations were limited to these three locations due to logistical constraints; however, patterns of crab abundance and burrow

morphology were first investigated at a larger number of sampling stations to ensure that the three more intensely studied locations typified the environments inhabited by *Austrohelice*. This wider-scale sampling also provided insight into the drivers of the observed crab-sediment interactions.

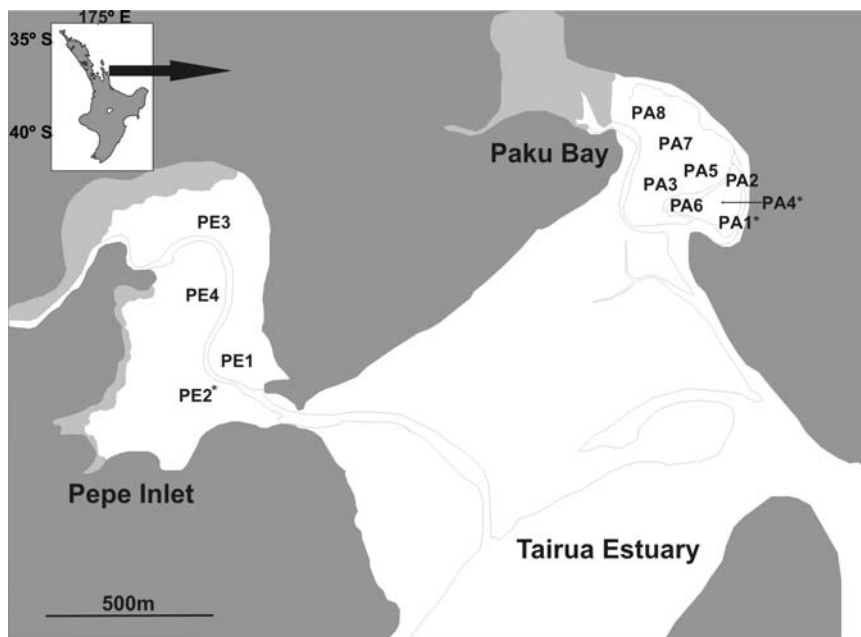
### **2.2.1 Study sites**

Studies were conducted in two sheltered embayments in Tairua Estuary, North Island, New Zealand (Figure 2.1). The two sites, Paku Bay and Pepe Inlet were selected for their high abundance of *Austrohelice*, similar inundation periods and tidal heights. Due to the close proximity of the two embayments and the range of *Austrohelice* habitats, sampling stations across both locations were treated as a continuous gradient of sedimentary variables. Sampling effort reflected the heterogeneity of each bay with four sampling stations in the fine sands of Pepe inlet (PE1 to PE 4) and eight in Paku Bay: two in mud (PA 1 & 2), two in muddy sand (PA3 & 4), two in fine sand (PA5 & 6) and two in medium sand with a gravel top layer (PA7 & 8). Sampling stations were not equidistant (most were  $\geq$  100 m apart) and reflected spatial distributions in sediment properties. The greatest distance between stations situated at the far sides of each bay (PA1 - PA8 and PE2 - PE3) was approximately 550 m and the closest stations between bays (PE3 and PA3) were around 1 km apart. All sampling was undertaken during the late spring (November) and summer (February) 2008 on spring tides.

### **2.2.2 Sediment parameters and crab abundance**

At each station, three 0.25 m<sup>2</sup> quadrats were placed on the sediment surface and all visible burrow openings were counted, noting the number >10 mm dia. Samples for grain size, chlorophyll *a* (chl *a*) and total organic matter content

(TOM) were then collected at random from inside each quadrat using a 2.8 cm diameter, 1 cm deep corer. Three replicate cores per quadrat were collected and pooled for each analysis. The remaining sediment in each quadrat was excavated to a depth of 20 cm, visually checking that no crabs were lost in the process, and sieved on a 1 mm mesh screen. Crabs and other large macrofauna were preserved in isopropyl alcohol for later identification and enumeration. Crab carapace width (CW) was measured to the nearest 0.1 mm using digital callipers and the sex of each mature crab (i.e., >5 mm CW, below which gender was indeterminate) recorded.

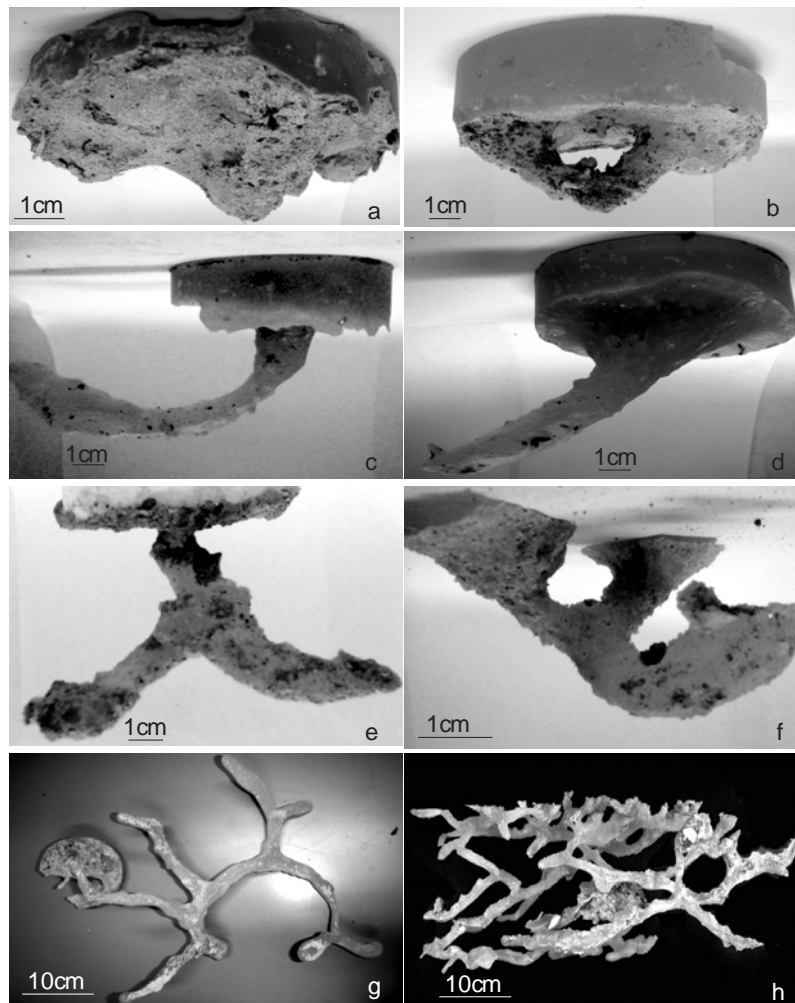


**Figure 2.1.** Insert, North Island, New Zealand. The arrow depicts the location of the study location, Tairua estuary, Coromandel peninsula. Main figure shows the proximity of the two bays and sampling stations. Shaded areas ■ denote mangroves and fringing vegetation. The grey line indicates the channel edges at low tide.\* Indicates stations used to calculate sediment reworking rates.

### 2.2.3 Burrow morphology

A 1m<sup>2</sup> quadrat was arbitrarily positioned at each station with a 0.25m<sup>2</sup> quadrat placed at random within it. This smaller quadrat enabled a subset of the total burrow number to be counted and compared to previous burrow surveys at each station enabling correlative patterns in burrow morphology and density to be elucidated. At each station ten burrows were randomly selected from a numbered grid of 25 cells (20\*20 cm, labelled 1 to 25) within the 1 m<sup>2</sup> quadrat. Only one burrow per cell was cast, and prior to pouring the resin, each burrow opening was measured across both axes. Burrow casts were not collected from PA8, as this area had been subject to disturbance, leaving very few visible burrows present. A PVC collar (either 6 cm or 12 cm in diameter depending on the size of the burrow opening) was placed on to the sediment surface, separating the burrow opening from its surroundings. Catalysed polyester resin (Norski products) was poured in to each burrow until flush with the sediment surface. Resin casts were left *in situ* for 24 h to harden before being excavated from the sediment by hand. Casts were left to air dry for an additional 7 days before being thoroughly cleaned of residual sediment with a brush. Casts were analysed morphometrically by dividing each burrow in to its component shapes (e.g., cone shaped burrow entrance, cylindrical burrow shaft, etc). Surface area and volume were calculated from the linear dimensions of each component shape then summed. Burrow length was calculated similarly. Maximum depth was measured directly from the level of the sediment surface to the deepest point of the cast and the number of surface openings and overall burrow shape, irrespective of size, were recorded.

Eight different and distinct burrow forms were categorised across the 11 stations (Figure 2.2 a to h). These ranged from the simple ‘*cone*’, ‘*i*’ and ‘*j*’ shaped burrows to complex structures known as ‘*inverted y*’ and ‘*branching*’. Some burrows (‘*y*’ and ‘*u*’) were classified by their dual surface openings. Large matrices of interconnecting burrows were also observed in association with burrowing shrimp species. These burrows were described as ‘*complex*’.



**Figure 2.2.** Photographs of the 8 burrow forms found across the 11 stations cast. Burrow forms were classified as; (a), *cone*; (b), *u*; (c), *j*; (d), *i*; (e), *inverted y*; (f), *y*; (g), *branching*; (h), *complex* formed with other species, in this instance, alpheid shrimp.

#### **2.2.4 Burrow permanency**

Three stations from the original twelve were established for monitoring burrow permanency from which the rate of decay could be estimated. Each station had adult *Austrohelice* densities  $>10$  ind.  $0.25 \text{ m}^{-2}$  and best represented three distinct habitats found within the sediment gradient (Figure 2.3a); mud (PA1), muddy sand (PA4) and fine clean sand (PE2). Five  $0.25 \text{ m}^2$  plots marked at the corners with pegs (1 cm dia.) were created along a transect parallel to the incoming tide at lower mid-tide level. In each plot 10 burrows with an aperture  $> 10$  mm were measured and individually marked using numbered thin wire flags. On each visit, the presence/absence of flagged burrows was recorded and the total number of burrows ( $>10$  mm dia.) within each quadrat was counted to look for changes in burrow density over time. All fifteen quadrats were visited daily for one week, weekly for one month and monthly for two months.

#### **2.2.5 Burrow maintenance**

In unconsolidated sandy sediments *Austrohelice* clear their burrows just after the sand flat is exposed. Sediments are pelletised and removed from the burrow by the occupant crab. These pellets are usually dark in colour, relative to ambient surface sediments, and easily distinguished from feeding pellets. In muddy, cohesive sediments signs of burrow maintenance were not as apparent as lower bedload transport appears to reduce the frequency of burrow clearance (*pers obs*). Similarly in the coarsest grained stations, where a gravel top layer was present, pellets were not distinct, making measurements of burrow maintenance only possible in fine sand.

To measure the amount of sediment cleared from a burrow as the tide receded, six 0.25 m<sup>2</sup> plots were created 5 m apart on a transect running from the shore to the channel edge (as elevation changes were minimal) at PE1 (Figure 2.1). Each plot was positioned and marked with corner pegs (1 cm dia.) as soon as the tide uncovered the area. Sampling began 1 h after each plot was exposed to air, as burrow clearance by *Austrohelice* generally starts at this time. An approximate 8 minute lag between dewatering of each plot meant all sediment collection could be completed on one tide. To commence sampling, all burrows with excavated sediment surrounding the opening were individually marked with numbered fine wire flags. Each burrow opening was measured across both axes to the nearest millimetre and the pellets removed using a small steel spatula. Marked burrows were repeatedly sampled on an hourly basis until no further excavate was found (approximately 3 hours post-exposure). Transect surveys were repeated on three consecutive days with plots placed parallel to, but spaced 5 m away from, the previous day's site. The excavated sediment was frozen at -20° C until analysis for dry weight, TOM and grain size was conducted.

### **2.2.6 Sediment analyses**

TOM was determined through loss on ignition from dried sediments (105 °C for 24 h), after combustion for 5.5 h at 550 °C (Dean 1974). Sediments for particle size analysis were digested in 10 % hydrogen peroxide, to remove organic matter (Day 1965) before analysis on a Malvern mastersizer-S (300 FR lens) to determine grain size fractions in the range of 0.05 µm to 2000 µm. Chl *a* was determined from freeze dried sediment and extracted in 90 % acetone for 24 h before centrifugation; concentrations were determined fluorometrically, on a

Turner 10-AU fluorometer, using an acidification step to separate phaeophytin (phaeo) concentration from that of photosynthetic pigments (Arar and Collins 1997).

### **2.2.7 Data analysis**

Correlation coefficients (Pearson's  $r$ ) were calculated to determine relationships between crab and burrow density and sediment properties across all 12 stations. Correlation-based principal component analysis (PCA) was used to visualise the sediment gradient based on the measured sediment variables. All axes were normalised to enable comparison of Euclidean distances between sample points, irrespective of the measurement units. Highly correlated variables were excluded when  $r > 0.8$ . From this PCA three distinct stations were selected for the estimation of sediment reworking rates. To assess differences in crab size between stations a Kruskal-Wallis test was conducted with post-hoc multiple comparisons tests, as parametric analysis of variance (ANOVA) assumptions were not met. The number of burrows remaining through time was used to estimate burrow decay rates ( $k \text{ d}^{-1}$ ) by fitting an exponential decay model ( $Y=Y_0e^{-kt}$ ) using non-linear least squares regression with the Levenberg-Marquardt algorithm as the measure of estimation (Levenberg 1944). The decay constant of each sediment type was used to calculate the mean burrow permanency ( $Bp = 1/k$ ) in each of the three locations. One way ANOVA was used to test if burrow maintenance rates differed as a function of shore position. Type III sums of squares were used to perform this analysis due to the differing burrow number in each quadrat. Simple linear regression was used to establish if relationships between the dw sediment expelled and burrow aperture existed. All analyses

were computed using Statistica software (Stat Soft Inc, release 8) apart from PCA where Primer V6 (Primer-E Ltd) was used.

### 2.2.8 Model calculations

To calculate sediment reworking rates in the mud (PA1), muddy sand (PA4) and sand (PE2), resin cast data from each location were used to determine the average amount of sediment exhumed when a burrow is first created ( $Bg$  (g dw)) using the formula:

$$Bg = V * \rho$$

Where  $V$  is mean volume of adult burrows cast ( $\text{cm}^3$ ) in each station and  $\rho$  is the salt corrected dry bulk density of the sediment ( $\text{g cm}^{-3}$ ) from that location. Sediment reworking rates ( $SR$  ( $\text{g dw m}^{-2} \text{ SLM}^{-1}$ )) were then calculated for each of the three sediment types as follows:

$$SR = Bg * Cn * (SLM / Bp)$$

Where summer lunar month ( $SLM$ ) is a constant 28 days,  $Cn$  is the mean crab density ( $\text{ind. m}^{-2}$ ) and  $Bp$  is the mean crab burrow permanency (days) in each location. My equation, like that of Katz (1980) and Gardener et al (1987), assumes that the rates of burrow construction and collapse are equal i.e., a crab makes a new burrow each time an old burrow collapses. For the sand site only, the mean amount of sediment excavated during burrow maintenance ( $BM$  ( $\text{g dw m}^{-2} \text{ SLM}^{-1}$ )) was also calculated:

$$BM = Cn * (Se * Ti)$$

Where  $Se$  is the mean amount of sediment excavated ( $\text{g dw crab}^{-1} \text{ low tide}^{-1}$ ),  $Ti$  is the number of tidal exposures per lunar month (a constant 56, two exposures per day for 28 days). Therefore total sediment reworking ( $TSR$  ( $\text{g dw m}^{-2} \text{ SLM}^{-1}$ )) can be summarised as:

$$TSR = SR + BM$$

The increase in sediment surface area created by *Austrohelice* burrows was estimated from resin casts of adult crab burrows found in the 3 locations ( $n = 8$ ). Burrow density information from each location enabled estimations of the total increase in sediment surface area through *A. crassa* bioturbation. Similarly, total burrow volume of each area, based on burrow density, was also calculated. Upper and lower confidence intervals (95 %) around the mean were carried forward through each step of the calculation to gain an estimate of associated error.

## **2.3 Results**

### **2.3.1 Sediment surface properties**

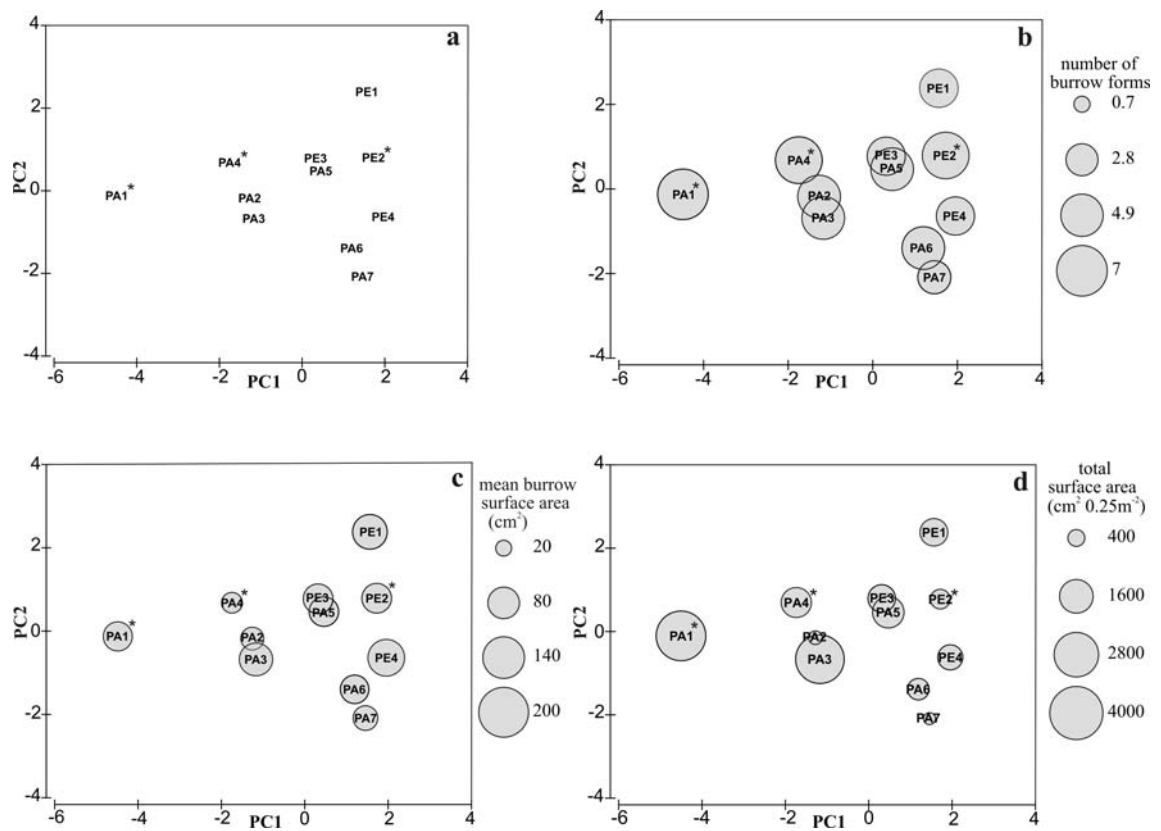
Sites spanned the range from fine silt-clay (mean grain size =  $22 \mu\text{m}$ ) at PA1 to medium sand with a gravel top layer (mean grain size =  $257 \mu\text{m}$ ) at PA8 (Table 2.1). The muddiest site, PA1, exhibited the greatest sediment TOM, silt-clay and chl *a* content. Silt-clay content ranged from 77.3 % to 10.4 % across the sediment gradient whilst total organic matter content ranged from 6 % in fine sediments down to 2.3 % in sand. Chl *a* concentration varied between stations from 18.3 to  $8.6 \mu\text{m g dw}^{-1}$ , with the highest concentration in the muddiest and lowest concentration in the coarsest sediments. Sediment properties showed strong, significant correlations with each other, indicating predictable relationships

between parameters across the spectrum of sites (Table 2.2). A two dimensional correlation-based principal component analysis ordination (PCA) of surface sediment properties showed that 65.5% of variation among sites were explained by median grain size and silt-clay content on PC1 (Eigenvalue 3.93), with a further 24.7% variation attributable to the biologically derived pigments (Chl *a* and phaeo) on PC2 (Eigenvalue 1.48 (Figure 2.3a)). This PCA also visually highlights the spread of the three stations chosen for the calculation of sediment reworking rates driven mainly by differences on axis PC1.

### **2.3.2 *Austrohelice* abundance and distribution**

*Austrohelice* populations showed a similar range in carapace width (CW) across 11 of the 12 sites, with a mean CW between 5.8 ( $\pm 2.3$ , 1 SD) at PA5 and 8.6 ( $\pm 3.7$ ) mm at PE3 (Figure 2.4a). PA3 was the only station where mean crab CW ( $9.8 \pm 2.7$  mm) was greater than any of the other sampled locations (K-W multiple comparisons test,  $p < 0.018$  in all cases). The stations with the greatest crab abundance were PA1, PA4 and PA7, with a peak density of 55.3 ( $\pm 7.1$ ) ind.<sup>-1</sup> 0.25 m<sup>-2</sup> at PA4 (Figure 2.4b). These three sites all had high silt-clay content despite differing in other sediment properties (Table 2.1). Burrow density ranged from 295 ( $\pm 44.17$ ) 0.25 m<sup>-2</sup> at PA1, through to 26 ( $\pm 2.65$ ) 0.25 m<sup>-2</sup> at PE1 (Figure 2.4c). Differences in burrow: crab ratio (Figure 2.4d) were observed across the sediment gradient, with the greatest number of burrows per crab occurring at the muddiest station PA1 ( $5.7 \pm 0.7$ ) with the closest association being 1.4 burrows per crab ( $\pm 0.3$ ) in fine clean sand (PE2). Crab population was split in to two categories; juveniles ( $< 5$  mm CW) and adults ( $>5$  mm CW) which were both shown to correlate significantly with burrow density ( $p < 0.001$ , Table

2.2). Strong correlations ( $p < 0.005$ ) with percentage silt-clay, porosity and TOM over that of grain size ( $p = 0.042$ ) were also apparent. Overall, burrow and adult crab density displayed similar relationships to measured sediment properties, the only exception being chl *a*, which correlated with burrow density only. The abundance of juvenile crabs followed that of the adult population in all but their association with mean grain size.



**Figure 2.3.** Two-dimensional correlation-based principal component analysis (PCA) ordination of the surface sediment properties across the sediment gradient (a). PC1 and PC2 account for 90.2% of the total variance across the 11 stations sampled. Increasing values on PC1 correlate positively with grain size and negatively with silt-clay content (65.5%, Eigenvalue 3.93). PC2 values positively correlate with sediment pigments (24.7%, Eigenvalue 1.48). Overlain bubble plots display changes in the number of burrow forms present (b), mean burrow surface area (c) and total burrow surface area (d) at each station. \* Indicates stations used to calculate sediment reworking rates.

**Table 2.1.** Surface sediment properties across the 12 stations sampled in Tairua Estuary. Standard deviations are given in parentheses (n = 3). Sites are ordered according to mean grain size, from finest (PA1) to coarsest (PA7).

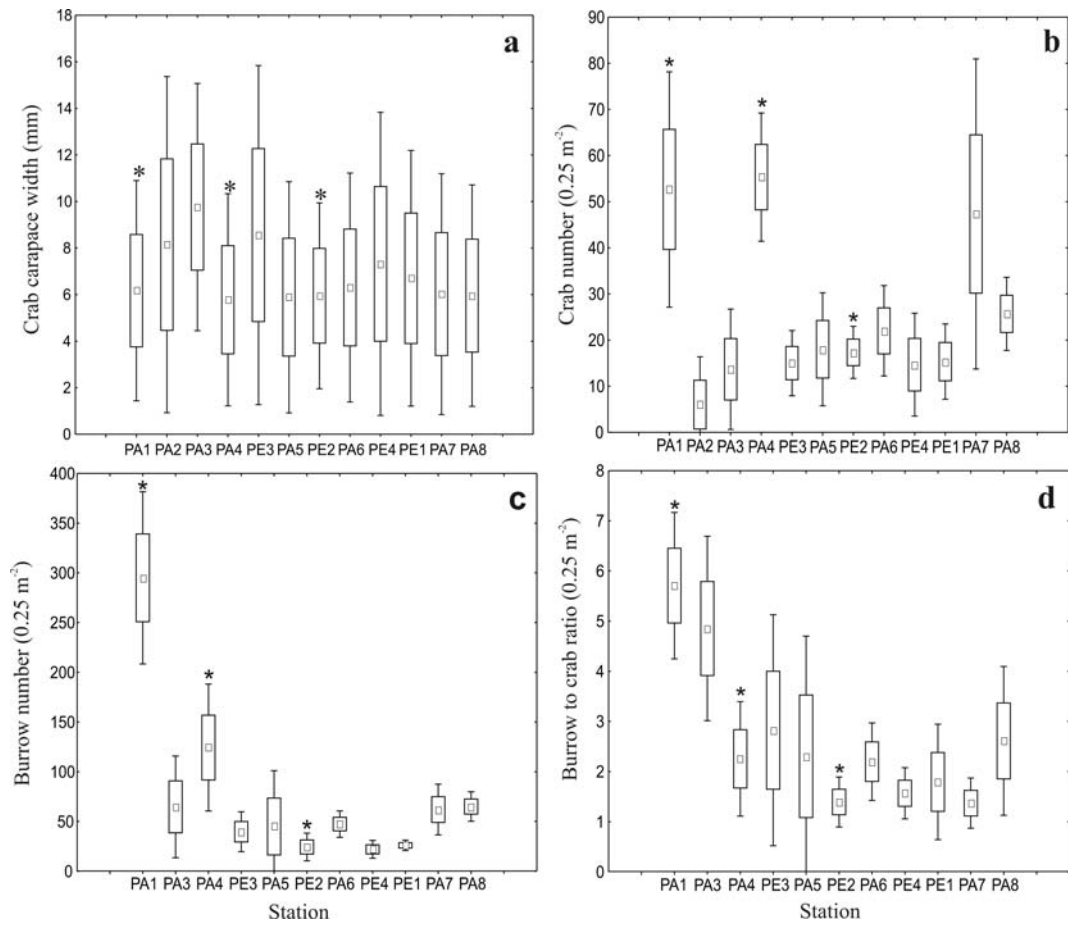
Station	TOM (%)	Chl <i>a</i> ( $\mu\text{g g}^{-1}$ )	Phaeo ( $\mu\text{g g}^{-1}$ )	Median grain size ( $\mu\text{m}$ )	Silt-clay (%)	Porosity	Water content (%)
<b>PA1*</b>	6.0 (0.13)	18.3 (0.9)	12.6 (2.4)	22 (3)	77.3 (3.8)	0.66 (0.01)	76.3 (4.0)
<b>PA2</b>	4.2 (0.70)	13.7 (6.4)	17.1 (12.0)	94 (62)	53.1 (24.3)	0.55 (0.03)	47.8 (6.0)
<b>PA3</b>	4.3 (0.46)	13.2 (2.5)	13.2 (2.0)	94 (47)	42.6 (19.1)	0.57 (0.00)	50.6 (0.4)
<b>PA4*</b>	4.4 (0.41)	17.1 (1.6)	17.1 (1.5)	96 (43)	42.1 (9.8)	0.58 (0.01)	53.4 (2.6)
<b>PE3</b>	3.9 (1.03)	14.9 (1.3)	19.2 (3.8)	162 (29)	19.9 (6.1)	0.49 (0.04)	31.7 (5.4)
<b>PA5</b>	3.8 (0.12)	15.7 (2.6)	15.7 (0.6)	168 (3)	23.1 (0.7)	0.44 (0.02)	30.0 (2.2)
<b>PE2*</b>	2.3 (0.03)	14.4 (2.9)	19.2 (3.8)	168 (16)	19.3 (3.3)	0.39 (0.01)	25.2 (0.9)
<b>PA6</b>	3.0 (0.16)	11.5 (1.0)	8.8 (5.3)	170 (9)	21.4 (9.8)	0.47 (0.01)	34.4 (1.4)
<b>PE4</b>	2.3 (0.33)	10.7 (4.3)	15.6 (4.0)	171 (34)	26.1 (14.4)	0.41 (0.04)	27.4 (5.0)
<b>PE1</b>	2.7 (0.35)	15.7 (5.5)	28.2 (24.4)	174 (7)	10.4 (0.4)	0.42 (0.03)	27.8 (3.2)
<b>PA7</b>	2.9 (0.23)	11.9 (2.3)	6.7 (1.3)	256 (22)	40.7 (1.1)	0.45 (0.02)	31.1 (2.0)
<b>PA8</b>	2.7 (0.45)	8.6 (0.7)	8.6 (0.8)	257 (39)	23.1 (5.54)	0.45 (0.07)	32.1 (0.8)

Values represent averages of 0-1 cm layer in all but granulometric samples which were taken to a depth of 2cm. TOM, total organic matter; Chl *a*, dry weight sediment chlorophyll *a*; Phaeo, dry weight sediment phaeopigment. \* Denotes stations used in sediment reworking calculations

**Table 2.2.** Pearson's r correlation coefficients calculated between *Austrohelice* densities, burrow densities and surface sediment properties from each of the 12 stations across the sediment gradient.

	Burrow density (0.25m <sup>-2</sup> )	Total <5mm CW	Total >5mm CW	TOM (%)	Med grain size (µm)	Silt-clay (%)	Chl <i>a</i> (µg g)	Phaeo (µg g)	Porosity
<b>Burrow density (0.25m<sup>-2</sup>)</b>	1								
<b>Total &lt;5mm CW</b>	<b>0.66***</b>	1							
<b>Total &gt;5mm CW</b>	<b>0.67***</b>	<b>0.81***</b>	1						
<b>TOM (%)</b>	<b>0.79***</b>	<b>0.43**</b>	<b>0.53**</b>	1					
<b>Med grain size (µm)</b>	<b>-0.62***</b>	-0.19	<b>-0.36*</b>	<b>-0.75***</b>	1				
<b>Silt-clay (%)</b>	<b>0.84***</b>	<b>0.57***</b>	<b>0.70***</b>	<b>0.78***</b>	<b>-0.70***</b>	1			
<b>Chl <i>a</i> (µg g<sup>-1</sup>)</b>	<b>0.41*</b>	0.21	0.21	<b>0.51**</b>	<b>-0.52**</b>	0.31	1		
<b>Phaeo (µg g<sup>-1</sup>)</b>	-0.09	-0.09	-0.2	-0.04	-0.16	-0.2	0.12	1	
<b>Porosity</b>	<b>0.75***</b>	<b>0.52**</b>	<b>0.50***</b>	<b>0.80***</b>	<b>-0.62***</b>	<b>0.68***</b>	<b>0.41*</b>	-0.16	1

Total <5mm CW, juvenile *Austrohelice* carapace width; total >5mm, adult *A. crassa* carapace width; TOM, total organic matter; Chl *a*, dry weight sediment chlorophyll *a*; Phaeo, dry weight sediment phaeopigment. Significant values are in bold \* p = < 0.05, \*\* p = < 0.01, \*\*\* p = < 0.001. Sediment values represent mean values (n = 3) of the 0-1cm later in all but granulometric samples which were taken to 2 cm depth.

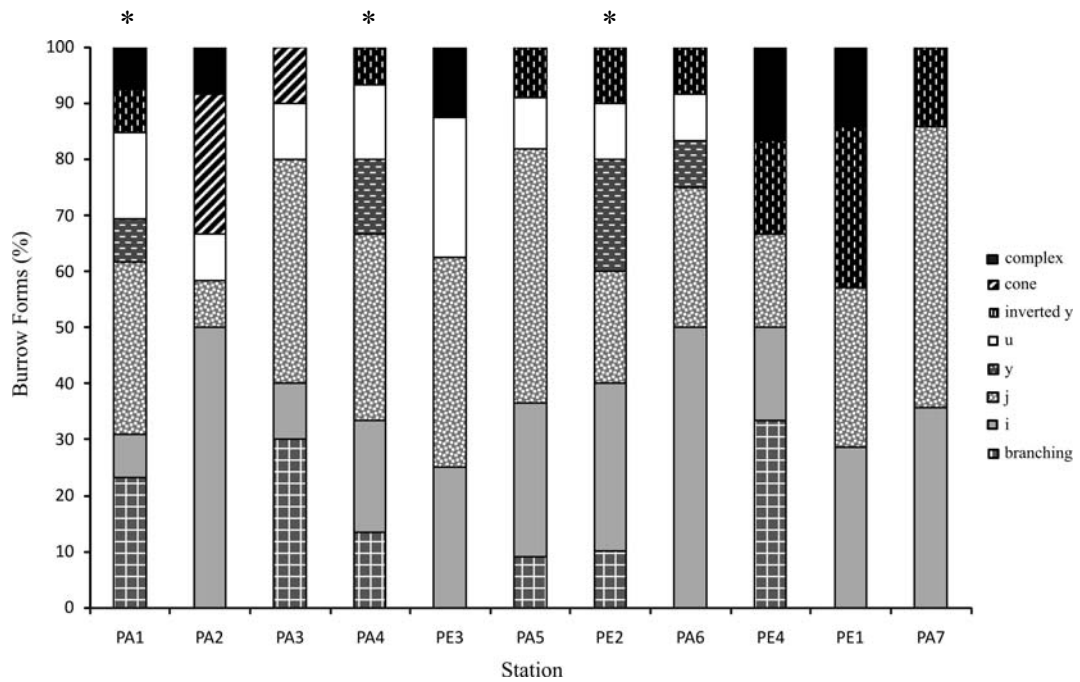


**Figure 2.4.** Box and Whisker plots of crab population size structure (a), mean *Austrohelice* density (b), burrow density (c) and the burrow to crab ratio (d) at each station. Stations are ordered according to mean grain size from finest (PA1) to coarsest (PA7). \* Indicates stations used to calculate sediment reworking rates. The central box indicates the mean, the surrounding box represents  $\pm 1$  standard deviation and the whiskers denote the upper and lower 95 % confidence intervals. Station PA2 was removed from Figure 2.3c and 2.3d due to the high density of *Alpheus* sp. burrows which were indistinguishable from *A. crassa* burrows at the sediment surface.

### 2.3.3 Burrow morphology

The most common burrow forms were that of ‘j’ and ‘i’ with ‘branching’ and ‘inverted y’ forms also occurring across the sediment gradient although more frequently in fine to medium sand (Figure 2.5). No burrow forms with multiple entrances (y, u) were observed in the three coarsest sediments (PE4, PE1 and PA7) and those described as ‘cone’ were cast at site PA2 and PA3 only. ‘Complex’ casts of mixed species found at the muddiest sites (PA1 and PA2) were created in conjunction with alpheid shrimp, whilst those in PE1, PE3 and PE4 were morphologically typical of callianassid species (Nickell and Atkinson 1995). These burrow matrices were excluded from all further analyses as it was impossible to disentangle the effects of the various crustacean burrowers.

Burrow diversity (i.e. the number of burrow forms cast at each sampling station), did not display predictable patterns across the sediment gradient despite the greatest number of burrow forms being found in the muddiest (7, PA1) and the fewest in the coarsest (3, PA7) station (Figure 2.3b). Patterns in mean burrow surface area (Figure 2.3c) were also inconsistent across the sediment gradient and did not show significant correlations with any of the measured sediment parameters ( $|r| < 0.55$ ,  $p > 0.08$ ). As mean burrow surface area was highly correlated with mean burrow volume, length and depth ( $r > 0.83$   $p < 0.001$ ), this pattern was similar for all burrow metrics. However, when scaled with burrow density, total surface area (and hence, other burrow metrics) showed a tendency to decrease with increasing grain size (Figure 2.3d,  $r = -0.71$ ,  $p = 0.014$ ).

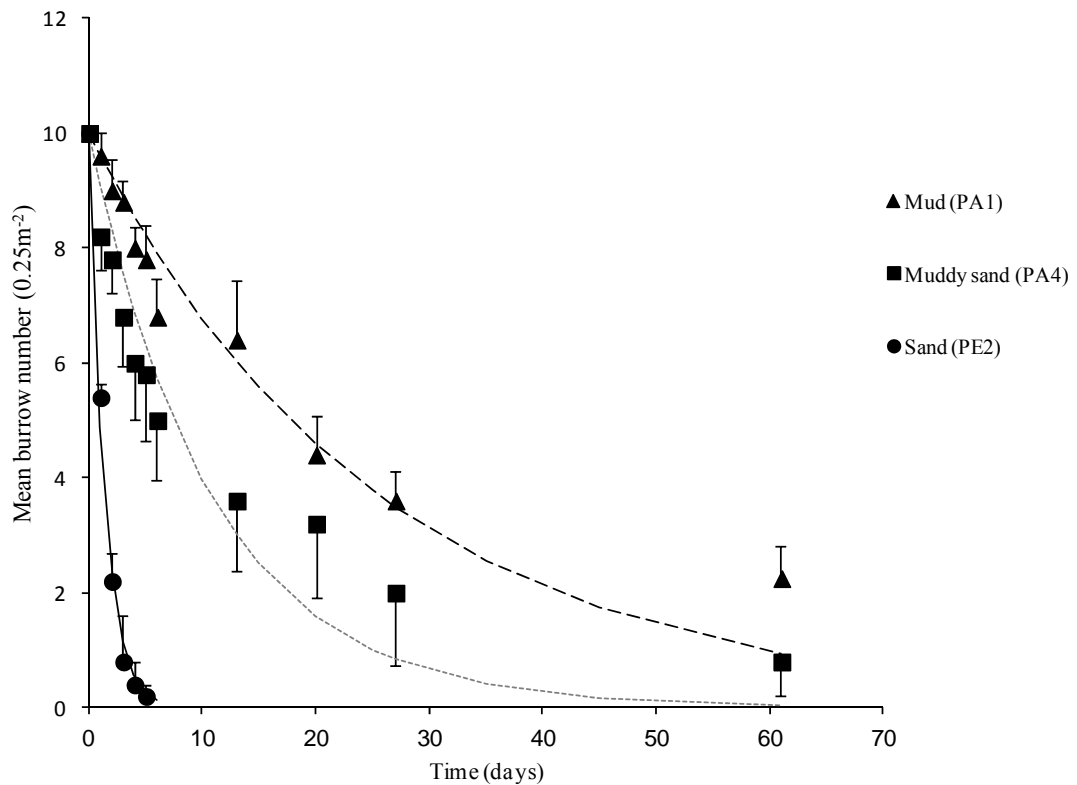


**Figure 2.5.** The percentage of differing burrow forms at each of the 11 stations which are ordered according to mean grain size with PA1 the finest and PA7 the coarsest. Burrows with more than one surface opening were counted as a single burrow structure, including ‘*complex*’ multi species casts. \* Denotes stations used to calculate sediment reworking rates between sediment types.

### 2.3.4 Burrow permanency

The permanency of burrows at each station showed distinct differences across the three sediment types (Figure 2.6). After six days of observations, all marked burrows at the sand location (PE2) had infilled. This differed greatly to the other two locations, which after two months of observations had 8 % ( $\pm 13$  SD, muddy sand, PA4) and 22.5 % ( $\pm 1.26$  SD, mud, PA1) of their marked burrows remaining. No major fluctuations in total burrow number per site were witnessed during the observational period, indicating a steady state in the rate of burrow formation and decay at each location. The fitted exponential decay models were all highly significant ( $p < 0.0001$ ;  $r^2 > 0.89$ ; Figure 2.5) with the decay constant

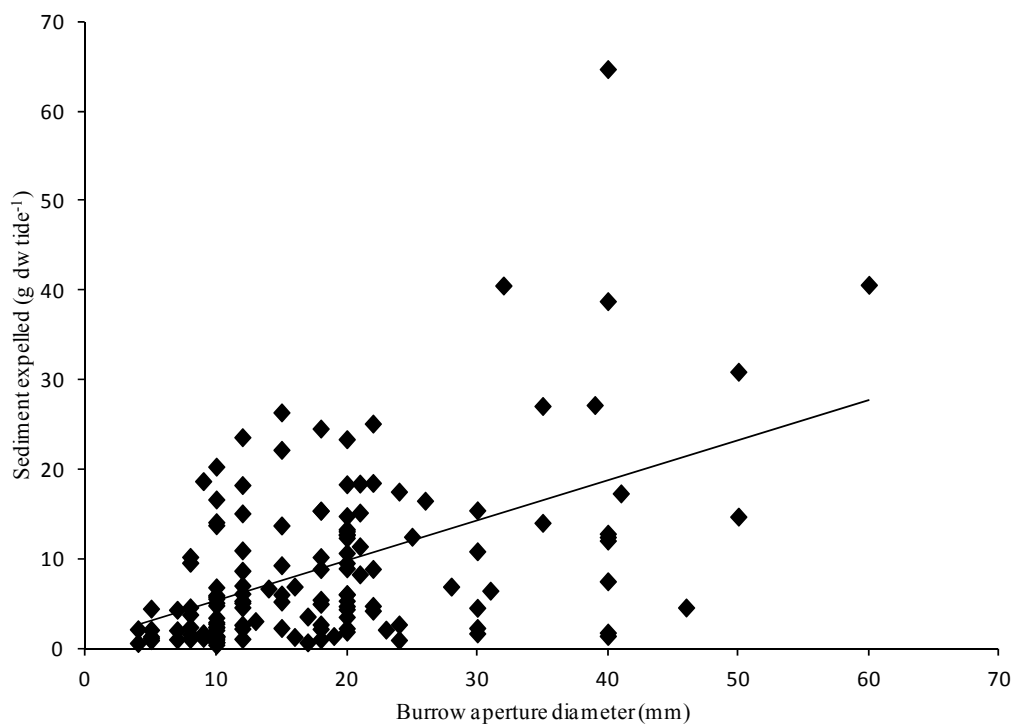
( $k$ ) differing by an order of magnitude between sand and mud. Sand showed the fastest rate of decline ( $k = 0.72$ , 95% CI = 0.63 - 0.81d<sup>-1</sup>), mud the slowest ( $k = 0.039$ , 95 % CI = 0.031 - 0.046 d<sup>-1</sup>), with muddy sand displaying more similarities with that of the mud ( $k = 0.092$ , 95 % CI = 0.068 - 0.117 d<sup>-1</sup>). The mean burrow permanency ( $1/k$ ) indicated a burrow would last on average 25.7 days in mud, 10.8 at the intermediate site and only 1.4 days in sand.



**Figure 2.6.** Mean number of marked burrows remaining as a function of time and sediment type. The fitted exponential decay models are: sand  $y = 10 * e^{(-0.720 * t)}$  ( $r^2 = 0.99$ ,  $p = < 0.0001$ ); muddy sand,  $y = 10 * e^{(-0.092 * t)}$  ( $r^2 = 0.89$ ,  $p = < 0.0001$ ) and mud  $y = 10 * e^{(-0.0390 * t)}$  ( $r^2 = 0.94$ ,  $p = < 0.0001$ ). Error bars denote standard error.

### 2.3.5 Sediment evacuation during burrow maintenance

The amount of sediment excavated during burrow maintenance at low tide was highly variable (Figure 2.7). The amount of sediment excavated ( $\text{g dw burrow}^{-1}$ ) did not differ with shore position across the 3 transects ( $F = 1.78$   $df = 5$   $p = 0.12$ ), so all data were pooled. Burrow aperture size was related to the amount of sediment excavated across all 141 burrows ( $r^2 = 0.25$   $p < 0.001$ , Figure 2.7). On average this material contained 2.5 % ( $\pm 0.6$  SD) TOM, fractionally lower than that of the surface sediment of the surrounding area (2.8 %  $\pm 0.9$  SD). Mean grain size of the pelletised material did not differ from that of the sediment surface ( $170 \mu\text{m} \pm 24$ ).



**Figure 2.7.** The relationship between burrow aperture size and the amount of sediment brought to the surface during burrow maintenance ( $r^2 = 0.25$ ,  $p = < 0.001$ ). All samples were collected from transects near station PE1.

**Table 2.3.** Sediment surface area extension and reworking estimates calculated for three differing sediment types; mud (PA1), muddy sand (PA4) and sand (PE2). Mean values are indicated in bold and the 95% confidence interval is given in parentheses. All values are for adult burrows only. Burrow maintenance samples were only collected at PE2.

	<b>Mud</b>	<b>Muddy Sand</b>	<b>Sand</b>
<b>Burrow density (# m<sup>-2</sup>)</b>	<b>207</b> (143 - 271)	<b>144</b> (134 - 154)	<b>30.7</b> (5.71 - 58.3)
<b>Burrow volume (cm<sup>3</sup>)</b>	<b>22.4</b> (17.5 - 53.4)	<b>9.5</b> (5.77 - 18.7)	<b>32.5</b> (11.7 - 37.4)
<b>Total burrow volume (cm<sup>3</sup> m<sup>-2</sup>)</b>	<b>4635</b> (2499 - 14439)	<b>1373</b> (774 - 2874)	<b>997</b> (66.6 - 2178)
<b>Burrow surface area (cm<sup>2</sup>)</b>	<b>68.6</b> (35.2 - 102)	<b>34.5</b> (25.7 - 43.3)	<b>71.0</b> (29.5 - 113)
<b>Total burrow SA (cm<sup>2</sup> m<sup>-2</sup>)</b>	<b>14180</b> (5027 - 27564)	<b>4968</b> (3446 - 6668)	<b>2180</b> (168 - 6588)
<b>% increase SA (m<sup>-2</sup>)</b>	<b>142</b> (50.3 - 276)	<b>49.7</b> (34.4 - 66.6)	<b>21.8</b> (16.8 - 65.8)
<b>Bg (g dw)</b>	<b>20.2</b> (6.75 - 33.6)	<b>11.0</b> (6.9 - 15.0)	<b>48.8</b> (17.5 - 80.1)
<b>Cn (ind. m<sup>-2</sup>)</b>	<b>141</b> (61.6 - 221)	<b>109</b> (29.0 - 190)	<b>48.0</b> (18.2 - 77.8)
<b>Bp (days)</b>	<b>25.7</b> (21.5 - 31.8)	<b>10.8</b> (8.57 - 14.8)	<b>1.39</b> (1.24 - 1.58)
<b>Median burrow depth (cm)</b>	<b>4.7</b>	<b>3.6</b>	<b>3.9</b>
<b>Available sediment (kg dw m<sup>-2</sup>)</b>	<b>42.3</b>	<b>41.4</b>	<b>57.7</b>
<b>SR (kg m<sup>-2</sup> SLM<sup>-1</sup>)</b>	<b>3.1</b> (0.37 - 9.7)	<b>3.1</b> (0.38 - 9.3)	<b>47.2</b> (5.7 - 141)
<b>% SR (SLM<sup>-1</sup>)</b>	<b>7.4</b> (0.87 - 22.9)	<b>7.5</b> (0.92 - 22.5)	<b>81.8</b> (9.8 - 244)
<b>Se (kg crab<sup>-1</sup> SLM<sup>-1</sup>)</b>	-	-	<b>0.56</b> (0.45 - 0.67)
<b>BM (kg m<sup>-2</sup> SLM<sup>-1</sup>)</b>	-	-	<b>26.9</b> (8.3 - 52.0)
<b>TSR (kg m<sup>-2</sup> SLM<sup>-1</sup>)</b>	-	-	<b>74.2</b> (14.0 - 192)
<b>% TSR (SLM<sup>-1</sup>)</b>	-	-	<b>129</b> (24.2 - 333)

*Bg*, burrow dry weight; *Cn*, crab density; *Bp*, burrow permanency; *SR*, sediment reworking rate; *SLM*, summer lunar month (28 days); *Se*, sediment excavated as maintenance pellets; *BM*, sediment excavated during burrow maintenance; *TSR* total sediment reworking rate including *BM* and *SR* values.

### 2.3.6 Differences in burrow surface area and sediment reworking with grain size

Total burrow wall surface area was estimated to average  $14180 \text{ cm}^2 \text{ m}^{-2}$  in mud, almost 3 times greater than the  $4968 \text{ cm}^2 \text{ m}^{-2}$  estimated for the muddy sand site and 6.5 times greater than the burrow surface area of  $2180 \text{ cm}^2 \text{ m}^{-2}$  in fine sand (Table 2.3). This equates to a mean increase in the sediment-water interface of 142 % (mud), 50 % (muddy sand) and 22 % (sand) through the presence of *Austrohelice* burrows. Total burrow volume displayed similar trends to that of increased sediment-water interface; total burrow volume was greatest in mud ( $4635 \text{ cm}^3 \text{ m}^{-2}$ ), which was 3.8 times greater than the  $1373 \text{ cm}^3 \text{ m}^{-2}$  at the intermediate site and 4.7 times greater than the  $997 \text{ cm}^3 \text{ m}^{-2}$  in sand (Table 2.3).

Rates of sediment reworking were very similar in both mud and muddy sand locations, (about  $3.1 \text{ kg dw sediment m}^{-2} \text{ SLM}^{-1}$ ), whilst reworking in sand was much greater ( $47.2 \text{ kg dw sediment m}^{-2} \text{ SLM}^{-1}$ ) (Table 2.3). These estimates were converted to monthly percentages (using the median burrow depth to calculate the volume of sediment available to crabs) to enable comparisons across locations and times. On average 7.4 % of the sediment volume available to *Austrohelice* was reworked monthly in summer at both the mud and muddy sand locations. Sand proved much more dynamic with almost 82 % of the sediment volume being reworked per month. The greatest variance in burrow reworking estimates was evident at the sandy station (95% CI = 9.8 % - 244 %). The lower estimate for sand is still greater than the mean sediment reworking rate of both other sediment types, indicating functionally important differences in rates of sediment mixing.

Burrow maintenance also contributed to sediment reworking rates in sand, the average amount of sediment excavated for maintenance purposes from adult burrows were incorporated into total sediment reworking rates (*TSR*) (Table 2.3). It was assumed that crabs showed similar circa-tidal rhythms, excavating equivalent amounts of sediment irrespective of the time of low tide. Including these extra sediment expulsions increased the upper estimate of sediment reworking to 333 %, the mean to 129 % and the lower estimate to 24 %, generating a total mean sediment reworking rate over 17 times greater than that of muddy sand or mud per lunar month with an average of  $74.2 \text{ kg m}^{-2} \text{ SLM}^{-1}$ . Based on this calculation the entire sedimentary area available to *Austrohelice* (to a median depth of 38.5 mm in this instance) would be turned over 1.3 times each month at site PE2.

## **2.4 Discussion**

This study demonstrates that the sediment environment in which *Austrohelice* resides can alter its primary mode of bioturbation from a burrow builder in cohesive sediments to that of a bulldozer in sandier sediments. These differences in organism behaviour and activity affect functionality across sediment types. This suggests a need to understand both organism natural history and the environmental context of an organism if we are to develop adequate surrogates for ecosystem functioning using biological traits analysis (Suding et al. 2008). Recognition of the importance of natural history and environmental context will also help us comprehend the myriad of ecosystem services derived from seafloor ecosystems and better predict how they may respond to habitat change.

#### 2.4.1 Extension of the sediment-water interface

When all highly correlated mean burrow metrics (length, depth, volume and surface area) were assessed across the sediment gradient, no obvious differences associated with sediment type were apparent due to the variation in burrow forms and sizes within each station (Figures 2.3 and 2.5). However, when surface area was scaled with burrow density (giving the total burrow surface area), trends across the sediment gradient were evident; with greatest surface area in mud and lowest in the coarsest sand (Figure 2.3 c). Indeed, when considering the three locations where sediment reworking was estimated, the muddiest station displayed a much greater total burrow surface area than either of the other two stations despite mean burrow surface area and volume being greater in sand (Table 2.3). Muddy sand showed a reduced mean burrow surface area and volume compared to the other two stations, likely caused by a reduction in mean burrow length and fewer funnel shaped burrow apertures. Burrow lumen were observed to be larger and more symmetrical in sand than either of the other two locations. This potentially acts as a stabilising mechanism for structures in less cohesive sediments.

Morrissey et al. (1999) found *Austrohelice* burrows were of a simpler morphology in sand with burrows up to a factor of 14.8 times larger in mud. I found that although the number of burrow forms present did not show predictable relationships with sediment type across the entire sediment gradient, the greatest numbers of burrow forms were cast in the muddiest sediments and fewest in the coarsest sediments but these were not always the simplest forms. However, some loss of complexity was indicated by the lack of burrows with multiple surface

openings in coarser sediments, potentially elevating the observed burrow to crab ratio found in muddier habitats (Figure 2.4 and Figure 2.5).

#### **2.4.2 Sediment reworking**

Cohesive sediments were shown to be much more static than non-cohesive sediments. Rates of reworking were very similar in mud and muddy sand as, despite a significantly larger number of adult crabs being present in the mud, burrow permanency was longer (Table 2.3). Although burrows had greatest median depth in mud, the density of sediment was lower than in either of the other two habitats, leading to differences in the available dry weight of sediment for crabs to exhume. This equated to over an order of magnitude difference in the percentage volume of sediment reworked by *Austrohelice* between sand and muddier sediments. The main driver of this difference (in conjunction with organism density) is that of burrow permanency. A 20 % increase in silt-clay content meant burrow permanency in muddy sand was almost 8.5 times that of sand alone. A further 35 % increase in silt-clay doubled the mean burrow life from that of muddy sand, making burrows in the muddy location over 18 times more stable than that of fine, clean sand. My assumption, that for every burrow that collapses a new one is formed, appeared valid as total burrow density in each location maintained a steady state throughout the observation period. This also indicates that the burrow markers did not have any adverse effects on crab behaviour.

Burrow maintenance rates in sand contributed greatly to the total reworking rates (Table 2.3). In combination with the burrow construction based estimates, this activity meant *Austrohelice* would completely turn over the available sediment

volume 1.3 times each summer lunar month. The excavated sediment did not differ greatly in grain size or TOM from that of the sediment surface. This again highlights that sediment mixing is frequent. Although burrow maintenance data were not collected at the mud and muddy sand locations, it is assumed that bedload transport would be greatly reduced in more cohesive, lower energy environments and hence the frequency of burrow maintenance would be less. Therefore, whilst the inclusion of burrow maintenance rates in mud and muddy sand may have increased total sediment reworking rates fractionally (had these measurements been possible), the relative differences between the three locations would likely remain the same.

#### **2.4.3 Primary effects of *Austrohelice* in cohesive sediments**

In mud and muddy sand *Austrohelice* primarily altered its environment through the extension of the sediment-water interface. This increases the depth of oxygen penetration, enhancing biogeochemical exchange and creates new and varied habitats for microbial communities altering the metabolic breakdown of organic matter (Kristensen and Blackburn 1987, Glud 2008). Passive burrow irrigation through tidal flushing may further speed up reaction rates irrespective of burrow occupancy, enhancing solute transport across the sediment water interface (Kristensen 1984). This contribution to nutrient exchange is likely to relate to burrow morphology, permanency and orientation in to the prevailing flow (Ray and Aller 1985, Huettel and Gust 1992, Libelo et al. 1994, Ridd 1996). Extension of the sediment-water interface is the typical mechanism by which burrow builders influence their environment. Previous studies on decapod crustaceans have documented increases in sediment-water interface ranging from 20 – 310 %

(Katz 1980, Dworschak and Pervesler 1988, Griffis and Chavez 1988, Witbaard and Duineveld 1989, Coelho et al. 2000). My estimates for all three locations fall within this range. However, this study has proven the importance of including the dynamic element of sediment reworking in discussions of such estimates. Due to the short lived nature of burrows in sand, the increases in burrow surface area alone may be misleading.

#### **2.4.5 Primary effects of *Austrohelice* in non-cohesive sediments**

Regular burrow collapse in sandier sediments meant that although *Austrohelice* continued to create burrows, their impacts through increased burrow surface area were short lived (2 to 3 tides). *Austrohelice* primarily destabilised the sediment surface in sand, repressing the redox potential discontinuity (RDP) and subducting organic matter through frequent burrow collapse; characteristics normally attributed to bulldozing bioturbators (Lohrer et al. 2004, Osinga et al. 1997, Hollertz and Duchene 2001, Widdicombe and Austen 1998). For example, *Echinocardium cordatum* has been demonstrated to affect the top 6 cm of sediment creating continual slumping similar to that of derelict burrows (Lohrer et al. 2005). In all habitats where bioturbation occurs and particularly where turnover is rapid, meiofaunal and macrofaunal communities will be greatly affected by this continual disturbance (Thrush 1988, Botto and Iribarne 1999, Lohrer et al. 2008).

Increased sediment reworking in non-cohesive sediments also suggests a higher turnover of carbon standing stock. Microphytobenthic communities are likely to respond to frequent displacement and burial, as the energetic cost of reorientation at the sediment surface will differentially affect species. Biofilms that are

perpetually disrupted may not bind the sediment matrix adequately, leading to decreased sediment stability and increased bedload transport (Miller et al. 1996). However, the presence of bioturbating macrofauna has previously been shown to increase O<sub>2</sub> uptake and CO<sub>2</sub> production by 30-70 % which may act as a ‘trade off’ for microphytes living in dynamic systems (Kristensen et al. 1992, Hansen and Kristensen 1997).

Sediment reworking can affect the bioavailability of pollutants and contaminants in sediments (Petersen et al. 1998, Menone et al. 2006). Sediment reworking by *Austrohelice* has previously been shown to affect the bioavailability of heavy metals through the influence of their bioturbation activity on acid volatile sulphides and FeS<sub>2</sub> (Morrisey et al. 1999). *Austrohelice* also plays a crucial role in remediation of terrigenous sediment impacts. They can survive deposition events and through mixing and re-oxygenation alter the rates of transport and sequestration of terrigenous material (Gibbs et al. 2001, Norkko et al. 2002, Thrush et al. 2003).

#### **2.4.6 Seasonal elements/temperature related effects: Adjustments to estimations**

Several studies have shown that burrowing crab species including *Austrohelice* display patterns of seasonality in their burrow building (Wolfrath 1992, Sivaguru 2000, McCraith et al. 2003). This manifests as changes in morphology such as burrow length, altered activity and burrow building rates. Spring and summer appear to be the most active seasons for burrowing crabs in relation to sediment mixing, irrespective of sediment location. *Austrohelice* densities do not differ seasonally (Sivaguru 2000), which indicates that any observed changes in activity

rates are likely to be caused by temperature change as inherent sediment properties do not differ greatly between seasons. When considering the calculations in this study, I captured the likely maximal rates of bioturbation activity to highlight the differences across sediment types. If these values were extrapolated to an annual level, it is likely that mean sediment mixing and surface area increase would yield overestimates. Mean annual sea and air temperatures in the locality of this study range from 20.1 ( $\pm 1.7$ ) – 13.6 ( $\pm 1.2$ ) °C and 19.9 ( $\pm 2.0$ ) – 10.9 ( $\pm 2.1$ ) °C respectively (Giles 2002, NIWA CliFlo database 2009), therefore seasonal reworking patterns may be more detectable in the colder southern regions of New Zealand where seasonal temperature variation can be greater.

Circatidal and circadian rhythms can alter the behavioural responses of some crustaceans. Unlike many burrowing crabs, *Austrohelice* behaviour is not affected by the day/night cycle, indeed *Austrohelice*'s peak activity period is at high tide (Williams et al. 1985). Therefore my maintenance rate assumption that behaviour is similar on both day and a night tides was justified. This also indicates that seasonal responses to changes in photoperiod are unlikely to alter behaviour of this organism dramatically. As burrow permanency was monitored for two months, differences in activity rates through alterations of tidal amplitude were captured.

## **2.5 Conclusions**

To assess broad-scale patterns in ecosystem functioning, species have previously been grouped according to their functional or biotic traits to reduce the variability within biological data (Pearson and references therein 2001, Bremner et al. 2006,

McGill et al. 2006). To model relationships between such functional groups and sediment dynamics, Swift (1993) proposed organisms should be rated according to their 'bioturbation potential'. Such models, including those with increased nuances such as organism biomass (Gilbert et al 2007, Sanders et al. 2007) do not yet acknowledge that the functionality of individuals within a species may differ according to its sedimentary context. These alterations are not only about potential shifts in the *rates* of particular processes, but may even include, as illustrated by *Austrohelice*, fundamental shifts in the *types* of processes occurring. Few studies have touched upon how environmental variability directly affects organism behaviour to the degree that its functionality within an environment is altered (Biles et al. 2003, Escapa 2008, Sassa and Watabe 2008). This current study demonstrates that the behaviour and performance of a dominant organism may determine the degree of ecosystem functioning under different environmental conditions. This is likely to be expressed by larger bodied 'bioengineers' or those present in high densities across a wide habitat spectrum. Understanding the functional plasticity of key bioturbating species is vital if we are to ensure that predictive models elicit an accurate organism response under different environmental scenarios.

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## Chapter 3

# Context-specific bioturbation mediates changes to ecosystem functioning

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### **3.1 Introduction**

The processes that drive ecosystem functioning often involve complex relationships between organisms and their environment. In marine ecosystems, biological perturbation (bioturbation) of sediments is widely acknowledged to affect ecosystem processes by altering fluxes of both energy and matter across strong geochemical gradients. Processes, such as organic matter remineralisation, primary production, sediment transport and nutrient cycling are often measured as proxies for ecosystem health and functioning as they act as indicators of environmental change (Widdicombe and Austen 1998, Peterson and Heck 2001, Lohrer et al. 2004, Webb and Eyre 2004, Thrush et al. 2006). Development of assessment tools for ecosystem-based monitoring and management is becoming increasingly important as global anthropogenic pressures on natural environments continue to grow and management focus shifts to address issues of loss of function and concomitant ecosystem services. Therefore understanding organism-sediment interactions and consequently the underpinning mechanisms by which changes across environmental gradients are mediated, is essential for better

prediction and interpretation of ecosystem functioning (Williamson et al. 1999, Suding et al. 2008).

Soft-sediment environments are some of the most widespread habitats on the planet incorporating most of the world's coastal zones and estuaries (Snelgrove 1999). By physically reworking the sediment they live in, bioturbators increase the energy flow across the sediment-water interface, subducting organic and labile material whilst introducing oxygen to greater depths than would otherwise be the case (Aller and Yingst 1978, Kristensen et al. 1985, Hollertz and Duchêne 2001, Botto and Iribarne 2000). In shallow water ecosystems, pelagic primary production is reliant on benthic processes that recycle nutrients back to the overlying water column (Sündback et al. 2003, Gibbs et al. 2002). Many of these systems have sufficient light penetration to support benthic primary production by microphytobenthos, tightly coupling photosynthesis with the flux of inorganic nutrients to the water column (Sündback et al. 1991, 2000). Bioturbators can positively affect microphytobenthic populations by enhancing mineralisation rates and increasing availability of ammoniacal nitrogen, or negatively affect production through grazing and subduction (Lohrer et al. 2005, Tang and Kristensen 2007). Therefore, the interactions between benthic primary producers, bioturbation and the sediment characteristics should be accounted for to correctly interpret estuarine and coastal ecosystem processes in sedimentary systems.

Even the most ubiquitous macrobenthic species show some habitat preferences contributing to changes in densities across environmental gradients (Ysebaert and Herman 2002, Thrush et al. 2003a). The degree to which increased proximity to one another influences ecosystem processes is, in part, governed by an organism's

biological or functional traits (trophic guild, mobility and lifestyle mode). For example, burrow-building species have been shown to alter the diffusion dynamics of porewater solutes through their proximity to one another (Aller and Aller 1998, Gilbert et al. 2003), whilst differences in grazing intensity at the sediment surface can alter the direction and degree of sediment-water solute exchange through the impact on microphytobenthic populations (Marinelli 1992). Increased organism density and therefore increased availability of metabolic products such as  $\text{NH}_4^+$  can also stimulate microbial metabolism, affecting nitrification/denitrification rates (Henriksen et al. 1983, Kristensen 1985). Hence, changes in organism density can exert strong control over ecosystem processes such as nutrient cycling (Widdicombe and Austen 1998, Lohrer et al. 2004, D'Andrea and DeWitt 2009, Sandwell et al. 2009).

Often, species are categorised to a functional group by their biological traits to infer wide scale patterns in ecosystem functioning (Norling et al. 2007, Suding et al. 2008, Bremner et al. 2006). By definition, some functional traits indicate a shift in organism behaviour such as the facultative switch between feeding modes in some benthic organisms under differing environmental regimes (Riisgård and Kamermans 2001, Marinelli and Williams 2003). However few studies to date have considered that single species can perform differing ecological functions dependent on their sediment environments, a phenomenon likely to be of particular importance in systems where single species dominate the biomass (Sassa and Watabe 2008). Rarer still are those studies which combine interactions between habitat, organism behaviour and density to infer changes to ecosystem processes (McCraith 2003, Escapa 2008). Here I consider not only context-

specific functioning of organisms but also their density dependent effects, to create more robust models of organism-sediment relationships and their associated biogeochemical processes.

Burrowing crabs play important roles in ecosystem functioning (Lee 1998, Kostka et al. 2002, McCraith et al. 2003, Wang et al. 2010). They are often found in high densities and can significantly alter the sediment-water interface through burrow construction modifying bedload transport dynamics, affecting sediment penetrability, erodibility and increasing sediment mixing (Botto and Iribarne 2000, McCraith et al. 2003, Gutiérrez et al. 2006, Escapa et al. 2007, Needham et al. 2010, Wang et al. 2010). Here I demonstrate how the mud crab *Austrohelice crassa* (herein *Austrohelice*), can have context-specific effects on biogeochemical processes through sediment induced changes to its primary bioturbational role. Shifts in functionality are mediated through differences in burrow permanency and consequentially, sediment reworking rates between cohesive and non-cohesive sediments (Needham et al. 2010). *In situ* benthic chambers were used to measure the rate of solute flux ( $O_2$ ,  $NH_4^+$ ,  $PO_4^{3-}$ ,  $NO_3^-$ ,  $NO_2^-$ ) in both a sand (S) and muddy-sand (MS), in relation to *Austrohelice* density. Flux incubations were conducted in both daylight and at night to establish the relationships between microphytobenthic photosynthetic  $O_2$  production, microphytobenthic nutrient uptake and crab bioturbation in the two sediment types. I hypothesised that the observed differences in sediment reworking rates would be detectable in the flux of solutes across the sediment-water interface due to the differing mechanisms facilitating their utilisation or release.

Increasing crab density was predicted to reduce and potentially alter the microphytobenthic community through increased grazing pressure, in-turn affecting sediment oxygen concentrations, gross primary production and nutrient release irrespective of sediment type. However, changes in sediment reworking rates and hence *Austrohelice*'s primary bioturbational role between sand and muddy-sand sediments, were predicted to create significant between site differences in the magnitude of solute fluxes at equivalent crab densities. Due to the transient nature of burrows in sand (lasting ~1.4 d, Needham et al. 2010) collapse and subduction of microphytobenthos was anticipated to reduce productivity compared to the more physically stable muddy-sand burrows (lasting ~11 d, Needham et al. 2010). Regular destabilisation of the sediment matrix through burrow collapse may also alter diagenic pathways and processes in sandy sediments, enhancing remineralisation rates and porewater flux in association with increasing *Austrohelice* density. As burrow longevity is greater in muddy-sand, these structures likely create diverse, well established microbial communities within the burrow walls. Such communities exert strong chemical control over biogeochemical processes altering the pathways and magnitude of solute fluxes. In the case of nitrogen recycling, the close coupling of nitrification/denitrification pathways in burrow walls has been well documented (Kristensen 1985 and refs therein, Gilbert et al. 1998, Webb and Eyre 2004). Having said this, uncoupled nitrogen dynamics through burrowing crab activity has also previously been seen (Botto et al. 2005). Potential rates of nitrification/denitrification and nitrate reduction generally reflect the state of the microbial population. I therefore predicted that stronger relationships between these processes would occur in muddy-sand sediments compared to those in sand, and that the increased

sediment-water interface associated with greater crab (and hence burrow) density, would further amplify reaction rates.

## **3.2 Methodology**

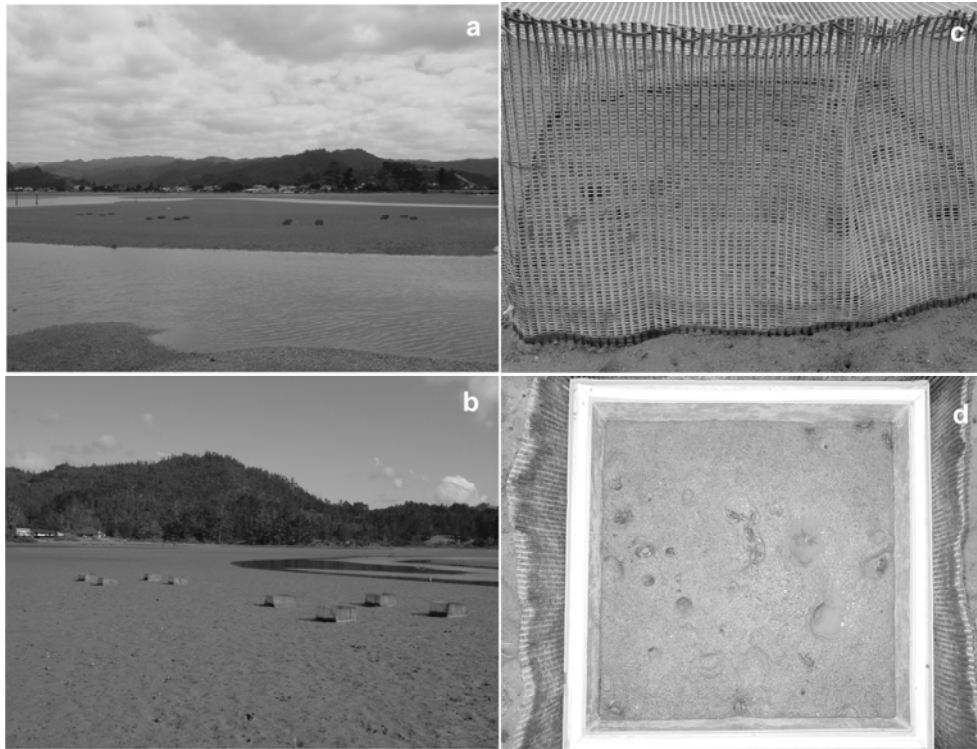
### **3.2.1 Study site and experimental treatments**

This study was conducted in Tairua estuary (36° 59' 57.56" S, 175° 51' 04.09" E), Coromandel Peninsula, New Zealand, in the mid-intertidal zone during summer 2008. The two sediment types, S (sand) and MS (muddy-sand) were chosen as differences in crab behaviour affecting sediment stability had previously been recorded in these sites (Needham et al. 2010). Site S was categorised as a fine to medium sand and site MS as a fine sand with high silt-clay content (see results). In each sediment type a randomised complete block design was employed, whereby 16 cages (60\*60\*40 cm, L\*W\*H) were installed in blocks of four spanning a total distance of ~ 45 m parallel to the incoming tide (Figure 3.1 a and b). Crab density treatments of 0, 15, 25 and 35 ind. 0.36 m<sup>-2</sup> cage, equating to densities of 0, 42, 70, 98 ind. m<sup>-2</sup>, were created with one replicate in each of the four blocks (n = 4). I used only mature crabs with an approximate carapace width (CW) of 10 mm, which were collected from the same location within Tairua estuary. Our high treatment density was less than the maximum observed in natural *Austrohelice* populations of this estuary; up to 252 ind. m<sup>-2</sup> in muddy-sand and up to 190 ind. m<sup>-2</sup> in sand have previously been recorded (Needham et al. 2010). However, these estimates included a high proportion (~ 50%) of juveniles (CW < 5 mm) that did not create large, deep burrows and therefore had limited bioturbation potential. Compared to the peak densities of larger adult crabs (> 8

mm CW; S = 71, MS = 86 ind. m<sup>-2</sup>; Needham et al. 2010, H. Needham *pers obs.*), our maximum treatment density was slightly higher than the maximum treatment density, to buffer against potential crab loss (see results).

To establish each cage, sediment was excavated to 20 cm depth (i.e. well below the average burrow depth, Needham et al. 2010). The excavated sediment was sieved on a 2 mm mesh screen to remove all large macrofauna. Each cage (constructed from a single piece of 3\*6 mm nylon mesh (Taylor Built Ltd) and woven at the seams), was set into an excavated hole, leaving the top 20 cm of the cage walls visible above the ambient sediment surface. Sieved sediment was placed back inside each cage and levelled before weaving on an inset lid. As coarser sediments are more adapted to periodic resuspension and disturbance, site S was left for 2 weeks whilst site MS was left for 3 weeks, to re-establish chemical gradients, microphytobenthic and faunal communities prior to crab introduction (Davis and Lee 1983).

Individual *Austrohelice* were randomly assigned to cages according to the treatment densities and allowed 18 d to establish themselves at site S and 22 d at MS prior to flux measurements. This allowed the crabs to rework the sediment into a more natural state as sediment at site MS showed greater burrow density due to increased longevity (Needham et al. 2010). Cages were monitored regularly for signs of sediment alteration, physical damage, crab mortality and burrow number (Figure 3.1 c). No alterations to the sediment surrounding the cages were observed in either sediment type and burrow number appeared proportional to each treatment in all but one instance (see results).



**Figure 3.1.** The randomised complete block design of 16 cages at site M, Paku Bay (a), and 8 of the 16 cages at closer range, site S, Pepe Inlet (b). Burrowing behaviour was not altered by the cage enclosures (c) and benthic flux chamber bases were placed within cages 12 h prior to experiments (d).

### 3.2.2 Flux incubations

Benthic chambers at S and MS were deployed on consecutive spring tides (Figure 3.1 d). At high tides, the depth of water covering the chambers was approximately 1.25 m. Incubations were paired (daylight and night) to account for interactions with microphytobenthos. All water from within the chambers drained with the tide between the two incubation periods. Chamber bases (0.25 m<sup>2</sup>) were placed within the 0.36 m<sup>2</sup> cages 12 h prior to running incubations. Perspex domes were fitted on an incoming tide, entrapping on average 36 L of water. A recirculating water pump intermittently mixed the chamber water to stop stratification without resuspending sediments. Midge™ oxygen loggers (Eureka

Environmental engineering, Texas) were placed in a cradle on a wall of each chamber away from sampling ports to measure water oxygen concentration at 5 min intervals. As biological reactions and solute exchanges can be driven by alteration in temperature and light levels, three Hobo loggers and eight tidbit loggers (Onset computing corporation) logging every 5 min, were randomly assigned to chambers across treatments. Additional temperature and light sensors were placed on the sediment surface at an unmanipulated ambient water sampling station located between the chamber blocks.

Water samples were collected through 2 m of 3.2 mm dia. nylon tube capped with a luer lock valve, to minimise sediment disturbance. A one-way valve, placed on the opposing wall to the sampling port allowed external water to be drawn into the chamber to compensate for sample water removal. Ambient water samples, drawn from the ambient water station close to the chambers, were used to correct for nutrients drawn back in to the chamber. Once the chambers were sealed, one clear and one dark 1 L bottle were filled with ambient water and secured at the sediment surface to enable water column processes at the experimental site to be factored out of flux calculations.

Sampling began once all chambers were sealed and fully submerged. After discarding the first 20 ml to clear the tubing, 50 ml water samples were collected via syringe every 45 min until the tide receded 4 to 5 h later. After each sampling period, water samples were pressure filtered through a swinnex housed 24 mm Whatman GF/C filter into an acid washed container. Samples were kept on ice in the dark prior to freezing. Solute fluxes were determined through linear regression of concentrations as a function of time, chamber volume and sediment

surface area. These rates were corrected for the addition of replacement water drawn into each chamber at the time of sampling.

After diurnal incubations were completed, two burrows within each chamber were randomly selected and cast using a catalysed polyester resin (Norski products) to check burrow morphology had not been affected by caging. Sediment reworking rates were also calculated from these burrow volumes. A 13 cm dia., 15 cm deep macrofaunal core ( $0.01 \text{ m}^2$ ) was also taken from each chamber and sieved over a  $500 \mu\text{m}$  mesh to determine the biomass and identity of any other bioturbators present. Three 28 mm dia., 1 cm deep sediment cores were collected and pooled from each chamber and the ambient station (where *Austrohelice* were also present) for granulometry, sediment pigment and total organic matter content (TOM). All samples were frozen in the dark immediately post-collection. The sediment from within each chamber as well as the perimeter material (i.e. that still enclosed in the cage but not included within the chamber) was then excavated and sieved separately on a 2 mm mesh to collect the crabs.

### **3.2.3 Laboratory analyses**

Inorganic nutrient species ( $\text{NH}_4^+$ ,  $\text{NO}_3^-$ ,  $\text{NO}_2^-$  and  $\text{PO}_4^{3-}$ ) were analysed colorimetrically on a Lachat CQ8000 Flow Injection auto analyser (DKSH Ltd) using standard Lachat QuikChem<sup>®</sup> methods. TOM was determined through loss on ignition from dried sediments ( $110 \text{ }^\circ\text{C}$  for 24 h), after combustion for 5.5 h at  $550 \text{ }^\circ\text{C}$  (Dean 1974). Sediment grain size fractions were determined using a Malvern mastersizer-S (300 FR lense, range  $0.05 - 2000 \mu\text{m}$ ) after digestion in 10% hydrogen peroxide (Day 1965). Pigments were extracted from freeze-dried sediment and steeped in 90% acetone for 24 h before centrifugation. Chlorophyll

*a* (chl *a*) and phaeophytin (phaeo) content was determined fluorometrically, before and after acidification on a Turner 10-AU fluorometer (Arar and Collins 1997). Macrofauna were stained using rose bengal, grouped by major taxa, counted and blotted wet weighed (BWW). All crabs were sized (CW) using digital callipers and counted. Burrow casts were classified and analysed morphometrically as described in Needham et al. (2010).

### **3.2.4 Data analyses**

Due to the variability in the number of *Austrohelice* collected from the chambers post-incubation (see results), analysis was conducted using multiple linear regression with backwards selection to determine the effects of crab flux chamber density and sediment properties on dissolved solute fluxes. Light intensity, temperature and macrofauna BWW (excluding crabs), were also included as predictor variables in initial (full) models. Multicollinearity among predictor variables was avoided by examining the variance inflation factors and condition indices. Variables were eliminated using a backwards selection procedure (SAS 9.1.3) unless significant at  $\alpha = 0.10$ . The significance of final models was evaluated at  $\alpha = 0.05$ , and goodness of fit was assessed using adjusted  $r^2$  and Akaike's Information Criterion (AIC) values. Assumptions of homogeneity of variance and normality were evaluated by plotting residuals vs predicted values, with normal probability plots and Shapiro Wilk's tests on residuals. Homogeneity of slopes tests were conducted to elucidate if density dependent effects were similar between the two sediment types. If no interaction occurred, analysis of co-variance (ANCOVA) was used to determine the main effects (site/density). Any significant co-variables highlighted in the multiple-linear regressions were

omitted from this analysis and corrected partial residual values were used where necessary. Sediment reworking values were derived using formulas and burrow permanency data from Needham et al. (2010). Mann-Whitney non-parametric U tests were conducted to look at differences in reworking, burrow surface area and burrow:crab ratios between sediment types, as the data were not normally distributed.

### **3.3 Results**

#### **3.3.1 Sediment properties and crab/sediment relationships**

Sediments properties in the cages were not substantially different from the surrounding ambient sediment at either site indicating there were no long-term effects of the establishment procedure (Table 3.1). Between site differences in median grain size and silt-clay content were as expected, with many of the other sedimentary variables similar across sites (see supplementary material Table A.1 for details). Correlations between *Austrohelice* density and surface sediment properties showed similar trends at both sites, but the strength of correlations varied (Table 3.2). At both sites crab density was negatively correlated with sediment pigments (chl *a*  $p = 0.001 - 0.02$ , phaeo  $p = 0.03 - 0.02$ ), TOM (not significantly in S  $p = 0.11$ , marginally at MS  $p = 0.049$ ), and silt-clay content (site S,  $p = 0.001$ ) though not significantly in MS ( $p = 0.14$ ) whereas median grain size was positively correlated with crab density at both sites ( $p = 0.03 - 0.04$ ).

Burrow structures were not affected by the cage enclosures. All burrow casts were the same morphological forms as previously described from these sites, most commonly ‘i’ an often short, oblique angled straight burrow (Site S = 67%, MS =

39 %) and 'j' an oblique angled burrow with a terminal hook or chamber (site S = 17%, MS = 30%). As seen previously, burrow morphotypes showed no correlation with either crab density or sediment type (Needham et al. 2010). Data across treatments were pooled at each site (n = 24 casts), to assess if burrow surface-area and sediment reworking rates altered as a function of sediment type. Burrows had a greater median depth at site S (6.1 cm) than MS (5.0 cm), as well as greater mean volume (S =  $48 \pm 21 \text{ cm}^3$  ( $\pm \text{SD}$ ), MS =  $25 \pm 10 \text{ cm}^3$ ) and surface area ( $91 \pm 35 \text{ cm}^2$  and  $58 \pm 18 \text{ cm}^2$  respectively). At site S, on average  $57 \pm 30 \text{ kg m}^{-2}$  ( $\pm \text{SD}$ ) each summer lunar month (SLM), was reworked opposed to only  $3.6 \pm 1.7 \text{ kg m}^{-2} \text{ SLM}^{-1}$  at site MS. This equates to a 16 fold increase in sediment reworking at site S. Mann-Whitney U tests showed significant differences in burrow surface area ( $p = 0.009$ ) and sediment reworking rates ( $p < 0.001$ ) between the two sediment types.

### **3.3.2 Organism density and biomass**

Evidence of crab mortality or cage breach was not obvious from the sediment surface. However, from the final number of *Austrohelice* recovered from each cage, losses (and occasional gains) occurred in both sediment types and across density treatments (Table 3.3). On average 83% of the total number of crabs recovered from a given cage were found inside the incubation chamber, a value comparable to the proportion of the cage area occupied by the chamber (70%). This indicates that crabs did not avoid or aggregate at the perimeter of the cage and therefore the presence of the cage did not greatly influence burrow position. Data from one flux chamber in MS were omitted from all analyses due to the presence of three large thalassinidean shrimp. With no obvious sign of disruption

to the cage or lid observed, a breach of the mesh cage walls below the sediment surface most likely occurred. Correlations between burrow and crab density were only seen at site MS (Pearson's correlation  $p = 0.019$ , at site S  $p = 0.15$ ). Overall burrow:crab ratios were lower in site S than MS (Mann-Whitney U test,  $p = 0.02$ ) indicating that burrow permanency (and therefore the number of refuges available) was greater at MS, a phenomenon previously recorded in the natural environment (Needham et al. 2010). This suggests that crab behaviour was not greatly compromised by the presence of our cages. Both biomass (BWW) and abundance of other macrofauna within the caged sediments were dominated by small polychaetes, which were able to migrate through the mesh cage.

**Table 3.1.** Mean (SD) sediment properties of caged and ambient sediments at each site.

<b>Property</b>	<b>Ambient S</b>	<b>Caged S</b>	<b>Ambient MS</b>	<b>Caged MS</b>
<b>med grain size (<math>\mu\text{m}</math>)</b>	179 (8)	170 (14)	114 (3)	131 (14)
<b>silt-clay (%)</b>	11.2 (3.2)	14.3 (2.6)	36.8 (2.4)	37.8 (9.7)
<b>TOM (%)</b>	3.65 (0.21)	4.12 (0.60)	4.29 (0.30)	3.69 (1.26)
<b>Porosity</b>	0.51 (0.03)	0.58 (0.03)	0.57 (0.02)	0.59 (0.09)
<b>chl <i>a</i> (<math>\mu\text{g g}^{-1}</math>)</b>	11.9 (2.9)	9.28 (2.13)	8.46 (2.71)	8.16 (3.34)
<b>Phaeo (<math>\mu\text{g g}^{-1}</math>)</b>	19.1 (4.4)	21.8 (5.3)	15.7 (4.4)	10.6 (6.3)

Ambient: sediment from the surrounding area with natural *Austrohelice* populations; Caged: mean of all cages irrespective of crab density; TOM: total organic matter; Chl *a*: dry weight sediment chlorophyll *a*; phaeo: dry weight sediment phaeophytin.

**Table 3.2.** Correlation (Pearson's coefficient) between *Austrohelice* density and surface sediment properties. Significance values \*  $p < 0.05$ , \*\*  $p < 0.01$ , \*\*\*  $p < 0.001$ . Above diagonal indicates relationships at site S and below diagonal at site MS.

	<b>Crab density (m<sup>-2</sup>)</b>	<b>Chl <i>a</i> (µg g<sup>-1</sup> dw)</b>	<b>Phaeo (µg g<sup>-1</sup> dw)</b>	<b>Porosity</b>	<b>TOM (%)</b>	<b>Silt-clay (%)</b>	<b>Grain size (µm)</b>	<b>BWW (g m<sup>-2</sup>)</b>
<b>Crab density (m<sup>-2</sup>)</b>	-	-0.74***	-0.54*	0.07	-0.41	-0.73***	0.52*	-0.43
<b>Chl <i>a</i> (µg g<sup>-1</sup> dw)</b>	-0.59*	-	0.65**	0.15	0.42	0.60*	-0.48	0.23
<b>Phaeo (µg g<sup>-1</sup> dw)</b>	-0.59*	0.83***	-	0.56*	0.74***	0.37	-0.34	0.39
<b>Porosity</b>	-0.52*	0.93***	0.91***	-	0.63**	0.02	-0.26	0.41
<b>TOM (%)</b>	-0.52*	0.90***	0.94***	0.97***	-	0.44	-0.58	0.65**
<b>Silt-clay (%)</b>	-0.40	0.17	0.13	0.09	-0.06	-	-0.87***	0.48
<b>Grain size (µm)</b>	0.57*	-0.66**	-0.60*	-0.69**	-0.58*	-0.48	-	-0.42
<b>BWW (g m<sup>-2</sup>)</b>	-0.51	-0.06	-0.03	-0.01	0.05	-0.16	0.36	-

TOM: total organic matter; Chl *a*: sediment chlorophyll *a* concentration; phaeo: sediment phaeophytin concentration; BWW: blotted wet weight of macrofauna (excluding *Austrohelice*).

**Table 3.3.** Initial and final *Austrohelice* densities and benthic community composition.

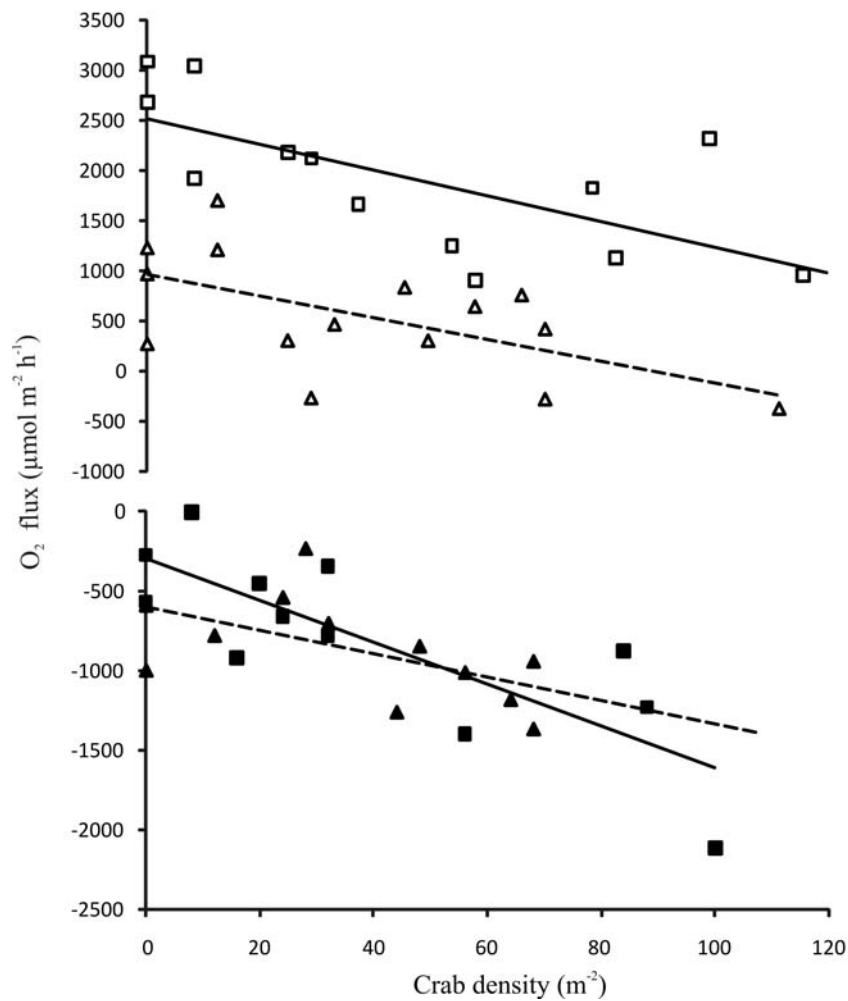
Site	Initial cage density (m <sup>-2</sup> )	Final cage Density (m <sup>-2</sup> )	Crabs in chamber (%)	Burrow:crab ratio	Annelids (m <sup>-2</sup> )	Other fauna (m <sup>-2</sup> )	BWW (g m <sup>-2</sup> )
<b>S</b>	0	6	100	-	1500	200	35.5
	0	6	100	-	700	100	15
	0	0	-	-	100	100	0.3
	0	3	100	-	1900	200	11.6
	42	28	60	2.8	600	100	2.6
	42	6	100	6.0	1500	0	4.8
	42	36	85	1.0	500	0	0.7
	42	31	64	2.0	100	0	0.1
	70	59	62	1.4	500	0	2.5
	70	53	74	1.1	200	0	0.3
	70	59	90	0.8	0	100	1.1
	70	28	90	0.1	700	0	1.6
	98	84	80	0.6	500	0	1.8
	98	70	80	0.9	600	0	1.2
	98	87	94	0.6	500	100	2.9
98	81	97	0.8	900	0	0.9	
<b>MS</b>	0	0	-	-	400	200	2.4
	0	0	-	-	200	100	23.9
	0	8	67	-	600	0	3.7
	0	0	-	-	300	100	5.2
	42	14	60	5.0	500	400	4.5
	42	22	100	2.9	200	100	0.9
	42	36	85	2.0	100	200	4.1
	42	22	75	3.7	0	0	0
	70	42	80	2.6	300	0	0.5
	70	53	84	1.3	100	100	4.5
	70	56	85	1.2	100	0	0.7
	98	45	88	1.7	500	100	6.7
	98	76	100	1.2	300	100	2.5
	98	22	88	2.1	100	0	0.1
	98	70	68	1.4	0	100	77.4

Chamber crabs: the percentage of the final cage density within the incubation chamber; BWW: blotted wet weight.

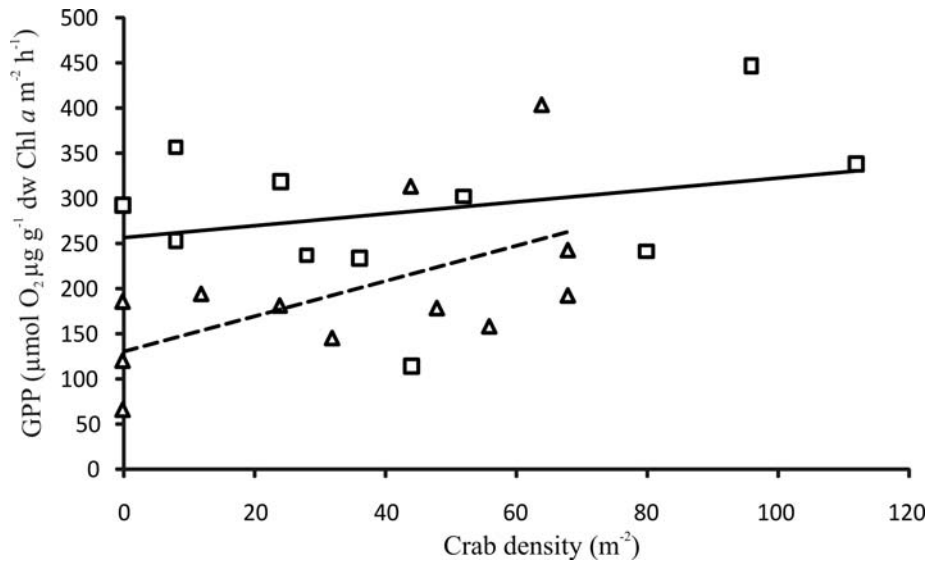
### 3.3.3 O<sub>2</sub> fluxes and primary productivity estimates

Leaks, through improper attachment of the chamber lids at night were identified in three of the chambers at site S (crab densities 0, 56 and 116 m<sup>-2</sup>) and one chamber at site MS (108 crabs m<sup>-2</sup>). These measurements were therefore excluded from all analyses.

At both sites sediments acted as a source of oxygen during daylight and a sink for oxygen at night (Figure 3.2). Multiple linear regression models for both daylight and night incubations in each sediment type were significant and explained 27 – 57% of the variability in O<sub>2</sub> flux, with crab density being the greatest significant predictor at both sites (Table 3.5). During daylight the slope of the relationship between crab density and O<sub>2</sub> efflux did not differ with site (Table 3.5). However a significant between site difference in O<sub>2</sub> flux was observed ( $p = <0.001$ ; Table 3.5), with rates approximately 3.8 times greater in site S than MS (adjusted means, S = 1873 and MS = 496  $\mu\text{mol O}_2 \text{ m}^{-2} \text{ h}^{-1}$ ). A significant crab density\*site interaction at night ( $f = 4.47$ ,  $p = 0.046$ ) indicated that differences in the relationships between crab density and O<sub>2</sub> flux between sediment types occurred. During the night when microphytes were no longer photosynthesising, O<sub>2</sub> influx into both sediment types was observed in all chambers (Figure 3.2). O<sub>2</sub> influx increased with increasing crab density due to greater respiration demands, being most pronounced at site S where TOM was also negatively correlated with O<sub>2</sub> flux (Table 3.4  $p = 0.08$ ). However, partial residual plots without this variable showed 61% of the variation was explained by density alone.



**Figure 3.2.** O<sub>2</sub> flux as a function of *Austrohelice* density (using residual data where appropriate, see Table 3.4) at site S (square) and MS (triangle). Daylight is denoted by open symbols and night by closed symbols. Regression line is solid for site S (day:  $y = -2513 - 53x$ ,  $r^2 = 0.31$ ,  $p = 0.024$ , night:  $y = -254 - 53x$ ,  $r^2 = 0.61$ ,  $p = 0.011$ ) and dotted for site MS (day  $y = -44.4x + 954$ ,  $r^2 = 0.30$ ,  $p = 0.026$ , night  $y = -594 - 44.4x$ ,  $r^2 = 0.27$ ,  $p = 0.041$ ). Positive values (efflux) indicate sediment release and negative values (influx) imply sediment utilisation.



**Figure 3.3.** Gross primary production (GPP, after normalising data for microphytobenthic biomass) as a function of *Austrohelice* density at site S (square) and MS (triangle). Regression line is solid for site S ( $y = 274 + 2.1 * x$ ,  $r^2 = 0.31$ ,  $p = 0.056$ ) and dotted for site MS ( $y = 132 + 7.7 * x$ ,  $r^2 = 0.34$ ,  $p = 0.045$ ).

*Austrohelice* density was negatively correlated with chl *a* concentration in both sediment types (Table 3.2). The slope of the regression was greater in site MS than S (0.25 vs. 0.16) but the difference was not significant (homogeneity of slopes  $p = 0.34$ ). When gross primary production estimates (GPP = daylight O<sub>2</sub> flux - night O<sub>2</sub> flux), were normalised for microphytobenthic biomass (i.e. sediment chl *a* content), crab density was shown to have a positive, marginally significant ( $p = 0.050$ ) effect on GPP (Table 3.5, Figure 3.3). Between site differences were more significant ( $p = 0.01$ ) with adjusted means of 292 and 204  $\mu\text{mol O}_2 \mu\text{g}^{-1} \text{dw chl } a \text{ m}^{-2}, \text{h}^{-1}$  in site S and MS respectively.

### 3.3.4 Nutrient fluxes

*Austrohelice* density was the only significant predictor of  $\text{NH}_4^+$  flux, explaining between 52 and 67 % of the variance in the regression models (Table 3.4). Both sediments showed greater  $\text{NH}_4^+$  fluxes with increasing crab density in daylight and at night. However, homogeneity of slope tests showed significant density\*site interactions, demonstrating that between site differences in the effect of *Austrohelice* density on  $\text{NH}_4^+$  flux were detected (Table 3.5). Between site differences were more significant during daylight ( $f = 17.5$ ,  $p = <0.001$ ), than at night ( $f = 5.5$ ,  $p = 0.028$ ) with fluxes being over 4.3 times greater at site MS than S in daylight at the highest crab densities. In daylight,  $\text{NH}_4^+$  was taken up by both sediments until *Austrohelice* density exceeded approximately 60 crabs  $\text{m}^{-2}$  (Figure 3.4a). After this point (in most instances),  $\text{NH}_4^+$  was released to the water column to a greater (MS) or lesser (S) degree. At night, sediment influx of  $\text{NH}_4^+$  also occurred in crab exclusion plots in both sites, despite the absence of photosynthesis.

$\text{NO}_3^-$  and  $\text{NO}_2^-$  flux did not show any significant diurnal patterns associated with crab density or sediment type (Table 3.4). Other significant models for predicting patterns in  $\text{NO}_2^-$  and  $\text{NO}_3^-$  fluxes were influenced by sediment properties such as TOM, silt-clay content and porosity. At site MS  $\text{NO}_3^-$  was nearly always taken up by sediment (Figure 3.4b), displaying a greater influx in daylight (mean =  $-46.9 \pm 35.4$  SD) than at night ( $-5.02 \pm 6.5$ ), yet fluxes of  $\text{NO}_3^-$  and  $\text{NO}_2^-$  (in combination,  $\text{NO}_x$ ) in both sediments were very low. Similarly, fluxes of  $\text{PO}_4^{3-}$  were low compared to that of  $\text{NH}_4^+$  and  $\text{O}_2$  (Figure 3.4c). Crab density did not significantly affect  $\text{PO}_4^{3-}$  fluxes during the day in either sediment type and variability was not

further explained by any of the measured parameters (Table 3.4). At night,  $\text{PO}_4^{3-}$  ( $\log_{10} \text{PO}_4^{3-}$ ) efflux was positively influenced by crab density in site S only, increasing with sediment oxygen demand.

**Table 3.4.** Significant multiple linear regression models of the effects crab density and sediment properties on dissolved solute fluxes.

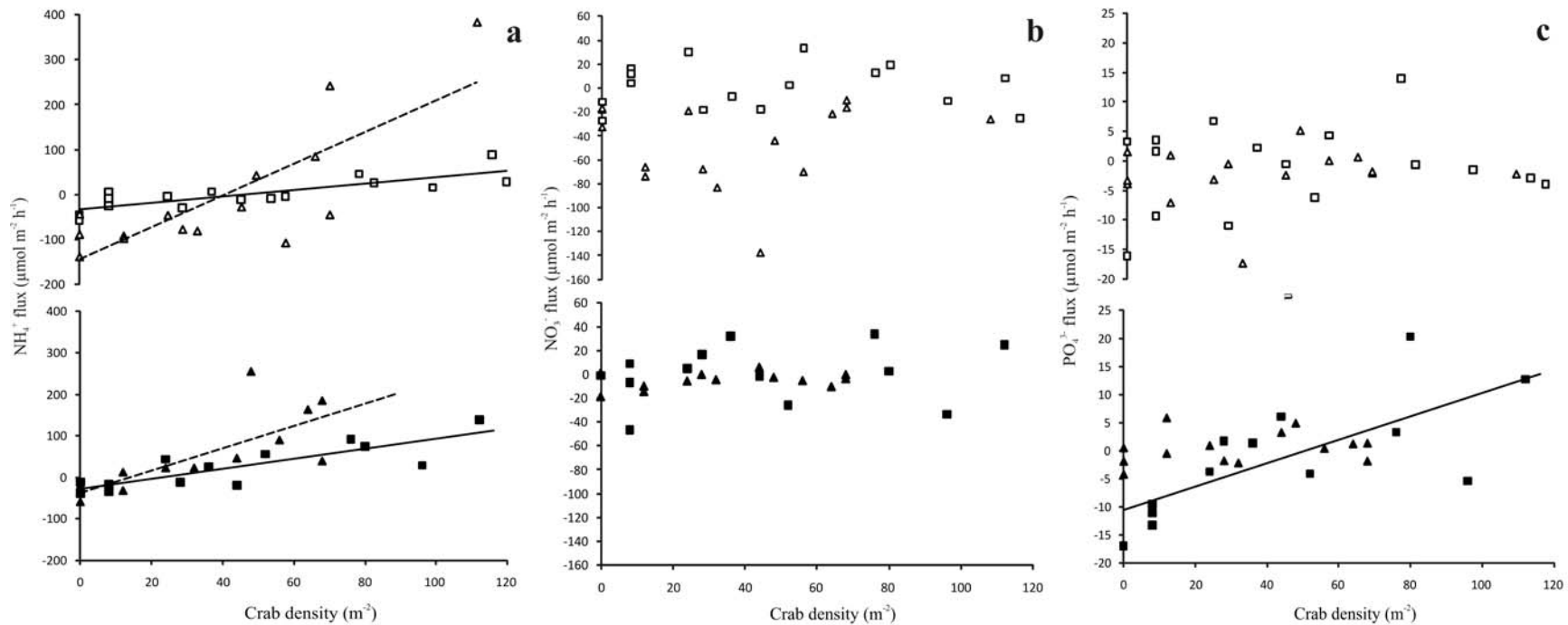
Solute	Site	Day/Night	Predictors	$\beta$ coefficient	p	Overall regression	
						adj $r^2$	p
$\text{O}_2$	S	day	density	-0.61	0.024	0.31	0.024
		night	density	-0.74	0.005	0.57	0.014
			TOM	-0.39	0.076		
$\text{O}_2$	MS	day	density	-0.59	0.026	0.30	0.026
		night	density	-0.04	0.041	0.27	0.041
$\text{NH}_4^+$	S	day	density	0.58	<0.001	0.67	<0.001
		night	density	0.79	<0.001	0.65	<0.001
$\text{NH}_4^+$	MS	day	density	0.73	<0.001	0.60	<0.001
		night	density	0.59	0.003	0.52	0.003
$\log_{10}\text{PO}_4^{3-}$	S	night	density	0.56	0.021	0.34	0.021
$\text{NO}_3^-$	S	night	porosity	-0.76	0.006	0.47	0.006
$\text{NO}_2^-$	S	night	TOM	-0.71	0.004	0.56	0.007
			silt-clay	0.62	0.010		

TOM: total organic matter; density: *Austrohelice* density.

**Table 3.5.** Comparisons of solute fluxes between sites in daylight and at night. Partial residual data were used for O<sub>2</sub> flux at night, Site S. GPP (gross primary production) has been normalised for microphytobenthic biomass ( $\mu\text{mol O}_2 \mu\text{g g}^{-1} \text{dw Chl } a \text{ m}^{-2}, \text{h}^{-1}$ ).

Test	Factor	Df	MS	F	p
<b>Homogeneity of slopes</b>					
O <sub>2</sub> day	site*density	1	33512	0.09	0.757
O <sub>2</sub> night	site*density	1	418538	4.47	<b>0.046</b>
GPP	site*density	1	9919	1.88	0.186
NH <sub>4</sub> <sup>+</sup> day	site*density	1	73948	17.54	<b>&lt;0.001</b>
NH <sub>4</sub> <sup>+</sup> night	site*density	1	12563	5.48	<b>0.028</b>
<b>ANCOVA</b>					
O <sub>2</sub> day	density	1	4633509	14.01	<b>&lt;0.001</b>
	site	1	13572726	41.05	<b>&lt;0.001</b>
GPP	density	1	23857	4.34	<b>0.050</b>
	site	1	43948	8.00	<b>0.010</b>

Density: *Austrohelice crassa* density



**Figure 3.4.** Nutrient fluxes as a function of *Austrohelice* density at site S (square) and MS (triangle). Daylight is denoted by open symbols and night by closed symbols. Regression line is solid for site S and dotted for site MS. Positive values (efflux) indicate sediment release and negative values imply sediment utilisation (influx). (a)  $\text{NH}_4^+$  flux (S day:  $y = -33.1 + 2.93*x$ ,  $r^2 = 0.67$   $p < 0.001$ , night:  $y = -27.62 + 4.84*x$ ,  $r^2 = 0.65$   $p < 0.001$ . MS day:  $y = -144 + 14.6*x$ ,  $r^2 = 0.60$   $p < 0.001$ , night:  $y = -37.6 + 18.8*x$ ,  $r^2 = 0.52$ ,  $p = 0.003$ ). (b)  $\text{NO}_3^-$  flux; no significant relationships with *Austrohelice* density was found. (c)  $\text{PO}_4^{3-}$  flux; only site S (night) showed a significant relationship with *Austrohelice* density ( $y = -10.63 + 0.83*x$ ,  $r^2=0.34$   $p = 0.021$ ).

### **3.4 Discussion**

The presence of *Austrohelice* was linked to differences in solute fluxes between sand (S) and muddy-sand (MS) environments, altering ecosystem functioning between habitats. Significant density-dependent effects on O<sub>2</sub> and NH<sub>4</sub><sup>+</sup> flux were also apparent. However, variation in the magnitude of change associated with crab density between sites highlighted the different interactions between *Austrohelice* and its environment in each sediment type. These changes related to the functional attributes of *Austrohelice* that were modified by environmental conditions. Patterns in both burrow:crab ratios and sediment reworking rates across treatments showed significant between site differences. Greater silt-clay content and hence increased sediment cohesion in muddy-sand (Table 3.1) resulted in longer lasting burrow structures and a greater burrow: crab ratio overall. Although burrow dimensions and therefore sediment-water interface were greater in sand, their transient nature is likely to weaken their influence on sediment geochemistry because if burrows are short-term, microbial communities cannot easily establish (Marinelli et al. 2002). Such differences highlight the context-specific nature of *Austrohelice* bioturbation on ecosystem processes.

#### **3.4.1 *Austrohelice* effects on sediment properties and primary production**

At both sites, crab density influenced sediment properties in similar ways, but to differing degrees (Table 3.2). The sand site displayed a highly significant negative correlation between silt-clay content and crab density consistent with the shift in functionality between sites. Increased sediment reworking is often associated with a winnowing of fine particles which are easily transported with the tide (Graf and Rosenberg 1997). However, such clear correlation in muddy-

sand may have been masked by greater variability in the (naturally higher) silt-clay content. As grazing pressures were assumed to be the same across both sites at equivalent *Austrohelice* densities, the more significant negative correlation between chl *a* and crab density in sand is likely to be influenced by increased microphyte reburial through burrow collapse and construction. Nevertheless, GPP was enhanced with increasing crab density when differences in microphytobenthic biomass, through increased deposit feeding were accounted for (Figure 3.3). This indicates that microphytes were more productive at greater crab densities, likely driven by the increased availability of  $\text{NH}_4^+$ , the preferentially used nitrogen source by microphytobenthos, coupled with a potential release from  $\text{CO}_2$  limitation through increased crab respiration. Also a reduction in microphytobenthic biomass may decrease intraspecific competition for resources between microphytes, increasing productivity (Morrisey 1988).

As chl *a* content was used as a proxy for microphyte biomass it is also possible that increased grazing pressure may have changed the microphytobenthic community composition between sites, altering the productivity per pigment concentration through species shifts (Falkowski and Kiefer 1985). Top-down grazer control on microphyte biomass, resulting in lower benthic primary production, has been well documented in estuarine systems (Asmus and Asmus 1985, Andersen and Kristensen 1988, Webb and Eyre 2004), yet studies which estimate microphyte efficiency in the presence of macrofauna provide greater insight in to benthic interactions. Indeed, previous studies which consider this have also concluded that benthic primary production can be stimulated through

macrofaunal bioturbation, particularly in the case of vertical mixers (Lohrer et al. 2004, Sandwell et al. 2009, Rodil et al. 2011).

### 3.4.2 Oxygen fluxes

Between site differences in (normalised) GPP were driven by the greater efflux of O<sub>2</sub> during the day in the sand site (Figure 3.2). Differences in light attenuation between sediment types through variations in physical properties such as grain size will influence microphytobenthic photosynthesis and diffusion of O<sub>2</sub> from the sediments. Light penetration and backscatter is greater in coarser sediment than fine, enabling photosynthesis to occur at greater depth in the sediment profile (Paterson et al. 1998). Bioturbation has previously been seen to have a greater influence on oxygen consumption in diffusion-dominated muddy sediment opposed to advective-dominated sands. Mermillod-Blondin and Rosenberg (2006) demonstrated that U-shaped burrow builders increased O<sub>2</sub> consumption in diffusive systems due to their strong influences on microbial processes. The opposite effect was true in more permeable sediments where changes in water circulation only moderately influenced microbial processes. Microphytobenthic species assemblages are also likely to differ with grain size, altering community production rates between locations (Heip et al. 1995). However, relationships between *Austrohelice* density and O<sub>2</sub> flux in daylight were similar in both sites despite fluxes being nearly four times greater in sand than muddy-sand, indicating crab respiration dominated sediment O<sub>2</sub> demands (Figure 3.2).

At night O<sub>2</sub> influx increased with crab density in both sediments due to increased respiration pressures within the chambers (Figure 3.2). *Austrohelice* does not show strong circadian rhythms, but instead shows peak activity around high tide

(Williams et al. 1985). Therefore, organism behaviour was assumed to be similar in both day and night chamber deployments. Nonetheless, differing interactions between sediments and crab density were observed between sites at night, with the greatest influx of O<sub>2</sub> occurring in site S. TOM was a significant predictor of O<sub>2</sub> flux in site S which, in conjunction with the increased availability of NH<sub>4</sub><sup>+</sup> and greater porewater exchange, indicates some enhancement of remineralisation through bioturbation activity. Vertical mixing of sediments has been well documented for enhancing remineralisation rates through the constant movement of particles between reaction zones, increasing overall benthic metabolism (Aller 1994). Increased remineralisation and sediment mixing through bioturbation can also influence the adsorption/desorption pathways of PO<sub>4</sub><sup>3-</sup> (Slomp et al. 1998). However, the increased PO<sub>4</sub><sup>3-</sup> efflux in sand at night (Figure 3.4c) may also be due to the release of porewater nutrients associated with higher crab densities and hence, sediment reworking. This effect may be masked in daylight due to microphyte utilisation.

### **3.4.3 Inorganic nitrogen fluxes**

Benthic organisms excrete ammonium through metabolic activities, contributing to the overall flux of NH<sub>4</sub><sup>+</sup>. Increased NH<sub>4</sub><sup>+</sup> flux with increasing crab density was observed in both sediment types during daylight and at night (Figure 3.4a). Similar flux rates between sites in crab exclusion plots in both daylight and at night indicated that sedimentary driven differences were minor. Where crabs were excluded or present in low numbers, NH<sub>4</sub><sup>+</sup> was taken up by the sediment, indicating utilisation by microphytes and bacteria. However, with increasing crab density, excretion rates are likely to have outweighed autotrophic demand

leading to a release of excess  $\text{NH}_4^+$  to the overlying water. This shift from influx to efflux occurs at densities above  $60 \text{ ind. m}^{-2}$  in both sediment types and is more pronounced in muddy-sand where  $\text{O}_2$  efflux and GPP were generally lower (Figures 3.2 and 3.3). Despite similarities in the fluxes between sediments when crabs were excluded,  $\text{NH}_4^+$  fluxes were of greater magnitude in muddy-sand than sand diurnally, indicating that these changes in responses were *Austrohelice* mediated.

Crab nitrogen excretion rates were assumed to be the same at each site. Consequently, the amplified efflux of  $\text{NH}_4^+$  at site MS was attributed to stimulation of  $\text{NH}_4^+$  production through microbial mineralisation pathways within the crab burrow walls (Braeckman et al. 2010). Established burrows provide a stable interface for these geochemical exchange gradients to develop (Aller and Yingst 1978), unlike the more transient burrow structures in sand. In cohesive sediments, where diffusive processes dominate, burrows act as macropores that produce strong fluxes at the sediment-water interface (Mermillod-Blondin and Rosenberg 2006). Flows over these reactive burrow surfaces greatly influence microbial processes. With increased crab density, galleries of burrows were formed in site MS amplifying these reactions and further enhancing N-cycling. Irrigation through persistent crab movement into and out of burrows, as well as passive irrigation through tidal flow in the natural system, may also affect  $\text{NH}_4^+$  efflux to some degree by creating pressure differentials (Williams et al. 1985, Ray and Aller 1985).

Similar  $\text{NO}_3^-$  influxes between sites were also observed where crabs were excluded, the magnitude of which were equivalent in daylight and at night, yet

*Austrohelice* density driven trends were not detected at either site (Figure 3.4b). Persistent, albeit low levels of  $\text{NO}_3^-$  influx in muddy-sand, indicated that dissimilatory nitrate reduction may have been promoted in anoxic areas of burrow walls (Kristensen et al. 1985), even when  $\text{O}_2$  production was enhanced at the sediment surface. However, burrow morphology was not correlated with *Austrohelice* density in either site. Uptake by microphytes may also have contributed to  $\text{NO}_3^-$  influx in muddy-sand during daylight, particularly in lower crab densities where  $\text{NH}_4^+$  influx was also measured. Low  $\text{NO}_3^-$  and  $\text{NO}_2^-$  ( $\text{NO}_x$ ) fluxes at these sites were not unexpected as denitrification rates are often witnessed to be greater than nitrification rates in marine sediments, resulting in little available  $\text{NO}_3^-$  to diffuse out of sediments. Nitrogen efflux in coastal habitats therefore consists mainly of  $\text{NH}_4^+$  (Kemp et al. 1990, Trimmer et al. 1998, Thrush et al. 2006) and in New Zealand,  $\text{NH}_4^+$  has previously been seen to make up 100 % of the measured dissolved inorganic nitrogen in coastal systems (Lohrer and others, 2004, 2010, Sandwell et al. 2009).

*Austrohelice* is a key bioturbating species in the regulation of nutrient cycling and remineralisation rates in both muddy-sand and sandy environments and shows strong density driven changes to solute exchange. Changes in the bioturbational role of *Austrohelice* were most notable in the flux of  $\text{NH}_4^+$ ; the key source of inorganic nitrogen in these systems. *Austrohelice* bioturbation also facilitated higher benthic primary production per unit of chl *a* in both sediment types, increasing with crab density. This unpredicted result may be facilitated through an increase in *Austrohelice* excretory products ( $\text{NH}_4^+$  and  $\text{CO}_2$ ) with greater crab density, which may act as a trade-off against increased grazing pressure.

### ***3.5 Conclusions***

The importance of faunal activities for the regulation of ecosystem processes is frequently associated with individual species and their functional or biological traits (Bornsdorff and Pearson 1999, Norling et al. 2007, Bremner et al. 2006). Other studies have concluded that differing bioturbation modes do not have comparable effects on biogeochemical processes under different sediment conditions due to hydrological shifts between environments (Mermillod-Blondin and Rosenberg 2006, Volkenborn et al. 2010). Our study highlights that an organism's contribution to ecosystem functioning can also be context-specific and although different sediment properties can create changes in fluxes, this is an oversimplification of the processes at work. How widespread the phenomenon of habitat induced functional plasticity actually is for other species, requires further exploration. Integrating behavioural information into functional studies will broaden conceptual frameworks and further develop accurate predictive tools for ecosystem based monitoring and management.

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## Chapter 4

# Density and habitat dependent effects of *Austrohelice crassa* burrows on sediment erodibility

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### **4.1 Introduction**

Soft sediment ecosystems are the most extensive environments on the planet including large areas of the intertidal zone (Snelgrove 1999). It has long been established that bioturbating fauna influence the flux of matter to and from the benthos through their disruption to the geotechnical properties of the sediment matrix (Meadows and Meadows 1991, Murray et al. 2002, Meysman 2006) affecting sediment erosion and deposition by several orders of magnitude (Grant 1983, Paterson and Black 1999, Widdows et al. 1998). Such modification to the benthic environment has the capacity to alter ecosystem functioning by affecting the rates and pathways of processes such as nutrient cycling, primary production, and organic matter remineralisation (Snelgrove 1997, Lohrer et al. 2004, Webb and Eyre 2004, Thrush et al. 2006). Despite biological interactions being highlighted as a key process in determining particle flux, relatively few studies have attempted to establish the links between bioturbation and sediment stability (Graf and Rosenberg 1997 and references therein, Fernandes 2006, Widdows 2009). Studies on burrow building species are particularly lacking, considering

the number of habitats in which they dominate in both number and biomass (Botto and Iribarne 2000, Escapa et al. 2007, 2008, Widdows 2009, Needham et al. 2010).

Burrow construction modifies the structure of sediments as both the sediment matrix and interstitial porewater are mixed during the building process (Botto and Iribarne 2000, Nowell and Jumars 1984, Escapa 2008). The formation of water filled burrow structures often results in a reduction of bulk shear strength, bulk density (particularly in cohesive sediments) and erosion thresholds, increasing the mass of sediment eroded especially where burrow densities are high (Grabowski et al. and references therein, 2011). However, these effects are unlikely to be universal because of the multifaceted nature of organism-sediment interactions. Consequentially, the capacity for individual species to influence sediment dynamics are still poorly understood and highly contested.

Attempts to group organisms in to one of two functional classifications, that of ‘stabilisers’ or ‘destabilisers’, have been limited in success because of an oversimplification of the processes and interactions at work (Jumars and Nowell 1984 and references therein). For example, the burrowing species *Nereis diversicolor* and *Corophium volutator* (herein *Nereis* and *Corophium*), have been classed as stabilisers as they increase sediment shear strength (Meadows and Tait 1989, Meadows et al. 1990). However, when bed erosion has been measured directly, *Nereis* has been categorised as both a sediment stabiliser at low flow speeds and a destabiliser after the onset of erosion (Fernandes et al. 2006). Moreover, Widdows et al. (2009) demonstrated density dependent effects of burrowing and surface deposit feeding by *Nereis* on bed erodibility. *Corophium*

has also been shown to exert strong seasonal density dependent effects on erosion thresholds through intense grazing of microphytes and resuspension of sediments (Gerdol and Hughes 1994, Dedeckere et al. 2000). However *Corophium* burrow caps were also shown to ‘armour’ the sediment, preventing erosion, whilst simultaneously increasing bed roughness and therefore increasing erosion potential (Grant and Danborn 1994). Such opposing interactions highlight the complex and contrasting influences a dominant species can have on the sediment surface and associated near bed hydrodynamics (Grant and Daborn 1994).

Differences in sediment stability between cohesive mud and non-cohesive sand naturally occur irrespective of benthic biota as transport is also heavily influenced by particle size, cohesion, water content and system hydrodynamics. Many studies have shown a correlation between erosion threshold and particle size (Grabowski et al. and references therein 2011), however most have focussed on non-cohesive sediments as the hydrodynamics of cohesive particles are much less predictable. As key bioturbating species often reside across broad sedimentary gradients, organism-sediment interactions may differ due to changes in the inherent sediment properties surrounding them, in turn affecting erodibility (Escapa 2008, Widdows and Brinsley 2002).

The burrowing mud crab *Austrohelice crassa* (herein *Austrohelice*), is a key species in the regulation of ecosystem functioning in New Zealand estuaries (Gibbs et al. 2001, Thrush 2003, Needham et al. 2011), and has been shown to exhibit some degree of functional plasticity mediated by the sediment environment (Needham et al. 2010). This shift in functionality is attributed to differences in burrow permanency and consequentially, sediment reworking rates

between cohesive and non-cohesive sediments. These differences have been shown to modify the flux of nutrients to the overlying water column (Needham et al. 2011) and are likely to create differences in the erodibility between sediment types. As *Austrohelice* burrows are less stable in sand than in mud (1.4 days and 26 days respectively, Needham et al. 2010), sediment is turned over much more frequently, particularly in areas of high crab density. Sediment in these areas will be less consolidated than areas without crabs and consequently microbial biomass, and therefore cohesion, may be reduced. However, far greater burrow densities per unit area are often seen in mud due to a combination of both increased crab number and burrow longevity. Due to their close proximity to one another, alterations to the bed surface topography and increased roughness may occur, likely altering boundary layer dynamics (Baas and Best 2000, Fries et al. 1999, 2000, Widdows and Brinsley 2002, Widdows et al. 2000, 2004).

Here I explore the relationships between *Austrohelice crassa* burrow density and sediment type in two key habitats, a fine to medium sand and a cohesive sandy mud, to establish the role these burrows perform in sediment particle fluxes. Intact sediment cores containing burrows from these environments were subjected to flow simulations *ex-situ* in annular flumes. Burrow morphology is highly varied regardless of sediment type and organism density (Needham et al. 2010), therefore by using actual burrows instead of mimics we aimed to gain a greater appreciation of the structure-flow-sediment interactions in the natural environment. I hypothesised that in both sediment types, increasing burrow density would increase sediment erodibility. However due to the different interactions between organism and environment associated with the inherent differences in sediment properties, the degree to which erodibility was affected by

the presence of *Austrohelice* burrows would differ between sediment types. Further understanding and quantification of how intrinsically small-scale biotic processes can influence sediment stability at greater scales will greatly enhance the predictive capabilities and realism of hydro and sediment dynamic models (Widdows et al. 2004).

## **4.2 Methodology**

### **4.2.1 Study site and experimental treatments**

Sediments were collected from crab beds in the mid intertidal zone of Tairua estuary (36° 59' 57.56" S, 175° 51' 04.09" E), Coromandel peninsula, New Zealand, during summer over a 3 week period. At the two selected locations, classed as a cohesive sandy mud (herein called mud) and a non-cohesive fine to medium sand (herein called sand; Table 4.1), burrow counts and permanency observations have previously been made (Needham et al. 2010). *Austrohelice* comprised the majority of macrofaunal biomass at both sediment types and very few other macrofaunal species greater than 1 cm in length and/or diameter resided within the burrowed beds (*pers obs*), likely due to the high levels of crab generated bioturbation (Botto and Iribarne 2000). Local, small scale variations in burrow density within each crab bed were used to create burrow density treatments of 0, 19 and 100 burrows m<sup>-2</sup> in sand and 0, 100 and 400 m<sup>-2</sup> in mud. *Austrohelice* density has been shown to correlate with increasing mud content (Thrush et al. 2003), and these densities reflect the natural range of burrows (> 8 mm dia.) found in summer in these two areas of the estuary (*pers obs*, Needham et al. 2010). This burrow size hosts adult crabs and is common in both sediment types. As such they are assumed to dominate bioturbation and sediment mixing

effects. Overlap of the highest burrow density in sand and the lowest density in mud was deliberate so that some comparison between sediments could be made whilst still reflecting natural burrow densities for each sediment type. Zero density treatment samples were also collected from within the crab beds, as surrounding areas with few or no crabs likely indicated a shift to unsuitable conditions, introducing potential confounding factors to the sampling design.

#### **4.2.2 Sediment collection and erosion runs**

Erosion runs were carried out in annular flumes that followed the design of Widdows et al. (1998) and used the same operating procedures. Briefly, each of the two flumes were constructed from clear acrylic with a 64 cm outer and 44 cm inner diameter resulting in a 10 cm channel width, giving a total bed area of 0.17 m<sup>2</sup>. Each flume has a rotating motor driven lid whereby changes in water flow are regulated by modifying the revolutions per minute (rpm). Lid generated flow speeds were initially calibrated over a smooth 7 cm deep sponge bed using a downward facing micro-ADV (Acoustic Doppler Velocimeter; Sontek Ltd) inserted through the base of the flume, to generate a series of nominal flow velocities that were used to create a stepwise series of flow rates ranging from 0.05 – 0.45 m s<sup>-1</sup> (7-63 rpm).

Previous studies have shown no significant difference between erosion rates of *in situ* and cored inter-tidal sediments (Widdows et al. 2000, 2007). Therefore undisturbed sediment cores were collected using stainless steel corers matching the dimensions of the flume channel. On each collection day both sand and mud sediments were sampled, but density treatments were randomised. Each density treatment was replicated 3 times over the sampling period in each sediment type.

Care was taken to space burrows throughout the cores so that erosion would not be focussed in one area of the flume. Burrow orientation was also considered when positioning the corer to ensure as many intact burrow structures as possible were retained within the corer. Cores were taken to a depth of 7 cm which is deeper than median burrow depths in both sediments (3.9 cm in sand and 4.7 cm in mud, Needham et al. 2010). On each sample date 3 replicate cores (2.8 cm diameter, 1 cm deep), were also collected at random from inside the crab beds and pooled prior to analysis for grain size, chlorophyll *a* (chl *a*) and total organic matter content. Unlike other systems where chl *a* concentration has been seen to correlate with sediment stability (Underwood and Paterson 1993, Paterson and Black 1999), in areas where deposit feeding burrow builders dominate chl *a* has previously been classed as a poor predictor of sediment stability (Riethmüller et al. 2000, Fernandes 2006). This is due to the fact that burrow walls increase sediment-water interface increasing oxygen penetration and chl *a* content (Andersen and Meadows 1978, Davey and Partridge 1998), which can attenuate or counter potential grazing effects. Due to small spatial scale over which our samples were taken (within crabs beds) and the highly mobile nature of *Austrohelice*, disturbance and grazing pressure was assumed to be similar among density treatments, although differences between sediment types were expected.

Cores were returned to the laboratory in under 4 h post-collection. Small quantities of liquid nitrogen were poured precisely in to each burrow aperture using a funnel to fast freeze any inhabitants before carefully placing each core in the flume. This bypassed potential issues concerning irregular crab behaviour within the flume, particularly under high flow conditions where both erratic surface activity and reburial were enhanced (*pers obs*). Such behaviour may have

led to an artificial amplification of bed roughness and erosion and so was eliminated. After positioning each core, a 4 mm insert was added around the inner wall of the flume to fill the area left by the corers, reducing the total bed area to 0.16 m<sup>2</sup>. ‘Bubble wrap’ packing material following the shape of the channel was placed over the sediment surface to avoid disturbance before slowly filling the flume with artificial seawater (~30 ‰, 21 °C). Flumes were filled to a water depth of 25 cm above the bed. An optical backscatter sensor (OBS; Seapoint turbidity meter) was then placed vertically in the water column in to the direction of flow, 8 cm above the sediment surface. Sediments were allowed to settle overnight in the gently aerated flumes at a flow speed of 0.05 m s<sup>-1</sup>.

Prior to beginning erosion runs, aeration devices were removed and burrows recounted in case of overnight collapse. In two instances at low densities in sand (19 burrows m<sup>-2</sup>) replicates were discarded and recollected. Both flumes were run simultaneously. Water flow was created using the computer controlled rotating lid (LabVIEW software). An initial free stream velocity of 0.05 m s<sup>-1</sup> was maintained for 15 min. Based on flow calibrations, a stepwise increase in rpm creating a nominal increase of 0.05 m s<sup>-1</sup> in lid rotation speed took place every 15 min up to a maximum current speed of 0.45 m s<sup>-1</sup>. Voltage readings from the OBS were logged every second. These readings were calibrated against duplicate water samples collected during the 10<sup>th</sup> minute of each erosion step for each flume. Water samples, varying in volume depending on the suspended particulate matter (SPM) concentration (1L to 60 ml), were immediately vacuum filtered through a pre combusted GF/C filter washed down with distilled water and frozen for gravimetric analysis. Replacement seawater was added back to the flume to maintain a constant volume. Gravimetric samples were dried to a constant mass

(80 °C, 48 hrs) and used to create OBS calibration curves (sand  $r^2 = 0.97$ , mud  $r^2 = 0.97$ ) from which the mass of sediment eroded (ME;  $\text{g m}^{-2}$ ) and mean erosion rate (ER;  $\text{mg m}^{-2} \text{s}^{-1}$ ) at each step in the erosion sequence, were calculated. Erosion rates have previously been used in preference to other measures such as erosion threshold as indicators of sediment stability as this parameter does not just relate to the upper most layers of the sediment (Houwing, 1999). The critical velocity required to erode 1 g sediment ( $U_{1\text{crit}} \text{ m s}^{-1}$ ) was estimated from the linear relationship of  $\ln(\text{ME})$  and  $\ln(U)$  from each replicate ( $r^2 > 0.92$ , Widdows 1998, Roast 2004).

Sediment grain size fractions were determined using a Malvern Mastersizer-S (300 FR lense, range 0.05 - 2000  $\mu\text{m}$ ) after digestion in 10% hydrogen peroxide (Day 1965). A dispersant (Calgon) was also added to the mud samples to stop silt-clay consolidation. Organic matter content was quantified through loss on ignition from dried sediments (105 °C for 48 h), after combustion for 5.5 h at 550 °C (Dean 1974). Pigments were extracted from freeze-dried sediment samples and steeped in 90% acetone for 24 h before centrifugation. Chl *a* and phaeophytin (phaeo) content was determined flourometrically, before and after acidification, on a Turner 10-AU flourometer (Arar and Collins 1997). Dry bulk density (mass of wet weight/volume of wet sediment) and % water content (mass of water/mass of wet sediment) were also calculated from the sediment cores.

#### **4.2.3 Near-bed flow measurements**

To determine if bed shear stress altered as a function of burrow density in each sediment type, we conducted vertical flow velocity profiles and near bed turbulence measures using a downward facing micro-ADV. This device was

mounted through the base of the flume on a vertically moving racking system for fine control. Flow profiles were conducted on a separate occasion to erosion runs in case the presence of an ADV affected sediment entrainment rates. Only one replicate from each sediment type was used to characterise the near bed hydrodynamics as a function of burrow density. Flow speeds of 0.05, 0.15, 0.2 m s<sup>-1</sup> (i.e below the onset of erosion, see results) were profiled. Prior to this, the sampling volume of the ADV had been mapped to enable accurate positioning above the bed (Finelli et al. 1999, Jones et al. 2011). A velocity profile was recorded (30 s at 25 Hz) at 13 elevations ranging from 0.5 – 3.5 cm above the bed in burrowed sediment and at 11 points (0.5 cm to 2.5 cm) in zero density treatments. Compression of the boundary layer (a recognised limitation of annular flumes) meant bed roughness and/or shear stress are not calculable from the log profile of current speeds. Therefore turbulent kinetic energy (TKE) was used to calculate bed shear stress (Kim et al. 2000, Pope et al. 2006) as follows:

$$\text{TKE} = \frac{1}{2} \rho (\overline{u'^2} + \overline{v'^2} + \overline{w'^2})$$

Where  $\rho$  is the density of the fluid and  $u$  is the fluctuating flow in the streamwise direction.  $v$  and  $w$  denote cross channel and vertical components of the flow respectively. The ratio of TKE to bed shear stress ( $\tau_0$ ) is constant

$$\tau_0 = C_1 \text{TKE}$$

where  $C_1 = 0.19$  (Pope et al., 2006).

Turbulence measurements were made for 180 s at 25 Hz at 0.5 cm above the bed for each sediment, flow and treatment. This height was determined from the velocity profiles to be within the log layer in each instance.

#### **4.2.4 Statistical Analysis**

$U_{1\text{crit}}$  ( $\text{m s}^{-1}$ ) and the mass of sediment eroded at  $0.35 \text{ m s}^{-1}$  (ME  $0.35 \text{ g m}^{-2}$ ) were selected as indicators of sediment stability and erodibility for statistical analyses across the two sediment types. Within sediment type differences of  $U_{1\text{crit}}$  and ME  $0.35$  values among burrow density treatments were analysed using one-way analysis of variance (ANOVA). Two-way ANOVA was conducted to assess if between sediment type differences in these two parameters at comparable burrow densities (zero and  $100 \text{ burrows m}^{-2}$ ) were statistically significant ( $p = 0.05$ ). As variance was not homogeneous for ME  $0.35 \text{ (g m}^{-2}\text{)}$  values, these data were log transformed prior to analysis in order to meet test assumptions. Post-hoc Tukey tests were conducted where significant differences were identified.

#### **4.3 Results**

Sediment characteristics within the two selected sediments were distinct from each other (Table 4.1) as was expected from their visual appearance. Silt-clay content (particles  $< 63\mu\text{m}$ ) was approximately 10 times greater in mud, with a much smaller median grain size ( $119 \mu\text{m}$ ) than sand ( $226 \mu\text{m}$ ). Due to these factors dry bulk density was  $1/3^{\text{rd}}$  greater in sand than in mud. Chl *a* content, a proxy for microphytobenthos biomass, organic matter and water content were all approximately two times higher in mud than sand. Despite samples being pooled across the density treatments, the variance in chl *a* content was lower in mud (coefficient of variation (COV): mud = 0.10, sand = 0.45), whereas the variance between replicates of organic matter content displayed greater uniformity in sand (COV: sand = 0.03, mud = 0.18). Median grain size and silt-clay content showed

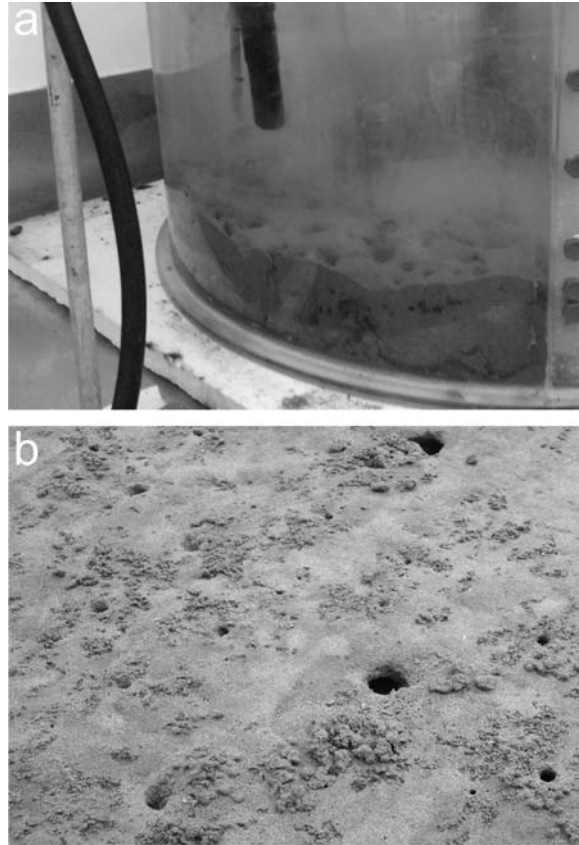
more within sediment type variability in mud, potentially indicating crab mediated changes to the sediment surface.

**Table 4.1.** Sediment properties (0-1 cm) of the two selected sediment types in Tairua Estuary. Three samples were collected and pooled on 6 sample dates interspersed throughout the three week study period. Standard deviations are given in parentheses.

<b>Sediment property</b>	<b>Sand</b>	<b>Mud</b>
Chl <i>a</i> ( $\mu\text{g g}^{-1}\text{dw}$ )	9.3 (3.0)	18.5 (2.5)
Phaeo ( $\mu\text{g g}^{-1}\text{dw}$ )	1.4 (0.8)	4.1 (2.0)
Organics (%)	2.8 (0.1)	5.3 (0.9)
Water content (%)	30.1 (1.0)	59.7 (10.9)
Dry bulk density ( $\text{g cm}^3$ )	1.5 (0.02)	1.05 (0.1)
Silt-clay (%)	5.9 (1.3)	63.5 (15.2)
Med grain size ( $\mu\text{m}$ )	226 (13.6)	119 (95.4)

Chl *a*: sediment chlorophyll *a* content; Phaeo: sediment phaeopigment concentration.

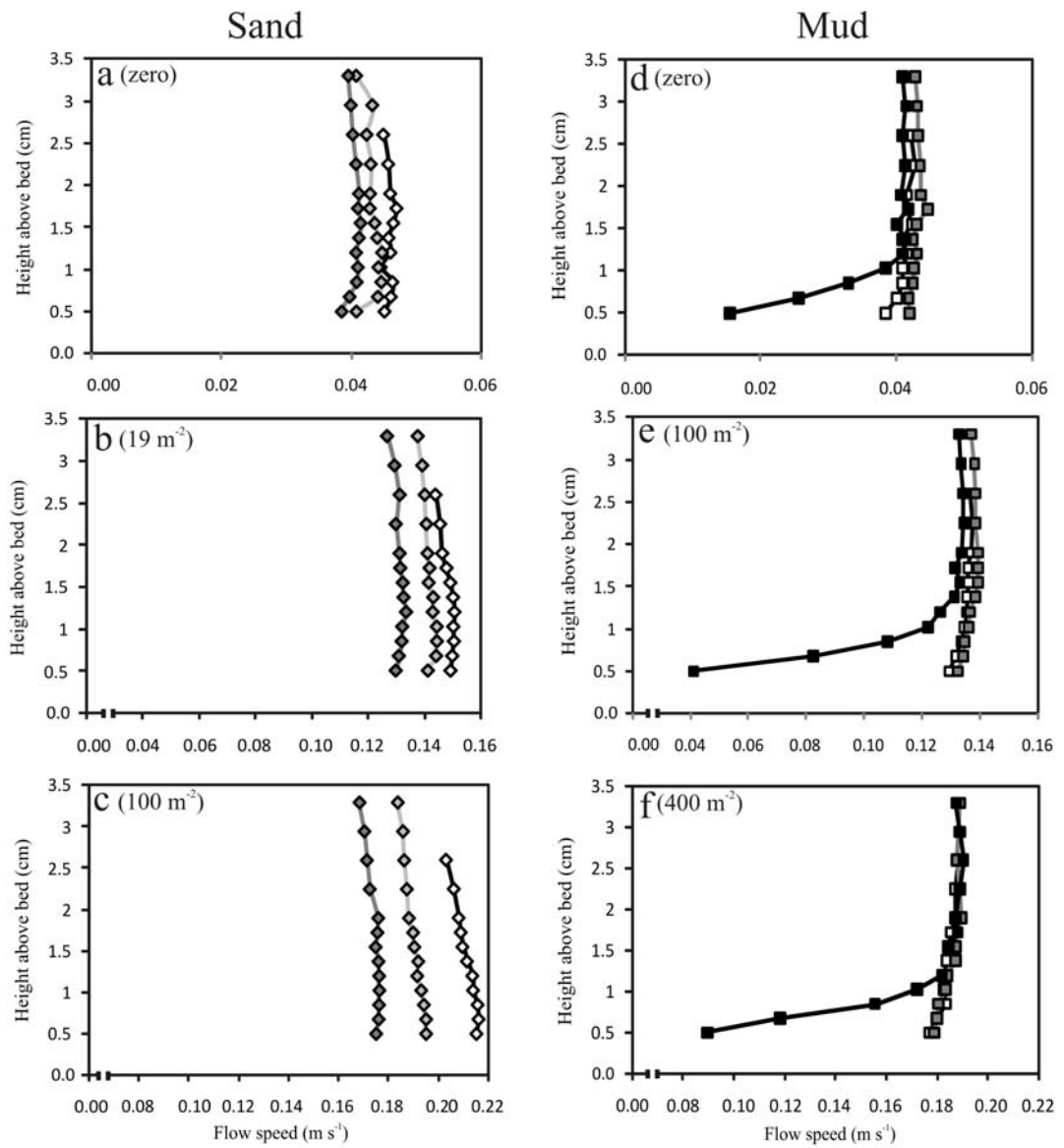
Visual inspection of the sediment confirmed an altered surface topography in the presence of crab burrows. In mud increased undulations between burrow openings were most noticeable at the greatest burrow densities ( $400 \text{ ind. m}^{-2}$ , Figure 4.1a). In sand, surficial sediment pellets created during burrow clearance on an ebbing tide were often present (Figure 4.1b) and therefore collected in the burrowed cores. At burrow densities of  $100 \text{ ind. m}^{-2}$  these could increase bed height by 5-10 mm. This pelletisation was not as apparent in cohesive sediments where burrow debris is sluiced out in a more liquid form, notable as a darker colouration around the burrow entrance.



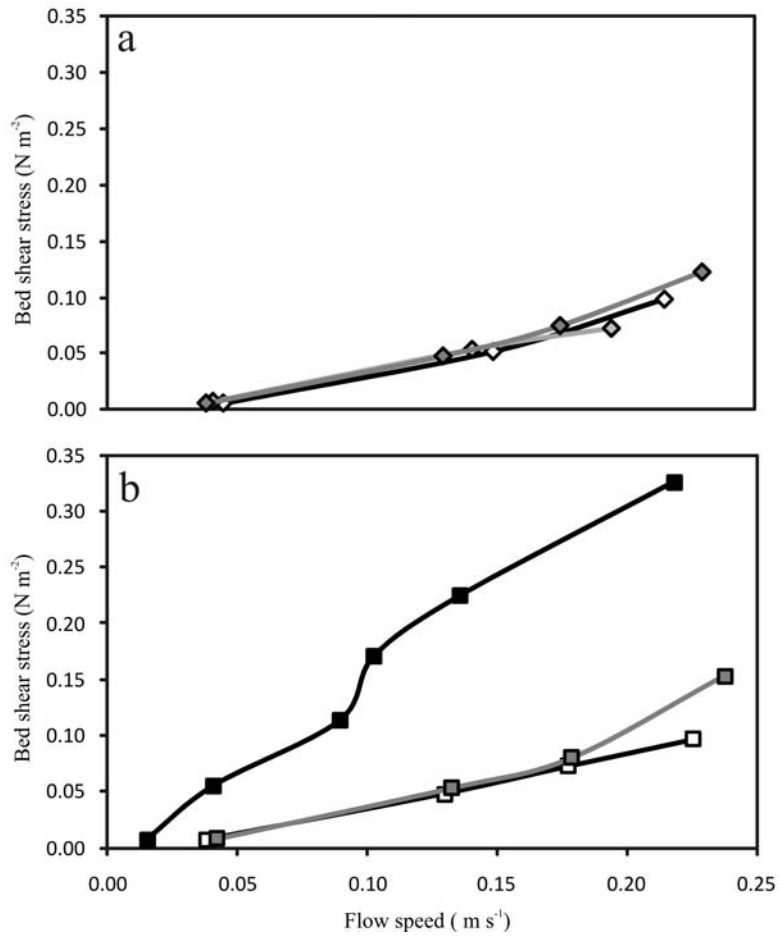
**Figure 4.1.** Surface undulations seen at the highest density treatment (400 burrows  $\text{m}^{-2}$ ) in mud (a) and surficial pelletised deposits observed in sandy sediment (b).

#### **4.3.1 Near-bed hydrodynamics**

In sand, an increase in burrow density was associated with an increase in the amount of surficial pelletised sediment. Velocity profiles showed greater drag associated with this increase in bed roughness, reducing flow speed with increasing burrow density at each nominal flow velocity (Figure 4.2a-c). At nominal flow speeds of  $0.05 \text{ m s}^{-1}$  and  $0.15 \text{ m s}^{-1}$ , there was a 12 % reduction in the depth integrated flow velocity from the zero to high density treatments which widened to 18 % at the nominal flow speed of  $0.2 \text{ m s}^{-1}$ . Nevertheless bed shear stress showed no distinct differences associated with increased burrow density in sand (Figure 4.3a).



**Figure 4.2.** Near bed flow velocity profiles as a function of; sediment type (sand and mud), nominal flow speed  $0.05 \text{ m s}^{-1}$  (a and d),  $0.15 \text{ m s}^{-1}$  (b and e), and  $0.2 \text{ m s}^{-1}$  (c and f) and burrow density. Symbol colour indicates burrow density treatment from zero (white),  $16 \text{ m}^{-2}$  (light grey),  $100 \text{ m}^{-2}$  (dark grey) in sand, and zero (white),  $100 \text{ m}^{-2}$  (dark grey) and  $400 \text{ m}^{-2}$  (black) in mud.



**Figure 4.3.** Bed shear stress (estimated using TKE method) in sand (a) and mud (b) as a function of mean depth integrated (0.03-0.35 m) flow speed. Symbol colour indicates burrow density from zero (white), 16 m<sup>-2</sup> (light grey), 100 m<sup>-2</sup> (dark grey) in sand, and zero (white), 100 m<sup>-2</sup> (dark grey) and 400 m<sup>-2</sup> (black) in mud.

In mud, where an increase in shallow pits and mounds was observed with increasing burrow density ( $\sim \pm 2$  cm above/below bed height, Figure 4.1a), little evidence of any drag effect between treatments were detected. Having said this, at the greatest burrow density treatment (400 m<sup>-2</sup>) all nominal flow velocities were greatly reduced until a height of 1.25 cm above the bed was reached (Figure 4.2d-f), although, bed shear stress in this region was still high (Figure 4.3b). Due to the high density of burrows in this treatment, it is likely that the ADV detected an

eddy in the lee of a burrow structure, a region of low flow but high turbulence, influencing bed shear measurements.

#### **4.3.2 Sediment stability and erosion rates**

Both sediment types showed different and distinct patterns of erosion associated with *Austrohelice* burrow density. In sand, burrow densities of 19 m<sup>-2</sup> displayed the greatest reduction in sediment stability among treatments over the sequence of flow speeds (Figure 4.4). In all three treatments some variability amongst replicates was apparent, but always occurred above flow speeds of 0.35 m s<sup>-1</sup>, i.e. after the onset of type II erosion, whereby the integrity of the deeper sediment layers are no longer intact. Counter intuitively, in mud the total mass of sediment eroded over the erosion sequence was greatest in the zero burrow treatment and reduced with increasing burrow density. Similarly variability between replicates also reduced with burrow density. Erosion rates followed a similar pattern to ME (Figure 4.5) with erosion onset generally occurring at lower flow speeds in mud than sand.

Burrow density did not affect  $U_{1crit}$  in either mud or sand (Table 4.2, Figure 4.6a), however, ME 0.35 highlighted distinct patterns in erosion for each sediment type. In sand a unimodal pattern in ME 0.35 values was observed whereby at burrow densities of 19 m<sup>-2</sup> sediment erosion was 2.5 and 3.5 times higher than the zero and 100 m<sup>-2</sup> density treatments respectively (Figure 4.6b). Despite a 5 fold increase in burrow number between the two burrowed treatments, at a density of 100 burrows m<sup>-2</sup>, erosion was reduced to levels similar to that of unburrowed sediment. Variance within the 19 m<sup>-2</sup> density treatment was also proportionally greater than the other two treatments. Significant differences between the two

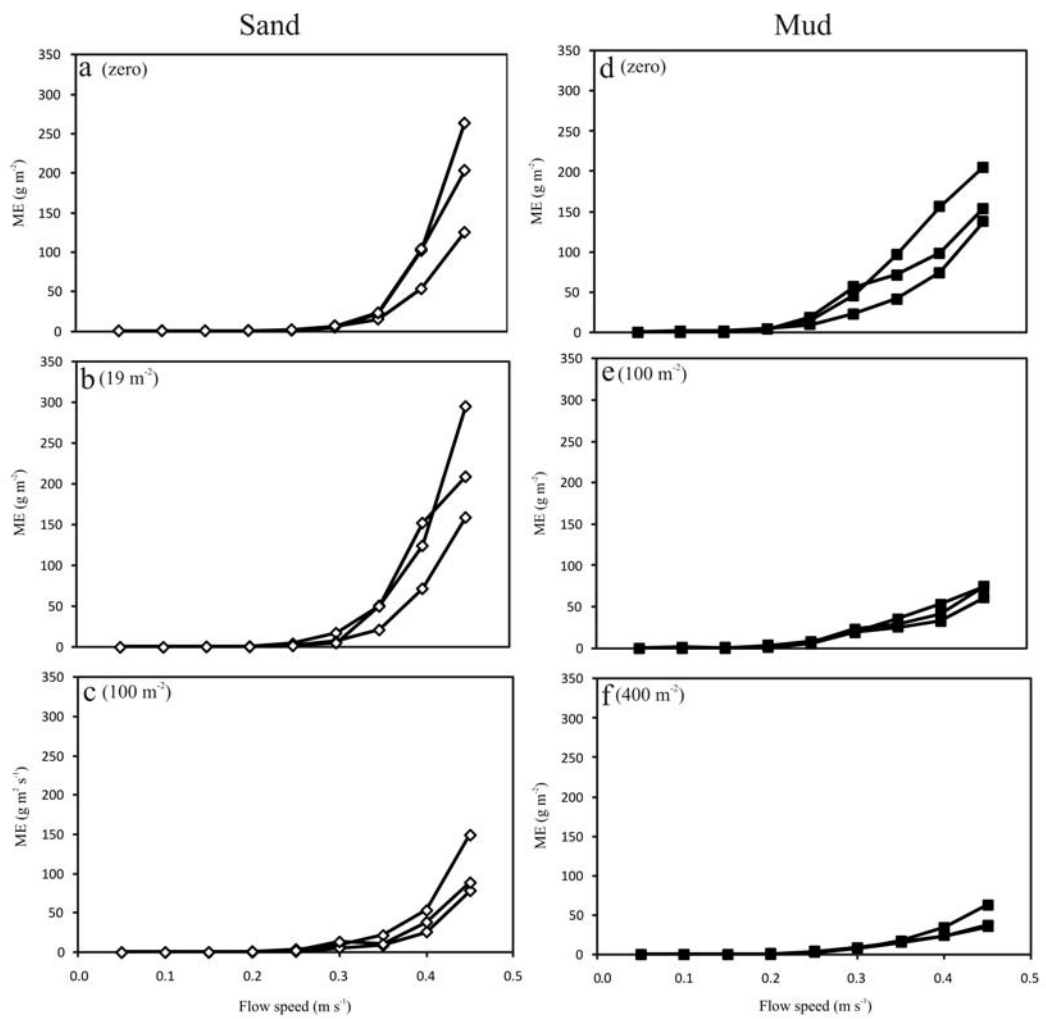
burrowed treatments were observed ( $p = 0.016$ , Table 4. 2), as were marginally significant differences between zero and the 19  $\text{m}^{-2}$  burrow treatment ( $p = 0.065$ ).

In mud, a linear decline in ME 0.35 as a function of increasing burrow density was measured. In this habitat, the zero density treatment was significantly different from both the 100  $\text{m}^{-2}$  treatment ( $p = 0.038$ ) and the 400  $\text{m}^{-2}$  burrow treatment ( $p = 0.002$ ) with a respective 53 and 75% reduction in the mass of sediment eroded. However, only a marginally significant difference between the two burrow treatments was detected ( $p = 0.071$ ) indicating that the presence of burrows, not the density, may be the key factor in sediment stabilisation.

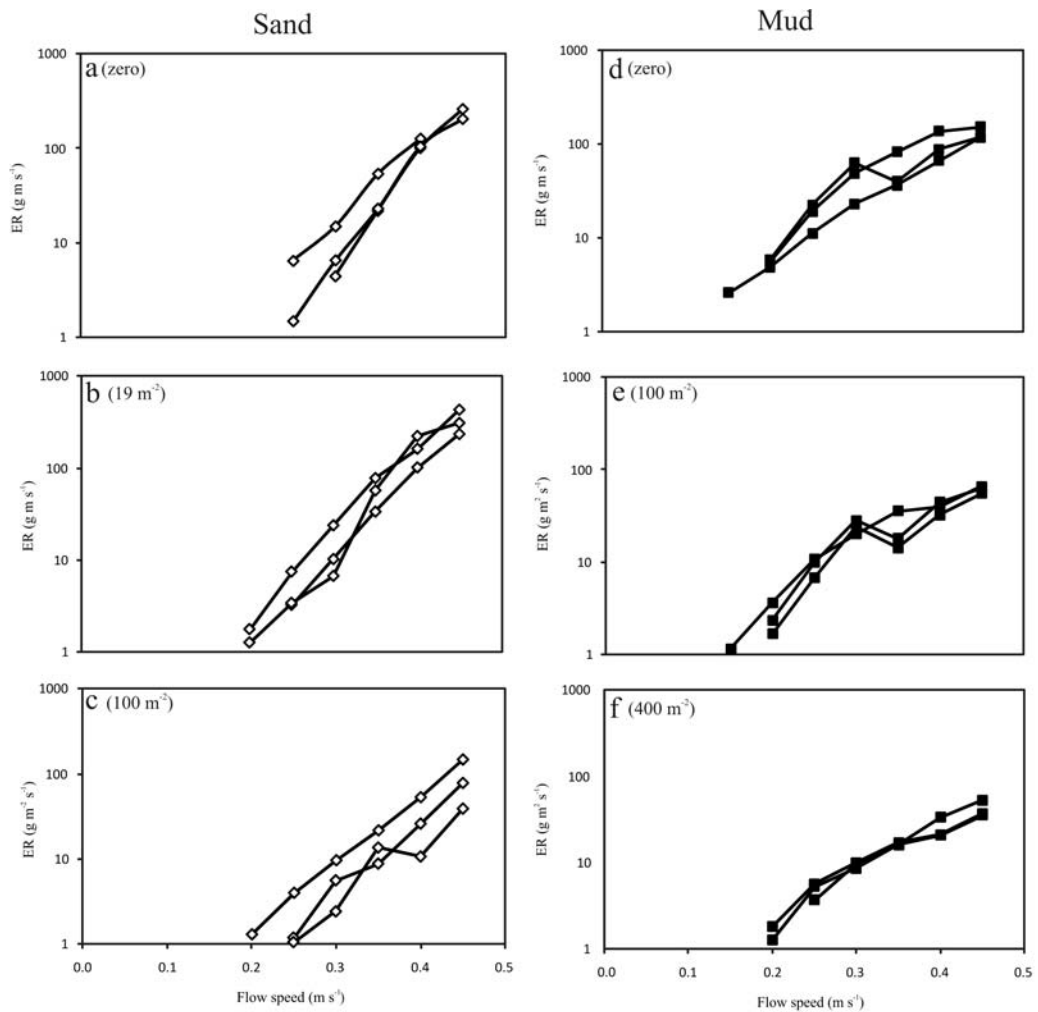
**Table 4.2.** Results of a one way analysis of variance testing within sediment type differences in  $U_{1\text{crit}}$  ( $\text{m s}^{-1}$ ) and ME 0.35 ( $\text{g m}^{-2}$ ) as a function of burrow density.

<b>Sediment</b>	<b>Dependent</b>	<b>Source</b>	<b>df</b>	<b>MS</b>	<b>F</b>	<b>p</b>
Mud	$U_{1\text{crit}}$ ( $\text{m s}^{-1}$ )	density	2	5.86	0.99	0.426
		error	6	5.93		
	logME 0.35 ( $\text{g m}^{-2}$ )	density	2	0.25	18.49	<b>0.003</b>
		error	6	0.01		
Sand	$U_{1\text{crit}}$ ( $\text{m s}^{-1}$ )	density	2	5.29	0.99	0.424
		error	6	5.33		
	logME 0.35 ( $\text{g m}^{-2}$ )	density	2	0.23	8.71	<b>0.017</b>
		error	6	0.03		

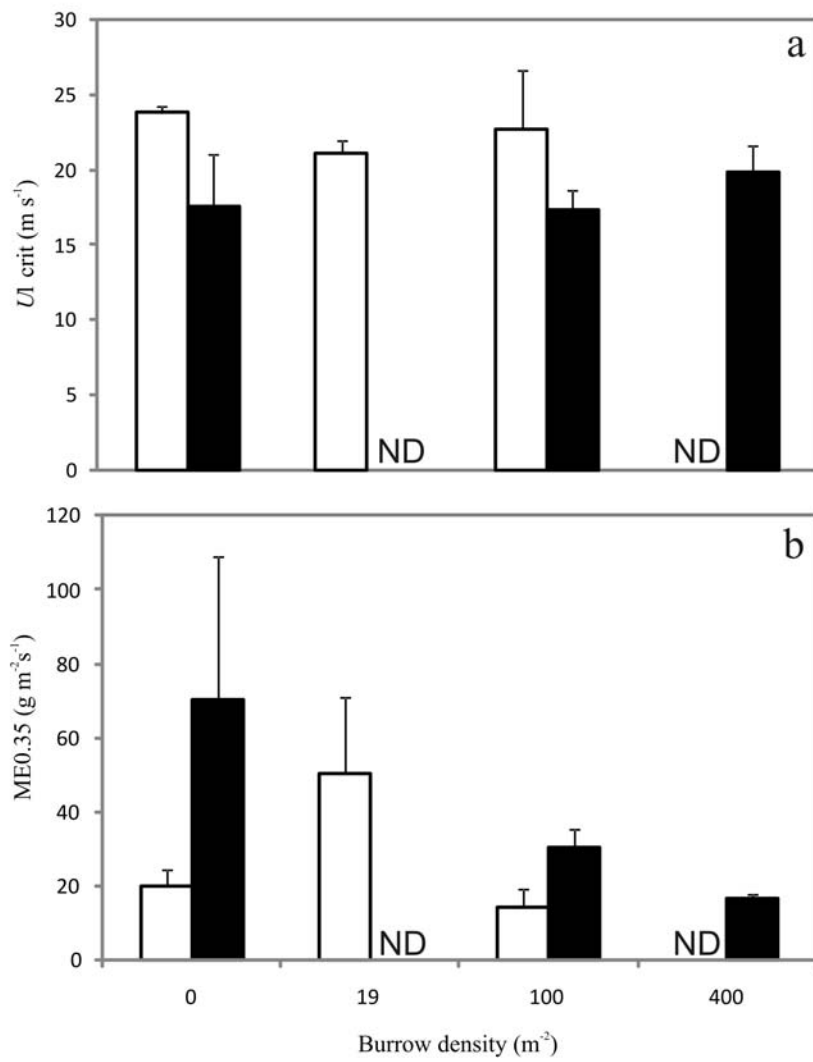
Density: *Austrohelice* burrow density



**Figure 4.4.** Relationship between the mass eroded (ME) and the nominal flume free-stream flow speed as a function of sediment type and *Austrohelice crassa* burrow density treatments (given in parentheses). Data from the three replicates of each treatment are displayed.



**Figure 4.5.** Relationship between the erosion rate (ER) and the nominal flume free-stream flow speed as a function of sediment type and *Austrohelice crassa* burrow density treatments (given in parentheses). Data from the three replicates of each treatment are displayed.



**Figure 4.6.** The critical erosion velocity required to erode  $1g$  sediment  $m^{-2}$  (a) and the mass of sediment eroded at a flow speed of  $0.35 m s^{-1}$  (b), as a function of burrow density and sediment type. White bars indicate sand, black bars indicate mud and ND not determined. Error bars indicate standard deviation ( $n=3$ ).

**Table 4.3.** Results of a two way analysis of variance testing between sediment type differences in  $U1_{crit}$  ( $m s^{-1}$ ) and ME 0.35( $g m^{-2}$ ) as a function of burrow density (zero and 100 burrows  $m^{-2}$ ).

<b>Dependent</b>	<b>Source</b>	<b>df</b>	<b>MS</b>	<b>F</b>	<b>P</b>
$U1_{crit}$ ( $m s^{-1}$ )	sediment	1	102	13.74	<b>0.006</b>
	density	1	1.24	0.167	0.693
	sediment*density	1	0.55	0.074	0.792
	Error	8	7.44		
logME 0.35 ( $g m^{-2}$ )	sediment	1	0.52	27.11	<b>0.001</b>
	density	1	0.17	8.694	<b>0.018</b>
	sediment*density	1	0.02	0.874	0.377
	error	8	0.02		

Density: *Austrohelice* burrow density.

A two-way ANOVA detected significant sediment type effects for  $U1_{crit}$ , being ~20% higher in sand than mud (Figure 4.6a, Table 4.3  $p = 0.006$ ) but no significant burrow density effects were detected for this measure. Alternatively, (log) ME 0.35 displayed significant differences for both sediment type ( $p = 0.0008$ ) and burrow density treatments ( $p = 0.018$ ). Zero density treatments were significantly different from each other ( $p = 0.01$ ), and differences between zero burrows in mud and 100  $m^{-2}$  burrows in sand were also significant ( $p = 0.002$ ). At a burrow density of 100  $m^{-2}$ , significant differences were marginal ( $p = 0.065$ ) between the two sediment types. No significant sediment\*density interaction was detected ( $p = 0.38$ ), indicating that the effect of burrows at the two comparative densities was similar between sediment types.

## **4.4 Discussion**

The presence of *Austrohelice* burrows was shown to have unpredicted effects on sediment stability, primarily reducing erosion rates in all but the lowest burrow density in sand (19 burrows m<sup>-2</sup>). My findings therefore directly contradict the assumption that increased bioturbation increases sediment erodibility. Distinct between sediment type differences in sediment entrainment patterns were also observed associated with burrow density.

### **4.4.1 Patterns of erodibility in sand**

In sand, the velocity required to erode 1 g of sediment ( $U_{1\text{crit}}$ ) was similar among treatments (Table 4.2). However after erosion onset a unimodal pattern in the mass of sediment eroded was observed (ME0.35), indicating burrow density affected sediment erodibility. Previous studies on burrow building species have also seen a decoupling of the initiation of sediment transport (i.e.,  $U_{1\text{crit}}$ ) from the subsequent erosion rate (as indicated by ME0.35), with the latter proving to be a better predictor of biotic and physical erosion controls (Grant and Danborn 1994). Unexpectedly, ME 0.35 in the zero and high burrow density (100 m<sup>-2</sup>) treatments was more similar to each other and significantly lower than the 19 burrow m<sup>-2</sup> density treatment. A reduction in the variability between replicates in each treatment was also associated with increasing sediment stability. Factors controlling this unimodal response were not apparent from either the flow velocity profiles (Figure 4.2), or bed shear stress measurements (Figure 4.3). In comparison to other burrowing decapods, *Austrohelice* did not dramatically alter the sediment topography even at high burrow densities (Nowell et al. 1981, Ziebis et al. 1996, Rowden et al. 1998) but increasing bed roughness, associated with the

greater quantity of surficial pellets, accounted for the reduction of free stream velocity between treatments. This observed pattern did not however indicate why erosion rates were so much greater at a density of 19 burrows  $\text{m}^{-2}$ .

The reduction in mass of sediment eroded (ME 0.35) in burrow densities of 100  $\text{m}^{-2}$  may be influenced by two factors. Firstly, frequency of surficial pellets increased with burrow (and hence crab) density. This labile material may act as 'hotspots' for microphytobenthic activity, aiding in stabilisation of the sediment surface (Murray et al. 2002). However, bedload transported material was apparent in this high burrow density treatment once flow speeds  $> 0.25 \text{ m s}^{-1}$  were reached, indicating that pellets were readily eroded. This indicates that reduced ME 0.35 at the higher burrow densities may in fact reflect higher deposition and subduction of bedload transported material rather than a reduction in erosion rates *per se*.

A previous study, mapping the flow dynamics around pits similar to *Austrohelice* burrow openings, demonstrated a reduction in suspended sediment transport (Friedrichs et al. 2009). This was attributed to partial flow separation between the main channel and the burrow cavity where a recirculating vortex occurred. Particles trapped in this way facilitated deposition within the structure, potentially indicating that the frequency of burrow collapse observed in sand at this location (Needham et al. 2010) is also aided by high rates of infilling. Indeed, unlike at lower densities, complete burrow collapse was not observed in the 100 burrow  $\text{m}^{-2}$  treatment, but wearing and scour around burrow apertures was evident. Therefore higher erosion rates at burrow densities of 19  $\text{ind m}^{-2}$  may actually reflect the fact that fewer burrows are present to trap bedload material and that greater erosion

may occur at higher burrow densities, but as material is immediately sequestered back to the bed, the effects are less apparent. Where burrows are absent, the smoother sediment surface requires faster flow for erosion onset (Figure 4.5). However at high nominal flow rates ( $> 0.35 \text{ m s}^{-1}$ ) rapid entrainment occurs (Figure 4.4, 4.6) as the structure of deeper sediment layers also give way.

Several studies have demonstrated the ability of crab species to facilitate sediment trapping (Iribarne et al. 1997, 2000, Escapa et al. 2008, Botto et al. 2006). Differences in deposition and erosion rates have been related to habitat dependent flow conditions and trapping rates has been linked to burrow morphology. Funnel shaped burrow openings of decapods have been seen to increase the amount of bedload transported particles trapped in burrows (Witbaard and Duineveld 1989, Nickell and Atkinson 1995, Iribarne 1997, Botto et al. 2006). When compared to tubular apertures Escapa et al. (2008), found funnel shaped burrow openings trap twice the amount of sediment under the same conditions. Small sediment particles trapped in funnels have also been attributed to an increase in sediment stability and reduced bedload transport for other grapsid crabs (Botto and Iribarne 2000). *Austrohelice* displays a wide variety of burrow morphology which is independent of sediment type or density (Needham et al. 2010), therefore variance in ME 0.35 values between replicates in each treatment may be attributable to both changes in burrow morphology and the position of the burrow aperture relative to the main direction of flow. Trapping of sediment could positively affect crabs by increasing the amount of labile material within burrows, acting as a sink for organic material and hence a food source for the organism (Botto et al. 2006).

Burrow permanency can be over 18 times greater in cohesive mud when compared to non-cohesive sand (Needham et al. 2010). As burrows collapse occurs as frequently as every 2 to 3 tides in sand, recent shifts in burrow density among treatments may also have lowered or modified erosion thresholds among treatments, increasing variance between replicates. This includes the zero burrow treatment as sediment was collected from within crab beds in each sediment type.

#### **4.4.2 Patterns of erodibility in mud**

As seen in the sand treatments, mud erosion rates and thresholds were decoupled as  $U_{crit}$  did not show any significant differences among burrow density treatments but a reduction in the total mass of sediment eroded (ME 0.35) was observed with increasing burrow density. Again, a reduction in variability among treatments was associated with increased sediment stability. Previous studies on burrow building organisms in muddy sediments have shown the opposite effect on sediment stability to that observed here, in that increased burrow density has resulted in amplified erosion rates (Fernandes et al. 2006, Widdows et al. 2009). However some stabilising effects by the worm *Nereis virens* at low flow velocities have been documented (Fernandes et al. 2006), although above  $U_{crit}$  a positive relationship between the mass of sediment eroded and organism density occurred. Organisms like nereidid worms which line their burrows with a mucous secretion, can actually increase erosion rates past that of unbound sediments once the surface integrity is compromised, as sediment aggregates are resuspended (Luckenbach 1987). As grapsid crabs do not line their burrows, it stands to reason that the processes governing erodibility will differ between these taxa.

Unlike in sandy environments, the greater presence of finer, lighter sediment particles in muddy sediment indicates bedload transport, and hence the proportion of material trapped in burrows, is likely to be reduced. Instead, material deposited at the sediment surface by crabs may serve to reduce erodibility. Crab activity and behaviour have also previously been hypothesised to play an important role in sediment transport. *Chasmagnathus granulata* (now *Neohelice granulata*) produces long lasting clay laden surface deposits, reducing erosion potential by creating a surficial barrier (Botto and Iribarne 2000). Similarly, *Austrohelice* does not pelletise cohesive muddy sediments when clearing its burrow, but instead sluices fine material from the burrow in a radial pattern around the burrow aperture as the tide ebbs. In the cohesive mud, bed shear stress was elevated in burrowed sediments, most markedly in the highest density treatment ( $400 \text{ m}^{-2}$ , Figure 4.3), even though a reduction in flow speed at the bed was measured (Figure 4.2d-e). Although this increase in shear stress may have been anomalous, due to the unavoidable close proximity of the ADV to burrow mounds and pits at this density, this indicated the potential for greater erosion existed despite a comparative reduction in ME 0.35.

Sediment cores were collected at low tide and were subjected to a 4 hour de-watering period prior to settling them in the flume. During summer months sand and mud flats in North Island New Zealand can reach temperatures in excess of  $25^{\circ}\text{C}$  (Read 1984, H. Needham *unpublished data*). Such temperatures may help consolidate the surficial layer, in essence ‘baking’ the clay sluice on to the surface, retarding erosion. Although rehydration of the cores occurred prior to each flume run, this increase in fine particles ( $< 63\mu\text{m}$ ) in the sediment matrix may bind and also smooth the surface, reducing drag at a micro scale. An

increase in burrow number would therefore increase the area over which this sluice layer covers, influencing stability. Having said this, only a marginal significant difference between the two burrowed sediment treatments was observed in mud despite a 4 fold increase in burrow density, indicating that a critical burrow mass may have already been reached at 100 ind. m<sup>-2</sup>.

#### **4.4.3 Between sediment differences at comparative burrow densities**

The two sediment types were deliberately chosen to reflect a dichotomy of sediment properties as erodibility generally relates to dry bulk density which is reduced through greater water and/or organic content (Amos et al. 1997). Cohesive muds generally retain more water on emersion than non-cohesive sands due to their lower porosity. Surficial biofilms, which are most often greater in fine muddy sediment, can also reduce evaporation potential at low tide and bind the sediment increasing stability (Underwood and Paterson 1993, Christie et al. 2000, Yallop et al. 2000).

Organic content in mud was double that of sand, but the lower variability between replicates in sand likely reflected uniformity through more frequent sediment mixing (Needham et al. 2010). Similarly chl *a* content (a proxy for microphytobenthos) in mud was also approximately double that of sand, however, across the two comparable treatments in both instances ME 0.35 was greater in mud. This indicates that, as previously seen for burrow builders, differences in chl *a* content is not necessarily a good indicator of stability (Riethmüller et al. 2000). Composition of the microphyte community is rarely explored in studies of this nature, but can also have significant effects on erodibility, as populations are likely to differ with sediment type. For example, the presence of diatoms at the

sediment surface can create high erosion thresholds by 'armouring' the sediment with their hard silica shells (Tolhurst et al. 2003). Detailed investigations of microphyte populations would therefore be greatly advantageous when comparing stability of different sediment types.

Although the mass of sediment entrained at a density of 100 burrows m<sup>-2</sup> showed similarity between sediment types, this most likely reflects the different modes by which sediment is transported in the two differing habitats. In muddy sediments lighter silt particles remain in suspension and once eroded were easily detected by the OBS. In sand much of the eroded material is transported as bedload and, when present, can be trapped in burrows. As sandy environments are often more dynamic than muddy areas, burrows act to reduce the amount of sediment transported from the system. This further highlights the need to determine structure-flow-sediment interactions between sediment types.

#### **4.5 Conclusions**

Sediment mediated differences in organism behaviour were likely to have contributed to sediment stability effects, through differences in burrow clearance techniques, burrow permanency and burrow aperture morphology between the two sediment types. As *Austrohelice* is active both in high and low tide periods, their physical presence at the sediment surface may also increase bed roughness beyond that seen in this experiment, further influencing sediment erodibility and transport. Studies which have considered sediment stability at wider scales have often yielded highly variable results, both spatially and temporally due to the numerous biotic and abiotic factors at play (Widdows et al. 2000, Widdows and Brinsely 2002, Lucas et al. 2003, Thrush et al. 1996). This study highlights some

of the complexities of small-scale sediment processes and the need to establish organism-sediment interactions amongst sediment types. Integration of such data will aid to elucidate patterns in sediment transport at greater spatial scales.

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## Chapter 5

### General summary and conclusions

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#### **5.1 Summary**

*Austrohelice crassa* has proven to be a key regulator of ecosystem processes in New Zealand estuaries by influencing its physical and biogeochemical surroundings. As such, this species contributes to the maintenance of ecosystem functioning and the consequent delivery of goods and services provided by these environments. This thesis highlights the value of assessing organism characteristics and behaviour alongside organism density in order to mechanistically investigate ecosystem level processes, as the degree to which *Austrohelice* influences both chemical and particle fluxes has proven to be highly context-specific.

Chapter 2 of this thesis was conducted primarily to elucidate organism-sediment interactions across natural sediment gradients. As much previously gathered information was either lacking or anecdotal, I set out to establish the ecological background of this organism and quantify natural history information for the purpose of integrating it in to ecosystem function based questions. By coupling a sequence of basic measurements and observations I was able to demonstrate that *Austrohelice* shows functional plasticity, a phenomenon not previously documented for this organism. This chapter also provides the first published records of burrow permanency and sediment reworking rates for this species. I

demonstrated that although *Austrohelice* creates burrows in each sediment environment, differences in organism density and burrow permanency drive shifts in the role of *Austrohelice* between sediment types. In cohesive sediments *Austrohelice* mainly increases sediment water interface augmenting habitat complexity, whereas in non-cohesive sediments *Austrohelice*'s primary role is that of a sediment mixer due to the frequency of sediment reworking. These differences in the bioturbational role of *Austrohelice* between sediment types indicated that the impact of the crab on ecosystem functioning was likely to be highly habitat dependent.

In Chapter 3, I tested the hypothesis that the functional plasticity of *Austrohelice* among sediment types would be reflected in measures of solute exchange; a process often used as a proxy for ecosystem functioning. *Austrohelice* regulated nutrient cycling, creating strong density driven effects on solute exchanges. Greater crab densities increased sediment O<sub>2</sub> demand and the flux of NH<sub>4</sub><sup>+</sup> from the sediment, indicating much of the response was physiologically driven. Clear interactions between *Austrohelice* and microphytobenthos were also detected in both habitats. Despite lowering microphyte standing stock through deposit-feeding, *Austrohelice* increased benthic primary production per unit of chlorophyll *a*, a phenomenon not previously described for this species. As hypothesised, this experiment also revealed important context-specific differences, most notably for NH<sub>4</sub><sup>+</sup> fluxes, which were higher in cohesive sediments where burrows and their associated microbial communities were most stable. This chapter highlights the need to integrate interactions between organism behaviour and habitat type into functional group studies to broaden conceptual frameworks and avoid oversimplification of highly complex organism-sediment interactions.

Burrow density also showed context-specific effects on particle fluxes in the two sediment types examined in Chapter 4. To the best of my knowledge, this is the first flume study to attempt to quantify the effects of crab burrows on sediment erodibility. Results were counterintuitive, particularly when compared with other bioturbating species. Increasing burrow density reduced sediment erodibility in cohesive muddy sediments, whilst in non-cohesive sands the presence of burrow structures had more complex effects. A unimodal pattern in the mass of sediment eroded ( $ME\ 0.35\ m\ s^{-1}$ ) occurred in sand, whereby sediment appeared least stable at low burrow densities. Such effects were linked back to the observations made in Chapter 2, in that the observed patterns were likely driven by the context-dependent interplay between organism and environment. Pelletisation of material in the sandy sediment increased bed roughness and slowed flow velocities with increasing burrow density, which did not adequately reflect the observed patterns in sediment erosion. The reduction in the mass of sediment eroded ( $ME\ 0.35$ ) at burrow densities of  $100\ m^{-2}$  was likely due to an increase in the trapping of bedload transported material by burrows. In the cohesive muddy sediments, a linear decrease in erosion associated with increased burrow density was attributed to the high concentration of fine particles (silt-clay) which are sluiced out of burrows on an ebbing tide, creating both a smoothing and consolidating effect on the sediment surface at a micro scale.

## ***5.2 Scaling up small-scale experiments to ecosystem-wide impacts***

Studies which solely address small-scale processes may be of limited value if their application to a wider ecological context cannot be demonstrated. Scaling up of controlled experiments can aid in answering both regional and sometimes globally

relevant questions and has been highlighted as a pressing, yet somewhat overlooked issue in ecological research (Schneider et al. 1997, Thrush and Lohrer *in press*). I wanted to test the feasibility of scaling up from my small-scale benthic chamber experiments detailed in Chapter 3, to system level nutrient exchanges in a small (~0.5 km<sup>2</sup>) estuarine inlet. To do this, water samples were collected from the constrained channel mouth of Pepe Inlet, Tairua, hourly for 48 h during summer. Net fluxes were calculated based on the difference in nutrient concentrations of water entering the estuary mouth on a flood tide and leaving on the ebb at the constrained channel opening. An FSI current metre logged speed, pressure, depth and direction of flow (see Appendix 2, section 2.1 for greater methodological detail and tables of results).

The calculated net input or export of nutrients of Pepe Inlet showed some agreement with the scaled chamber flux values (Tables A 2.1 and A 2.2). Due to the range in crab densities used in the manipulation experiment of Chapter 3, the span of scaled minimum, median and maximum values of each nutrient species (Table A 2.1) was relatively broad in each instance, always ranging from influx (min) to efflux (max). Net flux values were of the same order of magnitude as scaled chamber fluxes and often fell within the ranges predicted from the chambers.

*Austrohelice* density was only a significant predictor of NH<sub>4</sub><sup>+</sup> and PO<sub>4</sub><sup>3-</sup> (night) fluxes in Pepe Inlet (Chapter 3), therefore closer agreement between absolute values was expected for these nutrients. I predicted that Pepe Inlet would be a source of NH<sub>4</sub><sup>+</sup> in both daylight and at night due to the high densities of *Austrohelice* present throughout the inlet. Somewhat surprisingly this appeared

not to be the case in daylight. Scaled chamber fluxes showed a possible maximum efflux of 3.5 kg tide<sup>-1</sup> but also potential influx of 1.16 kg tide<sup>-1</sup> (Table A 2.1). However, net flux calculations showed an uptake by the inlet of 7.62 kg tide<sup>-1</sup> (Table A 2.2). Such differences indicate the high internal demand by microphytobenthos and other photosynthetic organisms during daylight despite some augmentation of NH<sub>4</sub><sup>+</sup> by *Austrohelice*. Although scaled chamber fluxes underestimated this demand, this pattern is still supported by the findings of Chapter 3. High microbial demand for this nutrient was indicated by consistent uptake of NH<sub>4</sub><sup>+</sup> by sediment at both low *Austrohelice* densities and in exclusion chambers in both daylight and at night.

Differences between flux rates calculated in the two ways described are not surprising considering that benthic chambers do not integrate tidal flow, which will undoubtedly influence reaction rates and porewater exchange in these sandy, advectively driven sediments. Chamber based experiments are therefore important tools for enabling insight in to the biological activities and mechanisms which drive geochemical changes, but direct scaling does not adequately represent the nutrient cycling processes at work in this habitat. Further replication over natural faunal communities and across a greater proportion of Pepe Inlet, as well as sampling of other nutrient sources will aid to build a more comprehensive picture of nutrient cycling at this spatial scale. However this ‘back of the envelope’ calculation is useful as it further demonstrates *Austrohelice*’s functional importance as a regulator of nutrient cycling and highlights where the focus of further work should be.

### ***5.3 Conclusions and suggestions for future research***

Collectively, the studies which constitute this thesis have shown the importance of incorporating environmental variability when assessing an organism's impact on ecosystem processes. Organism behaviour can be directly affected by the sediment environment, in turn altering the degree to which it contributes to ecosystem functioning. This is particularly important when considering larger bodied 'bioengineers' or those species present in high densities across a wide habitat spectrum. The degree to which functional plasticity, as expressed in *Austrohelice crassa*, exists in other key species requires further exploration, as studies which integrate behavioural differences between sediment types are lacking from the current literature. Observational studies, such as those carried out in Chapter 2 are infrequently conducted with ecological questions in mind, yet this information can often help to elucidate the sometimes counterintuitive or variable results from complex ecological systems at greater spatial and temporal scales (Hewitt et al. 2007). Indeed, the lack of integration of even the most basic natural history information has been highlighted as a major barrier for the development of the functional group concept (Pearson 2001, Petchey 2004) which is proving an important tool in the development of ecosystem-based management (Frid et al. 2008).

Working with a highly mobile organism such as *Austrohelice crassa* proved challenging when manipulating density. Caging experiments have in the past come under criticism through their potential to modify local flow dynamics (Nowell and Jumars 1984). Although I believe that 'cage effects' were minimal, given the lack of scour or difference in appearance of sediments inside and

surrounding the cages (Chapter 3), placing a structure in an otherwise structure poor environment is less than ideal (Dayton and Oliver 1980). Having said this, the merits of conducting a field based manipulative experiment still outweigh that of *ex-situ* laboratory manipulations, in that natural variability within the systems can be measured rather than controlled for. As the interactions between an organism and its environment are complex and non-linear, the ecological ‘noise’ captured through such experiments is insightful for establishing differing interactions and ecosystem responses between sediment types or locations.

As Tairua estuary was extensively sampled for this thesis, expansion of site level replication would be a desirable next step. Increasing the number of different sediment types within this design would also give greater indication of the generality of *Austrohelice*’s functional plasticity. Conducting crab density manipulations and *in situ* chamber experiments is logistically challenging, expensive and time consuming, often adding constraints to experimental design. As I was restricted to mid-afternoon high spring tides, further chamber experiments would have been staggered over several months, likely introducing confounding effects through differing environmental and temporal factors such as turbidity, light and water temperature (Webb and Eyre 2004). Ideally, to negate temporal shifts from spatial studies on a wider scale, sampling across locations should be done simultaneously or in very quick succession. Pragmatically, this is not often achievable, but by accounting for shifts in properties such as temperature, light and weather conditions in the statistical design of a study, much can be achieved.

Addressing, rather than omitting temporal shifts in *Austrohelice crassa* behaviour and hence their effect on both nutrient and particle fluxes would also increase our knowledge regarding the generality of *Austrohelice* impacts on ecosystem processes. All measurements conducted in this thesis were deliberately done in summer as *Austrohelice* are at their most active and the availability of photosynthetically active radiation (for the microphytobenthos) is highest. Therefore this likely represents the maximal effect of *Austrohelice* in Tairua Estuary. However, *Austrohelice* is found throughout New Zealand and is more likely to be affected by seasonality in the South, where variations in temperatures and light levels are much greater.

More detailed hydrodynamic mapping of flow around burrows at differing densities in both the horizontal and vertical plane may aid in visualisation of the near bed dynamics at differing burrow densities would be a logical 'next step' from the experiments of Chapter 4. Most importantly, bedload transported material should be quantified between burrow densities in both the flume and field to validate my hypothesis that deposition of sediment in burrows reduces the apparent erosion rate at high burrow densities in sand (Chapter 4). As *Austrohelice crassa* burrows are morphologically diverse, care in creating realistic field deployable burrow arrays will be a crucial development.

Potential differences in both the intensity and quantity of sediment processed by *Austrohelice* whilst feeding may influence sediment disturbance through organism mobility and particle sorting. These factors are likely to contribute to both the observed differences in nutrient fluxes and the erodibility of surficial sediments between cohesive and non-cohesive sediments. *Austrohelice* is an adaptive and

opportunistic feeder, utilising an array of decaying organic matter sources including macroalgae, macrofauna and seagrass when available (Beer 1959, Fielder and Jones 1978, Hailes 2006). Further exploration of *Austrohelice*'s feeding strategies between sediment types using stable isotope analysis may therefore highlight differences in the energetic cost of living in more dynamic versus more static sedimentary environments. Coupling this with burrow morphometrics and bedload transport information may also address the importance of trapped material as a supplementary food source for *Austrohelice* between habitats.

Previous studies have suggested that lower intertidal areas are not inhabited by *Austrohelice* due to its inability to maintain burrows in poorly drained sediments. Saunders (1999) found *Austrohelice* to be an important component of the flounder, *Rhombosolea leporina* diet, particularly during summer, with others reporting remains of *Austrohelice* in both benthic and pelagic fish (Graham 1939, Kilner 1974, King and Clark 1984). Therefore shore position may also be linked to predator evasion, through reduction in submergence time. *Austrohelice* is one of the few mid to high intertidal crabs that is not physiologically adapted to spending long periods out of water as it does not have the accessory respiratory structures to facilitate uptake of atmospheric oxygen (Hawkins and Jones 1982). Consumption rates by land based predators such as gulls (*Larus* spp) and kingfisher (*Halcyon sancta*) have not been quantified. Future studies on the trophic links of *Austrohelice* and the benthic pelagic and even terrestrial environments would therefore be of value.

Very few other large bioturbating fauna were found to reside within *Austrohelice* beds in Tairua estuary. This thesis has demonstrated how *Austrohelice* modifies the sediment environment through its activities, altering sediment stability and disturbance to differing degrees associated with sediment type and density. This absence, particularly of filter feeding fauna, lends itself to the trophic group amensalism hypothesis (Rhoads and Young 1970) whereby sensitivity to *Austrohelice* induced disturbance results in physical separation of differing trophic modes.

Smothering of estuarine faunal communities following deposition of terrestrial sediments of considerable magnitude have been observed in New Zealand (Norkko et al. 2002, Thrush et al. 2003, Gibbs et al. 2001) primarily due to changes in land use. *Austrohelice* has been highlighted as the primary remediation species as it quickly colonises terrigenous clay caps (Thrush 2003). Although *Austrohelice* may aid oxygenation and turnover of sediment, mitigating effects of the terrigenous deposits, they have been shown to inhibit recovery of the former surface sediment assemblages and are likely to have a negative effect on colonists due to both feeding and sediment disturbance (Thrush 1988, Botto and Iribarne 1999, Thrush et al. 2003). Susceptibility is likely to be species specific, but indications are that such events may create long term regime shifts as increases in size, density and biogenic structures are often considered as a classical end point to successional change in soft sediment communities (Pearson and Rosenberg 1978). Indeed Norkko et al. (2002) found that in areas with low hydrodynamic flow community composition had not recovered after 408 days of monitoring. Shifts in community composition of this magnitude are likely to have consequential effects on ecosystem functioning and warrants further research.

### **5.3.1 Relevance to ecosystem based management**

In the advent of the ecosystem approach to marine monitoring and management, much headway has been made into assessing the functionality of benthic assemblages by analysing the particular types of organism trait groups that are present. Yet standardising methods for classification is fraught with problems due to the complexities of organism-sediment interactions (Gerino et al. 2003). This problem is not explicitly associated with marine benthos but instead is shared across animal ecology (Blaum et al. 2011). Petchey and Gaston (2006) proposed studies should focus on traits that were important to a specific function of interest when constructing functional groups, ignoring others which were deemed functionally uninformative. As such, in future research nutrient fluxes themselves could be used as a functional trait whereby species are classified by their impact on nutrient cycling among habitats. However, although the number of ways to group organisms in to functional components is expanding, ultimately without understanding variations in organism function at a species level, the degree of accuracy and predictive power of generated models will be limited.

Successful ecosystem based management relies on integration of research conducted across all levels of ecological organisation, as it recognises that ecosystem processes operate over wide spatial and temporal scales and must be managed accordingly (Christensen et al. 1996). Therefore observations and small scale experiments such as those conducted in this thesis are insightful, but to increase their generality, should be nested in to greater frameworks to assess how broad scale spatial and temporal processes interact with the observed outcomes (Thrush et al. 1996, Hewitt et al 1998). However, such long term extensive work

is outside the remit of this PhD thesis, but provides an exciting avenue I hope to explore as my career in ecology develops.

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## Appendix 1: Sediment properties Chapter 3

**Table A.1.** Sediment surface properties at each site.

Site	<b>Crab</b>						
	density (0.25 m <sup>-2</sup> )	Chl a (µg g <sup>-1</sup> dw)	Phaeo (µg g <sup>-1</sup> dw)	Porosity (p)	TOM (%)	Silt-clay (%)	Grain size (µm)
<b>S</b>	24	9.89	20.28	0.60	4.41	11.7	173
	2	10.68	27.57	0.62	5.11	17.6	155
	6	8.87	23.47	0.56	4.33	13.4	172
	13	8.73	22.79	0.62	4.36	17.4	150
	14	11.05	23.63	0.60	4.53	13.7	161
	2	9.74	24.58	0.59	3.99	14.5	166
	20	8.28	29.93	0.59	4.37	12.2	181
	2	10.50	28.68	0.60	5.20	15.2	171
	29	5.69	14.11	0.59	3.68	11.2	175
	19	4.98	13.18	0.54	3.77	12.4	177
	0	13.15	29.25	0.58	4.27	16.1	166
	11	8.95	18.22	0.57	3.33	10.2	198
	0	10.50	21.03	0.54	4.56	18.8	147
	28	6.45	16.71	0.56	3.35	11.3	194
	9	11.03	19.75	0.56	3.55	16.7	166
7	10.04	16.14	0.50	3.28	15.8	174	
<b>MS</b>	3	12.73	14.65	0.70	4.72	47.0	80
	0	15.03	25.04	0.75	6.64	30.7	107
	14	10.40	14.66	0.66	4.51	35.1	125
	12	6.38	7.35	0.52	2.95	33.0	156
	8	7.97	4.39	0.56	3.17	26.6	153
	27	6.48	6.83	0.58	3.29	29.2	136
	0	13.02	23.00	0.74	6.16	42.2	111
	7	7.33	7.05	0.54	2.99	42.9	115
	16	4.77	6.10	0.54	2.56	47.2	145
	3	5.42	10.63	0.57	3.53	37.2	102
	11	6.64	5.48	0.55	3.24	23.3	153
	0	10.53	9.58	0.59	3.21	61.0	114
	17	5.57	5.98	0.53	3.09	29.8	174
	17	5.55	7.15	0.50	2.65	40.7	134
	6	4.60	10.75	0.52	2.58	41.0	155

TOM: total organic matter; Chl *a*: sediment chlorophyll *a* concentration; phaeo: sediment phaeophytin concentration

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## Appendix 2

### Scaling Exercise

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#### ***A 2.1 Scaling nutrient fluxes***

To estimate the total flux of nutrients from Pepe Inlet, Tairua water samples were collected hourly for 48 h using an ISCO automated water sampler. An FSI current meter, positioned 40cm above the channel bed logged speed, pressure, depth and direction of flow (burst cycle of 5 minutes every 15 minutes at 4 Hz). Vertical profiles of salinity and temperature were taken from the middle of the narrow channel mouth hourly. Samples were kept cool inside the sampler with ice and collected at the end of a 24 h period, filtered through a Whatman GF/C filter into acid washed bottles and frozen. Nutrient analyses followed the methods detailed in section 3.2.3

As Pepe Inlet drains completely on a spring tide (Figure A 2.1), the tidal flux can be calculated as the difference between nutrient concentrations of water entering the estuary mouth on a flood tide and leaving on the ebb. The total volume of water entering and leaving the estuary was estimated by summing the hourly water volume (channel area \* water velocity) over each ebb and flood. Mean nutrient concentrations over the 3 h of peak ebb and flood flows were used to approximate the flux of nutrients in to and out of the inlet. Solute fluxes from Pepe Inlet were then estimated by multiplying the average peak flow concentration by the mean volume of water entering and leaving the inlet during a

tidal cycle. Sampling was conducted over a midday/midnight high tide so that the flux of nutrients in both daylight and at night could be kept distinct, being most similar to the flux chamber measurements. To simplify this ‘back of the envelope’ exercise, factors such as groundwater seepage, rainfall and riverine inputs, suspended sediment and salinity were not integrated in to this calculation. Flux chamber nutrient values were scaled to the surface area of Pepe inlet (determined through GIS) and tidal emersion period.



**Figure A 2.1.** Aerial view of Pepe Inlet, Tairua. White box denotes sampling station. Image courtesy of Google Earth.

## A 2.2 Results

**Table A 2.1.** Tidal fluxes of nutrients as measured from the channel mouth of Pepe Inlet Tairua. Negative net fluxes indicate an export of nutrients from the inlet.

		Nutrients (kg tide <sup>-1</sup> )		
		NH <sub>4</sub> <sup>+</sup>	NO <sub>x</sub> <sup>-</sup>	PO <sub>4</sub> <sup>3-</sup>
<b>daylight</b>	input	33.29	12.38	10.86
	output	25.67	8.12	11.85
	<b>net flux</b>	<b>7.62</b>	<b>4.25</b>	<b>-0.99</b>
<b>night</b>	input	29.11	12.45	10.38
	output	31.11	9.02	10.85
	<b>net flux</b>	<b>-2.00</b>	<b>3.43</b>	<b>-0.47</b>

Direct flux measurements showed Pepe Inlet to be a sink for ammoniacal nitrogen (NH<sub>4</sub><sup>+</sup>) during the day, but a source of NH<sub>4</sub><sup>+</sup> at night, further demonstrating the influence of microphytobenthos on nutrient cycling (Table A2.1). This is supported by my findings in Chapter 3, whereby high internal microbial demand for this nutrient was indicated by consistent uptake of NH<sub>4</sub><sup>+</sup> by sediment at both low *Austrohelice* densities and in exclusion chambers (day and night). In the benthic chambers regulation of NH<sub>4</sub><sup>+</sup> flux was mediated through *Austrohelice* excretion and bioturbation. Measured net uptake of 7.62 kg NH<sub>4</sub><sup>+</sup> tide<sup>-1</sup> in Pepe Inlet indicates that demand exceeds supply in this system during daylight, despite *Austrohelice* contributions being estimated at up to 3.5 kg tide<sup>-1</sup> at crab densities of 116 ind m<sup>-2</sup> (Table A.2.1). Median flux values, at densities which are most similar to a large proportion of this estuary (48 ind. m<sup>-2</sup>, see Figure 2.4), were however, much lower (0.003kg tide<sup>-1</sup>). Overall, in daylight *Austrohelice* bioturbation buffers the sink of NH<sub>4</sub><sup>+</sup> in this inlet by increasing supply for internal

processes. Tidal export ( $2 \text{ kg tide}^{-1}$ ) was almost double that observed at median crab densities in chambers ( $1.04 \text{ kg tide}^{-1}$ ) at night, but much lower than the predicted maximum of  $5.4 \text{ kg tide}^{-1}$ . However despite the lack of photosynthesis, some microbial utilisation is also inferred through the scaled chamber fluxes at low *Austrohelice* density. Therefore without the presence of *Austrohelice*, this system is likely to be highly  $\text{NH}_4^+$  limited.

**Table A 2.2.** Maximum and minimum nutrient fluxes from experimental chambers containing populations of *Austrohelice crassa* (Chapter 3) over one tidal inundation. Values encompass the range of crab densities used in the experiment ( $8 - 116 \text{ ind. m}^{-2}$ ) and are scaled to estuary size ( $\sim 0.45 \text{ km}^2$ ). Positive values indicate efflux of nutrients from the sediment.

	Chamber fluxes scaled to inlet size ( $\text{kg tide}^{-1}$ )		
	$\text{NH}_4^+$	$\text{NO}_x^-$	$\text{PO}_4^{3-}$
day min	-1.16	-1.13	-0.95
day median	0.003	0.27	-0.05
day max	3.46	1.31	1.21
night min	-1.30	-1.89	-1.14
night median	1.04	0.15	-0.10
night max	5.40	1.57	1.75

Pepe Inlet acted as a sink for  $\text{NO}_x^-$  in both daylight and at night, showing similar net flux rates in each instance. These results also indicate that denitrification rates likely surpass nitrification rates. Although this statement requires quantitative validation, previous studies of bioturbating crustaceans have also seen this effect due to the increasing microbial biomass of burrow walls (Webb and Eyre 2004, Botto et al. 2005). Denitrification rates are often witnessed to be greater than nitrification rates in marine sediments, resulting in little diffusion of  $\text{NO}_3^-$  across

the sediment-water interface. Similarly, scaled chamber fluxes showed little difference in  $\text{NO}_x^-$  fluxes between daylight and at night but no correlations between *Austrohelice* density and the flux of either  $\text{NO}_2^-$  or  $\text{NO}_3^-$  were found (Figure 3.3 a, b). Therefore the observed net uptake may potentially be driven by other biota in Pepe Inlet.

Patterns associated with  $\text{PO}_4^{3-}$  flux as a function of crab density were not evident from the benthic chambers in daylight (Figure 3.3c). However, at night increasing  $\text{PO}_4^{3-}$  efflux was associated with increasing crab density reaching a maximum flux of  $1.75 \text{ kg tide}^{-1}$ . At a system scale, a net export of  $\text{PO}_4^{3-}$  was observed both in daylight and at night being, somewhat surprisingly, approximately twice as high during the day ( $0.1 \text{ kg tide}^{-1}$ ). Nevertheless, these values were within the observed range of chamber flux rates (day;  $-0.95$  to  $1.21$ , night;  $-1.14$  to  $1.75$ ) and are therefore assumed to reflect actual processes in the inlet. Obviously, this exercise oversimplifies the system level biogeochemical processes at work, as other key sources and sinks of nutrients have largely been overlooked. One key factor may be the location of this inlet as coastal water passes over a large expanse of sandflat before arriving at Pepe Inlet where nutrient loading may be augmented before entering the inlet.