The lugworm *Abarenicola affinis* (Arenicolidae, Polychaeta) in tidal flats of Otago, southern New Zealand.

Stefan Görlitz

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I had a false belief…I thought I came here to stay…

we're all just visiting…all just breaking like waves…

the oceans made me…but who came up with love? E.V.

Table of Contents

Abstract

Lugworms (Polychaeta: Arenicolidae) occur in coastal sediments worldwide and can dominate the macrofauna of intertidal sand and mud flats. They have been recognised as ecosystem engineers due to their bioturbating and bioirrigating activities, which can profoundly influence sediment properties and other biota. In view of the potentially significant role of lugworms, the present study examined aspects of the biology and ecology of the endemic lugworm *Abarenicola affinis* in coastal environments of southern New Zealand.

Abarenicola affinis occur in tidal inlets along the Otago coast with a patchy distribution. Mean abundance ranged between 4 and 21 individuals per m^2 across four different tidal flats (Papanui, Hoopers, Purakaunui inlets, and Harwood in Otago Harbour), resulting in an overall mean abundance of 11 individuals per m^2. Two investigated lugworm populations in neighbouring inlets were stable across seasons, but exhibited differences in terms of their spatial distribution, biomass, body size, and burrow depth. Lugworm populations appeared to be limited by intertidal seagrass (*Zostera muelleri*), which had a significant negative influence on *Abarenicola affinis* abundance and biomass in one inlet. In laboratory experiments, seagrass root-rhizome matrices imposed restrictions on the burrowing ability of *Abarenicola affinis* but did not prevent lugworms from burrowing and feeding similar to those in unvegetated sediment. Lugworms in seagrass treatments, particularly small individuals which stayed within the root-rhizome matrix, processed less sediment than those in unvegetated treatments, suggesting that they may have exploited seagrass detritus as an additional food source. Sediment turnover by *Abarenicola affinis* was found to be stable over seasons, with lugworms being mostly active

when burrows were submerged during high tide. Defaecation frequencies were shorter for small lugworms than for large ones, whereas the faecal amounts increased with increasing lugworm size. An annual sediment turnover estimate for an intertidal *Abarenicola affinis* population was calculated at 24.4 kg sediment dry weight per m^2, equivalent to a sediment depth of 2 cm. Habitat modification by lugworms had little influence on the macrofaunal assemblage composition in one tidal flat, and abiotic factors such as tidal level and proportion of sediment fines best explained assemblage patterns. Manipulative small-scale exclusion of lugworms from otherwise densely populated areas did not result in significant changes in macrofaunal assemblages, but showed a subtle promotional effect of *Abarenicola affinis* on abundance of macrofauna, in particular dominant amphipods, at one of two sampling occasions. The effect was inferior to the high spatial variation in macrofaunal assemblages at the other sampling occasion.

The study indicates that the impact of *Abarenicola affinis* on sediment and associated biota is spatially dependent and may be generally weak. As the distribution of this species is influenced by abiotic and biotic habitat variables, those factors will have, in turn, a profound influence on its engineering capacity. *Abarenicola affinis* does not reach the dominance and ecological importance as documented for lugworm species in other parts of the world (e.g. *Arenicola marina* in Europe), due to smaller and patchier populations, relatively smaller sediment turnover capacity, and less distinct influences on macrobenthic infauna. Future research is needed to gain more information on the species' population dynamics, and to elucidate ways in which these lugworms interact with their abiotic and biotic environment in coastal ecosystems of New Zealand.

List of Figures and Boxes

List of Tables

Chapter 1 - General introduction

Taxonomy, morphology and global distribution of lugworms

The present thesis investigates the role of the marine lugworm *Abarenicola affinis* in tidal inlets of Otago, southern New Zealand. *Abarenicola affinis* is a member of the Arenicolidae, a small family of polychaetes that has a worldwide distribution (Wells 1964; Hutchings 2000). Arenicolidae are marine burrowing worms that live in coastal soft sediments, particularly of tidal flats, inlets and estuaries. To date, around 30 nominal species have been described, but the status of many (geographical) subspecies remains unclear (Rouse & Pleijel 2001). Arenicolidae comprises the four genera *Abarenicola*, *Arenicola*, *Arenicolides* and *Branchiomaldane*, of which the former two are caudate forms, i.e., they possess a non-setigerous tail, whereas the latter two are non-caudate forms, i.e., without tails (Wells 1959). The caudate genera *Abarenicola* and *Arenicola* are commonly known as lugworms and comprise most of the species within the Arenicolidae (Wells 1959). The phylogenetic position of the caudate genera within the Arenicolidae is not entirely clear. Based on morphological observations, they have been proposed to be an evolutionary derived group of the family (Bartolomaeus & Meyer 1999). In contrast, a recent genetic study indicates a greater genetic distance between *Abarenicola* and *Arenicola* than between *Arenicola* and the non-caudate forms *Arenicolides* and *Branchiomaldane* (Bleidorn *et al.* 2005). Although the two lugworm genera, *Abarenicola* and *Arenicola*, have many morphological features in common (Box 1), they have been separated on the basis of differences in the prostomium, mechanism of proboscis movement, number of oesophageal caeca, and position and length of the neuropodia (Wells 1959).

The genetic and morphological differences between *Abarenicola* and *Arenicola* are reflected in their separate global distribution. Taxonomic and geographic studies classified the global distribution of lugworms according to three large zones: a northern cool water zone, a central warm water zone and a southern cool water zone (Wells 1963, 1964). The boundaries between these zones correspond to the summer surface-water isotherms at 20°C. The temperature barriers of the water zones are the most likely factor impeding dispersal, resulting in endemic clusters of species in each zone. With few exceptions, *Abarenicola* species are confined to the southern hemisphere, whereas most *Arenicola* species occur in cool waters of the northern hemisphere. Wells (1963) also stated that species that are found in southern cool waters all belong to the genus *Abarenicola*. Nevertheless, the hypothesis of isotherms acting as physical barriers needs revision, as the southern Pacific lugworm *Abarenicola affinis chiliensis* has been shown to disperse from the cool water zone of southern South America to the warm water zone of northern South America (Moreno *et al.* 2007).

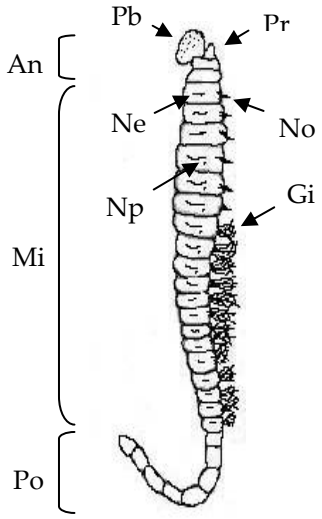
The first ecological studies on lugworms date back more than one hundred years (e.g. Ashworth 1903). To date, lugworms are one of the most researched organisms of tidal flat benthos, especially the North Atlantic species *Arenicola marina* (e.g. Wells 1966; Beukema & de Vlas 1979; Reise 1985; Riisgard & Banta 1998), and its North Pacific equivalent *Abarenicola pacifica* (e.g. Healy & Wells 1959; Swinbanks 1981; Krager & Woodin 1993; Linton & Taghon 2000). *Arenicola marina* populates approximately 70 to 90% of the European Wadden Sea (comprising several thousand km²) and is present throughout the entire tidal gradient (Beukema 1976; Reise 1985). The species accounts for a considerable amount of macrobenthic biomass (15 to 30%) and differs from other tidal flat

organisms such as bivalves and crustaceans by having relatively stable populations over time (Beukema *et al.* 1993; Flach & Beukema 1994; Reise *et al.* 1994; Reise *et al.* 2001). Whereas lugworms dominate tidal flats on the East Atlantic coast, they are less dominant on the West Atlantic and East Pacific side in the northern hemisphere (Reise 2002). In the eastern Pacific, the species *Abarenicola pacifica* and *Abarenicola vagabunda* occur in tidal bays of northern America (Kozloff 1983), but are mainly found in population patches with distinct boundaries (Healy & Wells 1959; Hobson 1967; Swinbanks & Murray 1981). Although lugworms appear also widespread along ocean coasts of the southern hemisphere, e.g., *Abarenicola affinis chiliensis* in Chile and *Arenicola loveni* in South Africa, they have been less researched in these parts of the world (Wells 1963; Lewis 2005; Moreno *et al.* 2007).

Box. 1. Morphology of lugworms (Abarenicola, Arenicola, Polychaeta)

Lugworms have a fully segmented body with a robust epidermis. The setigers are present as capillary notopodia (No), which support movement in the burrow, and hooked neuropodia (Ne), which are used to grip to the burrow wall. The body is externally divided into three regions. The anterior region (An) consists of the prostomium (Pr), the peristomium from which the papillae covered proboscis (Pb) is everted for burrowing and feeding, and a few non-setigerous segments. The middle region (Mi) is characterised by setigerous segments, most of them with branched, tufted gills (Gi) associated with the notopodia. The posterior region (Po) is without setigers and gills. The worms lack any kind of appendices. Adult lugworms range from 2.5 to 25 cm in body length, but larger specimens have been reported. Lugworms are gonochoristic. Gametes develop in the coelomic cavity and will be released through the nephridiopores (Np).

(Wells 1962, 1963; Cadman & Nelson-Smith 1993; Riisgard & Banta 1998; Bartolomaeus & Meyer 1999).



Box 1. Morphology of lugworms (*Abarenicola*, *Arenicola*, Polychaeta).

Lifestyle and trophic role of lugworms

Despite morphological and geographical differences, all lugworms have a similar lifestyle (Wells 1964; Fauchald & Jumars 1979; Rouse & Pleijel 2001). They are subsurface deposit-feeders living in intertidal and shallow subtidal soft sediments where they construct and occupy mucus-lined J-shaped burrows of up to 40 cm depth (Fig. 1). At the lower end of the tail shaft of the burrow the lugworm resides in a "feeding pocket" (Reise 1985). Burrows are completed to a U-shape when headward irrigation by the lugworm creates an upward flow of porewater and loosens the sediment, resulting in a sinking column of particles, namely the head shaft (Hobson 1967; Riisgard *et al.* 1996; Reise 2002). Lugworms feed upon the subsiding surface and subsurface sediment, as they digest organic matter associated with sediment grains and interstitial water (Hylleberg 1975; Riisgard & Banta 1998). The main components of their diet are microalgae and to a lesser extent meiofauna, bacteria and digestible detritus (Zebe & Schiedeck 1996; Andresen & Kristensen 2002; Leduc *et al.* 2006). The processed sediment is defaecated on the sediment surface in the form of coiled strings, which form a characteristic faecal cast (Fauchald & Jumars 1979; Reise 1985). Through their feeding and burrowing activity, lugworms turn over a substantial amount of sediment (Swinbanks 1981; Retraubun *et al.* 1996), e.g., equivalent to a sediment depth of up to 33 cm per year for *Arenicola marina* (Cadée 1976). At the sediment surface, pits and mounds, caused by subsiding sediment and accumulating faecal strings, generate a distinct landscape, the "lugworm flat" (Reise 1985). Respiration is achieved by a peristaltic movement of the worm body, pumping oxygenated water from the overlying water column into the burrow (Riisgard *et al.* 1996; Riisgard & Banta 1998; Meysman *et al.* 2005). This irrigation has also been shown to stimulate subsurface bacterial

growth which, in turn, facilitates microorganisms including those on which lugworms feed (see "concept of gardening" by Hylleberg 1975). Feeding, defaecation and irrigation are combined into an activity cycle that alternates with periods of rest (Wells 1953).

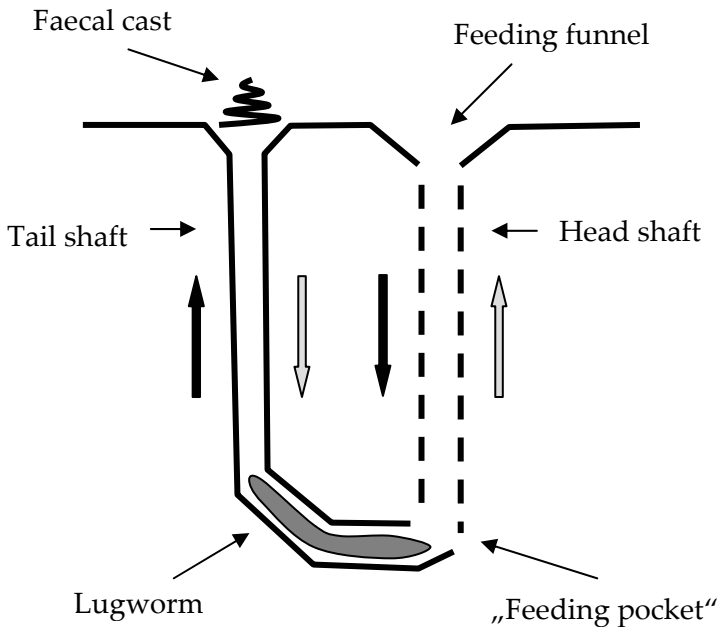


Fig. 1. Schematic presentation of a lugworm burrow. The arrows indicate the primary transport of particles (closed) and porewater (shaded) between sediment and overlying water through the tail shaft (mucus-lined, open) and the head shaft (permeable, sand filled) by feeding (upward flow of porewater and downward movement of sediment in the head shaft), defaecation (upward movement of sediment in the tail shaft) and irrigation (downward flow of porewater in the tail shaft) of the lugworm.

Due to their deep burrowing lifestyle, lugworms are able to avoid predation on tidal flats most of the time, except when they are defaecating on the sediment surface (Reise 1985). Whilst defaecation, lugworms are exposed to browsing ebb and flood predators regularly visiting intertidal flats, e.g., foraging fish and

decapod crustaceans when the tide is in, and coastal birds when the tide is out: all of which are mostly cropping the tail tips of lugworms, i.e., tail-nipping (de Vlas 1979; Bergman 1988; Hulscher 1996). Lugworms constitute a significant food source for these predators, e.g., approximately 10 to 30% of the annual production of *Arenicola marina* is removed by predation, and tail tips of this species have been found to contribute 22% to the total food intake of plaice (*Pleuronectes platessa*) in the Dutch Wadden Sea (de Vlas 1979). The tail loss is compensated by an increase in the length of the remaining tail segments. This compensation is important for the lugworm as the tail stores faeces, i.e., the longer the tail the less often lugworms have to defaecate and, consequently, the lower is the risk of predation (de Vlas 1979).

Ecosystem engineering by lugworms

In addition to playing an important trophic role in the tidal flat food web, lugworms are also important as physical ecosystem engineers (Riisgard & Banta 1998; Reise 2002). The concept of ecosystem engineering describes relationships between organisms and their environment that are not directly trophic or competitive (Jones *et al.* 1994). Ecosystem engineers are defined as those species that directly or indirectly modify habitat resource flow by causing state changes in the biotic and abiotic environment (Jones *et al.* 1994). Either by their physical presence (autogenic engineers) or by their activity (allogenic engineers), ecosystem engineers generate, modify and maintain habitats of different characteristics from the surrounding environment (Jones *et al.* 1994; Hastings *et al.* 2007). Prominent examples from marine tidal flats are seagrass and mussel beds (autogenic) and organisms that cause sediment disturbance such as

lugworms or thalassinid shrimps (allogenic). These organisms have a considerable influence on the habitat suitability for other species and, thereby, shape benthic community structures (e.g. Reise 2001, 2002; Berkenbusch & Rowden 2003; Bouma *et al.* 2009; Buschbaum *et al.* 2009).

In recent decades, investigations have increasingly focused on the role of lugworms as ecosystem engineers (e.g. Riisgard & Banta 1998; Volkenborn *et al.* 2007a; Wethey *et al.* 2008). The effects of lugworms on physical, chemical and biological sediment properties have been mainly studied for *Arenicola marina* (e.g. Huettel 1990; Riisgard *et al.* 1996; Kristensen 2001; Volkenborn *et al.* 2007a). Bioturbation and bioirrigation by this species displace both particles and porewater within the sediment and facilitate a close link between sediment and the overlying water column (Meysman *et al.* 2005; Volkenborn *et al.* 2007b). For example, selective swallowing of fine particles results in concentrations of coarser particles at lugworm feeding depth, while fine grains are defaecated on the sediment surface where they get resuspended by tidal currents and wave action (Baumfalk 1979; Retraubun *et al.* 1996; Zebe & Schiedeck 1996). The irrigation of the burrow oxygenates sediment to a depth where it would otherwise be anoxic and flushes out porewater nutrients and toxic metabolites (sulphides), which are replaced by oxygen-rich and nutrient-poor water from above the surface (Huettel 1990; Riisgard *et al.* 1996; Banta *et al.* 1999; Kristensen 2001). The pumping activity of lugworms also results in an advective flow of porewater through the permeable parts of the burrow, i.e., the "feeding pocket" and head shaft, from where it radiates in an upward direction (Meysman *et al.* 2005; Wethey *et al.* 2008). These hydraulic activities, namely bioadvection, can have conspicuous effects on sediment properties, biogeochemistry and other biota, and have been recently regarded as an engineering process independent

of bioturbation (Woodin *et al.* 2010). The effects of bioturbation and bioirrigation by lugworms are not confined to the vicinity of their burrows. Meso-scale and long-term experiments with *A. marina* revealed that this species may contribute to the maintenance of permeable sand and inhibits the succession of intertidal habitats from sandflats with low organic content towards organic-enriched mud flats (Volkenborn *et al.* 2007a, 2007b). Also, the spheres of lateral porewater advection, which extend multiple body lengths, may overlap in high densities of burrows resulting in a continuous area of porewater replacement at depth (Whethey *et al.* 2008).

The habitat modifications caused by lugworms influence the associated tidal flat benthos in both positive and negative ways (Riisgard & Banta 1998; Reise 2002; Volkenborn & Reise 2007). The sediment disturbance by lugworms decreases sediment stability and, thus, has a negative effect on some sedentary macrofauna such as tube-building amphipods and other polychaetes, e.g., by destroying their tubes and burrows and / or burying them under sediment (Brenchley 1981; Wilson 1981; Brey 1991; Flach 1992). As a consequence, the disturbed sediment is avoided by juveniles of many sedimentary benthic species of bivalves, amphipods and polychaetes (Brenchley 1981; Woodin 1985; Flach 1992). Furthermore, lugworm sediment reworking may inhibit the establishment of seagrass by burying the plants and seeds (Phillipart 1994; van Wesenbeeck *et al.* 2007). The surface structures generated by lugworms, i.e., feeding funnels and faecal casts, are avoided by most infauna due to their instability, but small mobile fauna such as copepods may accumulate in funnels during low tide exposure (Reise 1981; Wilson 1981). Also, the halo around fecal casts may attract small amphipods as they feed on organic particles flushed into the interstitial system of the cast sediment by above-ground currents (Huettel &

Gust 1992; Huettel *et al.* 1996; Lackschewitz & Reise 1998). The oxygenated burrows tend to increase abundance of small benthos as they attract meiofaunal and some macrofaunal species, e.g., nematodes, plathelminthes and amphipods, which have been shown to populate distinct sections of the burrow (Reise 1985; Lackschewitz & Reise 1998; Reise 2002). Burrow walls have been identified as locations of increased bacterial production and microheterotrophic activity in comparison to the sediment surface (Reichardt 1988). Similar to their impact on sediment properties, lugworm effects on the benthic community extend beyond burrows (Volkenborn & Reise 2006, 2007; Kuhnert *et al.* 2010). For example, *Arenicola marina* has been found to induce a functional shift in the benthic polychaete-community from assemblages dominated by suspension and surface deposit-feeding tube-builders to assemblages dominated by subsurface deposit-feeding discretely motile polychaetes (Volkenborn & Reise 2007).

Lugworms in New Zealand

In contrast to the extensive research in other parts of the world, relatively little is known about lugworms in the soft-sediment environments of New Zealand. Ashworth (1903) first described a New Zealand lugworm specimen, collected from Otago Harbour (Dunedin, South Island) that closely resembled a lugworm species known as *Arenicola assimilis* at that time. Based on his own morphological examinations and inadequate information about *Arenicola assimilis*, Ashworth named the New Zealand species A*renicola assimilis var. affinis*. Wells (1963) re-examined the specimen in question from Ashworth's collection and assigned it to a new species, *Abarenicola affinis affinis*, a subspecies

of the lugworm known as *Abarenicola affinis* at the time. He also re-defined two other lugworm species occurring in New Zealand, one collected from Plimmerton (Wellington, North Island) and one collected from subantarctic islands (Auckland Island, Campbell Island) as subspecies of *Abarenicola assimilis*, and named them *Abarenicola assimilis devia* and *Abarenicola assimilis insularium*, respectively. In recent taxonomic literature, the three geographic subspecies defined by Wells (1963) have been given species rank: *Abarenicola affinis* (endemic to the mainland of New Zealand), *Abarenicola devia* (in New Zealand and Australia) and *Abarenicola insularum* (on subantarctic islands of New Zealand and Australia, and Kerguelen Islands, Indian Ocean, France) (Glasby & Read 1998; Glasby *et al.* 2009). The former two, which both occur on the mainland of New Zealand, are morphologically distinguishable by the enlarged annuli of the first three setigers in *Abarenicola affinis*, whereas in *Abarenicola devia* the parapodial annuli are all of similar size (Wells 1963).

The lugworm *Abarenicola affinis* (Fig. 2) is sparsely distributed along the New Zealand coast (Wells 1963). Local populations have been reported from Manukau Harbour and Petone Beach in the North Island (Wear 1962; Wells 1963; Glasby *et al.* 2009), but these colonies appear to have declined in recent years and *Abarenicola affinis* is rarely found in its former habitat (Glasby *et al.* 2009; D Bell, G Read both pers. comm.). In the South Island, *Abarenicola affinis* has been reported from a greater number of locations than in the North Island, including Akaroa Harbour, Otago Harbour, Papanui Inlet, Hoopers Inlet, Blueskin Bay and Stewart Island (Wells 1963; Leduc *et al.* 2006; K Probert, G Read both pers. comm.).

Fig. 2. *Abarenicola affinis* (~ 60 mm total length) and faecal cast landscape in Hoopers Inlet, southern New Zealand.

Relatively little is known about the biology and ecology of *Abarenicola affinis* with published research mostly limited to anatomical and morphological descriptions (Ashworth 1903; Wear 1962; Wells 1963), and a series of physiological studies, which examined respiration characteristics (Barrow & Wells 1982; Wells 1982; Chadwick *et al.* 1984) and blood cells (Wells & Pankhurts 1980; Chung & Ellerton 1981). More recently, *Abarenicola affinis* has been included in a dietary study of intertidal benthos in southeastern New Zealand, and the species has been shown to feed mainly on microphytobenthos

and seagrass detritus (Leduc *et al.* 2006). In Otago Harbour, sediment disturbance by the polychaetes has been found to cause emigration of the sympatric New Zealand cockle *Austrovenus stutchburyi* in intertidal areas (Mouritsen 2004).

Study aim and thesis outline

Despite past research, there has been no published quantitative information on *Abarenicola affinis* populations, and no ecological study has investigated the role of this burrowing polychaete in coastal ecosystems of New Zealand. The aim of this thesis was to address this shortfall by assessing the species' biology and ecology. The following aspects are investigated: distribution and abundance of *Abarenicola affinis*, population characteristics, sediment turnover, effects on associated fauna and how seagrass affects the lugworms on tidal flats in southern New Zealand. It is intended to highlight the ecological function of *Abarenicola affinis* for the coastal sediment and benthos and to compare its role with lugworms from other coasts of the world. Due to the paucity of information on *Abarenicola affinis*, the chapters build on each other with examinations in part being based on information gained in previous chapters.

In detail, the chapters are structured as followed:

Chapter 2 assesses the density and distribution of *Abarenicola affinis* populations in tidal inlets of the Otago coast, southern New Zealand, and evaluates the use of faecal casts as a proxy for density.

Chapter 3 investigates the characteristics of two *Abarenicola affinis* populations in neighbouring tidal inlets across seasons, and relates the distribution patterns of *Abarenicola affinis* to habitat variables in these inlets.

Chapter 4 examines the sediment turnover by *Abarenicola affinis* in relation to season, tidal stage and lugworm size in the field and laboratory, and estimates the annual sediment turnover of an intertidal *Abarenicola affinis* population.

Chapter 5 assesses the influence of *Abarenicola affinis* bioturbation on associated macrofaunal assemblages in a tidal inlet, based on descriptive data and a small-spatial exclusion experiment in the field.

Chapter 6 examines the burrowing ability, spatial persistence and sediment turnover by *Abarenicola affinis* in sediments containing seagrass (*Zostera muelleri*) in a laboratory experiment.

Chapter 7 comprises general conclusions of the results, assesses the ecosystem engineering capacity of *Abarenicola affinis* in intertidal sediments, and recommends on future research.

Chapter 2 - Density and distribution of the lugworm *Abarenicola affinis* (Arenicolidae, Polychaeta) in tidal flats of the Otago coast, southern New Zealand

Introduction

In contrast to rocky shores with their conspicuous epibenthos, sedimentary intertidal flats are mainly populated by a cryptic infauna, recognisable from tube caps, faecal mounds and feeding pits indicating an abundance of life below the surface of mud and sand (Reise 1985; Raffaelli & Hawkins 1996; Bertness 2007). Large burrowing polychaetes of the genera *Abarenicola* and *Arenicola* (Arenicolidae, Polychaeta), known as lugworms, are common and often dominant members of intertidal sediment communities worldwide (Healy & Wells 1959; Wells 1964; Hutchings 2000; Reise *et al.* 2010). Lugworms are deposit-feeding sand swallowers that construct and maintain J-shaped burrows of up to 40 cm depth (Riisgard & Banta 1998; Reise 2002). Although lugworms spend most of their time below the sediment surface, their presence on tidal flats is readily recognisable by conspicuous faecal casts adjacent to their burrow openings (Fig. 3) (Fauchald & Jumars 1979; Reise 1985). Lugworms offer significant food to fish and birds regularly visiting tidal flats (de Vlas 1979; Reise 1985), but may be even more important as ecosystem engineers by irrigating and reworking the sediment with significant effects on sediment properties, biogeochemistry and other biota (Riisgard & Banta 1998; Reise 2002; Volkenborn & Reise 2007; Volkenborn *et al.* 2007a).

The distribution of lugworms on tidal flats has been researched mainly in the northern hemisphere (e.g. Beukema & de Vlas 1979; Swinbanks & Murray 1981; Reise *et al.* 2001). In the northern European Wadden Sea, the species *Arenicola marina* is widely distributed, representing the largest lugworm population worldwide (Reise *et al.* 2010). Approximately 70 - 90% of the 4700 km² tidal flats are populated by this species with average densities of 20 to 40 individuals per m² and local maxima of 150 individuals per m² (Beukema 1976; Farke *et al.* 1979; Reise 1985; Reise *et al.* 2001). On the North American Pacific coast, lugworms are less dominant and more patchily distributed in comparison to their European equivalents. There, the species *Abarenicola pacifica* populates parts of the tidal flats, with reported average densities of 20 individuals per m², but local concentrations of up to 1000 individuals per m² have also been observed (Healy & Wells 1959; Swinbanks 1981; Wilson 1981). Although lugworms have been described from coastal areas in the southern hemisphere, e.g., South Africa, South America, southern Australia (Wells 1963; Lewis 2005; Moreno *et al.* 2007), less quantitative information is available. A recent study on the South Pacific lugworm *Abarenicola affinis chiliensis* recorded average densities of 110 individuals per m² in subtidal waters of southern Chile and revealed that lugworms can dominate the biomass of subtidal macrobenthic communities (Moreno *et al.* 2007).

Studies investigating the distribution of lugworms with respect to tidal level have revealed a variety of patterns (Hobson 1967; Beukema & de Vlas 1979; Swinbanks & Murray 1981; Cadman 1997). Some lugworm species are mainly confined to the high intertidal zone, e.g., *Abarenicola pacifica* (Hobson 1967; Swinbanks & Murray 1981), whereas others occur in low intertidal zones, e.g., *Abarenicola vagabunda* (Hobson 1967) and *Arenicola defodiens* (Cadman 1997),

with co-occurring species occupying different intertidal zones with distinct monospecific beds (Hobson 1967; Cadman 1997). The common European lugworm *Arenicola marina* populates all intertidal zones (Beukema 1976; Beukema *et al.* 1983; Reise *et al.* 2001) but occurs at maximum adult densities at mid-tide level (Beukema & de Vlas 1979; Farke *et al.* 1979).

Fig. 3. Scattered faecal casts on the sediment surface of a tidal flat (left), and *Abarenicola affinis* faecal strings adjacent to a burrow opening (right).

In some studies, the observed distribution patterns were related to changes in sediment characteristics and hydrodynamics across different intertidal zones. Lugworms avoid, for example, upper intertidal areas where sediments are too muddy, as well as lower intertidal areas where hydrodynamic disturbance is

too high to enable them to become established (Hobson 1967; Beukema & de Vlas 1979). Other factors that may play a role in lugworm distribution along the tidal gradient are increased desiccation or fluctuations in temperature and salinity with increasing shore height, i.e., tidal exposure (Reise 1985; Cadman 1997; Zipperle & Reise 2005). In addition, food availability, i.e., sediment organic content, has been related to lugworm distribution (Longbottom 1970), and species-specific larval and juvenile settlement may also be responsible for distinct population patterns of lugworms in tidal flats (Hobson 1967; Farke *et al.* 1979).

The present study investigated the abundance and distribution of the lugworm *Abarenicola affinis* in southern New Zealand tidal inlets. The species is endemic to New Zealand, where it occurs sparsely in the North Island, but has been reported from several locations in the South Island (Wells 1963; Leduc *et al.* 2006; Glasby *et al.* 2009). There is, however, no published information on the density and distribution of *Abarenicola affinis*. As lugworms burrow deep into the sediment (up to 40 cm, Reise 2002), direct sampling by sediment cores is limited in space and time. The present study assessed the counting of faecal casts at the sediment surface as a measure for *Abarenicola affinis* density. This method has been used in studies of other lugworm species, where it provided reliable estimates of lugworm density (Farke *et al.* 1979; Swinbanks & Murray 1981; Flach & Beukema 1994; Reise *et al.* 2001). First, the ratio between numbers of faecal casts and individuals of *Abarenicola affinis* within the same area was determined to provide a conversion factor for lugworm density. Second, based on this ratio, surveys were conducted to assess the density and distribution of *Abarenicola affinis* in tidal inlets along the Otago coast, southern New Zealand.

Material and Methods

Study sites and field sampling

The study was carried out in four tidal inlets of the Otago coast, southern New Zealand (Fig. 4). The study sites were Papanui Inlet, Hoopers Inlet (both 4 km²), Purakaunui Inlet (1.6 km²), and Harwood (in Otago Harbour, 46 km²). In each inlet, the intertidal sampling area comprised between 1 and 2 km² with tidal flats being non-coherent in Papanui and Hoopers inlets and coherent in Purakaunui Inlet and at Harwood. Study sites were characterised by semidiurnal tides with mean tidal ranges varying between 0.4 m in Hoopers Inlet and 1.5 m at Harwood (Heiss *et al.* 2000; Albrecht & Vennell 2007).

To evaluate faecal cast density in relation to *Abarenicola affinis* abundance, data were collected in Papanui and Hoopers inlets. A total of 145 sediment cores of 20 cm diameter (314 cm² area) and 40 cm depth were collected in July (winter) and December 2007 (summer), as well as March (autumn), June (winter) and September 2008 (spring), with 10 - 15 cores collected on two sampling days per month per inlet. The number of faecal casts within each core was recorded prior to excavation of the core and collection of *Abarenicola affinis* by sieving (1 mm mesh).

Densities of *Abarenicola affinis* faecal casts were recorded during low tide in August 2007 (winter) in Papanui, Hoopers, and Purakaunui inlets, and at Harwood, over 10 sampling days in total. The sea surface water temperature over the sampling period ranged between 6.8 and 8.9°C, recorded in Otago Harbour (Portobello Marine Laboratory, unpubl. data). Sampling was done during calm and dry weather conditions. In each inlet, faecal casts were

counted along perpendicular transects every 10 m within a 0.25 m² quadrat. Transects were sited haphazardly along the shoreline, but were at least 200 m apart, and varied in length between 150 and 700 m. In Papanui and Hoopers inlets and at Harwood, 8 transects were sampled from the shoreline to the low tide waterline. In Purakaunui Inlet, the water recedes from the entire inlet at low tide and, therefore, 4 transects were sampled between opposite shorelines.

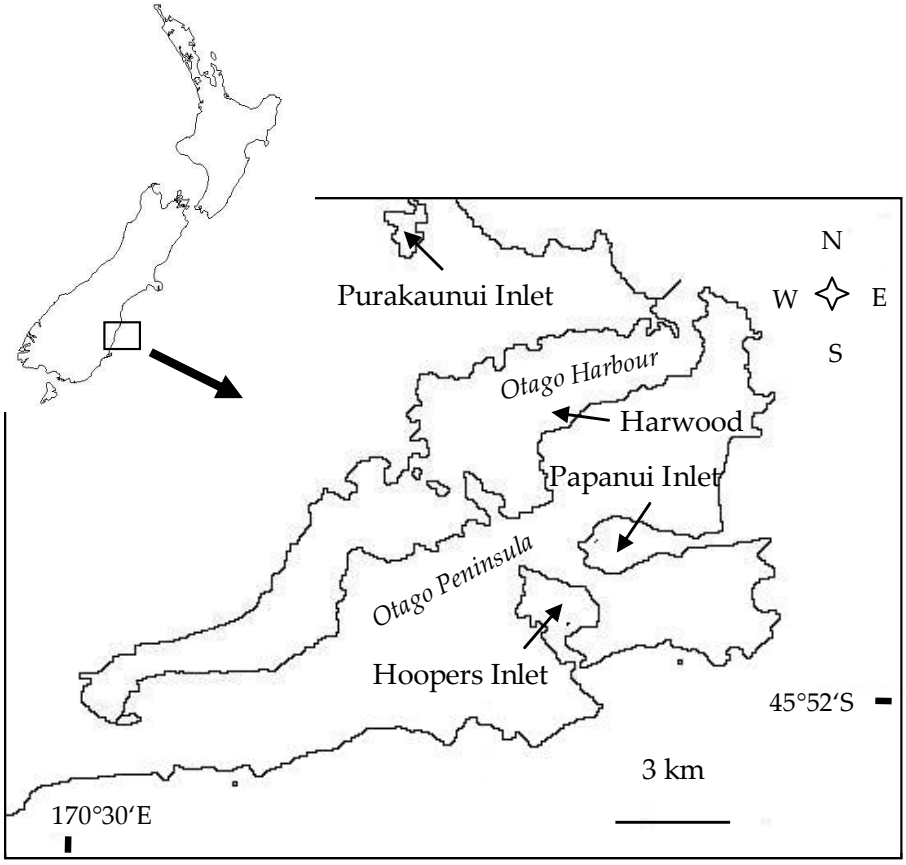


Fig. 4. Location of the study sites Papanui, Hoopers, and Purakaunui inlets and Harwood (Otago Harbour) on the Otago coast, southern New Zealand.

In September 2007 (spring), the distribution of *Abarenicola affinis* with respect to different intertidal zones was examined in Papanui and Hoopers inlets and at Harwood. Water temperatures ranged between 9.6 and 11.2°C (Portobello

Marine Laboratory, unpubl. data). Purakaunui Inlet was excluded from this part of the study as the water recedes completely during low tide. At each study site, sampling stations were established in the high intertidal zone, i.e., in close proximity to the shoreline, in the mid intertidal zone, i.e., midway between the shoreline and low tide waterline, and in the low intertidal zone, i.e., close to the low tide waterline. Intertidal zones corresponded to 8 - 9, 5 - 6, and 2 - 3 h of exposure per semidiurnal tidal cycle, which was visually assessed prior to sampling. In each inlet, 18 sampling stations were established, 6 in each intertidal zone. To incorporate lateral heterogeneity at the site, sampling stations were combined in six blocks with each block containing one sampling station of each intertidal zone (Fig. 5). At each sampling station, *Abarenicola affinis* faecal casts were counted within six haphazardly distributed 0.25 m^2 quadrats. Sediment parameters were assessed by collecting two sediment cores per station to analyse grain size composition and total organic matter content (same core, 4.7 cm diameter, 10 cm depth), as well as chlorophyll *a* content (2.5 cm diameter, 2 cm depth). The latter two parameters indicated potential food availability for lugworms, i.e., total available organic material and concentration of microphytobenthos, respectively (Longbottom 1970; Leduc *et al.* 2006).

Sediment samples were processed in the laboratory. The samples were wet sieved to extract the fines fraction (< 63 μm), then dried to constant weight (60°C, 48 h) and mechanically sieved to divide grain size fractions (1000, 500, 250, 125 and 63 μm) (McManus 1988). The total organic matter content was determined by loss on ignition (500°C, 4 h) (Buchanan & Kain 1971). Sediment chlorophyll *a* samples were freeze dried (- 50°C, 48 h), homogenised, boiled in

90% ethanol, and subsequently analysed using a spectrophotometer (Sartory 1982).

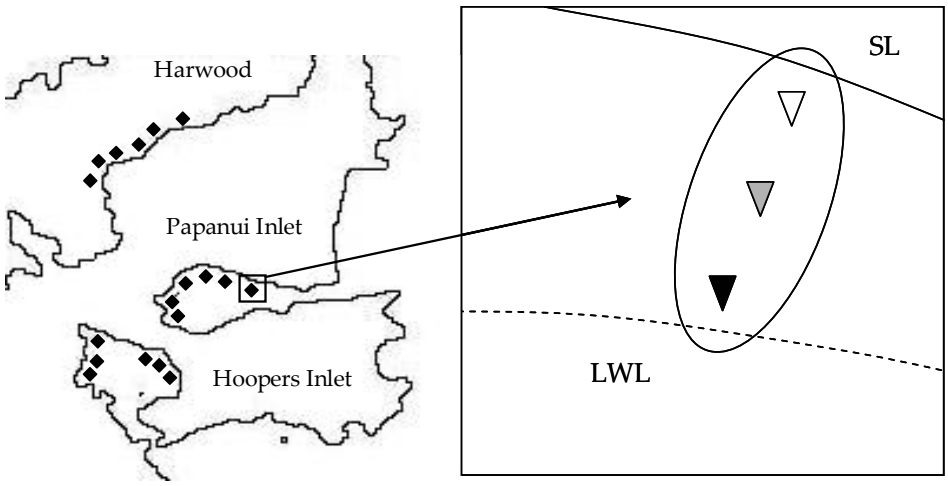


Fig. 5. Sampling blocks (♦) in Papanui and Hoopers inlets, and at Harwood containing sampling stations (triangles) in each intertidal zone (high = open, mid = shaded, low = closed; SL = Shoreline, LWL = Low tide waterline) that were each sampled with 6 replicate quadrats (0.25 m^2).

Data analysis

The relationship between number of faecal casts and number of *Abarenicola affinis* was established using simple linear regression (Quinn & Keough 2002). The established ratio between both parameters was subsequently used to obtain lugworm densities from the recorded faecal cast countings, which were presented as mean values per m^2. The proportional area covered by *Abarenicola affinis* on tidal flats was estimated using the number of quadrats containing *Abarenicola affinis* in relation to the total number of quadrats. Differences in lugworm abundance across intertidal zones were separately tested for each inlet by one-way randomised block ANOVA (Underwood 1997). It was assumed that haphazardly placed blocks represent random sampling as

required for ANOVA. Significant differences were subsequently analysed by post-hoc Tukey HSD test (Underwood 1997). Prior to analysis, data were assessed for normality and homogeneity by Kolmogorov-Smirnov and Cochran tests, respectively (Underwood 1997). Simple linear regression was used to test for relationships between lugworm abundance and sediment parameters, i.e., mean grain size, proportion of fines, total organic matter and chlorophyll *a* contents, in each inlet and over inlets combined. Statistical analyses were conducted using Statistica 6 (StatSoft Inc.).

Results

Evaluation of lugworm faecal cast counts

There was a highly significant relationship between faecal cast density and *Abarenicola affinis* abundance ($R^2 = 0.88$, $p < 0.001$) (Fig. 6). In 107 of 145 sampling cores, numbers of faecal casts and lugworms were equal. In 26 cores, fewer faecal casts than lugworms were found, whereas in 12 cores, faecal cast number exceeded lugworm abundance.

Overall, 226 faecal casts were associated with 246 individuals resulting in an faecal cast : lugworm ratio of 1.00 : 1.09. Mean ratios varied slightly across sampling months, but lugworm abundance was underestimated by faecal cast counts consistently, except for September, when overall numbers were the same (Table 1).

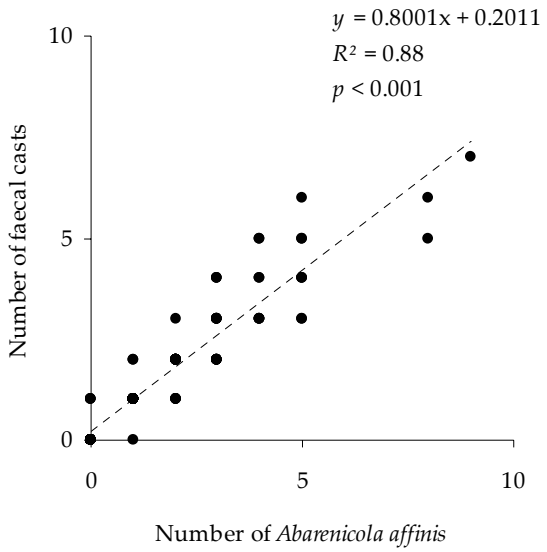


Fig. 6. Relationship between number of faecal casts and number of *Abarenicola affinis* per sediment core (20 cm diameter, 40 cm depth), sampled between July 2007 and September 2008 in Papanui and Hoopers inlets, southern New Zealand (n = 145). (Note: data points overlap.)

Table 1. Mean ratios between number of faecal casts and number of *Abarenicola affinis* (n = 25 - 30 per sampling month) in sediment cores (20 cm diameter, 40 cm depth) sampled between 2007 and 2008 in Papanui and Hoopers inlets, southern New Zealand.

Sampling month	No. of faecal casts : No. of *Abarenicola affinis*
July 2007 (winter)	1.00 : 1.05
December 2007 (summer)	1.00 : 1.11
March 2008 (autumn)	1.00 : 1.19
June 2008 (winter)	1.00 : 1.11
September 2008 (spring)	1.00 : 1.00
Overall	**1.00 : 1.09**

Lugworm density and spatial expansion in tidal inlets of Otago

Using the overall ratio, recorded faecal cast densities were corrected by the factor 1.09 to estimate *Abarenicola affinis* densities. Data combined across all inlets revealed that *Abarenicola affinis* populates tidal flats of the Otago coast with a mean density of 11.1 individuals per m² covering 42.7% of the intertidal area. The highest density within a 0.25 m² quadrat was 34 individuals (= 136 individuals per m²), recorded in Papanui Inlet.

The four study sites differed in mean density of *Abarenicola affinis* with highest density in Hoopers Inlet (21.3 ± 26.7 individuals per m²) followed by Purakaunui and Papanui inlets, where densities were relatively similar (9.3 ± 20.8 and 10.2 ± 19.6 individuals per m²), whereas at Harwood, lugworm density was considerably lower (3.8 ± 12.8 individuals per m²). In each inlet, *Abarenicola affinis* populated only parts of the tidal flats. Regarding the frequency of occurrence, lugworms were most widely distributed in Hoopers Inlet covering 73.2% of the intertidal area. In this inlet, faecal casts were also evident in subtidal regions. In Papanui and Purakaunui inlets and at Harwood, lugworms did not occupy the majority of the tidal flats as they occurred in 26.4 - 41.0% of the intertidal area (Table 2).

Mean abundance of transects varied between 0.2 and 46.4 individuals per m², with highest variation in Hoopers Inlet (5.8 - 46.4 individuals per m²), and least variation at Harwood (2.1 - 6.1 individuals per m²). There was also spatial variation within transects, particularly in Papanui and Purakaunui inlets and at Harwood, with standard deviations on average being 2.6 to 3.2 times higher than mean values (n = 4 / 8).

Table 2. *Abarenicola affinis* density per m² (mean values ± SD, *n* = 210 - 361) and proportion of intertidal area occupied by lugworms in tidal inlets of southern New Zealand, sampled in August 2007.

Study site	*Abarenicola affinis* density (m²)	*Abarenicola affinis* area (%)
Papanui Inlet	9.3 ± 20.8	41.0
Hoopers Inlet	21.3 ± 26.7	73.2
Harwood / Otago Harbour	3.8 ± 12.8	26.4
Purakaunui Inlet	10.2 ± 19.6	30.0
Overall	**11.1 ± 21.6**	**42.7**

Lugworm distribution across different intertidal zones

The distribution of *Abarenicola affinis* with respect to intertidal zones showed variation across inlets and also high variation within intertidal zones (Fig. 7). In Papanui Inlet and at Harwood, *Abarenicola affinis* were most abundant in the high intertidal zone and decreased in abundance towards lower intertidal zones. The opposite pattern was observed in Hoopers Inlet, where lugworm density increased from the high intertidal towards the low intertidal zone.

One-way ANOVA revealed a significant difference in *Abarenicola affinis* density across intertidal zones in Papanui Inlet (Table 3). Lugworms were significantly more abundant in the high intertidal zone compared with the mid (Tukey HSD test, $p = 0.015$) and low intertidal zones (Tukey HSD test, $p = 0.005$). In Hoopers Inlet and at Harwood, the differences in lugworm abundance across intertidal zones were not significant.

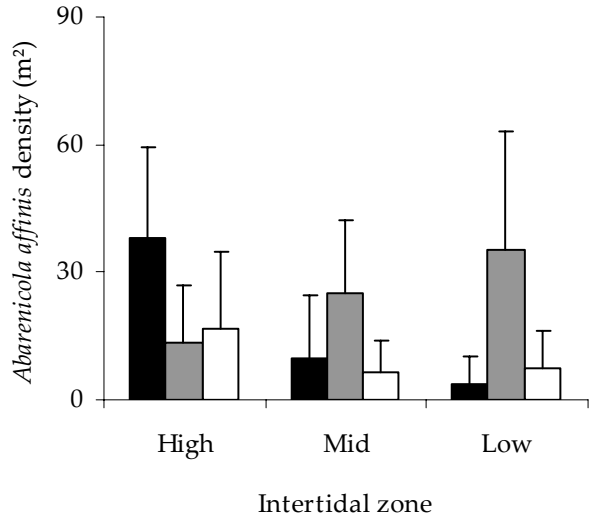


Fig. 7. *Abarenicola affinis* density per m² (mean values ± SD, *n* = 6) in the high, mid and low intertidal zones in Papanui (closed) and Hoopers inlets (shaded) and at Harwood (open), southern New Zealand, sampled in September 2007.

Table 3. Results of one-way ANOVA (factor intertidal zone) for *Abarenicola affinis* density (*n* = 6) across different intertidal zones in tidal inlets of southern New Zealand, sampled in September 2007 (significant value in bold).

Study site	One-way ANOVA		
	df	*F*	*p*
Papanui Inlet	2	10.28	**0.004**
Hoopers Inlet	2	1.71	0.229
Harwood / Otago Harbour	2	1.25	0.329

Sediment characteristics in the studied tidal flats

The study sites generally were characterised by fine to muddy sands with relatively low organic matter content (Table 4). In areas where *Abarenicola affinis* was present, sediment parameters were within the same range as in areas

where the species was absent. Sediment inhabited by lugworms ranged from 55 to 233 μm in mean grain size, 1 to 64% in fines, 0.4 to 1.6% in total organic matter content, and 1.4 to 12.2 μg / g sediment dry weight in chlorophyll *a* content.

At Harwood, sediment was of relatively similar character in all intertidal zones showing no corresponding pattern to lugworm distribution (Table 4). No significant relationships between lugworm abundance and sediment parameters were found (R^2 = 0.01 - 0.12, p = 0.165 - 0.749, n = 36). In Papanui Inlet, sediment in the high intertidal zone, where lugworms were significantly more abundant, was slightly finer with higher organic matter and chlorophyll *a* contents than in the lower intertidal zones (Table 4). Linear regression showed that lugworm abundance correlated significantly with sediment mean grain size and proportion of fines (R^2 = 0.31 / 0.23, p = 0.017 / 0.046, n = 36), but not with organic matter and chlorophyll *a* contents of the sediment (R^2 = 0.06 / 0.01, p = 0.329 / 0.737, n = 36). In Hoopers Inlet, the amount of sediment fines, as well as organic matter and chlorophyll *a* contents decreased from the shoreline towards the low intertidal zone, opposite to lugworm abundance (Table 4). In this inlet, variation in sediment parameters was notably high within intertidal zones. A significant negative relationship was found between lugworm abundance and chlorophyll a content of the sediment (R^2 = 0.33, p = 0.013, n = 36), whereas there was no relationship with the other sediment parameters (R^2 = 0.16 - 0.18, p = 0.083 - 0.097, n = 36).

Table 4. Sediment parameters (mean values ± SD, n = 6) across different intertidal zones in tidal inlets of southern New Zealand, sampled in September 2007.

Study site	Parameter	Intertidal zone		
		High	Mid	Low
Papanui	Mean grain size (μm)	139 ± 13	144 ± 9	147 ± 2
Inlet	Fines fraction (%)	5.9 ± 3.0	3.7 ± 2.1	5.0 ± 2.0
	Total organic matter (%)	0.81 ± 0.13	0.67 ± 0.16	0.69 ± 0.08
	Chlorophyll *a* (μg / g sediment dry weight)	4.6 ± 2.5	3.3 ± 1.2	2.7 ± 0.5
Hoopers	Mean grain size (μm)	113 ± 34	140 ± 58	136 ± 28
Inlet	Fines fraction (%)	22.4 ± 26.0	15.6 ± 24.6	10.6 ± 16.2
	Total organic matter (%)	1.15 ± 0.62	0.79 ± 0.36	0.69 ± 0.25
	Chlorophyll *a* (μg / g sediment dry weight)	8.3 ± 5.5	4.4 ± 3.5	2.5 ± 0.9
Harwood/	Mean grain size (μm)	151 ± 1	161 ± 16	157 ± 17
Otago	Fines fraction (%)	1.5 ± 0.6	1.0 ± 0.4	1.2 ± 0.4
Harbour	Total organic matter (%)	0.56 ± 0.12	0.55 ± 0.20	0.46 ± 0.04
	Chlorophyll *a* (μg / g sediment dry weight)	3.3 ± 1.7	2.6 ± 0.7	3.5 ± 0.9

Among inlets, a general trend could be observed between lugworm abundance and sediment parameters (Table 4). The tidal flat at Harwood, which contained the fewest lugworms, provided the coarsest sediment with lowest organic matter and chlorophyll *a* contents. The finest and organic-richest sediment with highest chlorophyll *a* content was found in Hoopers Inlet, where lugworm abundance was highest. Sediment parameters were intermediate in Papanui Inlet, with lugworm abundance being also intermediate. This trend, however, was not reflected by the results of the regression analyses combining sampling stations from all three sites, i.e., no significant relationships between lugworm

abundance and the measured sediment parameters were found (R^2 = 0.01 - 0.06, p = 0.088 - 0.999, n = 54). It was notable that a few sampling stations contained considerably higher amounts of sediment fines (17.1 - 66.2%, n = 6) compared with all other sampling stations (0.7 - 10.2%, n = 48). A second analysis, excluding these extreme muddy samples, showed significant relationships between lugworm abundance and proportion of sediment fines (R^2 = 0.23, p = 0.001, n = 48) and organic matter content of the sediment (R^2 = 0.12, p = 0.017, n = 48), whereas there were no significant relationships with mean grain size and chlorophyll a content of the sediment (R^2 = 0.02 / 0.04, p = 0.183 / 0.394, n = 48).

Discussion

Lugworm density and spatial expansion in tidal inlets of Otago

The number of faecal casts was significantly related to the number of *Abarenicola affinis* and, thus, faecal cast density provided a reliable estimate for lugworm abundance. Faecal cast counting resulted in an overall underestimation of 9% agreeing with other studies on lugworm faecal cast numbers that underestimated densities by 6% (*Arenicola marina*, Farke *et al.* 1979; Flach & Beukema 1994). However, overestimation by faecal cast counting has also been observed in lugworms (*Abarenicola pacifica*, Swinbanks & Murray 1981; Krager & Woodin 1993). Temporal variation in the relationship between faecal casts and lugworm abundance, which was found to be slight in this study, has been linked to seasonal changes in feeding activity of the lugworms (Reise *et al.* 2001). Lower feeding activity may result in the capture of lugworms, which had produced no cast prior to sampling, whereas in turn, high feeding activity may result in higher faecal cast numbers than lugworms in the same

area. In the present study, underestimation by faecal cast counting became more apparent in higher lugworm abundances, which may have been caused by the capture of lugworms from adjacent burrows that deviated into the excavated sediment core at depth.

The overall density of *Abarenicola affinis* was 11.1 individuals per m² ranging from 3.8 to 21.3 individuals per m² in the studied inlets, with a maximum local abundance of 136 individuals per m². These densities lay at the lower range of lugworm abundances reported from other parts of the world (Swinbanks 1981; Farke *et al.* 1979; Reise *et al.* 2001; Moreno *et al.* 2007). Similar to *Abarenicola affinis*, the North American lugworm *Abarenicola pacifica* has been found at densities of 0.5 to 20.0 individuals per m², but local patches may contain more than 200 individuals per m² (Swinbanks 1981), and maximum density was reported with 1000 individuals per m² (Wilson 1981). In the European Wadden Sea, the lugworm *Arenicola marina* occurs at densities of over 40 individuals per m² in tidal flats of relatively similar size to the present study location (< 10 km²) (Farke *et al.* 1979; Reise *et al.* 2001), and at densities of 14 to 36 individuals per m² over larger spatial scales (> 50 km²) (Beukema 1992). Maximum densities of this species have been reported with 150 individuals per m², but may be mainly associated with juvenile patches, whereas adult densities rarely exceed 85 individuals per m² (Cadée 1976; Farke *et al.* 1979). The South American lugworm *Abarenicola affinis chiliensis* has been shown to occur in higher density than presently found for *Abarenicola affinis*, reaching mean densities of 134 individuals per m² in a subtidal area (3 km²) of southern Chile (Moreno *et al.* 2007). Subtidal occurrence was similarly noted for *Abarenicola affinis* in Hoopers Inlet, but was not quantified.

The spatial expansion of *Abarenicola affinis* showed that the populations were patchily distributed. Lugworms were limited to less than half of the intertidal area at Harwood, as well as in Papanui and Purakaunui inlets, whereas they populated the majority of tidal flats in Hoopers Inlet. Apart from high variation among inlets, there was also high variation across transects within inlets, and within transects, which indicated that patchiness occurs at different spatial scales. A similar patchy distribution was found for *Abarenicola pacifica* in northern America, where the lugworms showed population boundaries characterised by drastic density declines and patchiness within populations (Hobson 1967; Swinbanks & Murray 1981; Krager & Woodin 1993). In comparison, *Arenicola marina* is extensively distributed in northern Europe occurring in approximately 70 - 90% of 4700 km² tidal flat area (Beukema 1976; Reise 1985). Such differences in the distribution success of lugworm populations at different coasts of the world may be caused by biotic interactions (competition and predation), but may also depend on the mere areal size of coherent zones of intertidal flats which are expansive in the European Wadden Sea, but smaller in isolated, relatively small-sized tidal inlets on the Otago coast. A large absolute population size, as in *Arenicola marina* (an estimated 1 billion, Reise *et al.* 2010), may generate sufficient offspring to occupy all potential areas, while dispersal in small and isolated populations may be insufficient to reach all potential sites at a time. Population patchiness in lugworms, as observed in the present study, may be also related to larval dispersion (Hobson 1967; Wilson 1981). Larval dispersal is pelagic in *Arenicola marina* (Farke & Berghuis 1979), but it has been shown for other lugworm species such as *Abarenicola pacifica*, that pelagic phases can be absent in larvae, resulting in settlement near adult burrows and, thereby, potentially limiting the spatial expansion of the lugworm population (Wilson 1981).

Lugworm distribution in relation to intertidal zones and sediments

Lugworm distribution across intertidal zones showed no consistent pattern among inlets, indicating that lugworm distribution along the tidal gradient is habitat-dependent and that tidal submergence is not a general key factor. In Hoopers Inlet, lugworm abundance was negatively related to chlorophyll *a* content of the sediment, which was measured to indicate concentration of microphytobenthos, an important food source for *Abarenicola affinis* (Leduc *et al.* 2006). The observed relationship is difficult to explain, i.e., an increase in microphytobenthos seems unlikely to be associated with a decrease in habitat suitability for lugworms. Chlorophyll *a* measurements, however, may have not reflected microphytobenthos productivity, which can be indirectly influenced by sediment grain size composition (Jones *et al.* 2011). The muddier sediment contained greater amounts of chlorophyll *a* than the sandier sediment, but microphytobenthos productivity may have been negatively influenced by the reduced sediment permeability causing a reduction in light penetration, solute flux, and resuspension that potentially results in lower turnover of algal biomass (Blanchard *et al.* 2001; Billerbeck *et al.* 2007). In Papanui Inlet and at Harwood, similar distribution patterns were found with highest lugworm abundance in the high intertidal zone (which was significant in Papanui Inlet), but both sites differed in their sedimentary characteristics. In Papanui Inlet, *Abarenicola affinis* distribution was related to sediment grain size, i.e., lugworm were more abundant in finer sediment which occurred mostly in the high intertidal zone. A higher amount of sediment fines may promote lugworms, as they mainly ingest sediment particles of smaller sizes (< 250 μm in *Abarenicola pacifica*, Hylleberg 1975; Fauchald & Jumars 1979), which has been attributed to their feeding mechanism (Baumfalk 1979). When feeding, the lugworm protrudes its proboscis into the sediment, and particles become adhered to the

mucus-covered papillae of the proboscis. Smaller particles have a greater chance to stick to the proboscis, whereas large particles will fall off more readily, before the proboscis is withdrawn and the sediment swallowed (Baumfalk 1979). Also, as observed in the present study, an increase in organic matter was often associated with an increase in proportion of sediment fines. This association has been similarly found in other studies, and has been related to the increase in surface area of the sediment facilitating micro-organisms (Newell 1965; Longbottom 1970; Hylleberg 1975; Cadman 1997). Fine, organically enriched sediment provides better feeding grounds for lugworms as more nutriments can be obtained from the ingested sediment (Longbottom 1970). *Abarenicola affinis* may, therefore, have also been attracted by slightly higher organic contents in the high intertidal zone of Papanui Inlet. However, sediment parameters did not change as drastically as lugworm abundance declined from high towards lower intertidal zones. At Harwood, lugworm distribution appeared unrelated to sediment parameters, i.e., the latter changed little across the tidal flat, whereas lugworm abundance decreased from the high towards lower intertidal zones. The results of the three study sites suggested that other factors than the measured sediment parameters, which could be site-specific, may play a role in lugworm distribution patterns within inlets.

Across inlets, *Abarenicola affinis* density showed a general increase from the coarsest and organic-lowest site (Harwood) towards the muddiest and organic-richest site (Hoopers Inlet). The findings support an earlier suggestion that this species prefers habitats with higher mud and organic contents of the sediment (Glasby *et al.* 2009). In the present study, this trend was only significant when excluding very muddy samples from the analysis. Sediment mud content may also be a limiting factor in lugworm distribution (Longbottom 1970; Beukema

1976). For example, *Arenicola marina* is absent in mud deposits of mean grain sizes lower than 80 μm, most likely due to the inability of the lugworm of maintaining and irrigating burrows (Longbottom 1970; Beukema 1976). In the present study, *Abarenicola affinis* was found in mud deposits of < 80 μm mean grain size indicating the ability to sustain in such extreme conditions. However, lugworm abundance was inconsistent and they were also absent in some of the muddiest sediments (>20% sediment fines) which suggested that there could be some limitation due to the high mud contents. The results of the regression analyses with and without data from the muddiest samples (17.1 - 66.2% sediment fines) suggested a positive relationship between *Abarenicola affinis* abundance and amount of sediment fines as long as the sediment does not become too muddy.

In two of three sites (Papanui Inlet, Harwood), *Abarenicola affinis* appeared to be mostly confined to the high intertidal zone. Such pattern could be also related to the hydrodynamic regime of tidal flats (Hobson 1967; Beukema 1976). For example, in a tidal bay of the North American Pacific coast, False Bay, the lugworm *Abarenicola pacifica* populates only upper intertidal parts as the species appears to be unable to establish burrows in lower intertidal parts due to the strong disturbance by currents and waves action (Hobson 1967). A preference of *Abarenicola affinis* for sheltered habitats has also been reported (Glasby *et al.* 2009), and may explain, in part, the pattern observed at Harwood. This tidal flat is characterised by a higher mean tidal range (1.5 m) than Papanui (1.15 m) and Hoopers inlets (0.43 m) and is located in a larger and deeper tidal bay (Otago Harbour, 46 km², tidal channel depth = 10 m) compared with the inlets (~ 4 km², tidal channel depth 1 - 2 m) (Heiss *et al.* 2000; Albrecht & Vennell 2007), suggesting a more stressful environment in lower intertidal zones, i.e., stronger

currents and waves action. In comparison, Hoopers Inlet represents a relatively calm environment with less hydrodynamic disturbance (pers. obs.), probably resulting from the constricted entrance of the inlet (Albrecht & Vennell 2007): a situation from which lugworms may benefit in lower intertidal zones.

Apart from abiotic environmental factors, biotic interactions can contribute to distribution patterns of tidal flat benthos, particularly in sheltered and smaller tidal flats, where biological effects have a stronger impact on habitat complexity (Reise 1985). Biotic interactions may have an influence on *Abarenicola affinis* distribution patterns in Otago tidal flats. For example, in Papanui Inlet and at Harwood, the scarceness of lugworms in lower intertidal zones coincided with extensively distributed seagrass in the same area. The distribution of lugworms may be limited by seagrass beds due to burrow inhibition (Brenchley 1981; van Wesenbeeck *et al.* 2007). Supportive to this suggestion is the absence of seagrass in Hoopers Inlet, where lugworms spread in greater numbers into lower intertidal zones.

Conclusions

Abarenicola affinis is patchily dispersed across tidal inlets of the Otago coast, and may not reach mean densities or local maxima reported for other lugworm species in the world. Across tidal inlets, *Abarenicola affinis* abundance increased with increasing contents of fine particles, organic matter and chlorophyll *a* in the sediment. Distribution patterns across intertidal zones and relationships between lugworm abundance and sediment parameters were inconsistent among inlets, indicating habitat-related complexity in the species' distribution.

Chapter 3 - Populations of the southern lugworm *Abarenicola affinis* (Arenicolidae, Polychaeta) in two neighbouring tidal inlets

Introduction

Lugworms, sedentary burrowing polychaetes of the genera *Abarenicola* and *Arenicola*, are an important component in shallow marine sediments worldwide, often dominating in macrobenthic biomass (Wells 1964; Wilson 1981; Moreno *et al.* 2007; Reise *et al.* 2010). On the North European Atlantic coast, lugworms cover roughly 70 - 90% of tidal flats and may contribute up to 30% to the macrobenthic biomass (Beukema 1976; Reise 1985; Reise *et al.* 1994). In other parts of the world, lugworms are less dominant and often patchily distributed in the tidal zone, e.g., *Abarenicola pacifica* in northern America (Hobson 1967; Swinbanks 1981). Lugworm densities on tidal flats have been reported with up to 150 individuals per m^2, but local maxima may reach 1000 individuals per m^2 (e.g. Beukema & de Vlas 1979; Farke *et al.* 1979; Wilson 1981; Reise *et al.* 2001).

Population studies on lugworms have been mainly conducted on the European species *Arenicola marina* (e.g. Beukema & de Vlas 1979; Flach & Beukema 1994; Reise *et al.* 2001). The populations of this species are relatively stable over time, which distinguishes them from populations of most other intertidal benthic species that tend to vary conspicuously across seasons and years (Beukema 1992; Beukema *et al.* 1993; Flach & Beukema 1994; Reise *et al.* 2001). *Arenicola marina* populations are characterised by low mortality, high juvenile survival, considerable longevity (up to 6 years), and many year classes within a

population (Beukema & de Vlas 1979; Reise 1985). Stable population sizes have been mainly associated with the density-dependent regulation between juveniles and adults (Flach & Beukema 1994; Reise *et al.* 2001).

In general, lugworms are gonochoristic with female and male gametes developing over several months in the coelomic fluid of the body (Mayes & Howie 1985). Gametes are released during periodical spawning, e.g., within a few weeks, which may occur several times per year (Farke & Berghuis 1979; Wilson 1981). Larval dispersion and juvenile migration is pelagic in *Arenicola marina* (Farke & Berghuis 1979; Reise 1985), but may be brief or absent in other lugworm species such as suggested by Wilson (1981) for *Abarenicola pacifica*. In *Arenicola marina*, juveniles assemble in distinct areas outside high adult densities, often in upper intertidal zones (so called "nursery areas"), resulting in size-related distribution patterns of this species on tidal flats with a general increase in lugworm size towards lower intertidal zones (Farke *et al.* 1979; Reise *et al.* 2001). In studies on *Arenicola marina*, the population structure has been characterised by bimodality with two distinctive cohorts of juveniles and adults (Beukema & de Vlas 1979; Farke *et al.* 1979).

The distribution of lugworm populations has been related to a number of different habitat characteristics such as inundation periods, hydrodynamics and sediment properties (e.g. Hobson 1967; Longbottom 1970; Beukema 1976). Lugworms may show maximum densities at high, mid or low-tidal levels (Beukema & DeVlas 1979; Swinbanks & Murray 1981; Cadman 1997), and patterns have been related to environmental factors changing along the tidal gradient, e.g., sediment characteristics, hydrodynamic stress or food availability (Hobson 1967; Longbottom 1970; Beukema & de Vlas 1979). Also, larval

dispersion and juvenile migration may play a role in determining lugworm distribution patterns (Hobson 1967; Farke *et al.* 1979; Reise 1985). For example, juveniles of *Arenicola marina* change habitats several times during their development on tidal flats in order to avoid predation and environmental extremes (Reise 1985).

The endemic lugworm *Abarenicola affinis* is relatively common in tidal flats of southern New Zealand, but little is known about the population biology. Published information is mostly limited to the reporting of the locations of lugworm populations (Wells 1964; Leduc *et al.* 2006; Glasby *et al.* 2009). On the Otago coast in southern New Zealand, two adjacent tidal inlets, Papanui and Hoopers inlets, both support populations of *Abarenicola affinis* (Chapter 2). A survey of these populations showed different distribution patterns between the two inlets. In Papanui Inlet, lugworms were patchily distributed and concentrated in the high intertidal zone, whereas in Hoopers Inlet, lugworms were spread across all intertidal zones at relatively high density (Chapter 2). Both inlets vary in their hydrodynamic and sedimentary regimes (Albrecht & Vennell 2007; Chapter 2), but differ also in the occurrence of the seagrass *Zostera muelleri*, which is extensively distributed in Papanui Inlet, but lacking in Hoopers Inlet (Mills & Berkenbusch 2009; Chapter 2). This present study investigated the variation of these two lugworm populations residing in different habitats. Population characteristics such as overall density, biomass, body size, size distribution, sex ratio and burrow depth were recorded for each population over four consecutive seasons and compared. The abundance and biomass of *Abarenicola affinis* were related to habitat variables in each inlet, including tidal level, sediment parameters, and distribution of seagrass.

Material and Methods

Study sites and field sampling

The study was conducted in two neighbouring tidal inlets of the Otago coast, southern New Zealand, which were Papanui and Hoopers inlets (Fig. 8). Both inlets are of similar size (4 km²) and characterised by semidiurnal tides, with mean tidal ranges of 1.15 m in Papanui Inlet and 0.43 m in Hoopers Inlet; the lower mean tidal range in the latter inlet is caused by a highly constricted entrance channel (Albrecht & Vennell 2007). A notable difference between the inlets is the occurrence of the seagrass *Zostera muelleri* in Papanui Inlet, where it covers extensive parts of the intertidal area, often in fragmented patches (Mills & Berkenbusch 2009; pers. obs.), whereas Hoopers Inlet contains no seagrass (pers. obs.).

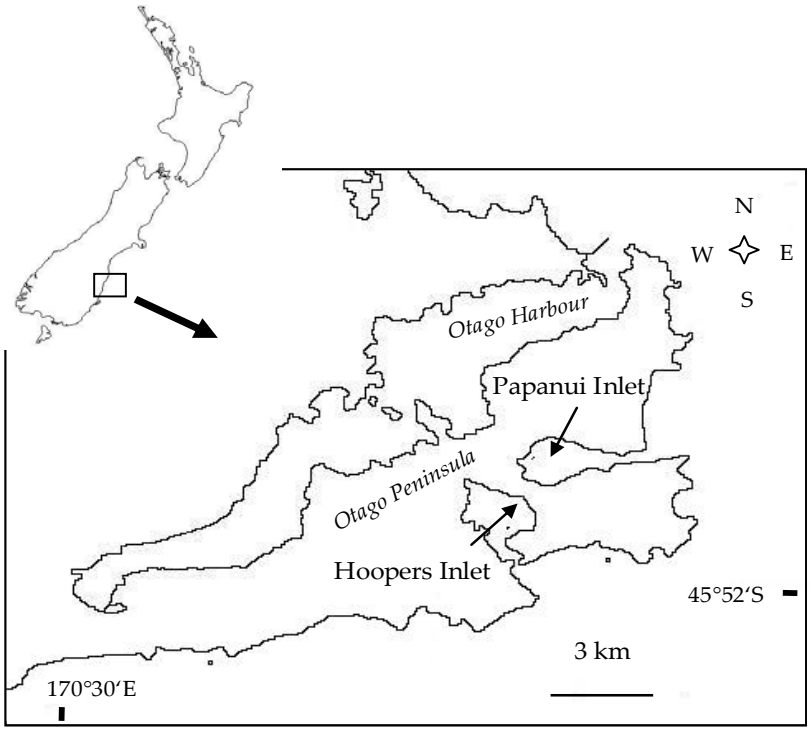


Fig. 8. Location of the intertidal study sites (arrows) in Papanui and Hoopers inlets on the Otago coast, southern New Zealand.

In each inlet, an intertidal sampling area of 0.5 km² was selected within the largest coherent intertidal part of the inlets. In both sampling areas, low tide exposure time ranged between 2 and 9 h per semidiurnal tidal cycle (visually assessed over 12 h), and corresponded with distance from the shore. This measure was used as a proxy for tidal level.

Seasonal sampling was conducted in both inlets in summer (December) 2007, autumn (March), winter (June) and spring (September) 2008. The sea surface water temperatures (averaged over 4 sampling days per season) were 15.4, 15.9, 9.0, and 11.9°C, respectively, recorded in Otago Harbour (Portobello Marine Laboratory, unpubl. data). In each inlet, the intertidal sampling area was divided into 90 sampling points, and the position of points and their distance to the shoreline were established by GPS. In each season, 15 randomly chosen points were sampled by collecting a sediment core of 20 cm diameter (314 cm² area) and 40 cm depth. Sample size was limited due to the effort of lugworm collection regarding the nature and depth of their burrows. Sampling depth was determined in preliminary studies, which showed that *Abarenicola affinis* burrow depth does not exceed 40 cm in the study area. Each sampling core was divided into 10 cm sediment sections, which were sieved individually (1 mm mesh) to collect lugworms and determine their burrowing depth. In Papanui Inlet, seagrass leaves within the sampling core were cut off at the sediment surface prior to excavation of the core. Seagrass roots, rhizomes and debris in the top 10 cm of the sediment were collected during sieving. At each sampled point, two additional sediment cores were collected to analyse sediment grain size composition and total organic matter content (same core, 4.7 cm diameter, 10 cm depth), as well as chlorophyll *a* content of the sediment (2.5 cm diameter, 2 cm depth).

Laboratory analysis

All *Abarenicola affinis* were anaesthetised for 3 h in 7% magnesium-chloride, fixed in 4% formalin, and subsequently preserved in 70% ethanol. Lugworm body measurements included total and thorax lengths, recorded with calipers (± 0.5 mm). To determine sex, a single drop of coelomic fluid was extracted from the mid-region of the worm body using a hypodermic needle, and examined under a compound microscope for the presence of gametes (Fig. 9). The minimum diameter (µm) was measured for eight haphazardly chosen oocytes (♀) or sperm platelets (♂) using image analysis software (AnalySIS LS). When fewer than eight gametes were found, all were measured. To determine the ash-free dry weight (AFDW, ± 0.0001 g), lugworms were dried to constant weight (60°C, 48 h) and subsequently combusted (500°C, 4 h).

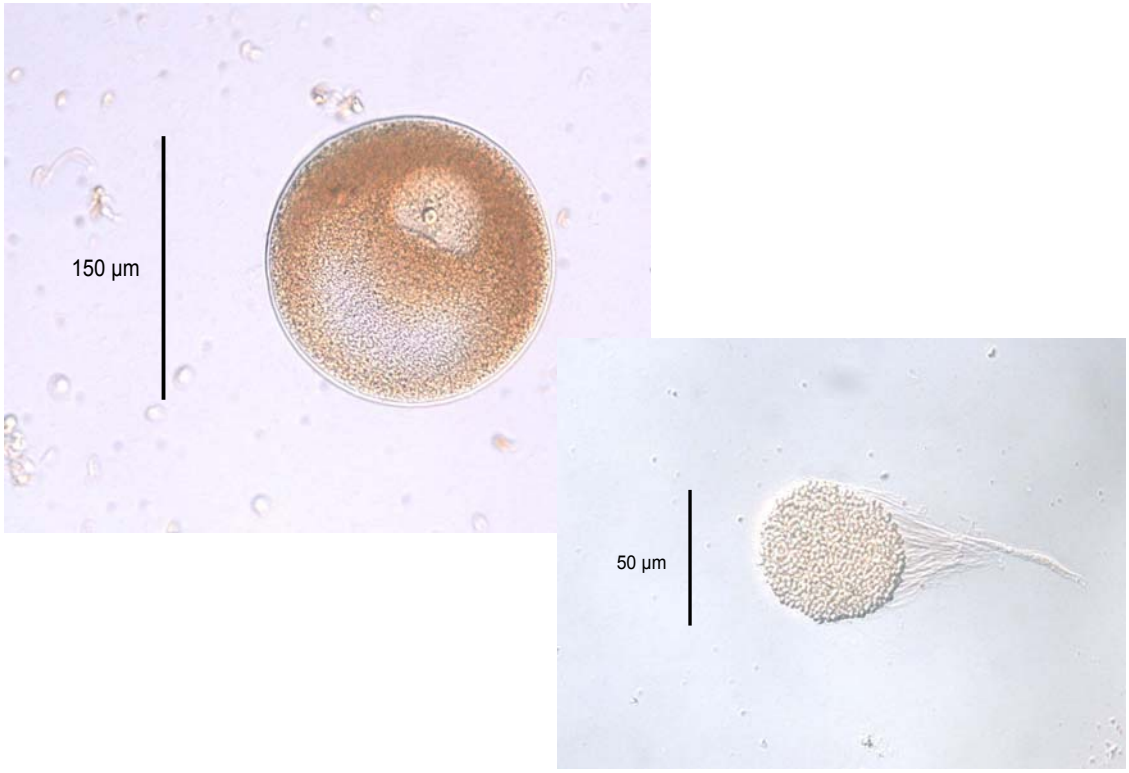


Fig. 9. Female (oocyte) (left) and male gametes (sperm congregated in a platelet) (right) of *Abarenicola affinis*.

Sediment samples were wet-sieved to extract the fines fraction (< 63 μm), dried (60°C, 48 h), and mechanically sieved to determine grain size fractions (1000, 500, 250, 125 and 63 μm) (McManus 1988). The total organic matter content of the sediment was determined by loss on ignition (500°C, 4 h) (Buchanan & Kain 1971). Sediment chlorophyll *a* samples were freeze dried (- 50°C, 48 h), homogenised, boiled in 90% ethanol and subsequently analysed using a spectrophotometer (Sartory 1982). Seagrass leaves, roots, rhizomes and debris were rinsed with freshwater, dried (60°C, 48 h) and weighed (± 0.001 g).

Data analysis

Examined *Abarenicola affinis* population parameters included density, biomass and thorax length. Thorax length was selected instead of total length due to the occasional occurrence of incomplete worm tails. One-way ANOVA (Underwood 1997) was applied to test for differences across seasons in each population, and for differences between both populations, combining data from all seasons. Prior to analysis, data were tested for normality and homogeneity of variances by Kolmogorov-Smirnov and Cochran tests, respectively (Underwood 1997). When data were non-normally distributed, ANOVA was still accepted due to its robustness against non-normality, especially under a balanced design with large sample numbers (Underwood 1997). When necessary, data were square-root or $\log_{10}$-transformed to achieve homogeneity of variances (Underwood 1997). Population density data between inlets remained heterogeneous after transformation; this heterogeneity only compromises the outcome of ANOVA when test results are significant (increased probability of Type I error, see Underwood 1997) and, therefore, ANOVA results were considered reliable as test results were non-significant.

The size-frequency distribution of each population was evaluated by categorising lugworms into 8 arbitrary size classes; 11-20, 21-30, 31-40, 41-50, 51-60, 61-70, 71-80 and 81-90 mm thorax length. The sex-ratio was determined by the relationship between the number of lugworms containing oocytes (♀) and the number of lugworms containing sperm platelets (♂).

Multiple linear regression (Quinn & Keough 2002) was used to examine the relationship between *Abarenicola affinis* distribution and the measured habitat variables in each inlet, with data combined across all seasons to assess general patterns. *Abarenicola affinis* density (individuals per 314 cm²) and biomass (g AFDW per 314 cm²) were used as dependent variables. Predictor variables included distance from the shore (m), sediment mean grain size (μm), sediment fines (%), as well as total organic matter (%) and chlorophyll *a* contents of the sediment (μg / g sediment dry weight). In Papanui Inlet, where seagrass was present, seagrass above-ground and below-ground biomasses (both g dry weight) were included. Below-ground biomass consisted of roots, rhizomes and debris (top 10 cm of the sediment). Prior to analysis, co-correlation of variables was assessed by matrix plots (Quinn & Keough 2002). In Papanui Inlet, mean grain size and sediment fines were co-correlated ($R^2 = 0.7$, $p < 0.001$), as were seagrass above-ground and below-ground biomasses ($R^2 = 0.5$, $p < 0.001$), leading to the omission of mean grain size and seagrass above-ground biomass. Residuals were graphically assessed for normality and homogeneity of variances, using probability plots and plots of residuals against predicted values, respectively (Quinn & Keough 2002). *Abarenicola affinis* density and biomass data were subsequently $\log_{(x+1)}$-transformed. Statistical analyses were conducted using Statistica 6 (StatSoft Inc.).

Results

Sediment and seagrass parameters in the intertidal sampling areas

The intertidal sampling areas in Papanui and Hoopers inlets consisted of relatively similar grain size composition with mean grain sizes of 145 ± 6 μm and 148 ± 1 μm, respectively (both n = 60, data from all seasons). In Papanui Inlet, the sampling area contained muddier sediment (fines fraction: 4.15 ± 2.51%, maximum 13.2%), whereas the amount of sediment fines was lower in Hoopers Inlet (2.11 ± 0.57%, maximum 3.6%, both n = 60). In both tidal flats, total organic matter content of the sediment was low with mean values of 0.64 ± 0.13% in Papanui Inlet, and 0.55 ± 0.09% in Hoopers Inlet (both n = 60). Sediment in Hoopers Inlet contained slightly higher amounts of chlorophyll *a* (5.0 ± 2.3 μg / g sediment dry weight) compared with Papanui Inlet (3.7 ± 1.4 μg / g sediment dry weight) (both n = 60). Seagrass above-ground and below-ground biomasses in Papanui Inlet were on average 0.143 ± 0.148 g dry weight and 3.833 ± 2.486 g dry weight, respectively (both n = 60), whereas no seagrass occurred in Hoopers Inlet.

Lugworm population characteristics in Papanui and Hoopers inlets

The density, biomass and individual size of both *Abarenicola affinis* populations varied little across seasons, indicating relatively stable populations in both inlets (Table 5). In Papanui Inlet, lugworm abundance and biomass were highest in autumn, whereas in Hoopers Inlet, the highest seasonal abundance occurred in summer, and the highest biomass was recorded in autumn. Results from one-way ANOVA showed no significant differences in *Abarenicola affinis* density, biomass and thorax length across seasons in each inlet (Table 6).

Table 5. *Abarenicola affinis* density and biomass per core (314 cm²) (mean values ± SD, *n* = 15), and thorax length (mean values ± SD, *n* = 19 - 31) in summer, autumn, winter, and spring (December 2007, March, June, September 2008, respectively) in Papanui and Hoopers inlets, southern New Zealand.

Site	Season	No. of sampling cores	No. of individuals	Mean density ± SD	Mean biomass (g AFDW) ± SD	Mean thorax length (mm) ± SD
Papanui	Summer	15	21	1.4 ± 1.4	0.033 ± 0.047	31.2 ± 8.6
Inlet	Autumn	15	29	1.9 ± 2.5	0.047 ± 0.063	27.4 ± 5.4
	Winter	15	20	1.3 ± 1.9	0.033 ± 0.050	30.0 ± 6.3
	Spring	15	19	1.3 ± 1.4	0.045 ± 0.068	31.0 ± 7.4
	Overall	**60**	**89**	**1.5 ± 1.8**	**0.040 ± 0.056**	**29.6 ± 6.9**
Hoopers	Summer	15	31	2.1 ± 1.5	0.107 ± 0.122	43.4 ± 10.5
Inlet	Autumn	15	22	1.5 ± 1.1	0.163 ± 0.118	47.6 ± 13.8
	Winter	15	21	1.4 ± 1.1	0.101 ± 0.086	41.9 ± 11.8
	Spring	15	22	1.5 ± 1.2	0.100 ± 0.077	43.6 ± 14.7
	Overall	**60**	**96**	**1.6 ± 1.2**	**0.118 ± 0.102**	**44.1 ± 12.5**

Both populations were of similar overall density, but lugworms were considerably larger in Hoopers Inlet resulting in comparatively higher population biomass in this inlet. These differences were consistent across all seasons, and most pronounced in autumn, when lugworms were on average 20 mm larger in Hoopers Inlet than in Papanui Inlet. Maximum total lengths and biomasses of lugworms were 175 mm and 0.3982 g AFDW in Hoopers Inlet, and 110 mm and 0.0971 g AFDW in Papanui Inlet. One-way ANOVA showed no significant differences in density between the two populations, but revealed significantly higher biomass and greater individual size in Hoopers Inlet compared with Papanui Inlet (Table 6).

Table 6. Results of one-way ANOVA (factor season) for *Abarenicola affinis* density and biomass per core (314 cm²) (n = 15), and thorax length (n = 19 - 31) in Papanui and Hoopers inlets, southern New Zealand, and results of one-way ANOVA (factor inlet) for *Abarenicola affinis* density, biomass (n = 60, data from all seasons) and thorax length (n = 89 / 96, data from all seasons) (significant values in bold).

Abarenicola affinis parameters	Seasonal comparison						Inlet comparison		
	Papanui Inlet			Hoopers Inlet					
	df	*F*	*p*	*df*	*F*	*p*	*df*	*F*	*p*
Density	3	0.41	0.750	3	0.98	0.410	1	0.17	0.682
Biomass (g AFDW)	3	0.28	0.837	3	1.31	0.280	1	30.44	**< 0.001**
Thorax length (mm)	3	1.63	0.190	3	0.82	0.489	1	101.37	**< 0.001**

Both populations of *Abarenicola affinis* were characterised by unimodal size distributions in each season (Fig. 10). In Papanui Inlet, lugworms of the size class 31-40 mm thorax length were most abundant in all seasons except autumn, when smaller individuals (21-30 mm thorax length) dominated. In Hoopers Inlet, a greater range of size classes was found with medium sized lugworms (41-50 mm thorax length) dominating the population in all seasons except spring, when smaller individuals (31-40 mm thorax length) were highly abundant. In both populations, large lugworms were scarce in winter.

In Papanui Inlet, there was a female biased sex ratio in all seasons (sex ratios ♀ : ♂ from 1.0 : 0.4 to 1.0 : 0.8) except autumn, when males dominated (sex ratio ♀ : ♂ of 1.0 : 1.8). In Hoopers Inlet, females were more abundant in all seasons (sex ratios ♀ : ♂ from 1.0 : 0.3 to 1.0 : 0.9). It occurred that lugworms could not be sexed due to the absence of gametes in the coelomic fluid sample (0 - 9 individuals per inlet and season). In Papanui Inlet, females and males were of

similar size (mean thorax length ♀ 31.6 ± 6.2 mm, ♂ 31.5 ± 6.7 mm, *n* = 31 / 27), whereas in Hoopers Inlet, females were slightly smaller than males (mean thorax length ♀ 44.0 ± 12.5 mm, ♂ 48.9 ± 11.7 mm, *n* = 45 / 32).

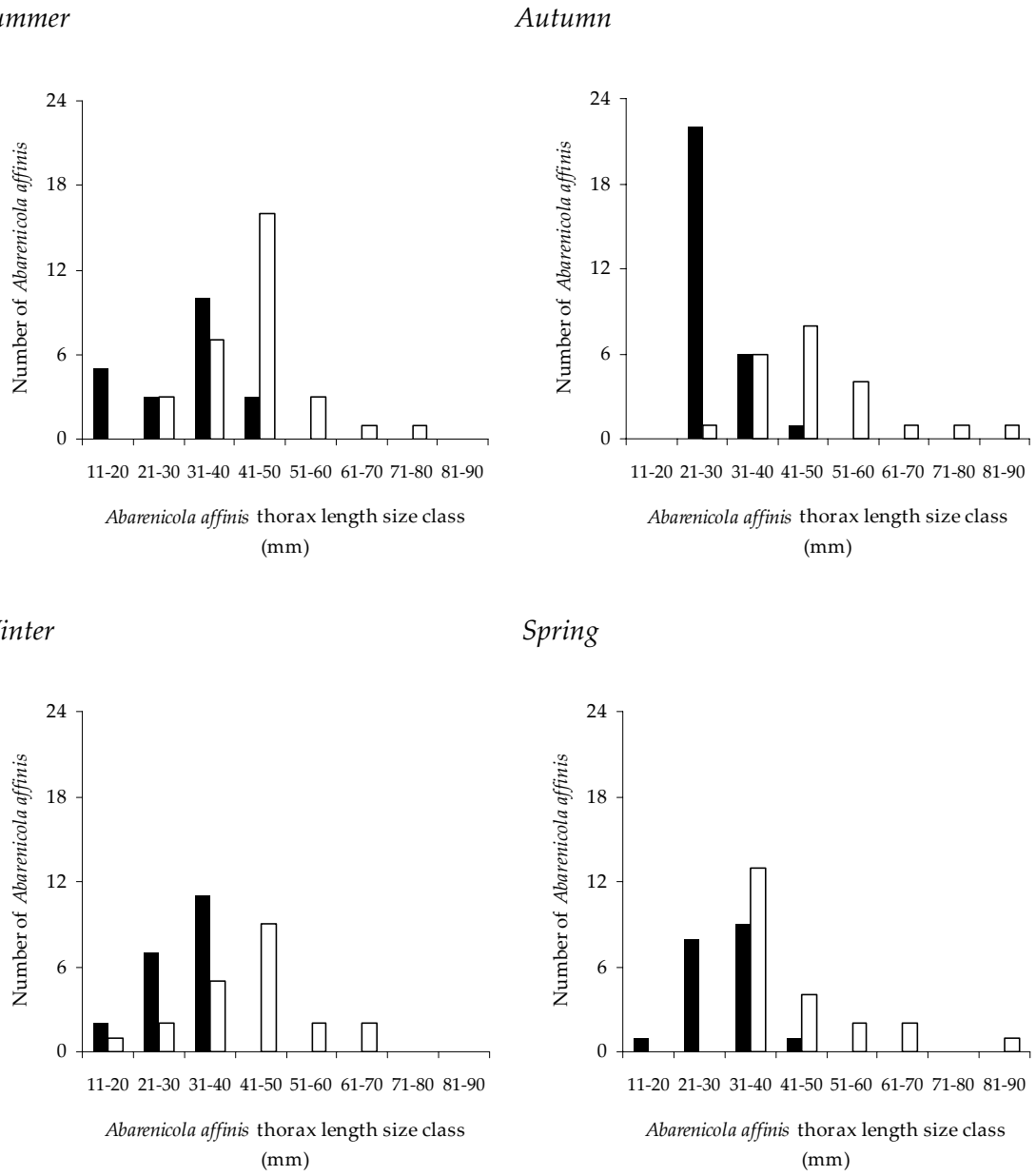


Fig. 10. Size-frequency distributions of *Abarenicola affinis* in summer, autumn, winter, and spring (December 2007, March, June, September 2008, respectively) in Papanui (closed) and Hoopers inlets (open), southern New Zealand.

Combined data from both populations and across seasons showed that the smallest gamete-carrying individuals of *Abarenicola affinis* ranged between 20 and 23 mm thorax length in both sexes. Lugworms of the size class 11-20 mm thorax length did not contain gametes in their coelomic fluid, indicating immaturity. In general, there was great variation in gamete sizes in all seasons. Overall, female oocytes ranged between 18 and 209 μm diameter, and male sperm platelets ranged between 15 and 76 μm diameter. On average, sperm platelets were 47 ± 9 μm in diameter (n = 452). Female lugworms contained oocytes of 3 distinctive size classes with mean diameters of 55 ± 12 μm (n = 291), 101 ± 14 μm (n = 345) and 156 ± 15 μm (n = 249). In both populations, the proportion of females with large-sized oocytes was highest in winter (83% in each population), but lower in other seasons (33 – 67%).

In each population, lugworm burrow depth was related to thorax length, i.e., large individuals burrowed in deeper sediment sections than small individuals (Fig. 11). Because of the larger individual sizes in the Hoopers Inlet population, mean burrow depth was greater in this inlet (32.7 ± 7.8 cm, n = 96) than in Papanui Inlet (23.6 ± 6.9 cm, n = 89). In Papanui Inlet, most *Abarenicola affinis* (48%) were found between 20 and 30 cm depth, and did not occur at greater depths (Fig. 11). In contrast, 44% of all excavated lugworms were captured below 30 cm depth in Hoopers Inlet.

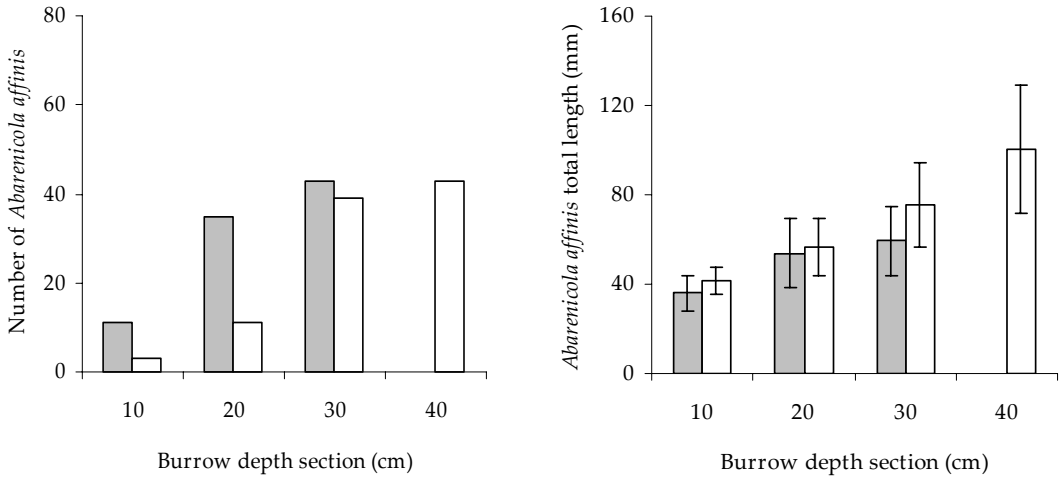


Fig. 11. Total number of *Abarenicola affinis* in different burrow depth sections (left), and total length (mm) (mean values ± SD, *n* = 3 - 43) per burrow depth section (right) in Papanui (shaded) and Hoopers inlets (open), southern New Zealand, sampled between summer 2007 and spring 2008.

Lugworm distribution patterns in relation to habitat variables in Papanui and Hoopers inlets

In Papanui Inlet, the distribution of *Abarenicola affinis* was significantly influenced by habitat characteristics, as revealed by multiple linear regression analysis (Table 7). The combination of measured habitat variables explained 68 and 71% of the variation in lugworm density and biomass, respectively. Semi-partial correlation coefficients, which indicate the relative importance of each variable to both lugworm parameters, were significant for distance from the shore and seagrass below-ground biomass; both were negatively related to lugworm density and biomass. In addition, the proportion of sediment fines was significantly positively related to lugworm biomass. In contrast to Papanui Inlet, the measured habitat variables did not explain variation in lugworm abundance and biomass in Hoopers Inlet (Table 7).

Table 7. Results of the multiple linear regression analyses of *Abarenicola affinis* density and biomass and habitat variables in Papanui and Hoopers inlets, southern New Zealand (combined data from all seasons, n = 60) (significant values in bold) ($R^2_{semipart}$ = squared semi-partial correlation coefficient, indicating the proportion of variance explained by the inclusion of the predictor variable).

Site	*Abarenicola affinis* density			*Abarenicola affinis* biomass		
	F	R^2	p	F	R^2	p
Papanui Inlet	22.75	0.678	**< 0.001**	26.93	0.714	**< 0.001**
Hoopers Inlet	0.90	0.077	0.490	0.94	0.080	0.464

Papanui Inlet	F	$R^2_{semipart}$	p	F	$R^2_{semipart}$	p
Fines fraction (%)	1.62	0.010	0.209	12.42	0.257	**< 0.001**
Total organic matter (%)	0.36	0.046	0.553	0.72	0.062	0.400
Chlorophyll *a* (μg/g dry weight sediment)	0.29	-0.041	0.596	0.17	-0.030	0.684
Distance from the shore (m)	39.09	-0.483	**< 0.001**	20.29	-0.328	**< 0.001**
Seagrass below-ground biomass (g dry weight)	4.87	-0.170	**0.032**	6.57	-0.187	**0.013**

Lugworm distribution in Papanui Inlet showed a zonational pattern, related to the tidal level and seagrass distribution. Figure 12 illustrates this pattern, showing that lugworms were most abundant in nearshore areas (within 100 from the shore), where seagrass was absent or at the lower range of biomass. Lugworm density decreased from the shoreline towards mid-intertidal areas, where seagrass biomass showed maximum values (~ 400 m from the shore). In lower intertidal areas, lugworms were absent and seagrass biomass was at a medium range. In Hoopers Inlet, lugworms were spread relatively evenly across all intertidal zones (Fig. 12).

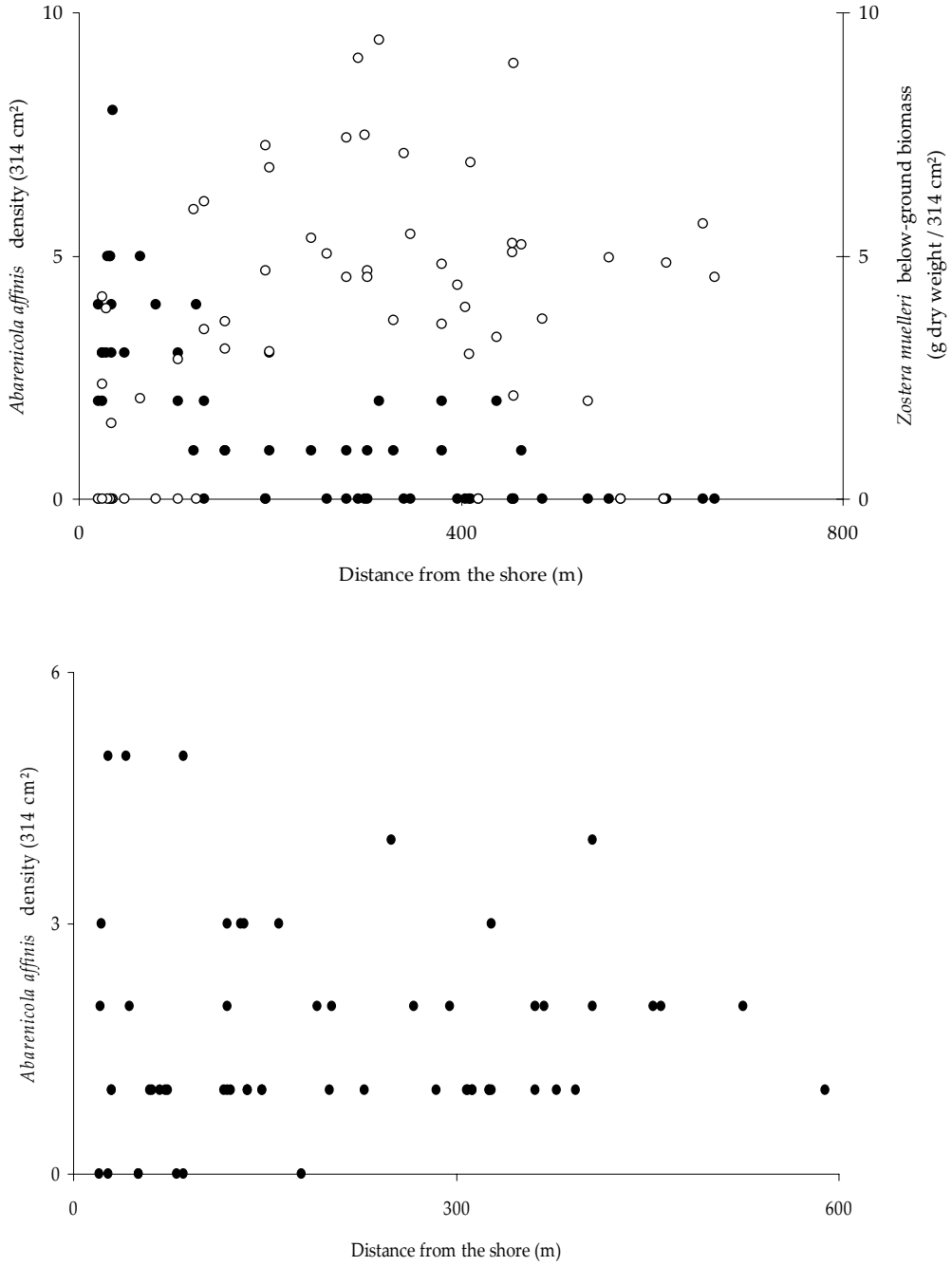


Fig. 12. *Abarenicola affinis* density (●) and seagrass (*Zostera muelleri*) below-ground biomass (○) at different distances from the shore in Papanui (above) and Hoopers inlets (below), southern New Zealand, sampled between December 2007 and September 2008. Note: There was no seagrass present in Hoopers Inlet.

In Papanui Inlet, lugworm biomass, but not density, was also positively related to the amount of fine particles in the sediment, i.e., finer sediment contained larger individuals. Lugworms of the two larger size classes were in sediment that contained a markedly higher proportion of fines than sediments containing smaller-sized individuals (Table 8). Individuals of the largest size class also only occurred in upper intertidal areas without seagrass, whereas smaller size classes were present across a wide range of distances from the shore and of seagrass below-ground biomass (Table 8).

Table 8. Ranges of sediment fines fraction (%), distance from the shore (m), and seagrass (*Zostera muelleri*) below-ground biomass in samples containing *Abarenicola affinis* individuals of different size classes, sampled between December 2007 and September 2008 in Papanui Inlet, southern New Zealand.

Size class (mm thorax length)	No. of individuals	No. of samples	Sediment fines fraction (%)	Distance from the shore (m)	Seagrass below-ground biomass (g dry weight)
11-20	8	6	2.6 - 7.2	24 - 380	2.356 - 6.815
21-30	40	20	2.2 - 13.2	20 - 380	0 - 9.433
31-40	36	21	4.0 - 13.2	20 - 464	0 - 9.433
41-50	5	3	6.3 - 13.2	20 - 81	-

Discussion

Variation in lugworm populations between two neighbouring tidal inlets of southern New Zealand

In both inlets, there were no drastic changes in population overall density observed throughout the year. Water temperatures ranged from 9°C in winter to 15°C in summer indicating moderate conditions compared with

temperatures in habitats of other lugworms, e.g., *Arenicola marina*, where freezing conditions in winter can lead to a seasonal decline in adult population density (Reise *et al.* 2001). The decline is associated with adult migration into lower intertidal and subtidal regions in avoidance of temperature extremes and mortality due to ice (Reise 1985; Reise *et al.* 2001). Seasonal stability in *Abarenicola affinis* populations in both tidal inlets suggested that temperatures are perceived as not extreme by lugworms. Furthermore, the stable population sizes indicated some balance in recruitment and mortality. Such balance has been particularly reported for *Arenicola marina* over year-intervals, i.e., this species successfully recovers from density declines after extremely cold winters (Beukema 1992; Flach & Beukema 1994; Reise *et al.* 2001). Flach & Beukema (1994) related these patterns to the selective settlement of juveniles in areas where adults are rare or absent, whereas in areas of high adult density, juveniles are excluded, probably due to food competition and sediment disturbance by adults. This density-dependant regulation supports the recovery of populations after severe winters, when areas vacated by adults, due to migration and mortality, are re-populated by juveniles expanding from their usual settlement areas (Reise *et al.* 2001). As a consequence, in years of low adult density recruitment is high and vice versa (Flach & Beukema 1994). In the present study, juvenile and adult *Abarenicola affinis* did not occur separately on the intertidal sampling areas and it is, therefore, unclear whether such density-dependent regulation operates in the observed populations. Pelagic phases and settlement of larvae of *Abarenicola affinis* have yet to be investigated. Pelagic phases during development can differ among lugworm species, i.e., they may occur several times (*Arenicola marina*, Reise 1985), but may also be brief or absent resulting in settlement near adult burrows (*Abarenicola pacifica*, Wilson 1981).

In the present study, sample sizes were limited due to the effort and time-consuming character of lugworm collection and parallel sampling of habitat variables. In terms of abundance, temporal variation within *Abarenicola affinis* populations could be probably better monitored by faecal cast counting, which gives a reliable proxy for real densities (Chapter 2) and covers larger areas in shorter amounts of time compared with core sampling.

Despite similar overall densities, the *Abarenicola affinis* population in Papanui Inlet consisted of significantly smaller individuals representing significantly less biomass than the population in Hoopers Inlet. Also, the smaller lugworm sizes resulted in a shallower population burrow depth in Papanui Inlet compared with Hoopers Inlet. There appears to be a general difference in individual sizes between both populations evident in similar unimodal size distributions, but different ranges of size classes, i.e., the lack of large size classes in Papanui Inlet. The underlying cause of the different population structures remains unclear. The lack of large individuals in Papanui Inlet could originate from different growth and longevity compared with the Hoopers Inlet population, but size-age relationships are unknown for this species. Lugworm growth rates may depend on external factors such as food availability, i.e., growth rates are faster in sediments of high organic concentration (Linton & Taghon 2000), however, organic content was relatively similar in both sampling areas. In other studies, premature mortality and adult migration into subtidal or remote locations have been identified as reasons for the absence of large individuals in lugworm populations (Lackschewitz & Reise 1998; Reise *et al.* 2001), but no such reason was evident in Papanui Inlet.

The size ranges of female and male gametes of *Abarenicola affinis* were similar to those recorded for other lugworm species (e.g. *Arenicola marina*, Pollack 1979; Rashah & Howie 1982; *Arenicola loveni*, M Gray pers. comm.). Oocytes of different size classes were present throughout the year, which has been similarly documented for *Arenicola marina* (Mayes & Howie 1985). The 3 distinct oocyte size classes in female *Abarenicola affinis* most likely represent different phases of oocyte development, and were similar to those used to assess the degree of female maturity in *Arenicola marina* (Rashah & Howie 1982; Mayes & Howie 1985). Mayes & Howie (1985) assessed stages of reproduction in female lugworms by the proportion of small, medium and large-sized oocytes to the total number of oocytes, with dominance of large-sized oocytes indicating that spawning is imminent. In the present study, oocytes were not counted, but the proportion of females with large-sized oocytes was highest in winter in both populations, suggesting that in most females, oocyte growth was at a later stage and spawning may occur shortly. Spawning at colder times of the year has been observed in other lugworm species and was associated with a seasonal drop in temperature below a threshold level, above which no spawning occurred (13 - 15°C were suggested for *Arenicola marina* in North European tidal flats, Farke & Berghuis 1979; Mayes & Howie 1985). In *Arenicola marina*, spawning may occur in intervals of several weeks during autumn and winter, and can also differ across populations in geographically separated habitats (Farke & Berghuis 1979; Pollack 1979). From the present study, exact spawning intervals remain unclear for the two investigated populations of *Abarenicola affinis*.

Bimodality in lugworm populations, which has allowed previous studies to distinguish between juvenile and adult cohorts, and determine temporal recruitment patterns (e.g. Beukema & de Vlas 1979; Reise *et al.* 2001), did not

occur in either population of *Abarenicola affinis*. Gamete observations indicated that juvenile (immature) *Abarenicola affinis* are less than 20 mm in thorax length. In Papanui Inlet, a strong cohort of the next larger size class (21-30 mm) dominated the population in autumn, suggesting that juvenile recruitment may have occurred in the preceding summer. This suggestion is supported by an observation made during macrofauna sampling in spring, where postlarval *Abarenicola affinis* (< 10 mm total length) occurred in samples collected in the study area (own unpubl. data). It has been reported for other lugworms such as *Arenicola marina* that postlarval recruitment occurs in spring and is followed by juvenile settlement in summer and autumn (Farke & Berghuis 1979).

Lugworm distribution in relation to physical habitat variables

In Papanui Inlet, the distribution of *Abarenicola affinis* was significantly related to distance from the shore, the proxy for tidal level, and amount of sediment fines, whereas measured physical habitat variables did not explain patterns in Hoopers Inlet. There was a difference in lugworm distribution in relation to distance from the shore between both inlets. Whereas lugworm abundance decreased from high towards lower intertidal zones in Papanui Inlet, they were evenly spread across intertidal zones in Hoopers Inlet. These patterns agreed with previous observations in both inlets, showing a significant decrease in lugworm abundance from high towards lower intertidal zones in Papanui Inlet, and a more homogeneous distribution of lugworms in Hoopers Inlet (Chapter 2).

Zonational lugworm distribution along tidal gradients, as observed in Papanui Inlet, has been associated with changes in hydrodynamic disturbance and

sediment types often co-correlating with tidal level and each other (Hobson 1967; Beukema 1976; Beukema & de Vlas 1979). For example, in high intertidal zones with low hydrodynamic disturbance, sediments can become too muddy for lugworms to sustain, probably due to their inability to maintain burrow irrigation in such mud deposits (e.g. *Arenicola marina*, Longbottom 1970; Beukema 1976). In low intertidal zones, strong hydrodynamic disturbance, e.g., by currents and waves action, may exclude lugworms due to the increased sediment instability (e.g. *Abarenicola pacifica*, Hobson 1967). Similar to the distribution of *Abarenicola affinis* in Papanui Inlet, the lugworm *Abarenicola pacifica*, which occurs in tidal bays of the northern American Pacific coast, populates upper intertidal regions, but is scarce in lower intertidal regions (Healy & Wells 1959; Hobson 1967; Swinbanks & Murray 1981). Whereas Healy & Wells (1959) related the observed pattern to the sediment types in their study location (False Bay, U.S.), with *Abarenicola pacifica* preferring muddier sediment in the high intertidal zone. Swinbanks (1981) found no such evidence in his study area (Boundary Bay, Canada), where upper intertidal areas were of low mud content (1%). A subsequent study in False Bay suggested that increased hydrodynamic stress rather than sediment type restricts *Abarenicola. pacifica* to the high intertidal zone, as lugworms did not survive in lower intertidal zones with unstable sediments caused by increased wave action (Hobson 1967). As *Abarenicola affinis* occurred mainly in the less exposed high intertidal zone of Papanui Inlet where mud content was relatively high, the findings support previous suggestions that the species prefers sheltered habitats with finer sediments (Glasby *et al.* 2009; Chapter 2). These sediments seemed to support large lugworms in Papanui Inlet, as biomass, but not density, was positively related to proportion of sediment fines, hence, the occurrence of the largest individuals in the upper intertidal zone only. However, sediment parameters

do not change markedly in this inlet from high towards lower intertidal zones, and are relatively similar to other tidal flats where *Abarenicola affinis* occurs (Chapter 2). Other physical factors may have played an additional role in lugworm distribution in Papanui Inlet. In other studies, factors such as tidal exposure, sediment desiccation, and tidal current regimes (limiting larval transport) have been suggested to be responsible for lugworm distribution patterns along the tidal gradient (Hobson 1967; Swinbanks 1981; Cadman 1997).

The influence of intertidal seagrass on lugworm distribution

The decrease in *Abarenicola affinis* abundance from high towards lower intertidal zones in Papanui Inlet was linked to the distribution of the seagrass *Zostera muelleri*, which seemed to impose limitations to the distribution of lugworms in an otherwise suitable habitat. The significant negative influence of seagrass below-ground biomass on abundance and biomass of *Abarenicola affinis* may be related to burrow restrictions in seagrass areas, as it has been observed for other lugworm species, e.g., *Abarenicola pacifica*, *Abarenicola clarapedii* (Brenchley 1982), and *Arenicola marina* (van Wesenbeeck *et al.* 2007). Seagrass binds sediments by a dense root-rhizome matrix below the surface, which negatively impacts on burrowing infauna such as lugworms, as it considerably reduces sediment penetrability (Brenchley 1982; Reise 1985; Siebert & Branch 2005; Berkenbusch *et al.* 2007; van Wesenbeeck *et al.* 2007). *Abarenicola pacifica* and *Abarenicola clarapedii* have been found to be hampered in their burrowing mobility by seagrass root-rhizome structures and this impact was more pronounced in large individuals, as they have greater difficulty to penetrate the seagrass matrix (Brenchley 1982). An increase in burrowing restrictions with increasing size such as observed by Brenchley (1982) would explain why large

Abarenicola affinis occurred primarily in unvegetated near-shore sediment, whereas lugworms of smaller size classes were also abundant in the adjacent seagrass bed.

In Papanui Inlet, lugworm density did not abruptly decline in the margins of the seagrass bed, but decreased steadily within the seagrass landscape towards the middle of the flat. At the same time, seagrass below-ground biomass increased and showed maximum biomass in the mid intertidal zone. It appeared that the relatively higher seagrass below-ground biomass in the mid intertidal zone of Papanui Inlet affected lugworms to a greater extent than the low biomass and more fragmented seagrass in upper intertidal regions. These observations agree with a study in three estuaries in northern New Zealand comparing distribution patterns of macrobenthic communities outside, at the edge, and inside of *Zostera muelleri* beds (van Houte-Howes *et al.* 2004). In this study, burrowing polychaetes have been found primarily in unvegetated sediment, but were also present at the edge of seagrass beds, where seagrass biomass was lower than inside the bed. This edge effect indicated a level of seagrass below-ground biomass that allowed burrowing organisms to colonise these areas, likely due to less burrowing restrictions (van Houte-Howes *et al.* 2004). The higher abundance of *Abarenicola affinis* in seagrass areas at the margin of the *Zostera muelleri* bed compared with seagrass areas in the mid intertidal zone may be associated with less burrowing restrictions due to relatively lower seagrass biomass in the upper intertidal region.

Similar to lugworms, other large benthic burrowers such as thalassinid shrimp (e.g. sandprawns, mud and ghost shrimps) can be limited in their distribution by seagrass (Brenchley 1982; Harrison 1987; Berkenbusch *et al.* 2007). In

particular, *Zostera muelleri* has been demonstrated to inhibit the ghost shrimp *Callianassa filholi* in Papanui Inlet; transplanted shrimp could not establish themselves in seagrass areas, most likely due to the restrictions on burrowing imposed by the seagrass root-rhizome matrix (Berkenbusch *et al.* 2007). In a tidal bay of southwestern Canada, the decline of burrowing mud shrimps (*Neotypea californiensis*) was related to the expansion of seagrass beds in the intertidal area (Harrison 1987). The lower intertidal limit of the shrimp population moved landwards over several years, and the upper intertidal limit of the seagrass bed coincided with this progression. Harrison (1978) suggested that the restriction on burrowing imposed by seagrass root and rhizome mats could explain, in part, the spatial limitation of the shrimp.

Conclusions

Two *Abarenicola affinis* populations residing in neighbouring tidal inlets of southern New Zealand were stable throughout the year and had similar densities, but differed significantly in their distribution, biomass and body size. Populations showed no distinct juvenile cohorts, but some observations (i.e., the highest proportion of females with large-sized oocytes in winter in both populations, and dominance of the post-juvenile size class in autumn in one population) suggested that spawning may occur in winter, and juvenile settlement in the following spring and summer. In the tidal inlet with seagrass, lugworms were restricted to the periphery of the inlet. The significant negative influence of seagrass below-ground biomass on *Abarenicola affinis* abundance and biomass indicated that seagrass root-rhizome matrices impose limitations to the lugworm population, possibly presenting a lateral barrier to lugworms in the mid intertidal zone, where seagrass biomass was highest. Large lugworms

seemed to occupy muddier sediment than small lugworms, but seagrass may also influence the size distribution as large lugworms were confined to unvegetated areas. In contrast, in the tidal inlet without seagrass, lugworms were spread across all intertidal zones with less variation in density, and also had significantly larger individual sizes, associated with deeper burrows. The findings highlight negative interactions between antagonistic habitat-modifiers, i.e., sediment stabilisers (seagrass) and destabilisers (lugworms) (Reise 2002; van Wesenbeeck *et al.* 2007; Bouma *et al.* 2009), indicating that such interactions can contribute to population patchiness in lugworms by inhibiting their distribution and possibly precluding them from suitable habitats. The findings emphasise the need to sample different habitats in order to understand the linkage between lugworms and their abiotic and biotic environment. More information is needed on population dynamics of *Abarenicola affinis*, in particular reproduction aspects such as spawning and recruitment in order to explain the underlying differences in the characteristics of the two populations.

Chapter 4 - Sediment turnover by the lugworm *Abarenicola affinis* (Arenicolidae, Polychaeta)

Introduction

Bioturbation is an important structuring process in marine soft-sediments and describes the sediment modifying activities of burrowing animals (Levinton 1995; Reise 2002; Bouma *et al.* 2009). Bioturbation, often coupled with bioirrigation (active flushing of burrows and surrounding sediment with overlying water), can have a substantial impact on physical, chemical and biological sediment properties (Graf & Rosenberg 1997; Cadée 2001; Pearson 2001; Meysman *et al.* 2005). To assess the impact of bioturbation and, thereby, an important aspect of the functioning role of an organism in its sedimentary environment, the sediment turnover has been quantified in various studies on intertidal and subtidal burrowers, including lugworms, thalassinid shrimps, fiddler crabs, echiuran worms, and maldanid polychaetes (Cadée 1976; Kudenov 1982; Berkenbusch & Rowden 1999; Hughes *et al.* 1999; McCraith *et al.* 2003).

One of the most prominent examples of marine bioturbators is the deposit-feeding lugworm (genera *Abarenicola*, *Arenicola*), which lives in J-shaped burrows in intertidal and subtidal sediments (Fauchald & Jumars 1979; Rouse & Pleijel 2001). For lugworms, the sediment turnover is part of their feeding and irrigation cycle (Wells 1953). Situated at the base of its burrow, the lugworm produces headward irrigation waves which loosen sediment particles and create a sinking column of sediment in front of the worm (Hobson 1967;

Fauchald & Jumars 1979). Lugworms ingest the subsided surface and subsurface sediment and digest organic material associated with grains and interstitial water (Hylleberg 1975; Riisgard & Banta 1998), before defaecating processed sediment back at the surface in form of characteristic faecal strings (Fauchald & Jumars 1979; Reise 1985). Some species have been shown to selectively feed on finer particles (< 250 μm grain size), with faeces characterised by a finer particle size and concentrated organic material (i.e. remains that were not digested by the lugworm), compared with the surrounding sediment (Hylleberg 1975).

While moving downwards following defaecation, lugworms irrigate their burrows by peristaltic body movements, pumping oxygenated seawater from the overlying water column into the burrow (Riisgard & Banta 1998). Suspension feeding by filtering seawater may occur, but is insignificant to their nutritional uptake (Hobson 1967; Riisgard *et al.* 1996). Hylleberg (1975) showed that both oxygenation of the burrow and increased organic matter in the faeces of lugworms facilitate subsurface bacterial growth, which in turn leads to an increase in microorganisms, upon which lugworms feed (*Abarenicola pacifica*, concept of "gardening" by Hylleberg 1975).

The defaecation rhythm of lugworms is irregular with alternating periods of activity and rest (Wells 1953). In field and laboratory observations, lugworms were spontaneously active after resting periods and defaecated in regular intervals during periods of high activity (Wells 1953; Retraubun *et al.* 1996). These irregular patterns can lead to a notable daily variation in the amount of sediment processed by lugworms (Cadée 1976). The feeding cycle is generated internally and may be modified to adjust to external changes (Wells 1950).

Measurements of lugworm sediment turnover have been used to assess their feeding activity in relation to physical and biological variables such as temperature, tidal stage and food concentration (Cadée 1976; Retraubun *et al.* 1996; Hymel & Plante 2000). Defaecation rates and the amount of expelled faeces may be reduced at lower temperatures in winter compared with summer (Cadée 1976; Retraubun *et al.* 1996). During low tide exposure, lugworms have been observed to slow down defaecation, and activity may cease until burrows become covered again by the incoming tide (Swinbanks 1981; Retraubun *et al.* 1996). Lugworms increase sediment uptake with increasing availability of digestible organic matter, but may reach a level of maximum absorption, characterised by a subsequent decrease in faecal amounts (Taghon & Greene 1990; Hymel & Plante 2000). In addition, the individual size of lugworms has an influence on the sediment turnover: small lugworms may defaecate at shorter intervals than large conspecifics (Wells 1953; Krager & Woodin 1993), and faecal amount generally increases with increasing lugworm size (Hylleberg 1975; Cadée 1976).

Quantifications of sediment turnover by the lugworm *Arenicola marina* revealed that this species reworks substantial amounts of sediment, i.e., replaces sediment equivalent to a depth of up to 33 cm per year (at a density of 85 individuals per m^2) in North European tidal flats (Cadée 1976). By doing so, *Arenicola marina* creates unstable sediments with increased resuspension rates, and, in combination with its irrigating activity, causes substantial changes to physical, chemical and biological sediment properties (Baumfalk 1979; Kristensen 2001; Meysman *et al.* 2005; Volkenborn *et al.* 2007a, 2007b), with significant effects on the structure of benthic tidal flat communities (Flach 1992; Riisgard & Banta 1998; Reise 2002; Volkenborn & Reise 2007; Kuhnert *et al.*

2010). By generating, modifying and maintaining habitats that accommodate distinct benthic assemblages, *Arenicola marina* represents an example within the concept of ecosystem engineering (*sensu* Jones *et al.* 1994) (see Chapter 1).

In view of the significance of lugworms overseas, the present study examined the sediment turnover by the lugworm *Abarenicola affinis,* which occurs in tidal inlets of southern New Zealand (Wells 1963; Glasby *et al.* 2009; Chapter 2). Little is known about the ecological role of this species, and there has been no assessment of its sediment turnover activity to date. The aim of the present study was to investigate factors that influence the sediment turnover activity of *Abarenicola affinis*, with studies carried out in the field and laboratory. Sediment turnover parameters were assessed across seasons, and in relation to temperature, food availability, tidal stage and individual size. Based on the observations, an annual sediment turnover estimate was calculated for an intertidal *Abarenicola affinis* population.

Material & Methods

Study site and field sampling

The study site was in Papanui Inlet (4 km^2), a tidal inlet located on the Otago Peninsula, southern New Zealand (Fig. 13). The inlet is characterised by semidiurnal tides with a mean tidal range of 1.15 m (Albrecht & Vennell 2007). The intertidal sampling area consisted of fine sand (mean grain size 145 μm) with an average proportion of 4% sediment fines (Chapter 3). The distribution of *Abarenicola affinis* in Papanui Inlet is patchy with lugworms primarily occurring in the high and mid intertidal zone (Chapters 2 & 3).

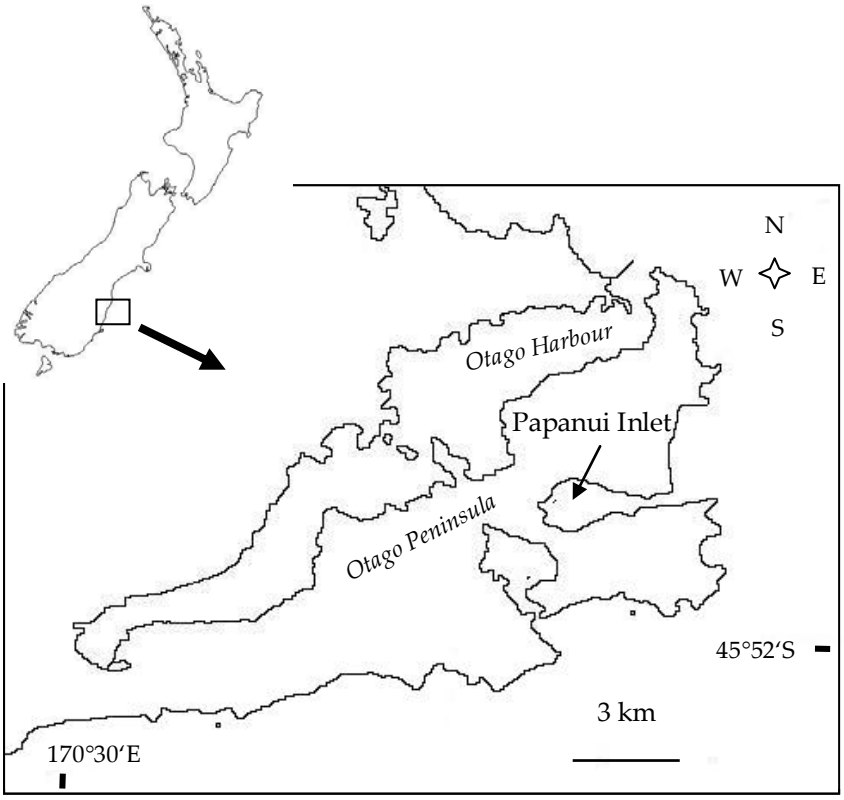


Fig. 13. Location of the intertidal study site (arrow) in Papanui Inlet on the Otago coast, southern New Zealand.

Abarenicola affinis sediment turnover was assessed across four consecutive seasons in summer (February), autumn (May), winter (August) and spring (November) 2009. Sea surface water temperatures (averaged over two sampling days per season) were 15.3, 9.3, 8.4, and 13.0°C, respectively, recorded in Otago Harbour (Portobello Marine Laboratory, unpubl. data). Sampling was carried out over 4 - 6 h during low tide, in calm and dry weather conditions. At the start of the study, four permanent sampling stations were selected in the high and mid intertidal zones and marked by GPS to ensure relocation (the low intertidal zone was not included due to the scarcity of lugworms in this zone). Each season, a total of 48 *Abarenicola affinis* burrows were observed, starting when sediment became exposed by the receding tide. In detail, 12 burrows

were chosen haphazardly in the vicinity of each sampling station, and marked by small labels placed adjacently. Faecal casts associated with the burrows were gently smoothed over by hand. During the time exposed, burrows were observed in 1-h intervals to record the deposition of a new faecal cast (i.e. defaecation rate) and to collect the expelled sediment (i.e. faecal amount). Each new faecal cast was photographed from above (including a scale bar), except in summer 2009, when no photographs were taken due to logistical reasons. Each cast was subsequently collected by carefully removing it from the sediment surface using a flat plastic slide, and rinsed into a container. At the end of the sampling period, 8 lugworms associated with burrows of collected faecal casts were excavated using a sampling core of 20 cm diameter (314 cm^2 area) to 40 cm depth, which was sieved (1 mm mesh) in the field. Also each season, two additional sediment cores were collected at each sampling station to determine total organic matter (4.7 cm diameter, 10 cm depth) and chlorophyll *a* contents of the sediment (2.5 cm diameter, 2 cm depth). Both parameters were used to assess food availability for lugworms, with the former parameter indicating total organic concentration in the surface and subsurface sediment layer upon which lugworms feed, and the latter parameter used as indicator for microphytobenthos, which represents a significant food source in the diet of *Abarenicola affinis* (Leduc *et al.* 2006).

To assess *Abarenicola affinis* sediment turnover in relation to tidal stage, burrow observations were also conducted during high tide in winter (August) and spring (November) 2009, during calm and dry weather conditions. The maximum height of the water column was 80 cm on sampling days. The same sampling stations and a similar sampling design to that of the low tide sampling were used. A total of 48 burrows were visited in 1-h intervals, starting

when the sediment became submerged by the incoming tide. As the collection of new deposited faecal casts was not possible underwater, they were photographed using an underwater camera (Fig. 14), as described for low tide sampling, and then gently smoothed over again. Owing to the time limitations imposed by the tide, records of newly deposited faecal casts (i.e. defaecation rate) could be made for every burrow (48), whereas photographs of faecal casts (i.e. faecal amount) were made for half of the burrows (24) per season. The data collection lasted 4 - 6 h, before burrows became exposed by the receding tide.

Fig. 14. Newly expelled faecal string of *Abarenicola affinis*, photographed underwater during high tide sampling in spring (November) 2009 in Papanui Inlet.

In the laboratory, photographs were analysed using computer software (Image J) in order to measure faecal string length and diameter (± 0.1 mm) for an estimated sediment volume per faecal cast, based on the assumption that faecal strings are cylinders. Faecal casts that were collected during low tide were dried to constant weight (60°C, 48 h) and weighed (± 0.001 g). Collected lugworms were anaesthetised for 3 h in 7% magnesium chloride, fixed in 4% formalin, and subsequently preserved in 70% ethanol. Thorax length was measured (using calipers ± 0.5 mm) instead of total length, as incomplete worms were captured

on occasion. To determine ash-free dry weight (AFDW, ± 0.0001 g), lugworms were dried (60 °C, 48 h) and subsequently combusted (500°C, 4 h). Total organic matter content of the sediment was determined by loss on ignition (500°C, 4 h) (Buchanan & Kain 1971). Sediment chlorophyll *a* samples were freeze dried (-50°C, 48 h), homogenised, boiled in 90% ethanol and subsequently analysed using a spectrophotometer (Sartory 1982).

Laboratory experiment

In the laboratory, the influence of temperature, simulated tidal stage and lugworm size was examined in more detail by observing the same individuals over several days. The experiment was conducted in two separate runs (16 days each) in summer (February) and winter (August) 2009 at the Portobello Marine Laboratory, University of Otago. Sediment and *Abarenicola affinis* were collected in the study area in Papanui Inlet. Sediment was collected relatively undisturbed by inserting a bottomless bucket (30 cm diameter) to 30 cm depth in an area that contained no lugworms. The bucket holding the sediment was excavated and the retained sediment was carefully transferred into another bucket of the same size, but with a bottom. A total of four buckets were filled this way. *Abarenicola affinis* were excavated using a sampling core (as described above), visually checked for being intact, and arbitrarily classed into two thorax length size groups: small (21 - 29 mm) and large individuals (36 - 50 mm).

In the laboratory, the buckets were set up with filtered flow-through seawater from Otago Harbour (Fig. 15). Water temperatures in the buckets were 15°C in summer (February) and 9°C in winter (August), measured by a thermometer. To simulate alternating low-high tide cycles, water flow was turned off and on

every 6 h, approximating the average exposure time at the collection site. During "low tide", the sediment was exposed to air by draining the water column through valves on the sidewall of the bucket. The valves were closed during "high tide" to allow re-submersion of the sediment to 10 cm water depth. This cycle was maintained continuously throughout the experiment. Lights were timed to coincide with the outside daylight period, and air temperature in the laboratory was similar to outside temperature. Each bucket contained 2 *Abarenicola affinis*, one of each size group, that were placed opposite each other on top of the sediment, resulting in a total of 8 lugworms per run. Due to the logistical effort of the experiment the number of buckets was limited and, therefore, two lugworms were placed in each bucket, which corresponded to densities at a lower range compared with the collection site (Chapter 3). At this density, interference within buckets was considered unlikely and lugworms were treated as replicates. When lugworms did not re-burrow within minutes of being placed on the sediment surface, they were replaced. In winter, the experimental set consisted of 7 lugworms, as one individual died during the experiment.

Each experimental run started after lugworms were given 48 h to acclimatise. Recordings were made on four dates, i.e., on day 3, 5, 8 and 9, over 12-h periods each (6 h "low tide" and 6 h "high tide", respectively), to incorporate daily variation in faeces production of singular individuals, as observed in earlier studies (Wells 1953; Cadée 1976). During each recording, buckets were observed at 1-h intervals to note the deposition of a new faecal cast (i.e. defaecation rate) and to collect the expelled sediment (i.e. faecal amount), as described above for the field sampling. The collection of faecal casts during "high tide" was possible after draining the water for one minute. This brief

disruption of the high tide simulation was considered unlikely to affect the lugworm's behaviour.

During each 12-h observation, a video camera recorded either one or two burrows (depending on coverage) with time lapse video recording of one second every 10 minutes, to determine the exact number of single defaecations by the observed lugworm and, thus, calculate an average amount of faeces expelled per single defaecation. Between both runs, a total of 10 lugworms, 5 of each size group, were recorded. Video recordings were similarly done in the second week of each experimental run, but without collecting faecal casts, to determine defaecation frequencies (± 10 minutes) for each individual. At the end of the experiment, lugworms were collected, processed and analysed as described above.

Fig. 15. Experimental set up, including video camera installation, in the laboratory in winter (August) 2009.

Data analysis

Examined sediment turnover parameters of *Abarenicola affinis* were the defaecation rate (active h / total h), and the faecal amount (g dry weight / h, or

mm^3 / h) during observation periods. The seasonal variation in defaecation rate and faecal amount was examined by one-way ANOVA (Underwood 1997). One-way ANOVA was also applied to test differences in sediment turnover parameters between low and high tides, combining field data from winter and spring. For tidal stage comparisons, faecal amount was expressed as volume (mm^3 / h), using photography as the consistent method for both tidal stages. During high tide sampling, faecal volume was determined for only half the number of observed burrows (see above) and, therefore, every second burrow from the low tide sampling was selected to achieve a balanced design. Prior to analysis, data were tested for normality and homogeneity of variances by Kolmogorov-Smirnov and Cochran tests, respectively (Underwood 1997). When data were non-normally distributed, ANOVA was still accepted due to its robustness to non-normality, especially under a balanced design (Underwood 1997). When necessary, data were square-root transformed to achieve homogeneity of variances (Underwood 1997). Simple linear regression (Quinn & Keough 2002) was used to relate sediment turnover parameters of *Abarenicola affinis* to thorax length, combining data from all seasons.

Results from the laboratory experiment were analysed by ANOVA. One-way ANOVA was used to test differences in defaecation rate and faecal amount between experimental summer and winter runs. Differences between simulated tidal stages and size groups were tested by two-way crossed ANOVA, with both runs combined, to assess whether differences between tidal stages are dependent on lugworm size. The mean faecal amount per single defaecation was determined for 10 individuals by dividing the amount of faeces expelled over 12 h by the number of single defaecations (obtained from video recording). Mean faecal amounts per single defaecation were subsequently related to

thorax lengths of individuals by simple linear regression.

To estimate the annual sediment turnover of the *Abarenicola affinis* population in Papanui Inlet, the mean faecal amount per lugworm per h was calculated for low tide (n = 192, all seasons combined) and high tide (n = 48, winter and spring combined). These two parameters represented the average faecal amount expelled by one individual in each hour of sediment exposure and submersion, respectively. High tide data were converted from volume into dry weight by using data collected during low tide in autumn, winter, and spring, when a total of 216 faecal casts were simultaneously photographed and collected. For these faecal casts, the relationship between volume and dry weight was established by simple linear regression (R^2 = 0.93, p < 0.001, n = 216). The resulting regression equations were used to convert volume into dry weight (y = 0.0012 * x + 0.0575) or vice versa (y = 773.869 * x - 32.321).

The mean faecal amount per lugworm per h of exposure or submersion was multiplied by the average daily period of the corresponding tidal stage in the high, mid and low intertidal zone of Papanui Inlet (Chapter 2) to obtain the daily faecal amount expelled by one individual in each intertidal zone. This value was multiplied by the mean population density in each zone (Chapter 2). Subsequently, data from all intertidal zones were averaged to obtain the faecal amount expelled per m² per day in the entire inlet. Values were then combined for the annual sediment turnover estimate of the entire lugworm population in Papanui Inlet. All statistical analyses were conducted using Statistica 6 (StatSoft Inc.).

Results

Field observations on lugworm sediment turnover

During low tide exposure, there was high variation in sediment turnover activity of *Abarenicola affinis* within each season, ranging from inactive to highly active individuals (defaecation rate 0 - 1 active h / total h). Between 8 and 15 individuals (of a total of 48) per season did not defaecate during low tide exposure, whereas the number of continuously active lugworms was lower with 1 - 4 individuals per season. The maximum amount of faeces expelled by one individual was 0.748 g dry weight / h.

The sediment turnover activity of *Abarenicola affinis* during low tide varied little across seasons, with mean defaecation rates of 0.32 - 0.42 active h / total h (each season n = 48), and similar values in autumn and spring, as well as in summer and winter (Table 9). One-way ANOVA showed no significant difference in defaecation rate across seasons (df = 3, F = 1.57, p = 0.197, n = 48). The mean faecal amount of *Abarenicola affinis* doubled from winter (0.064 ± 0.073 g dry weight / h, n = 48) to spring (0.130 ± 0.152 g dry weight / h, n = 48), whereas values in summer and autumn were similar, and lay between winter and spring values (Table 9). One-way ANOVA revealed that differences in faecal amounts across seasons were not statistically significant (df = 3, F = 1.78, p = 0.152, n = 48).

Total organic matter content of the sediment was within a similar range across seasons (below 1%), with slightly higher values in spring compared with the other seasons (Table 9). The seasonal pattern showed similarity with trends in *Abarenicola affinis* faecal amounts, i.e., at lowest organic contents in winter, lugworms expelled the smallest amount of faeces, whereas in spring, when

organic content was highest, lugworm faecal amounts were also largest. Chlorophyll *a* content of the sediment showed a seasonality related to water temperature, with highest values in summer, and lowest values in winter, whereas autumn and spring values were intermediate, but no corresponding pattern with lugworm sediment turnover parameters (Table 9).

Table 9. Sediment turnover parameters of *Abarenicola affinis* during low tides (mean values ± SD, each season n = 48), water temperature (averaged over sampling days, recorded in Otago Harbour, Portobello Marine Laboratory, unpubl. data), total organic matter and chlorophyll *a* contents of the sediment (mean values ± SD, each season n = 4) in summer (February), autumn (May), winter (August) and spring (November) 2009, in Papanui Inlet.

Season	Defaecation rate (active h / total h)	Faecal amount (g dry weight / h)	Water temperature (°C)	Total organic matter (%)	Chlorophyll *a* (μg / g sediment dry weight)
Summer	0.32 ± 0.29	0.090 ± 0.122	15.3	0.68 ± 0.07	8.2 ± 2.7
Autumn	0.42 ± 0.32	0.087 ± 0.115	9.3	0.64 ± 0.06	5.8 ± 2.4
Winter	0.33 ± 0.30	0.064 ± 0.073	8.4	0.61 ± 0.08	4.4 ± 1.0
Spring	0.41 ± 0.28	0.130 ± 0.152	13.0	0.79 ± 0.07	6.1 ± 1.9

The defaecation rate of *Abarenicola affinis* was related to tidal stage, as lugworms were notably less active when burrows were exposed to air during low tide (0.37 ± 0.29 active h / total h) compared with submerged burrows at high tide (0.63 ± 0.31 active h / total h), using combined data from winter and spring (each tidal stage n = 96). This difference in defaecation rate between tidal stages was significant (one-way ANOVA, df = 1, F = 36.79, p < 0.001). During high tide, at least 48% of individuals were active each h, whereas during low tide, the number of active individuals decreased with increasing time of exposure (Fig. 16). Similar to the activity patterns, lugworms expelled considerably smaller amounts of faeces during low tide compared with high tide, with mean faecal

volumes of 63.1 ± 115.9 mm³ / h and 193.3 ± 173.8 mm³ / h, respectively (winter and spring combined, each tidal stage n = 48). The difference in faecal volume between tidal stages was significant, as revealed by one-way ANOVA (df = 1, F = 27.05, $p < 0.001$).

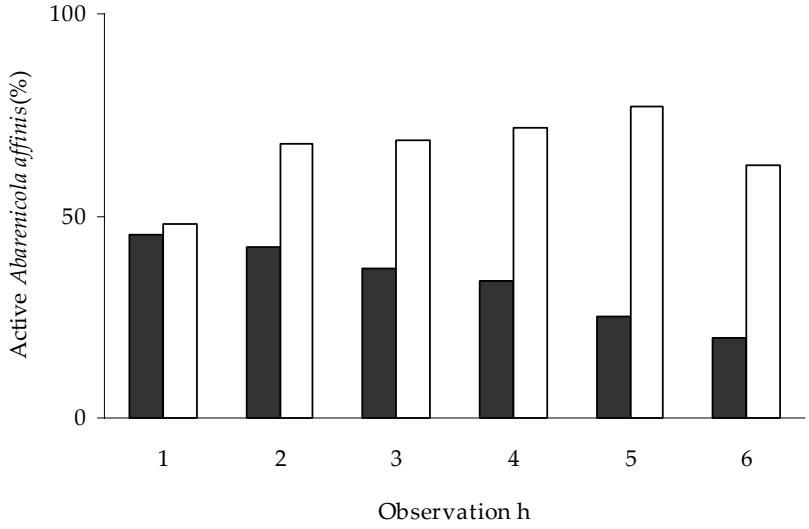


Fig. 16. Active *Abarenicola affinis* (%) per observation h during low (closed) (all seasons combined, n = 96 - 192) and high tides (open) (winter and spring combined, n = 48 - 96) in Papanui Inlet. Note: differences in n per tidal stage are caused by different observation periods (4 - 6 h), dependent on the position of lugworms on the tidal flat.

Defaecation rate and faecal amount of *Abarenicola affinis* related differently to individual size: there was no relationship between thorax length and defaecation rate (simple linear regression, p = 0.929, n = 32), but an increase in lugworm size corresponded with an increase in faecal amount (Simple linear regression, y = 0.0116 * x – 0.1359, R^2 = 0.56, $p < 0.001$, n = 32).

Laboratory observations on lugworm sediment turnover

In the laboratory, *Abarenicola affinis* were exposed to a simulated alternating 6 h low-high tide cycle over 16 days. During the experiment, lugworms were generally active during the experimental runs. The monitoring of lugworms at the 6-h intervals revealed that the longest resting period was 72 h (3 days), which was observed during the first few days of the experimental run in summer in one large individual. Resting periods longer than 24 h were only observed in the first week of both experimental runs, whereas in the second week, resting periods were usually less than 6 h and occurred mainly during "low tides".

The defaecation rate and faecal amount per individual were recorded over a total time of 48 h, in four separate 12-h recordings (encompassing 6 h of each tidal stage) to account for daily variation. The mean defaecation rate ranged between 0.33 and 0.69 active h / total h (both runs combined, n = 15), with mean faecal amounts of 0.330 ± 0.180 g dry weight / h, amounting to an average daily faeces output of 8.040 g dry weight per individual.

Water temperatures were 15°C in summer and 9°C in winter, which approximated the natural range observed in the field (see Table 9). Sediment turnover activity of *Abarenicola affinis* showed no variation between experimental runs with defaecation rates of 0.52 ± 0.12 active h / total h in summer (n = 8), and 0.57 ± 0.09 active h / total h in winter (n = 7). One-way ANOVA confirmed that there was no statistical difference in defaecation rate between both runs (df = 1, F = 0.77, p = 0.395). Similar to defaecation rate, faecal amounts varied little between summer and winter runs with 0.302 ± 0.157 g dry weight / h in summer and 0.368 ± 0.211 g dry weight / h in winter, and no

significant difference between both runs (one-way ANOVA, $df = 1$, $F = 0.48$, $p = 0.500$, $n = 8 / 7$).

Simulated tidal stages, i.e., the exposure and submersion of burrows, greatly influenced the sediment turnover activity of *Abarenicola affinis* (Table 10). The mean defaecation rate, averaged over both runs ($n = 15$), was nearly four times higher during "high tide" (0.86 ± 0.16 active h / total h) than during "low tide" (0.23 ± 0.11 active h / total h). Four individuals (of 15 in total) were continuously active each recorded h of submersion (24 h in total). Similar to defaecation rates, considerably greater amounts of faeces were expelled when burrows were covered by water, with a six-fold increase in faecal amounts during "high tide" (0.613 ± 0.325 g / h, $n = 15$) compared with "low tide" (0.089 ± 0.057 g / h, $n = 15$). Defaecation rate was not related to thorax length, whereas individual size had an influence on faecal amounts, i.e., large lugworms expelled greater amounts of faeces than small ones (Table 10). Results from two-way crossed ANOVA (factors simulated tidal stage, lugworm size) revealed significantly higher defaecation rates and faecal amounts during simulated high tide compared with simulated low tide, as well as significantly greater faecal amounts in large *Abarenicola affinis* compared with small ones (Table 10). The lack of a significant interaction between tidal stage and lugworm size in both sediment turnover parameters indicated that tidal stage effects were independent of lugworm size. The effect of tidal stage was highlighted by the notably greater amount of faeces expelled by small lugworms at "high tide" (0.374 ± 0.218 g / h, $n = 7$), compared with large lugworms at "low tide" (0.127 ± 0.045 g / h, $n = 8$).

Lugworms exhibited variation in the number of single defaecations (between 4 and 18) over 12 h. The mean faecal amount per single defaecation ranged

between 0.131 and 0.670 g and was significantly related to thorax length (simple linear regression, $R^2 = 0.94$, $p < 0.001$, $n = 10$) (Fig. 17).

Table 10. Sediment turnover parameters of small (21 - 29 mm thorax length) and large *Abarenicola affinis* (36 - 50 mm thorax length) (mean values ± SD, combined runs from summer and winter 2009, $n = 7 / 8$) during simulated low and high tides in the laboratory, and results from two-way crossed ANOVA (factors: simulated tidal stage, lugworm size, and interaction) (significant values in bold).

Parameters	Low tide		High tide	
	Small	Large	Small	Large
Defaecation rate (active h / total h)	0.21 ± 0.12	0.24 ± 0.09	0.83 ± 0.17	0.88 ± 0.13
Faecal amount (g dry weight / h)	0.047 ± 0.029	0.127 ± 0.045	0.374 ± 0.218	0.822 ± 0.222

	Tidal stage			Size group			Tidal stage x size group		
	df	*F*	*p*	df	*F*	*p*	df	*F*	*p*
Defaecation rate (active h / total h)	1	151.38	**< 0.001**	1	0.77	0.389	1	0.026	0.874
Faecal amount (g dry weight / h)	1	64.02	**< 0.001**	1	18.2	**< 0.001**	1	< 0.01	0.962

Defaecation frequencies, recorded for each individual over 12 h, were on average 53 ± 26 minutes ($n = 15$). There was a notable difference in frequencies between simulated low and high tides: when submerged, lugworms defaecated with relative regularity at intervals of 31 ± 12 minutes ($n = 15$). During exposure, defaecation was sporadic with resting periods of several h in 10 of 15 lugworms. Three individuals were inactive at "low tide", and were not included in the calculation of mean defaecation frequency, which was 180 ± 115

minutes (n = 12). There was also variation in defaecation frequency between small and large *Abarenicola affinis*, as small lugworms defaecated on average every 45 ± 13 minutes (n = 7), whereas large lugworms expelled faeces every 60 ± 35 minutes (n = 8). Whereas tidal stage-related differences in defaecation frequency agreed with findings from 1-h interval recording, lugworm size-related differences stood in contrast to 1-h interval recording, where similar defaecation rates were measured (Table 10).

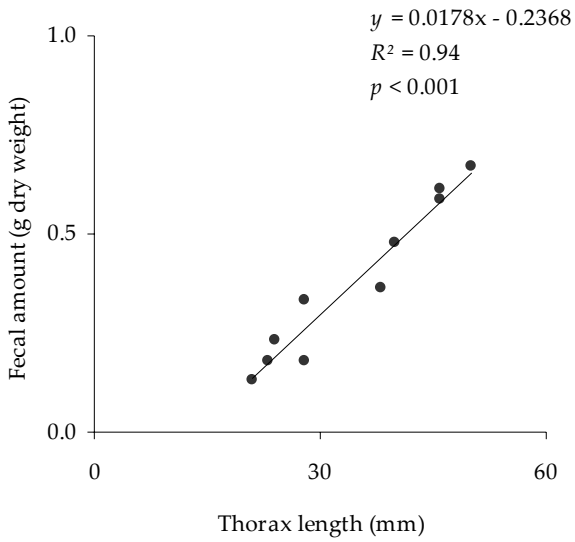


Fig. 17. *Abarenicola affinis* faecal amount per single defaecation (g dry weight) in relation to thorax length (mm), recorded in the laboratory, combining data from summer and winter runs 2009 (n = 10).

Annual sediment turnover by an intertidal lugworm population

The annual sediment turnover of the *Abarenicola affinis* population in Papanui Inlet was estimated for the high, mid and low intertidal zones of the inlet to account for the differences in tidal exposure / submersion and lugworm abundance in these zones. The sediment turnover estimate was based on two

parameters, which were the mean faecal amount expelled per individual per h during exposure (0.093 ± 0.121 g dry weight / h, all seasons combined, n = 192) and submersion (0.270 ± 0.218 g dry weight / h, winter and spring combined, n = 48). For each intertidal zone, these parameters were used to calculate the daily amount of faeces expelled by one lugworm (based on the average number of exposure and submersion h per day), accounting for the variation in sediment turnover associated with tidal stages (Table 11). Values were multiplied by *Abarenicola affinis* density in each zone to obtain the daily faecal amount expelled by the lugworm population in each zone and for the entire inlet, and then summed for the annual sediment turnover estimate, which was 24.4 kg dry weight per m². To express sediment turnover quantity as sediment depth, dry weight was converted into volume, and subsequently into sediment depth per m² (10 dm³ = 1 cm depth). Averaged over the entire inlet, *Abarenicola affinis* reworked sediment equivalent to a depth of 1.9 cm per year. Most sediment was reworked in the high intertidal zone due to the highest lugworm abundance in this zone. There, lugworms reworked sediment equivalent to a depth of 4 cm per year.

Table 11. Annual sediment turnover estimate of the *Abarenicola affinis* population in Papanui Inlet, expressed as dry weight (kg / m²) and sediment depth (cm / m²), accounting for population density (individuals per m²) and daily periods of exposure and submersion in different intertidal zones (Chapter 2).

Intertidal zone	Average daily exposure / submersion h	Daily turnover per individual (g dry weight)	Mean population density (m²)	Annual sediment turnover (kg dry weight / m²)	Sediment depth reworked per year (cm / m²)
High	16 / 8	3.648	38.0	50.598	3.9
Mid	12 / 12	4.356	9.8	15.581	1.2
Low	6 / 18	5.418	3.6	7.119	0.5
Overall		**4.474**	**17.1**	**24.433**	**1.9**

Discussion

Lugworm sediment turnover in relation to seasonal temperature and food availability

Abarenicola affinis reworked sediment at a relatively constant level throughout the year, with no significant seasonal variation in sediment turnover parameters recorded at low tide. Results from the laboratory experiment were consistent with field observations, as there were relatively similar defaecation rates and faecal amounts at summer and winter temperatures, recorded over several days including simulated low and high tides. The findings indicated that water temperature had no influence on *Abarenicola affinis* sediment turnover parameters. In terms of faecal amount, the present findings agree with field observations made by Plante & Mayer (1996), who found no significant differences in faecal amounts of the lugworm *Arenicola marina* across six seasonal sampling dates, with sediment temperatures spanning between 3.8 and 20.3°C. In other studies, however, a significant response of this species to seasonal temperature has been observed (Cadée 1976; Retraubun *et al.* 1996). Cadée (1976) measured ten times lower amounts of expelled faeces in winter (up to 400 ml / m^2), at sediment temperatures of 5°C, compared with summer (up to 4000 ml / m^2), when sediment temperatures were 22°C. Retraubun *et al.* (1996) recorded lower defaecation rates in autumn and winter (0.0 - 0.4 / h), compared with spring and summer (0.2 - 1.3 / h), with sediment temperatures varying between 6 and 15°C across seasons. In these studies, defaecation rate and faecal amount of *Arenicola marina* were positively correlated with temperature following the "bell curve" over the course of a year, i.e., highest and lowest values were found in summer and winter, respectively, whereas in spring and autumn values increased and decreased, respectively. Optimum

feeding rates in lugworms may occur over an intermediate temperature range of several degrees (e.g. 12 - 17°C for *Abarenicola pacifica*, and 14 - 20°C for *Arenicola marina*), with a decline in activity outside either side of the range (Plante & Jumars 1993; Retraubun *et al.* 1996). In the present study, the *in situ* water temperature range (8.4 - 15.3°C) may not have been sufficiently large to influence sediment turnover parameters of *Abarenicola affinis*, and it remains unclear, if or what temperature affects sediment turnover by this lugworm species. It is also to note that the present study measured water temperature instead of sediment temperature, with the latter presumably being somewhat higher in summer and lower in winter when sediment is exposed to air during low tide.

Similar to temperature, seasonal differences in food availability appeared to have little influence on sediment turnover parameters of *Abarenicola affinis*. A previous study demonstrated the ability of this species to adapt to seasonal changes in food availability (Leduc *et al.* 2006). The lower abundance of microphytobenthos in autumn and winter, indicated by lower chlorophyll *a* contents of the sediment, may have been compensated by the use of seagrass detritus as the main food source (Leduc *et al.* 2006). The results showed a general tendency of faecal amounts to increase with increasing organic matter content, but differences in the latter were small. In other studies, a similar relationship was found, i.e., an increase in organic concentration increased the amount of sediment processed by lugworms (de Wilde & Berghuis 1977; Hymel & Plante 2000). *Abarenicola affinis* faecal amounts were greatest in spring, coinciding with highest total organic matter contents, whereas lowest amounts of sediment were processed in winter, when both total organic matter and chlorophyll *a* were also lowest. Similar observations were made on *Arenicola*

marina by Cadée (1976), who suggested that the seasonality in sediment turnover quantity is related to food availability rather than temperature. This suggestion was based on the observation that the greatest faecal amounts were expelled in spring and early summer, before temperature peaked, but at a time when primary production of benthic microalgae was highest.

The sediment turnover activity and quantity of *Abarenicola affinis* were characterised by high variation within each season, as similarly reported for *Arenicola marina* on European tidal flats (Retraubun *et al.* 1996). Individual differences in lugworm activity have been attributed to the irregularity in defaecation patterns, e.g., the random occurrence of resting periods (which can last for several days) followed by regular defaecation over hours (Wells 1953; Hylleberg 1975; Cadée 1976; Retraubun *et al.* 1996). In *Abarenicola affinis*, irregular activity occurred mainly during low tide, and a potential seasonal influence may have been concealed by the lack of year-round observations during high tides, when lugworms defaecated more regularly. Findings from the laboratory experiment, however, indicated similar defaecation activity at summer and winter temperatures for both tidal stages.

Lugworm sediment turnover in relation to tidal stage and individual size

In situ observations demonstrated a significant influence of tidal stage on *Abarenicola affinis* sediment turnover, i.e., lugworms defaecated more often and expelled greater amounts of faeces during submersion at high tide, compared with exposure at low tide. The results support previous observations on other lugworm species (e.g. *Abarenicola pacifica*, *Arenicola marina*), relating defaecation activity to exposure and submersion of burrows (Swinbanks 1981; Retraubun *et*

al. 1996). In these studies, lugworms continued to defaecate during low tide, when their burrows stayed submerged, e.g., in tidal pools. The present study suggested that feeding processes, i.e., ingestion, digestion and defaecation, are regulated in accordance with tidal stage. The reduced activity of *Abarenicola affinis* during low tide may be the result of sediment oxygen depletion associated with the lack of oxygenated water. Oxygen deficiency forces lugworms to change their metabolism to anaerobic energy production (Schoettler *et al.* 1984), and lugworms have been shown to maintain feeding and defaecation activities only when the sediment remains sufficiently moist (Kermack 1955). In intertidal habitats, both lugworm abundance and sediment turnover activity may, therefore, be positively related to sediment wetness (Swinbanks 1981; Cadman 1997). The decrease in the number of active *Abarenicola affinis* with increasing time of exposure may be explained by ongoing desiccation impeding on feeding cycles. Although decreasing in numbers, some *Abarenicola affinis* were still active after several hours of exposure. In contrast, *in situ* observations on *Arenicola marina* showed that most individuals ceased defaecation within the first hour of exposure and did not defaecate until burrows were submerged again by the incoming tide (Retraubun *et al.* 1996). This difference in low tide-activity patterns between lugworm species may be, in part, explained by the sediment particle composition of the studied tidal flats. In the study on *Arenicola marina*, the tidal flat (Whitley Bay, U.K., northern Europe) consisted of medium sand (> 250 μm mean grain size), whereas the present study site in Papanui Inlet consisted of finer sand (145 μm mean grain size, 4% mud content) (Retraubun *et al.* 1996; Chapter 3). Coarser sediment retains less water during low tide than finer sediment, which could result in an earlier slow down of lugworm activity (Swinbanks 1981). For this reason, *Abarenicola affinis* in Papanui Inlet may have

been more able to continue feeding and defaecation during low tide compared with *Arenicola marina* in Retraubun's study (1996).

In addition to physical factors, sediment turnover activity patterns of *Abarenicola affinis* may have been influenced by predators. When sediment is exposed during low tide, foraging birds browse tidal flats in search of faecal casts appearing at the sediment surface: at this moment the posterior end of the lugworm is in reach of their bills ("tail-nipping") (Reise 1985; Hulscher 1996). In southern New Zealand, oystercatchers, and probably other waders, feed on *Abarenicola affinis* (K Probert pers. comm.), and a reduction in defaecation activity during low tide could lower the risk for lugworms to be attacked by these birds. There is, however, little information available about predation on lugworms during low and high tides. Studies on *Arenicola marina* showed that predation occurs at both tidal stages, either by birds or fish (de Vlas 1979; Reise 1985; Bergman 1988).

Laboratory results were consistent with findings from the field, showing a significant difference in *Abarenicola affinis* sediment turnover parameters between simulated tidal stages. Lugworms defaecated regularly at "high tide", whereas defaecation was sporadic at "low tide". The differences were more pronounced in the second week of the experiment, when regular defaecation at "high tide" resulted in resting periods no longer than 6 h. These observations indicate that the simulated tides supported regularity in lugworm activity patterns, i.e., feeding cycles, according to the external conditions (Wells 1950; Retraubun *et al.* 1996). In contrast, when kept under constant conditions, e.g., in permanently submerged sediment, feeding and defaecation activities of lugworms were found to be random (Wells 1950; Cadée 1976).

Recordings at 1-h interval showed no relationship between defaecation rates and lugworm size, whereas recordings at 10-minute interval revealed shorter defaecation frequencies in small lugworms compared with large ones, which has been similarly documented for *Arenicola marina* (Wells 1953) and *Abarenicola pacifica* (Krager & Woodin 1993). Findings of the present study indicated that 1-h intervals may have been too long to detect differences between small and large *Abarenicola affinis*. When continuously active at "high tide", *Abarenicola affinis* defaecated on average every 31 minutes (both size groups combined), which equals defaecation frequencies reported for other lugworm species, e.g., *Abarenicola pacifica* (30 min, Hylleberg 1975) and *Arenicola marina* (36 min, Retraubun *et al.* 1996). Fecal amounts of *Abarenicola affinis* gave a reliable indication of lugworm size in the field and laboratory. In comparison, other studies documented disproportional or poor relationships between lugworm sizes and faecal amounts (Hobson 1967; Cadée 1976; Krager & Woodin 1993). Faecal amounts per single defaecation were closely related to thorax length, and, therefore, could provide valuable estimates of lugworm length for non-invasive field observations (see also Chapter 2).

Annual sediment turnover and bioturbative impact by lugworms

Sediment reworking by *Abarenicola affinis* in Papanui Inlet was relatively stable throughout the year, as evident in little variation in faecal amounts (this study) and lugworm abundance (Chapter 3) across seasons. In contrast, there was spatial variation based on the heterogeneous distribution of this species in Papanui Inlet, with the majority of sediment reworked in the high intertidal zone. The annual sediment turnover estimate did not directly account for the distribution of lugworm sizes on the tidal flat, which may have an additional

influence on turnover estimates (Rowden & Jones 1993; Retraubun *et al.* 1996). In the present study, estimates were based on faecal amounts averaged over 192 individuals (per h of exposure) and 48 individuals (per h of submersion), representing a mean of all lugworm sizes within this population.

The studied lugworm population reworked annually 24.4 kg dry weight of sediment per m^2, equivalent to a sediment depth of 1.9 cm. Comparisons with sediment turnover estimates of other studies are difficult as field methods and calculations can differ widely. Similar to the present study, a number of studies have incorporated seasonal variation and tidal stages in their sediment turnover estimates, in particular for *Abarenicola pacifica* and *Arenicola marina* (Cadée 1976; Swinbanks 1981; Retraubun *et al.* 1996). The estimate for *Abarenicola affinis* is generally lower than those recorded for these other lugworm species. In case of *Abarenicola pacifica*, the annual sediment turnover has been estimated at 449 000 m^3 for an intertidal area of 8 km^2 in Boundary Bay, Canada, based on a population density estimate of $3.25 * 10^8$ individuals and faecal cast volumes collected on three sampling dates throughout the year (Swinbanks 1981). Converting the estimate in sediment depth per m^2 (10 dm^3 = 1 cm), *Abarenicola pacifica* turns over sediment equivalent to a depth of approximately 6 cm at a mean density of 41 individuals per m^2, which is higher than for *Abarenicola affinis* at a comparable mean density, e.g., in the high intertidal zone of Papanui Inlet. Considerably greater sediment amounts than those presented for both *Abarenicola* species were reported for *Arenicola marina* on European tidal flats (Cadée 1976; Retraubun *et al.* 1996). Cadée (1976), who combined seasonal data from several years and different tidal flats of the Dutch Wadden Sea, North Europe, estimated an annual sediment turnover equivalent to a depth of 14 and 33 cm at mean densities of 43 and 85 individuals per m^2, respectively.

Superimposed for the entire *Arenicola marina* population in the Dutch Wadden Sea (mean density 17 individuals per m^2), the estimate was equivalent to a sediment depth of 6 cm. This value is three-fold higher than found for *Abarenicola affinis* in the present study. A study of *Arenicola marina* at Whitley Bay, U.K., North Europe, which accounted for abundance and size-distribution at different distances from the shore, estimated the annual sediment turnover of the intertidal population to be equivalent to a sediment depth of 9 cm (Retraubun *et al.* 1996). In the European Wadden Sea, sediment turnover amounts of *Arenicola marina* exceed those of many other benthic organisms, and the species is recognised as the quantitatively most important bioturbator on tidal flats (Cadée 1976; Reise *et al.* 2010). Sediment reworking by this lugworm species can alter the entire sedimentary fabric, budget and chemistry (Baumfalk 1979; Huettel 1990; Kristensen 2001; Volkenborn *et al.* 2007a; Whethey *et al.* 2008), with significant effects on infaunal community compositions (Flach 1992; Reise 2002; Volkenborn & Reise 2006, 2007; Kuhnert *et al.* 2010). The notably lower amount of sediment reworked by *Abarenicola affinis* suggests a lower bioturbative impact on the sediment by the New Zealand species compared to its European counterpart. The difference could be due to species-specific differences in individual size, as the studied *Arenicola marina* populations contained larger individuals (up to 11 g wet weight, Cadée 1976; Retraubun *et al.* 1996) than the investigated *Abarenicola affinis* population (up to 3.28 g wet weight, own unpubl. data), likely resulting in greater amounts of faeces *per capita*.

Given these differences in individual size across lugworm species, it can be asked whether individuals of similar biomass would yield similar amounts of sediment turnover. Such comparisons are, however, difficult to make due to the

different observation and collection methods which were used in various studies on other lugworm species. A theoretical approach using data from the present and other laboratory studies shows that faecal amounts of *Abarenicola affinis* lie within the same range or higher than those of similar sized *Abarenicola pacifica*, whereas they are notably smaller than those of *Arenicola marina* at similar biomass. For example, in a study by Hobson (1967), *Abarenicola pacifica* of 1 - 3.5 g wet weight expelled on average 3.4 g sediment dry weight per day (under simulated tidal conditions), which is exceeded by similar sized *Abarenicola affinis* (0.18 - 2.77 g wet weight) in the present experiment (8.040 g sediment dry weight per day). Hylleberg (1975) recorded daily amounts of faeces of up to 4.5 and 15.0 g sediment dry weight for two *Abarenicola pacifica* individuals of 0.7 and 2.0 g wet weight, respectively, in the laboratory. In comparison, two similarly sized *Abarenicola affinis* from the present experiment weighing 0.8 and 2.2 g wet weight expelled 10.5 and 12.6 g sediment dry weight per day, respectively. In laboratory observations on *Arenicola marina*, individuals of 0.3 - 1.5 g wet weight produced 17 - 30 ml faeces per day (Cadée 1976). These amounts appear much larger than estimated faecal volumes produced by *Abarenicola affinis* of relatively similar size, i.e., individuals of 0.18 - 2.77 g wet weight produced 8 - 12 ml faeces per day (data converted to volume after regression equation, see Material and methods).

Sediment reworking by *Abarenicola affinis* in Papanui Inlet is confined mainly to the high intertidal zone, where lugworms are most abundant, exceeding densities of 100 individuals per m^2 (Chapter 2). As the species is patchily distributed in tidal flats of the Otago coast (Chapter 2), its bioturbative impact is likely to be spatially dependent and less widespread than that of *Arenicola marina*, which is extensively and relatively even distribution on tidal flats of

northern Europe (Reise 1985; Beukema *et al.* 1983; Beukema *et al.* 1993; Flach & Beukema 1994). The importance of lugworm concentrations as areas of high biogenic disturbance has been demonstrated in other studies (Swinbanks 1981; Krager & Woodin 1993). For example, *Abarenicola pacifica* has been found to assemble in high densities in tidal pools (up to 200 individuals per m^2, study site: Boundary Bay, Canada), where it reworks sediment equivalent to a depth of 10 cm in 100 days, exceeding by far the turnover estimate for the entire tidal flat (Swinbanks 1981). Krager & Woodin (1993) found that temporal persistence of lugworm concentrations was high, and suggested that spatial and temporal averages in sediment turnover estimates may conceal the importance of lugworm bioturbation for small-scale patches.

The local importance of *Abarenicola affinis* bioturbation may also be influenced by the distribution of other benthic burrowers that co-occur with lugworms in tidal flats of Otago, such as thalassinid shrimps (*Callianassa filholi*), maldanid polychaetes (*Macroclymenella stewartensis*) or mud crabs (*Helice crassa*, *Macrophthalmus hirtipes*) (Rainer 1981; Berkenbusch & Rowden 1998; Chapter 5). For example, *Callianassa filholi* is an effective bioturbator that turns over considerably greater amounts of sediment than *Abarenicola affinis*: the annual sediment turnover estimate of an intertidal shrimp population (mean density 16 individuals per m^2) in Otago Harbour, near the present study site (Fig. 13), has been estimated at 96 kg sediment dry weight per m^2, with data collected monthly over one year (Berkenbusch & Rowden 1999). Thus, the bioturbative importance of lugworms is likely to be influenced by the co-occurrence of these shrimps in intertidal habitats.

Conclusions

Sediment turnover by *Abarenicola affinis* varied little across seasons, and the lack of variation may be linked to only moderate changes in temperature (this study), as well as adaption of this species to seasonal changes in available food sources (Leduc *et al.* 2006). The potential influence of temperature and food concentration on *Abarenicola affinis* sediment turnover requires further research, e.g., in relation to the species' distribution along a latitudinal temperature gradient throughout New Zealand. Sediment turnover activity and quantity were significantly reduced at exposure during low tide, which agreed with previous findings on other lugworm species (Swinbanks 1981; Retraubun *et al.* 1996), and supports the generality of tidal stage effects on lugworm sediment turnover. Feeding cycles seemed to vary between small and large *Abarenicola affinis*, as small lugworms defaecated more often, but processed significantly less amounts of sediment compared with large lugworms. The annual sediment turnover estimate for *Abarenicola affinis* (equivalent to a sediment depth of 2 cm) suggests a smaller impact of this species on sediment properties compared with its European counterpart *Arenicola marina* (Cadée 1976). Sediment turnover by *Abarenicola affinis* is also largely exceeded by co-occurring ghost shrimps (Berkenbusch & Rowden 1999), indicating that the local importance of lugworm bioturbation may be further influenced by the distribution of other bioturbators in tidal flats of southern New Zealand.

Chapter 5 - Macrofauna associated with the lugworm *Abarenicola affinis* (Arenicolidae, Polychaeta)

Introduction

Marine bioturbating organisms can have a substantial impact on the benthic sedimentary environment: burrowing, feeding and irrigation activities modify the sedimentary budget, fabric and chemistry and, thereby, considerably impact on the habitat suitability for other species (Levinton 1995; Graf & Rosenberg 1997; Cadée 2001; Pearson 2001; Reise 2002). Positive effects of bioturbation have been linked to the maintenance of sediment permeability in otherwise cohesive mud flats, transport of oxygenated seawater to depth, and the provision of micro-habitats such as burrow constructs and surface structures (Dittmann 1996; Cadée 2001; Volkenborn & Reise 2007). In contrast, surface and subsurface sediment disturbance may result in the burial of organisms, and the unstable sediment matrix may be avoided by other tidal flat benthos (Suchanek 1983; Woodin 1985; Flach 1992; Berkenbusch & Rowden 2007). The impact of bioturbation on other biota can be influenced by environmental conditions, as well as population dynamics of the bioturbating organism and associated taxa (Posey 1986; Brey 1991; Sandnes *et al.* 2000; Berkenbusch & Rowden 2007; Volkenborn & Reise 2007).

Lugworms (genera *Abarenicola* and *Arenicola*, family Arenicolidae) are deposit-feeding burrowers in intertidal and subtidal sediments, where they often dominate macrobenthic abundance and biomass (e.g. Beukema 1976; Reise *et al.* 1994; Moreno *et al.* 2007). Lugworms rework the sediment constantly through

their feeding activities, i.e., ingestion of sediment at depth and deposition of faeces at the surface (Wells 1953; Cadée 1976; Fauchald & Jumars 1979). Also, they irrigate their burrows and surrounding sediment by pumping overlying seawater into the burrow, as well as creating upward and radiating porewater flows at feeding depth (Riisgard *et al.* 1996; Meysman *et al.* 2005). Previous studies, mainly conducted on the European species *Arenicola marina*, have demonstrated that both bioturbation and bioirrigation by lugworms affect physical and biogeochemical sediment properties such as particle size composition and distribution, organic content, permeability, as well as oxygen, nutrient and metabolite flux rates (Baumfalk 1979; Huettel 1990; Riisgard *et al.* 1996; Banta *et al.* 1999; Kristensen 2001; Volkenborn *et al.* 2007a).

Bioturbation by lugworms imposes changes to the structure of benthic sediment communities (Riisgard & Banta 1998; Volkenborn & Reise 2007). Sedentary macrofauna, e.g., tube-building polychaetes and amphipods, as well as juveniles of several bivalves, amphipods and polychaetes, avoid unstable sediments disturbed by lugworms (Brenchley 1981; Wilson 1981; Woodin 1985; Flach 1992). On the other hand, lugworm feeding funnels and faecal casts at the sediment surface may attract small mobile fauna such as amphipods and copepods, which has been linked to higher organic concentration in these structures compared with the surrounding sediment: funnels operate as particle traps during low tide, and cast sediment is flushed with organic particles by above-ground currents (Reise 1981; Brey 1991; Huettel & Gust 1992; Huettel *et al.* 1996; Lackschewitz & Reise 1998). Furthermore, lugworm burrows have been found to support small benthic animals which populate distinct sections of the burrow, e.g., nematodes, plathelminthes and amphipods (Reise 1985; Lackschewitz & Reise 1998). Sediment modifications imposed by lugworms can

extend beyond the vicinity of their burrows, and effects on meio- and macrobenthic communities have been documented over meso-spatial scales (hundreds of m^2) (Volkenborn & Reise 2006, 2007; Kuhnert *et al.* 2010).

In contrast to other parts of the world, little is known about lugworms and their potential effects on other macrobenthic organisms in tidal flats of New Zealand. In tidal inlets along the Otago coast, the lugworm *Abarenicola affinis* is commonly present, with mean densities of 11 individuals per m^2, and local maxima exceeding 100 individuals per m^2 (Wells 1963; Chapter 2). The influence of *Abarenicola affinis* on macrofaunal assemblages was examined in a descriptive field study and a manipulative field experiment, conducted in Papanui Inlet, south-eastern New Zealand. In this inlet, both macrofaunal assemblages and lugworm distribution have been related to spatial location on the shore in previous investigations (Mills & Berkenbusch 2009; Paavo *et al.* in press; Chapter 3). The descriptive field study compared macrofaunal assemblages across different intertidal zones, and related macrofaunal distribution to abiotic and biotic habitat variables, including *Abarenicola affinis* density and biomass. The experimental study examined whether small-scale exclusion of *Abarenicola affinis* from densely populated areas affects macrofaunal assemblage composition.

Material & Methods

Descriptive field study

The study was carried out in Papanui Inlet, a sheltered tidal inlet on the east side of the Otago Peninsula, southern New Zealand (Fig. 18). The inlet is

approximately 4 km² in area with 1 - 2 km² of tidal flats emerging in semidiurnal rhythms, with mean tidal ranges of 1.15 m (Albrecht & Vennell 2007). Lugworms are highly concentrated in the upper intertidal region of the inlet, but decrease in abundance towards lower intertidal regions (Chapters 2 & 3). The inlet is characterised by continuous and fragmented seagrass (*Zostera muelleri*) habitats (Mills & Berkenbusch 2009; Chapter 3).

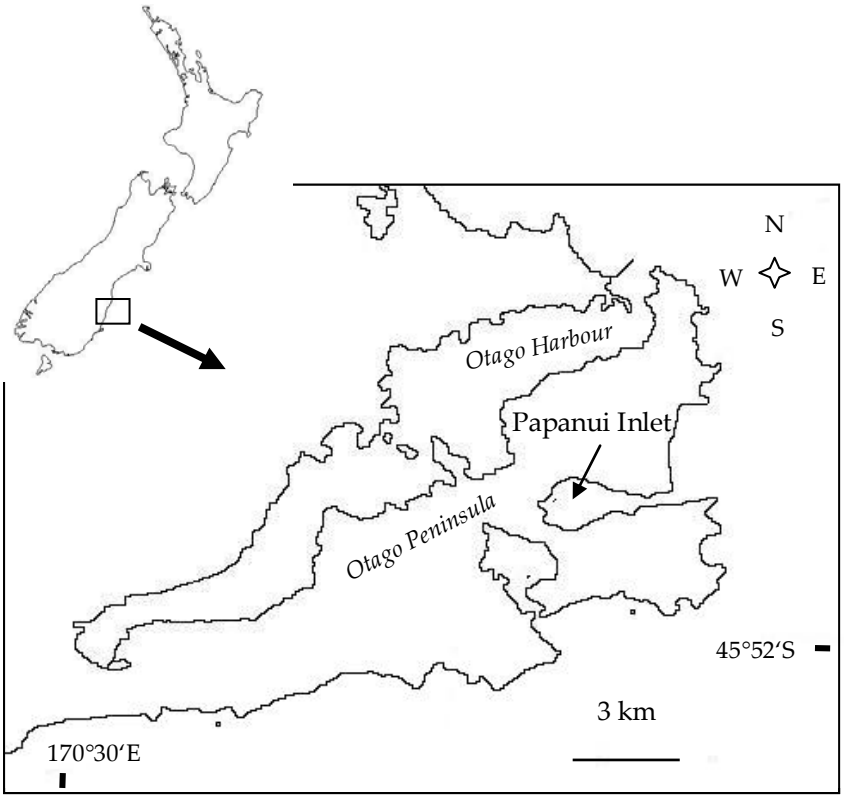


Fig. 18. Location of the intertidal study site (arrow) in Papanui Inlet, southern New Zealand.

Macrofauna was sampled on four seasonal dates in summer (December) 2007, autumn (March), winter (June) and spring (September) 2008, simultaneously to the sampling of lugworms, sediment parameters and seagrass biomass, which were collected and used as part of a different study on *Abarenicola affinis* in this inlet (Chapter 3). On an intertidal sampling area of 0.5 km², which was selected

within the largest coherent intertidal part of the inlet and stretched approximately 600 m from the shore to the low tide waterline, a grid of 90 evenly-spaced sampling points was established by GPS. In the sampling area, distance from the shore corresponded with low tide exposure time (2 - 9 h per semidiurnal tidal cycle, visually assessed over 12 h), and was used as a proxy for tidal exposure for each sampling point. Corresponding samples of macrofauna, *Abarenicola affinis*, sediment and seagrass were taken at 7 randomly chosen sampling points per season. Macrofauna was collected using a sediment core of 10 cm diameter (79 cm^2 area) to 10 cm depth. *Abarenicola affinis* were sampled using a sediment core of 20 cm diameter (314 cm^2 area) to 40 cm depth, which was sieved (1 mm mesh) at the field site to collect lugworms and transfer them into seawater-filled containers. Sediment was sampled using a core of 4.7 cm diameter to 10 cm depth to analyse grain size composition, proportion of sediment fines, and total organic matter content, and a core of 2.5 cm diameter to 2 cm depth to determine chlorophyll *a* content. Seagrass above-ground material was sampled by cutting off the leaves at the sediment surface within lugworm cores prior to excavation. Seagrass below-ground material, i.e., roots, rhizomes and debris in the top 10-cm depth section, was collected during sieving of lugworm cores.

In the laboratory, macrofaunal cores were sieved with seawater on a 500 μm mesh, stained with 1% Rose Bengal, fixed in 4% formalin, and subsequently preserved in 70% ethanol. Macrofauna was identified to the lowest practical taxonomic level (in most cases genus or species). *Abarenicola affinis* were anaesthetised for 3 h in 7% magnesium-chloride, fixed in 4% formalin, and preserved in 70% ethanol. Total lugworm length was measured using calipers (± 0.5 mm). Lugworms were dried to constant weight (60°C, 48 h) and

subsequently combusted (500°C, 4 h) to determine ash-free dry weight (AFDW, ± 0.0001 g). Sediment samples were wet-sieved to extract the fines fraction (< 63 μm), subsequently dried (60°C, 48 h) and mechanically sieved to divide larger grain size fractions (1000, 500, 250, 125 and 63 μm) (McManus 1988). Total organic matter content of the sediment was determined by loss on ignition (500°C, 4 h) (Buchanan & Kain 1971). Sediment chlorophyll *a* samples were freeze dried (- 50°C, 48 h), homogenised, boiled in 90% ethanol and subsequently analysed using a spectrophotometer (Sartory 1982). Seagrass above-ground and below-ground material was rinsed with freshwater, dried to constant weight (60°C, 48 h), and weighed (± 0.001 g).

Manipulative field experiment

The manipulative field experiment was conducted in the upper intertidal zone of Papanui Inlet, where lugworms are highly concentrated (Chapters 2 & 3). The experimental site comprised approximately 0.015 km², and was located between 50 and 100 m distance from the shoreline (approximately 7 - 8 h of exposure per semidiurnal tidal cycle) in unvegetated sediment bordered by a seagrass bed on the seaward side.

Abarenicola affinis was excluded in 1 m² plots by inserting a polyethylene net (1-mm mesh) at 10 cm sediment depth (Fig. 19). The net blocks the vertical shaft of lugworm burrows, preventing them from accessing the surface and, thereby, forcing them to emigrate from the area (Reise 1983). First, the top 10 cm sediment layer was carefully removed with a shovel and placed on a mat. Second, the net was inserted and the removed sediment was replaced on top of the net ("exclusion" treatment). To assess the effects of sediment disturbance by

digging, the same procedure was used in control plots without the insertion of a net, i.e., lugworms remained in their burrows ("control" treatment). Ambient plots were left untouched to provide additional and undisturbed control treatments with naturally occurring *Abarenicola affinis* ("ambient" treatment). Each treatment was replicated 6 times, arranged in experimental blocks (each block containing each treatment) to account for spatial heterogeneity at the experimental site (Fig. 19). Blocks were located haphazardly, but at least 30 m apart, with treatment plots within each block at least 3 m apart.

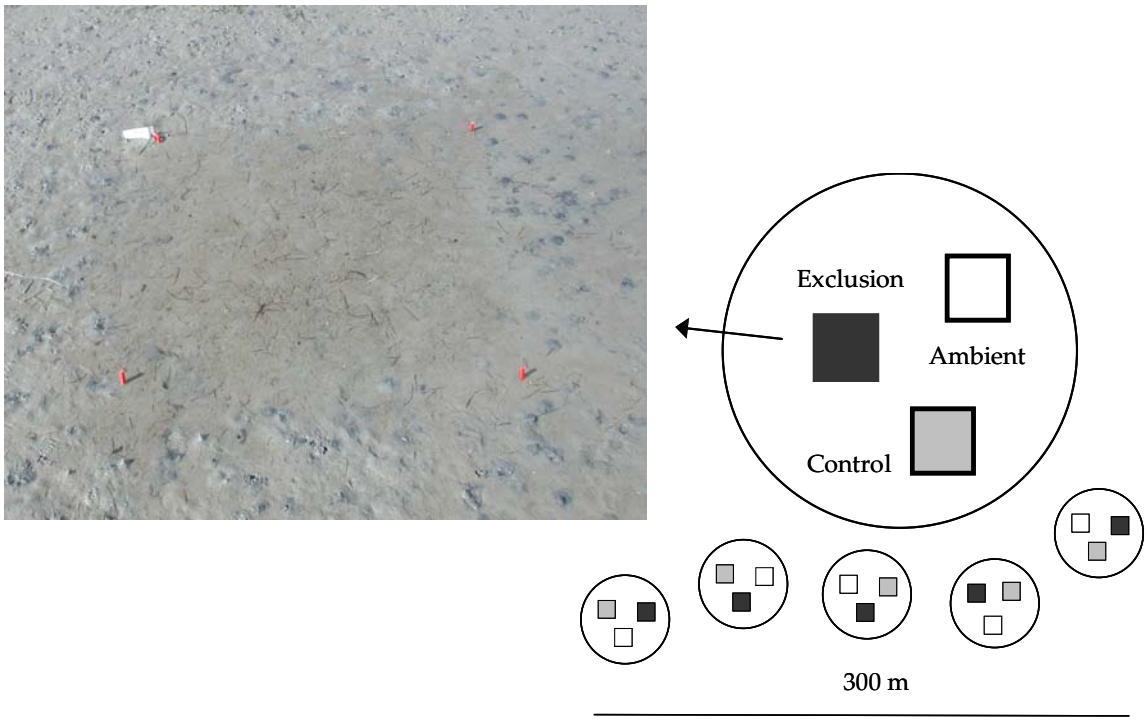


Fig. 19. Exclusion plot (1 m²) and experimental block design in the upper intertidal zone of Papanui Inlet.

The experiment was initiated in autumn (March) 2008, when the seasonal abundance of lugworms was highest (Chapter 3). Responses of macrofauna to lugworm exclusion were tested by sampling 1 month after set up in autumn

(April) 2008, and 8 months after set up in spring (November) 2008. *Abarenicola affinis* density in experimental plots was estimated by counting the number of faecal casts, which give a reliable proxy of lugworm abundance (Chapter 2). Counts were made every 10 days in the first month, and subsequently after 4 and 8 months, in calm and dry weather conditions.

Experimental plots were sampled for macrofauna and sediment parameters, the latter including grain size composition, proportion of fines, and total organic matter and chlorophyll *a* contents (same core sizes as in the descriptive field study). On each sampling occasion, both macrofaunal and sediment samples were taken from different areas within the plots to avoid repeated sampling of the same area. Samples were taken at least 10 cm from the edge of the plots to minimise edge effects. In control and ambient plots, attention was paid not to sample lugworm burrows or faecal casts. In the laboratory, macrofaunal and sediment samples were processed and analysed as described above for the descriptive field study.

Data analysis

Data were analysed by univariate and multivariate statistical techniques, using Statistica 6 (StatSoft Inc.) and PRIMER 6 (Plymouth Routine in Multivariate Ecological Research, Clarke & Gorley 2006). In the descriptive field study, macrofaunal assemblages were analysed by univariate community indices, including total number of individuals, total number of taxa, and Shannon-Wiener index of diversity (calculated by the DIVERSE function, Clarke & Warwick 2001). Assemblages were tested for differences across seasons by one-way ANOVA (Underwood 1997). When necessary, data were $\log_{10}$-transformed

to meet assumptions of normality and homogeneity of variances, tested by Kolmogorov-Smirnov and Cochran tests, respectively (applied to all ANOVA's in this study, Underwood 1997). When data remained heterogeneous after transformation, ANOVA was still considered reliable when test results were non-significant, as heterogeneity only compromises the outcome of ANOVA when test results are significant (increased probability of Type I error, see Underwood 1997). Multivariate differences in macrofaunal assemblages across seasons were tested by one-way ANOSIM (Clarke 1993). Prior to analysis, macrofauna abundance data were square-root transformed and ranked in a Bray-Curtis similarity matrix to balance dominant and rare taxa (applied to all ANOSIM's in this study, Clarke & Warwick 2001).

Seasonal sampling data were combined and grouped into high, mid, and low intertidal zones, corresponding to 0 - 100 m, 100 - 400 m, and 400 - 600 m distance from the shore, respectively (n = 9 / 10 per intertidal zone), to assess macrofaunal distribution across these zones. Differences in community indices across intertidal zones were tested by one-way ANOVA. Significant differences were subsequently analysed by post-hoc Tukey HSD test (Underwood 1997). Multivariate differences in macrofaunal assemblages were visually assessed by multi-dimensional scaling (MDS), and formally analysed by one-way ANOSIM. Taxa that primarily accounted for significant assemblage dissimilarities were determined by one-way SIMPER analysis (cut-off 40%, Clarke & Warwick 2001). The relationship between macrofaunal assemblage composition and corresponding habitat variables was analysed by the BIOENV procedure (Clarke & Warwick 2001). Variables included *Abarenicola affinis* density and biomass, mean sediment grain size, proportion of sediment fines, total organic matter and chlorophyll *a* contents of the sediment, seagrass above-ground and

below-ground biomasses, and distance from the shore (as proxy for tidal exposure). Prior to analysis, variables were graphically assessed for multivariate normality by draftsman-plots and tested for co-correlation by Spearman rank correlation (cut off value ρ = 0.95, Clarke & Warwick 2001). Mean sediment grain size and proportion of sediment fines were subsequently log_{10}-transformed to improve normality. There were no co-correlations and all variables were included in the analyses.

Macrofaunal assemblage compositions in experimental plots were analysed using univariate measures including total number of individuals, total number of taxa and Shannon-Wiener index. For 8-month sampling, differences in community indices were tested by two-way ANOVA, including treatment and block as factors, whereas data from 1-month sampling remained heterogeneous after transformation and, therefore, were tested for each factor by non-parametric Kruskal-Wallis test (Quinn & Keough 2002). For both sampling occasions, multivariate differences between treatments were visually assessed by MDS plots, and formally tested by two-way crossed ANOSIM without replication (Clarke & Warwick 2001), using treatment and block as factors.

Results

Macrofaunal assemblage patterns in Papanui Inlet

A total of 6783 individuals were counted, and 34 taxa were identified. Amphipods, comprising of 9 species overall, dominated in abundance (2913 individuals). The most abundant amphipods were *Paracorophium excavatum*, *Paracalliope novizealandiae* and *Torridoharpinia hurleyi*. Bivalves, comprising of 3

species (*Perrierina turneri*, *Arthritica bifurca* and *Nucula hartvigiana*), were also common (2203 individuals). Polychaetes contained the most taxa (11), but were less abundant than bivalves and amphipods (816 individuals). The most abundant polychaetes were *Capitella* sp., *Macroclymenella stewartensis*, *Scolecolepides benhami*, and Paranoidae. Oligochaetes were also abundant (577 individuals).

One-way ANOVA showed no significant seasonal variation in total number of individuals ($df = 3$, $F = 0.49$, $p = 0.670$), total number of taxa ($df = 3$, $F = 0.69$, $p = 0.567$), and Shannon-Wiener index ($df = 3$, $F = 0.65$, $p = 0.590$) of macrofaunal assemblages ($n = 7$ per season). Multivariate comparisons confirmed similar macrofaunal assemblages across seasons (one-way ANOSIM, *Global R* = 0.036, *P* = 0.264). Based on the non-significant results, seasonal data were combined to assess macrofaunal distribution across intertidal zones.

Univariate community indices showed differences across intertidal zones (Table 12). Macrofaunal abundance decreased from high towards lower intertidal zones, whereas number of taxa and diversity increased. Differences across intertidal zones were significant (Table 12), and post-hoc comparisons revealed that for each community indices, values from high intertidal assemblages were significantly different from those of mid and low intertidal assemblages (Tukey HSD test, $p < 0.05$, $n = 9 / 10$), whereas the latter two did not differ significantly from each other (Tukey HSD test, $p > 0.05$, $n = 9 / 10$). There was a notably higher variance of total numbers of individuals in the high intertidal zone compared with the mid and low intertidal zones (Table 12) corresponding with the heterogeneous distribution of some dominating taxa such as *Paracorophium excavatum*, Oligochaeta and *Capitella* sp..

Table 12. Community indices (sample size 78 cm²) (mean values ± SD, n = 9 / 10) in different intertidal zones of Papanui Inlet, sampled between summer (December) 2007 and spring (September) 2008, and results of one-way ANOVA (factor intertidal zone) (significant values in bold, asterisks indicate the significantly different intertidal zone (post-hoc Tukey HSD test, $p < 0.05$).

Community indices	Intertidal zone			One-way ANOVA results		
	High	Mid	Low	*df*	*F*	*p*
Total number of individuals	393 ± 294*	180 ± 93	161 ± 76	2	3.45	**0.047**
Total number of taxa	9 ± 2*	13 ± 2	14 ± 3	2	10.12	**< 0.001**
Shannon-Wiener index	1.11 ± 0.25*	1.45 ± 0.21	1.88 ± 0.18	2	28.51	**< 0.001**

Visual assessment of the MDS ordination of macrofaunal abundance data indicated different macrofaunal assemblages in the high intertidal zone compared with the mid and low intertidal zones (Fig. 20). Both of the latter accommodated assemblages that showed no clear distinction from each other.

One-way ANOSIM confirmed significant differences in macrofaunal assemblage composition across intertidal zones (*Global R* = 0.693, *P* = 0.001). Pair-wise tests revealed that high intertidal assemblages were significantly different from mid (*R* = 0.931, *P* = 0.001) and low intertidal assemblages (*R* = 0.992, *P* = 0.001), whereas no significant differences were found between assemblages of the latter zones (*R* = 0.058, *P* = 0.170). Taxa contributing the most to the dissimilarity between high and mid intertidal assemblages were the amphipod *Paracorophium excavatum* and the bivalve *Perrierina turneri*, of which the former was considerably more abundant in the high intertidal zone, whereas the latter showed markedly higher densities in the mid intertidal zone

(Table 13). Both taxa also best discriminated between high and low intertidal assemblages, together with the bivalve *Nucula hartvigiana*, which was more abundant in the low intertidal zone. Apart from *Paracorophium excavatum*, there were a few other taxa that occurred almost exclusively in the high intertidal zone (> 98% of individuals), which were Oligochaeta, *Capitella* sp., and *Scolecolepides benhami*.

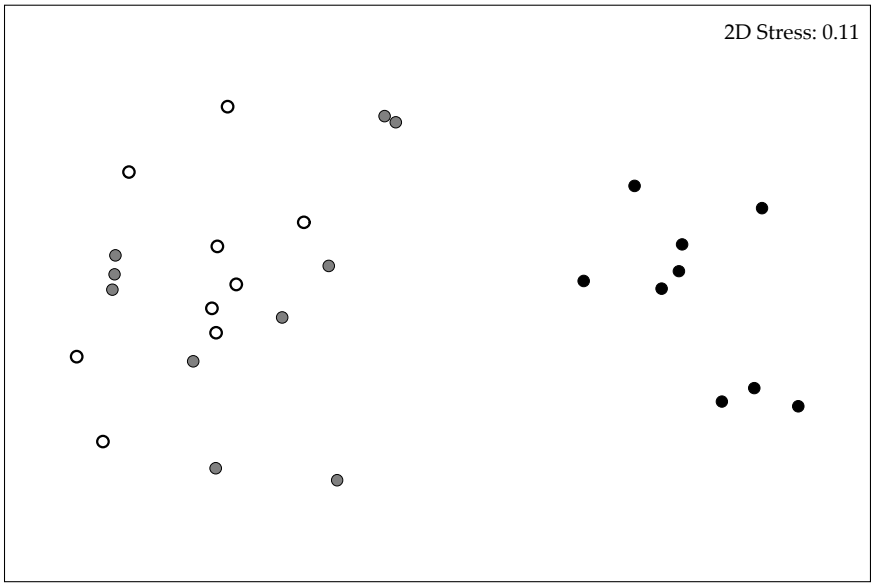


Fig. 20. MDS ordination of macrofaunal abundance data in different intertidal zones (high = closed, mid = shaded, low = open) of Papanui Inlet, sampled between summer (December) 2007 and spring (September) 2008.

Table 13. Results of one-way SIMPER analysis (cut-off 40%) of significantly different macrofaunal assemblages across intertidal zones of Papanui Inlet. Note: Mean abundances are calculated from root-transformed data.

High & Mid Average dissimilarity = 78.83%	Mean abundance High	Mean abundance Mid	Ratio of contribution dissimilarity	Percentage contribution (%)	Cumulative percentage contribution
Paracorophium excavatum	14.36	1.17	3.25	21.96	21.96
Perrierina turneri	0.98	7.35	1.37	10.75	32.71
High & Low Average dissimilarity = 81.43%	**Mean abundance High**	**Mean abundance Low**			
Paracorophium excavatum	14.36	0.60	3.28	21.48	21.48
Perrierina turneri	0.98	5.32	1.72	7.75	29.23
Nucula hartvigiana	0.16	4.64	1.56	7.14	36.37

Macrofaunal assemblage patterns were best explained by the combination of distance from the shore (the proxy for tidal exposure), and proportion of sediment fines (BIOENV, ρ = 0.802). The proportion of sediment fines was greater in the high intertidal zone (Table 14), with a maximum of 12.2% in the muddiest areas. The distance from the shore was the variable that alone best explained assemblage patterns, achieving second highest correlation (ρ = 0.774). *Abarenicola affinis* density and biomass, which were considerably higher in the high intertidal zone, and seagrass above- and below-ground biomasses, which showed higher values in the mid and low intertidal zones (Table 14), did not explain macrofaunal assemblage patterns. Also, total organic matter and chlorophyll *a* contents of the sediment, which were slightly greater in the high intertidal zone compared with lower intertidal zones (Table 14), had no explanatory power.

Table 14. *Abarenicola affinis*, seagrass and sediment parameters (mean values ± SD, *n* = 9 / 10) in different intertidal zones of Papanui Inlet, sampled between summer (December) 2007 and spring (September) 2008.

Parameters	Intertidal zone		
	High	Mid	Low
Lugworm density (individuals per 314 cm²)	3.8 ± 1.1	0.8 ± 0.8	0.2 ± 0.7
Lugworm biomass (g AFDW per 314 cm²)	0.1175 ± 0.0466	0.0112 ± 0.0138	0.0056 ± 0.0168
Seagrass above-ground biomass (g dry weight per 314 cm²)	0.009 ± 0.017	0.200 ± 0.117	0.147 ± 0.064
Seagrass below-ground biomass (g dry weight per 314 cm²)	0.756 ± 1.523	5.535 ± 2.043	4.544 ± 2.243
Mean sediment grain size (μm)	140 ± 11	147 ± 1	148 ± 1
Sediment fines (%)	7.3 ± 2.6	2.7 ± 0.7	2.8 ± 0.7
Total organic matter (%)	0.72 ± 0.18	0.61 ± 0.08	0.62 ± 0.14
Chlorophyll a content (μg / g sediment dry weight)	4.6 ± 1.6	3.1 ± 0.8	3.0 ± 0.7

Macrofaunal response to experimental lugworm exclusion

Abarenicola affinis were successfully removed from exclusion plots over the experimental period (Fig. 21). In control plots, in which sediment had been similarly disturbed as in exclusion plots, lugworms re-established their burrows within 24 h. Mean lugworm abundances were high in control and ambient plots throughout the experiment (> 40 individuals per m²), except for a decline in both of these treatments in winter (day 120, July 2008).

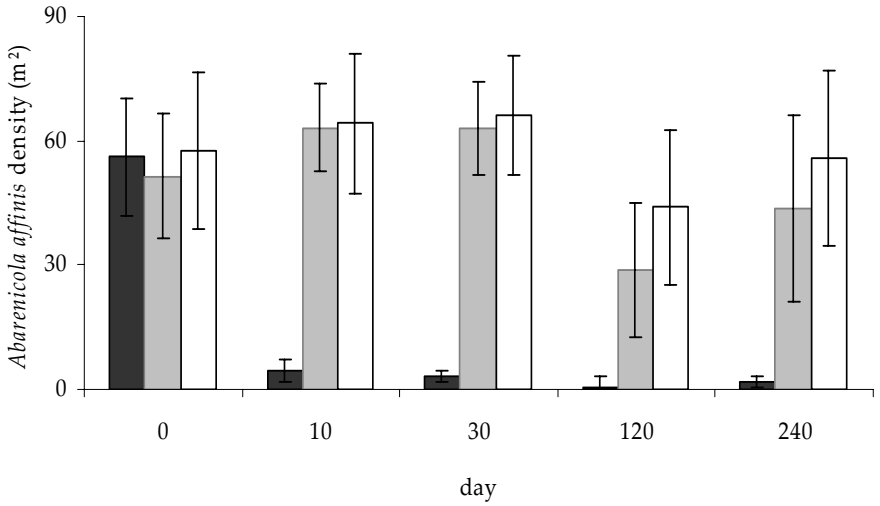


Fig. 21. *Abarenicola affinis* density (mean values ± SD, *n* = 6) on experimental plots: Exclusion (removal of lugworms by inserting a net at 10 cm depth) = closed, Control (sediment disturbance by digging without net insertion) = shaded, and Ambient (plots left untouched) = open, before (day 0) and after treatment set up (day 10 - 240) between autumn (March) and spring (November) 2008 in Papanui Inlet.

Experimental plots consisted of relatively muddy sediment with low organic matter content. Sediment parameters showed little variation across treatments and among sampling occasions (Table 15). These results indicated stable sedimentary conditions throughout the experiment and no lasting effects of initial sediment disturbance by digging, as well as no effect of lugworm exclusion on the measured sediment parameters.

Macrofaunal assemblages in experimental plots were characterised by a relatively low diversity with a total of 27 taxa. The most abundant species was *Paracorophium excavatum*, which contributed 71% to the total number of individuals (total number was 9012). Other common taxa were *Arthritica bifurca*, *Paracalliope novizealandiae*, *Torridoharpinia hurleyi*, *Scolecolepides benhami* and

Capitella sp., which together accounted for 25% of macrofaunal abundance overall.

Table 15. Sediment parameters (mean values ± SD, *n* = 6) from experimental plots (Exclusion = removal of lugworms by inserting a net at 10 cm depth, Control = sediment disturbance by digging without net insertion, Ambient = plots left untouched) at 1-month and 8-month sampling in autumn (April) and spring (November) 2008, respectively, in Papanui Inlet.

Sampling time	Treatment	Mean grain size (μm)	Fines fraction (%)	Total organic matter (%)	Chlorophyll *a* (μg / g sediment dry weight)
1-month	Exclusion	134 ± 8	8.7 ± 0.9	0.78 ± 0.07	5.5 ± 1.2
	Control	136 ± 6	8.4 ± 0.9	0.77 ± 0.13	4.4 ± 0.5
	Ambient	140 ± 5	8.4 ± 1.6	0.73 ± 0.10	5.2 ± 0.9
8-month	Exclusion	131 ± 9	9.0 ± 1.1	0.82 ± 0.06	5.0 ± 0.7
	Control	138 ± 7	8.9 ± 0.8	0.82 ± 0.07	4.7 ± 0.7
	Ambient	140 ± 8	8.5 ± 1.4	0.74 ± 0.07	4.4 ± 1.0

Macrofaunal assemblages showed no significant differences in univariate community indices across treatments 1 month after the treatments were set up (Table 16). There was spatial variation in macrofaunal assemblages, as revealed by a significant block factor for total number of individuals and Shannon-Wiener index (Table 16). A high degree of spatial variation was observed in the *Paracorophium excavatum* population, as these amphipods showed lower densities of one to two orders of magnitudes in blocks 3 - 6 (18.8 ± 13.0 individuals per 78 cm², *n* = 4), compared with blocks 1 - 2 (384.3 ± 52.3 individuals per 78 cm², *n* = 2). Visual assessment of MDS ordination showed the dispersion of macrofaunal assemblages related to blocks (Fig. 22). Multivariate comparisons showed no significant variation in macrofaunal assemblage

composition across treatments (two-way crossed ANOSIM, *Global R* = 0.033, *P* = 0.435), but a significant block effect (*Global R* = 0.630, *P* = 0.006). These results confirmed that similar assemblages from the surrounding sediment had re-colonised both types of manipulated treatments, whereas assemblages were heterogeneously distributed across the experimental site.

There were also no significant treatment effects on macrofaunal community indices after 8 months of *Abarenicola affinis* exclusion (Table 16). Nevertheless, macrofaunal abundances increased in control and ambient plots, but remained the same in exclusion treatments, when compared with abundances at 1-month sampling (Table 16, Fig. 23). In particular, *Paracorophium excavatum* densities were higher in control (222.0 ± 98.1 individuals per 78 cm², *n* = 6) and ambient plots (248.8 ± 42.7 individuals per 78 cm², *n* = 6), compared with exclusion plots (177.8 ± 23.2 individuals per 78 cm², *n* = 6). These differences were tested separately by one-way ANOVA, but were not significant (*df* = 2, *F* = 1.93, *p* = 0.180). In contrast to the 1-month sampling, no significant block effects in community indices were detected (Table 16). MDS ordination indicated that macrofauna was more homogeneously distributed at 8-month sampling compared with 1-month sampling, with assemblages also showing distinct separation from those of 1-month sampling (Fig. 22). Multivariate testing by two-way crossed ANOSIM revealed no significant differences in assemblage composition across treatments and blocks at 8-month sampling (treatment: *Global R* = 0.033, *P* = 0.434, block: *Global R* = 0.043, *P* = 0.368).

Table 16. Community indices (sample size 78 cm²) (mean values ± SD, n = 6) in experimental plots (Exclusion = removal of lugworms by inserting a net at 10 cm depth, Control = sediment disturbance by digging without net insertion, Ambient = plots left untouched), at 1-month and 8-month sampling in autumn (April) and spring (November) 2008, respectively, and results of Kruskal-Wallis test (1-month sampling) and two-way ANOVA (8-month sampling) (factors treatment and block) (significant values in bold).

Indices	1-month sampling			8-month sampling		
	Exclusion	Control	Ambient	Exclusion	Control	Ambient
Total number of individuals	239.2 ± 203.9	223.5 ± 186.8	222.5 ± 244.1	234.8 ± 33.6	278.0 ± 102.6	304.0 ± 48.4
Total number of taxa	8.8 ± 1.2	9.7 ± 0.5	10.0 ± 2.1	7.7 ± 1.6	8.5 ± 2.1	9.2 ± 2.3
Shannon-Wiener index	1.4 ± 0.4	1.4 ± 0.5	1.5 ± 0.4	0.9 ± 0.1	0.8 ± 0.2	0.8 ± 0.2

	Treatment			Block			Treatment			Block		
	df	*H*	*p*	*df*	*H*	*p*	*df*	*F*	*p*	*df*	*F*	*p*
Total number of individuals	2	0.82	0.665	5	14.46	**0.013**	2	2.19	0.163	5	2.19	0.137
Total number of taxa	2	1.70	0.428	5	8.26	0.143	2	1.13	0.360	5	2.13	0.145
Shannon-Wiener index	2	1.09	0.579	5	12.36	**0.030**	2	1.25	0.328	5	2.7	0.085

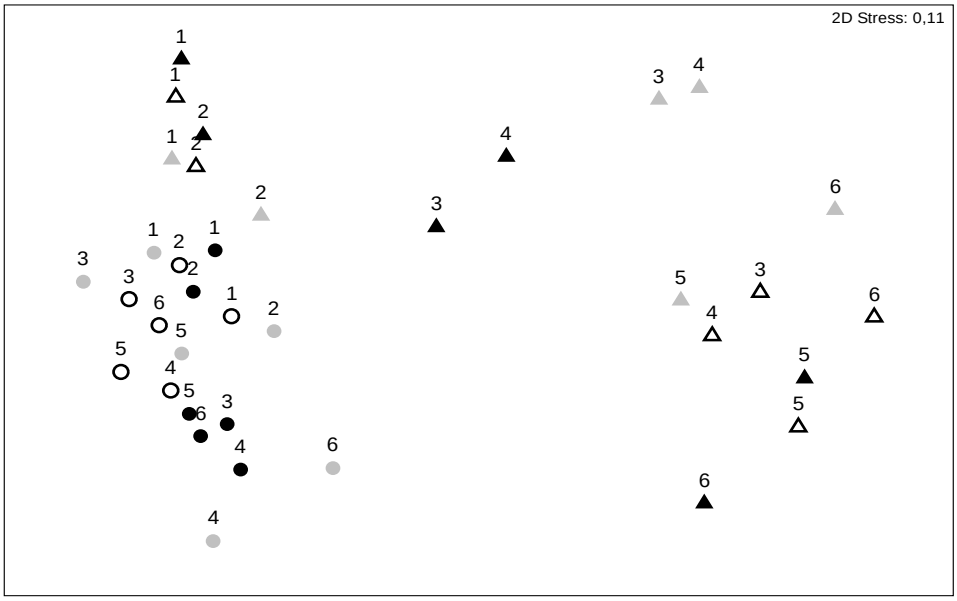


Fig. 22. MDS ordination of macrofaunal assemblages in experimental plots: Exclusion (removal of lugworms by inserting a net at 10 cm depth) = closed, Control (sediment disturbance by digging without net insertion) = shaded, Ambient (plots left untouched) = open, at 1-month sampling (triangles) and 8-month sampling (circles) in autumn (April) and spring (November) 2008, respectively, in Papanui Inlet. Numbers indicate experimental blocks.

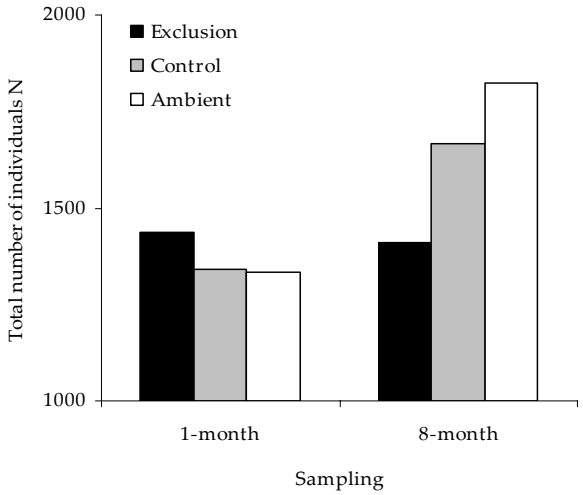


Fig. 23. Total number of individuals in 6 treatment plots of 1 m² each (Exclusion = removal of lugworms by inserting a net at 10 cm depth, Control = sediment disturbance by digging without net insertion, Ambient = plots left untouched) at 1-month and 8-month sampling in autumn (April) and spring (November) 2008, respectively, in Papanui Inlet. Note y-axis scale.

Discussion

Zonation of macrofauna in Papanui Inlet

Univariate and multivariate analyses revealed significant differences in macrofaunal assemblages across intertidal zones in Papanui Inlet. In particular, macrofaunal assemblages in the high intertidal zone were distinctively different from those in lower intertidal zones. High intertidal assemblages were characterised by greater abundance and fewer taxa, i.e., less diversity, compared with lower intertidal assemblages. Macrofaunal assemblage patterns were best explained by a combination of distance from the shore, the proxy for tidal exposure, and proportion of sediment fines, accounting for 80% of the variation in assemblage composition. Intertidal position in relation to tidal exposure appeared to be the main factor responsible for the distribution of macrofauna, as results from the BIOENV analysis confirmed distance from the shore to be the variable that alone best explained macrofaunal distribution.

Other studies have similarly documented distinct macrofaunal assemblage patterns in relation to intertidal zonation (Dankers & Beukema 1983; Peterson 1991; Dittmann 2000; Aerts *et al.* 2004; Rodil & Lastra 2004). Patterns associated with tidal exposure are generally related to the tolerance of organisms to increasing physiological stress with increasing exposure time, e.g., sediment desiccation, temperature and salinity fluctuations (Dankers & Beukema 1983; Reise 1985; Peterson 1991; Giménez *et al.* 2006). The pattern found in the present study indicated a shift in assemblage composition from lower intertidal zones which are exposed less than 50% of the time (< 6 h per semidiurnal tidal cycle) to the high intertidal zone with exposure periods of up to 75% of the time (7 - 9 h per semidiurnal tidal cycle, pers. obs.).

In addition to tidal exposure, macrofaunal zonation often results from other factors corresponding with tidal level such as physical (e.g. sediment composition) and / or biological (e.g. sediment vegetation) habitat zonation, as well as species interactions (e.g. predation) (Dankers & Beukema 1983; Reise 1985; Barry & Dayton 1991; Raffaeli & Hawkins 1996; Dittmann 2000). In agreement with previous studies at other coastal sites (e.g. Armonies & Hellwig-Armonies 1987; Thrush *et al.* 2003; Rodil & Lastra 2004; Giménez *et al.* 2006), the macrofaunal distribution in Papanui Inlet was related to the proportion of sediment fines. Sediment in the high intertidal zone contained higher proportions of fine particles compared with lower intertidal zones. The established relationship between sediment characteristics and the distribution and abundance of macrofauna, however, may be of a more complex nature as sediment characteristics are likely to co-correlate with other factors, e.g., hydrodynamic processes (Snelgrove & Butman 1994). In the absence of mechanistic studies, it remains difficult to indentify potential underlying mechanisms for the observed patterns. The distribution of sediment in tidal flats generally follows a pattern related to the hydrodynamic regime and settling behaviour of particles (Beukema 1976; Dankers & Beukema 1983; Dronkers 1984; Reise 1985; Hertweck 1994) and the greater proportion of sediment fines in the high intertidal zone indicated increased settlement of fine particles due to less hydrodynamic disturbance. Differences in macrofaunal assemblages across intertidal zones in Papanui Inlet may, therefore, be additionally linked to the hydrodynamic regime of the inlet. Hydrodynamic processes and current regimes can influence the distribution of macrobenthos, for example, by controlling the dispersal of larvae, or by reducing sediment stability through currents and wave actions, especially in lower intertidal zones (Beukema 1976; Reise 1985; Snelgrove & Butman 1994).

In the present study, the relative importance of tidal exposure and proportion of sediment fines for macrofaunal assemblage patterns was reflected in the distribution of dominant taxa. Intertidal assemblages were best discriminated by the corophiid amphipod *Paracorophium excavatum*, and the bivalves *Perrierina turneri* and *Nucula hartvigiana*: the amphipod occurred in higher density in the high intertidal zone, whereas the bivalves were more abundant in lower intertidal zones. The dominance of *Paracorophium excavatum* in the high intertidal zone agreed with previous observations at the same site (Ford *et al.* 1999; Paavo *et al.* in press), as well as with observations on a closely related and ecologically equivalent corophiid amphipod, *Corophium volutator*, in North European tidal flats (Jensen 1985; Beukema & Flach 1995; Hughes & Gerdol 1997). *Corophium volutator* populates mainly high intertidal zones often characterised by higher proportions of sediment fines, and has been shown to prefer muddier sediment to coarser sediment (Meadows 1964). However, *Corophium volutator* zonation in tidal flats has been also related to other factors such as tidal exposure determining the upper limit, and negative species interactions such as sediment disturbance and predation by other macrobenthos determining the lower limit of the amphipods' distribution (Roenn *et al.* 1988; Beukema & Flach 1995). In the absence of bioturbators and predators, *Corophium volutator* expanded into lower intertidal zones, i.e., appeared not to be limited by tidal submersion or sediment characteristics (Beukema & Flach 1995). Therefore, factors responsible for the scarceness of *Paracorophium excavatum* in lower intertidal zones of Papanui Inlet need to be closer investigated. The distribution of the dominant bivalves *Perrierina turneri* and *Nucula hartvigiana* can be well related to tidal exposure and sediment fines. Small suspension feeding bivalves such as *Perrierina turneri* are likely to avoid high intertidal zones due to short submersion periods and higher mud contents,

both factors imposing negative effects on their feeding activity and growth due to reduced feeding time and increased suspension of inorganic particle matter in the water column (Peterson & Black 1987; Vincent *et al*. 1994). In the case of *Nucula hartvigiana*, which is a deposit feeder, a preference for less muddy sediment has been similarly observed in a previous study examining abundances of this species along sand-mud gradients (Thrush *et al.* 2003).

Biological habitat modification by seagrass did not play a major role in determining macrofaunal assemblage patterns. In contrast, other studies have shown that the presence of seagrass can have a substantial influence on macrofaunal distribution on tidal flats (e.g. Bostroem & Bonsdorff 2000; Hovel *et al.* 2002; van Houte-Howes *et al.* 2004; Siebert & Branch 2005). Promotive effects of seagrass have been linked to an increase in habitat complexity, the provision of shelter, and increased organic matter content, i.e., food supply, in seagrass habitats compared with bare sediment (Orth *et al.* 1984; Bostroem & Bonsdorff 2000; Ford *et al.* 2001; Vizzini *et al.* 2002). Negative effects of seagrass have been related to burrow restrictions of sediment-dwelling organisms by cohesive root-rhizome matrices (Brenchley 1982; Siebert & Branch 2005). In particular, previous investigations in Papanui Inlet found significant influences of *Zostera muelleri* on the distribution of large bioturbators such as lugworms and thalassinid shrimps (Berkenbusch *et al.* 2007; Chapter 3). In this inlet, *Zostera muelleri* occurs patchily in the high intertidal zone, but seagrass beds become larger and more cohesive towards lower intertidal zones (Mills & Berkenbusch 2009; Chapter 3). The present study indicates that potential effects of seagrass habitat zonation on macrofaunal assemblages were overruled by physical habitat factors, i.e., tidal exposure and proportion of sediment fines. This finding supports a previous investigation that compared macrofaunal

communities in different sized seagrass patches in the same inlet, where differences in species composition between seagrass patch sizes were best explained by the position of patches in relation to tidal level (Mills & Berkenbusch 2009).

Macrofaunal response to lugworm bioturbation

Abarenicola affinis appeared to have no impact on macrofaunal distribution in Papanui Inlet. Although the significantly different macrofaunal assemblages in the high intertidal zone coincided with high lugworm abundances in this zone compared with lower intertidal zones, physical parameters such as tidal exposure and proportion of sediment fines had higher explanatory power. The findings of the descriptive study were supported by the absence of substantial effects of lugworm exclusion from otherwise highly occupied areas in the field experiment. Both findings suggested that macrofaunal assemblages were generally adapted to bioturbation by *Abarenicola affinis*.

Macrofaunal assemblages in Papanui Inlet were dominated by the small bivalve *Perrierina turneri* in the mid and low intertidal zones. This species has been shown to be susceptible to sediment disturbance by a large burrowing shrimp, *Callianassa filholi*, in a previous study (Berkenbusch *et al.* 2000). Negative effects on small free-living bivalves such as *Perrierina turneri* were associated with an increased suspension of inorganic particulate matter by bioturbation, interfering with suspension-feeding and leading to reduced growth and higher mortality (Murphy 1985). Due to the relatively exclusive distribution patterns of *Abarenicola affinis* and *Perrierina turneri* (i.e. lugworms occurred mainly in the high intertidal and bivalves mainly in lower intertidal zones), the findings of

the present study are inconclusive in terms of interactions between both species.

In the high intertidal zone, where lugworms were highly abundant, macrofaunal assemblages were dominated by *Paracorophium excavatum*, indicating co-existence of these amphipods with lugworms at relatively high density levels. *Paracorophium excavatum* also dominated macrofaunal assemblages in experimental plots with and without lugworms. In contrast to these observations, other studies have documented considerable negative impacts of the lugworm *Arenicola marina* on the distribution of the corophiid amphipod *Corophium volutator*, which is ecologically similar to *Paracorophium excavatum* (Ford *et al.* 2001), in North European tidal flats and shallow bays (Flach 1992; Flach & de Bruin 1993; Beukema & Flach 1995). Beukema & Flach (1995) observed distinct zonation-patterns in the distribution of both species in the Dutch Wadden Sea, i.e., *Corophium volutator* dominates upper intertidal and *Arenicola marina* lower intertidal zones, and suggested that the widely and evenly distributed lugworms restrict the distribution of the amphipod to the high intertidal zone. This suggestion was based on the response of *Corophium volutator* to manipulated *Arenicola marina* densities in experimental plots in the field (defaunated 1 m^2 plots were re-stocked with different lugworm densities ranging from 0 to 100 individuals per m^2): where lugworms had been excluded, *Corophium volutator* invaded these plots in high densities (Flach 1992; Flach & de Bruin 1993). *Corophium volutator* densities were already significantly lower in plots with lugworm densities of 10 individuals per m^2, and declined further with increasing abundance of lugworms. Flach (1992) suggested that the funnel-forming activities of *Arenicola marina* during feeding, i.e., downward sediment movement in the head shaft, forced the amphipod to move out of the area in

order to avoid burial. Low lugworm densities seemed to be sufficient to initiate this emigration due to a frequent change in the position of funnels, resulting in relatively constant disturbance of the area surrounding the lugworm burrow. In addition to funnel-forming activities, sediment deposition by *Arenicola marina* in the form of faecal casts at the surface can result in burial of amphipods, and these casts are mostly avoided by *Corophium volutator* (Brey 1991). The presence of lugworms on tidal flats was shown to have similarly negative effects on abundances of a co-occurring amphipod, *Corophium arenarium*, as well as other small macrobenthos living near the surface including polychaetes and bivalves (Brey 1991; Flach 1992, 1993; Beukema & Flach 1995).

Macrofaunal diversity at the experimental site was relatively low with assemblages dominated by few abundant species such as *Paracorophium excavatum*. This low diversity may have limited the spectrum of lugworm effects due to the absence of potentially sensitive species from the high intertidal zone.

In the field experiment, tube-building amphipods (*Paracorophium excavatum*) and other small macrofauna such as tube-building polychaetes (*Scolecolepides benhami*) and free-living bivalves (*Arthritica bifurca*) responded not as distinctively negative to lugworm bioturbation as found in previous studies on *Arenicola marina* (Brey 1991; Flach 1992, 1993). This contrast may be explained by differences in sediment turnover rates, which indicate bioturbation intensity, and can be crucial for macrofaunal responses, in particular for sedentary tube-builders living near the surface (Brenchley 1981; Wilson 1981; Brey 1991). For example, tube-builders are able to flush unwanted sediment from their tubes, but this ability is confined to a certain level of sediment deposition (Brenchley

1981). Relatively mobile fauna can move away from disturbed sediment and deposited faecal casts, but an increase in bioturbation rates lowers their chance to escape burial (Wilson 1981). A sediment turnover estimate for *Abarenicola affinis* in Papanui Inlet revealed relatively lower turnover amounts compared with *Arenicola marina* in European tidal flats: for the high intertidal zone, where the experimental site was located, an equivalent sediment depth of 4 cm per year is reworked at a mean density of 38 individuals per m² (Chapter 4), whereas at a comparable mean density, *Arenicola marina* would rework sediment to a depth of approximately 14 cm (Cadée 1976). The difference may be related to the relatively larger individual size of *Arenicola marina* compared with *Abarenicola affinis* in both quantitative studies. The relatively lower sediment reworking by *Abarenicola affinis* may explain the tolerance of tube-builders to lugworm bioturbation in the present study. This suggestion is supported by the findings of a study conducted at a nearby site, Otago Harbour, which investigated macrofauna in relation to bioturbation intensity by the ghost shrimp *Callianassa filholi*, comparing assemblages in naturally occurring low (~ 2.5 expulsion mounds per m²) and high shrimp densities (> 5 expulsion mounds per m²) (Berkenbusch *et al.* 2000). These shrimps have a considerably higher burrowing activity than *Abarenicola affinis* as they are more continuous burrowers and also turn over greater amounts of sediment than lugworms (four times greater annual sediment turnover estimate at comparable mean densities, Berkenbusch & Rowden 1999; Chapter 4). In contrast to the present study, *Paracorphium excavatum* responded negatively to an increase in bioturbation intensity by *Callianassa filholi*, i.e., had distinctively lower abundances in areas of higher shrimp density.

Data from 1-month sampling indicated that both types of manipulated treatments were re-colonised by the same species from the surrounding benthic community. However, macrofauna, in particular dominant *Paracorophium excavatum*, showed high spatial variation at the experimental site, resulting in considerably lower abundances in 4 of the 6 blocks. This variation may have concealed potential effects of lugworm exclusion. It has been suggested, that lugworm bioturbation effects can be less apparent in low abundant and spatially dynamic communities (Reise 1983; Flach 1992; Volkenborn & Reise 2007). At 8-month sampling, macrofaunal assemblages were more homogeneously distributed at the experimental site with relatively similar abundances and assemblage compositions across blocks. On this sampling occasion, macrofaunal abundances, in particular those of *Paracorophium excavatum*, tended to be lower in exclusion plots. This tendency suggested a subtle promotional effect of lugworms on abundances of macrofauna. Sediment parameters did not differ across treatments and, therefore, it seemed unlikely that this effect was related to the duration of lugworm exclusion. Instead, the observed tendency could be related to the spatial distribution of macrofauna at the time of sampling (spring), i.e., subtle promotional effects of lugworms became noticeable in abundant and homogeneous macrofaunal assemblages. These findings raise the need for future research spanning a longer experimental period addressing variation in macrofaunal assemblages and spatial persistence of lugworm patches.

The observed promotional effects on particularly *Paracorophium excavatum* density may be explained by the irrigation activities of lugworms. *Paracorophium excavatum*, as well as other corophiid amphipods, react to the level of oxygen, sulphide and ammonium ions in the sediment (Grant 1981;

Meadows *et al*. 1981; Ford *et al.* 2001). Oxygen is needed for respiration, whereas sulphide and ammonium ions, which are products of anaerobic microbial metabolism, i.e., inversely correlated to oxygen concentration in the sediment, are avoided by corophiid amphipods such as *Corophium volutator* (Grant 1981; Meadows *et al*. 1981; Janas & Szaniawska 1996). Lugworm irrigation activities oxygenate the subsurface sediment to a depth where it would otherwise be anoxic (Riisgard *et al.* 1996). This input of oxygen-rich water into anoxic sediments can further result in the removal or re-oxidation of toxic metabolites such as sulphides from or within the sediment (Banta *et al.* 1999; Kristensen 2001; Nielsen *et al.* 2003). It has been suggested that these irrigative inputs have promotional effects on small infauna inhabiting the subsurface sediment such as turbellaria and nematoda, as well as subsurface deposit-feeding polychaetes (*Scoloplos* cf. *armiger*), and that these effects may be pronounced in finer sediment (Reise 1983; Volkenborn & Reise 2006, 2007). Thus, a positive response of *Paracorophium excavatum* to the presence of *Abareniciola affinis* could be due to less sulphide and more oxygen in the sediment resulting from irrigation, under the condition that sediment reworking by lugworms does not exceed a tolerable level for the amphipods.

Conclusions

The present study showed that bioturbation by lugworms may not be an important factor in determining macrofaunal assemblage composition in tidal inlets of southern New Zealand. Physical factors such as tidal exposure and proportion of sediment fines were mainly responsible for the zonation of macrofauna, overruling biological habitat modification by both lugworms and seagrass. In the high intertidal zone, where lugworms were highly abundant,

macrofauna showed high spatial variation due to the heterogeneous distribution of dominating taxa. On a small spatial scale, a promotional effect of *Abarenicola affinis* bioturbation on abundance of macrofauna, in particular dominant *Paracorophium excavatum*, may exist, but appears to be weak and inferior to spatial variation in macrofaunal assemblages. *Paracorophium excavatum* which can be susceptible to bioturbation by other large-sized burrowers (Berkenbusch *et al.* 2000) tolerated sediment disturbance exhibited by lugworms, and seemed to benefit from habitat modifications by the latter. The findings indicated an opposite trend in the relationship between lugworms and corophiid amphipods compared with equivalent species in European tidal flats (*Arenicola marina* and *Corophium volutator*, Flach 1992; Beukema & Flach 1995), showing that the outcome of lugworm effects is variable and probably depending on species-specific levels of bioturbation intensity.

Chapter 6 - Burrowing by the lugworm *Abarenicola affinis* (Arenicolidae, Polychaeta) in vegetated (*Zostera muelleri*) sediment

Introduction

Two antagonistic processes of biogenic habitat transformation in tidal flats are destabilisation of the sediment by large bioturbators, e.g., lugworms and shrimps, and stabilisation of the sediment by cohesive below-ground structures such as those of seagrasses and tube-building organisms (Brenchley 1982; Reise 1985; Berkenbusch *et al.* 2007; Bouma *et al.* 2009). Both sediment stabilisers and destabilisers represent examples within the concept of ecosystem engineering (*sensu* Jones *et al.* 1994; Hastings *et al.* 2007), as they modify habitats either by their activity (allogenic engineering) or physical presence (autogenic engineering) and generate a complex and changing web of species interactions, mediated by the biogenically transformed sediment matrix (Reise 2002; Berkenbusch *et al.* 2007; Bouma *et al.* 2009). In tidal flats, the presence of either type of organism can negatively influence the distribution or functioning of the other type: bioturbation creates an unstable sediment matrix in which sedentary macrofauna or plants cannot establish, whereas, in turn, cohesive root- or tube-mats bind the sediment below the surface and inhibit reworking and burrowing activities (Wilson 1981; Brenchley 1982; Suchanek 1983; Flach 1992; Phillipart 1994; Dumbauld & Wyllie-Echeverria 2003; Siebert & Branch 2005; Berkenbusch *et al.* 2007). As a consequence, sediment destabilisers and stabilisers may show mutually exclusive distribution patterns when highly abundant, but may also

occur in mixed populations at lower densities (Reise 1985; Harrison 1987; Flach 1992; Phillipart 1994; Berkenbusch *et al.* 2007; Bouma *et al.* 2009).

Two prominent examples of antagonistic ecosystem engineers are lugworms and seagrasses (Phillipart 1994; van Wesenbeeck *et al.* 2007; Bouma *et al.* 2009). Lugworms are deposit-feeding bioturbators occupying deep burrows (up to 40 cm depth) of semi-permanent character (Krager & Woodin 1993; Retraubun *et al.* 1996; Reise 2002). Their feeding activity results in constant sediment turnover, i.e., lugworms create downward movement of surface and subsurface sediment that is ingested by them at depth, and, when processed, deposited back at the surface (Cadée 1976; Fauchald & Jumars 1979). These processes can inhibit the establishment of seagrass in intertidal areas which is most likely linked to the displacement or burial of seagrass plants and seeds (Phillipart 1994; van Wesenbeeck *et al.* 2007). Conversely, dense seagrass below-ground structures, i.e., root-rhizome matrices, may be difficult for lugworms to penetrate and have been shown to considerably reduce their burrowing ability within the sediment (Brenchley 1982; van Wesenbeeck *et al.* 2007).

In New Zealand, the lugworm *Abarenicola affinis* and the seagrass *Zostera muelleri* (previously *Zostera capricorni*) occur in tidal flats of shallow inlets and harbours, where they vary in distribution and biomass, often covering intertidal areas in patches (Wells 1963; Turner *et al.* 1999; Leduc *et al.* 2006; Mills & Berkenbusch 2009; Chapters 2 & 3). *Zostera muelleri* has been found to develop dense below-ground structures of roots and rhizomes that may adversely affect macrofauna and large bioturbators (van Houte-Howes *et al.* 2004; Berkenbusch *et al.* 2007). In Papanui Inlet, a sheltered tidal inlet on the Otago coast, *Abarenicola affinis* and *Zostera muelleri* share the same habitat in both

monospecific and mixed populations (Chapters 2 & 3). Lugworms populate mainly upper intertidal areas where they can be highly abundant (> 100 individuals per m^2, Chapter 2). Within an adjacent seagrass bed that extends parallel to the shoreline and covers the majority of mid and low intertidal areas, lugworms decline notably and are rarely present further than 300 m from the shoreline (Chapter 3). A previous investigation in this inlet showed that lugworm density and biomass was negatively influenced by seagrass below-ground biomass, suggesting that *Zostera muelleri* reduces habitat suitability for lugworms and restricts their distribution to the periphery of the inlet (Chapter 3). The aim of the present study was to investigate the effects of *Zostera muelleri* on *Abarenicola affinis* by testing whether the presence of seagrass in sediment has an influence on the burrowing activities of the lugworm.

Material & Methods

Laboratory experiment

In the laboratory experiment, lugworms were added to vegetated and unvegetated sediment collected from the field to examine their burrowing and sediment turnover activity in relation to seagrass presence and absence. The experiment was conducted in October 2009 at the Portobello Marine Laboratory, Dunedin, southern New Zealand. *Abarenicola affinis*, sediment containing *Zostera muelleri*, and bare sediment were collected from the nearby tidal flat in Papanui Inlet (see Chapter 3). The sediment was collected relatively undisturbed by inserting a bottomless bucket (30 cm diameter) to 30 cm depth in an area that contained no lugworms. The bucket holding the sediment was excavated and the retained sediment was carefully transferred into another

bucket of the same size, but with a bottom. In bare areas, it was initially checked that the sediment did not contain any seagrass material below the surface such as roots, rhizomes or debris. A total of 8 buckets were filled: 4 of vegetated (Fig. 24) and 4 of unvegetated sediment. *Abarenicola affinis* were excavated using a sampling core of 20 cm diameter (314 cm^2 area) to 30 cm depth. Each core was carefully sieved (1 mm mesh) in the field, and retained individuals were visually checked for being intact and transferred into seawater-filled containers. Collected lugworms were grouped into small (17 - 25 mm thorax length) and large individuals (32 - 51 mm thorax length) representing members of the smaller and larger size classes of this population, respectively (Chapter 3).

In the laboratory, the buckets were supplied with filtered seawater from Otago Harbour (10°C), with the water flow regulated on 6-h intervals to simulate alternating low-high tide cycles, approximating the average exposure time at the collection site in Papanui Inlet. During "low tide", the sediment was exposed to air by draining the water column through valves on the sidewall. These valves were closed during "high tide" to allow re-submersion of the sediment to 10 cm water depth. The cycle was maintained throughout the experimental period of 4 days. The lights were timed to coincide with the actual daylight period and temperature in the laboratory was near outside temperature. In vegetated treatments, seagrass leaves were cut off at the sediment surface to allow for clear visibility and collection of faecal casts during the experiment.

Four *Abarenicola affinis* individuals, two of each size group, were placed alternately and clockwise on top of the sediment in each of the 8 buckets

resulting in 32 lugworms in total, with each treatment (sediment with and without seagrass) containing 16 lugworms, 8 of each size group. Due to the logistical effort of the experiment the number of buckets was limited and, therefore, 4 lugworms were placed in each bucket corresponding to mid-ranges of densities at the collection site (Chapter 3). At this density, interference within buckets was considered unlikely and lugworms were treated as replicates. After re-burrowing, lugworms were acclimatised for 12 h before further observations commenced.

Fig. 24. Experimental bucket with vegetated (*Zostera muelleri*) sediment (seagrass leaves were cut off before commencing observations) (left), and extracted seagrass below-ground matrix (right).

The burrowing ability of *Abarenicola affinis* was tested by recording the re-burrowing time at the beginning of the experiment and burrow depth at the end of it. Re-burrowing time was defined as the time from the first sediment penetrating move of a lugworm until the complete burial of its body. At the end of the experiment, the sediment was carefully removed from the buckets to collect *Abarenicola affinis* individuals, and note the depth (in 10-cm sections) to which they had burrowed.

The spatial persistence of lugworms was examined by recording changes in the position of burrow openings, i.e., tail shafts, and measuring the distance at which burrows had been moved. Data were recorded in 6-h intervals over a total period of 84 h with recording intervals matching the simulated tidal stages during the experiment. Recording consisted of taking photographs of each bucket from above, including a scale bar placed at exactly the same position each time. In the subsequent analysis of photographs, burrow movements were noted and measured (± 1 mm) using computer software (Image J).

The sediment turnover by lugworms was examined by recording the frequency with which sediment is deposited at the surface, i.e., defaecation rate, and quantifying the amount of expelled sediment, i.e., faecal amount (Cadée 1976; Retraubun *et al.* 1996; Hymel & Plante 2000; Linton & Taghon 2000). The photographs taken at 6-h intervals were inspected for newly expelled faecal casts to broadly document defaecation activity over 84 h. The defaecation rate and faecal amount were determined in more detail on day 3 of the experiment by recording and collecting freshly deposited faeces every h over 12 consecutive h. Observation periods included 6 h of "low tide" and "high tide", respectively, to account for variation in sediment turnover by *Abarenicola affinis* with respect

to tidal stage (Chapter 4). At the beginning of observations, sediment in the buckets was smoothed over. Faecal casts were collected by carefully removing each one from the sediment surface with a plastic slide, and rinsing it into a container. During "high tide", faecal casts were collected after draining water in the bucket for one minute: this brief disruption was considered unlikely to affect *Abarenicola affinis*' behaviour. The collected faecal casts were dried to constant weight (60°C, 48 h) and weighed (± 0.001 g).

Following their collection at the end of the experiment, lugworms were anaesthetised (3 h in 7% magnesium-chloride), fixed in 4% formalin, and subsequently preserved in 70% ethanol. Thorax length was measured using calipers (± 0.5 mm): this variable was selected over total length as lugworm tails are fragile and may be damaged during sampling. Lugworm ash-free dry weight (AFDW, ± 0.0001 g) was obtained after drying (60°C, 48 h) and subsequently combusting (500°C, 4 h) each individual. In vegetated treatments, seagrass below-ground matrices were extracted (Fig. 24) and rinsed in freshwater, after which they were dried to constant weight (60°C, 48 h) and weighed (± 0.001 g).

Data analysis

Examined parameters were re-burrowing time (seconds), distance of movement of burrow openings in 84 h (cm), defaecation rate (active h / 12 h) and faecal amount (g dry weight / h). Differences between treatments and size groups were tested by two-way crossed ANOVA (Underwood 1997), treating lugworm individuals as replicates and including interactions (replicates: treatment n = 16, size group n = 16, interactions n = 8). Prior to analysis, data were tested for

normality and homogeneity of variances by Kolmogorov-Smirnov and Cochran tests, respectively (Underwood 1997). If data were not normally distributed, ANOVA was still accepted due to its robustness to non-normality under a balanced design (Underwood 1997). When necessary, data were square-root transformed to achieve homogeneity of variances (Underwood 1997). Faecal amount data remained heterogeneous after transformation. As this heterogeneity compromises the outcome of ANOVA by increasing the probability of a Type I error when test results are significant (Underwood 1997), ANOVA was considered reliable as the test result was non-significant. Statistical analyses were conducted using Statistica 6 (StatSoft Inc.).

Results

Burrowing ability and spatial persistence of lugworms in sediments with and without seagrass

Seagrass root-rhizome matrices in vegetated sediments were dense (see Fig. 24) and extended to a sediment depth of 20 cm. On average, seagrass below-ground biomass was 19.363 (± 4.792) g dry weight in the upper 10 cm and 8.368 (± 2.535) g dry weight in the lower 10 cm depth section. Lugworm size groups were comparable between treatments with relatively similar thorax lengths and biomasses, i.e., large lugworms had approximately twice the thorax length and six times higher biomass than small lugworms (Table 17).

Table 17. *Abarenicola affinis* length and biomass, and recorded burrowing and sediment turnover parameters for groups of small and large individuals (mean values ± SD, *n* = 8) in vegetated (*Zostera muelleri*) and unvegetated sediment in the laboratory (October 2009).

Abarenicola affinis	Vegetated sediment		Unvegetated sediment	
	Small	Large	Small	Large
*T*horax length (mm)	20.1 ± 2.6	40.5 ± 7.0	21.3 ± 2.6	39.6 ± 5.6
Biomass (g ash free dry weight)	0.0226 ± 0.0125	0.1477 ± 0.0678	0.0248 ± 0.0093	0.1514 ± 0.0681
Burrowing and sediment turnover parameters				
Re-burrowing time (seconds)	424.0 ± 239.0	1267.9 ± 473.7	195.5 ± 82.2	542.6 ±167.2
Burrow movement (active 6-h intervals in 84 h)	2.5 ± 1.3	1.8 ± 1.3	1.6 ± 1.8	1.3 ± 1.0
Distance of burrow movement in 84 h (cm)	5.2 ± 3.7	11.9 ± 9.4	3.2 ± 3.2	5.6 ± 6.7
Defaecation activity (active 6-h intervals in 84 h)	11.0 ± 2.3	9.5 ± 4.2	12.3 ± 1.7	9.9 ± 4.1
Defaecation rate (active h / 12 h)	0.52 ± 0.24	0.39 ± 0.24	0.65 ± 0.19	0.33 ± 0.27
Faecal amount (g dry weight / h)	0.117 ± 0.061	0.315 ± 0.215	0.239 ± 0.145	0.286 ± 0.265

In vegetated treatments, *Abarenicola affinis* re-burrowing time was approximately twice as long for both size groups compared with unvegetated treatments (Table 17, Fig. 25). In both treatments, large lugworms took generally longer to re-burrow than small ones, and took considerably longer than small individuals when re-entering sediment containing seagrass. Two-way crossed ANOVA revealed that differences were significant for both treatment and size group comparisons (Table 18). There were no significant

interactions, indicating that treatment effects were independent of lugworm size. The longest re-burrowing time recorded was 1771 seconds (= 29 minutes and 31 seconds) in one large individual in vegetated sediment, whereas the shortest re-burrowing time was 80 seconds by a small lugworm in unvegetated sediment. Most lugworms re-burrowed continuously until the thorax was covered, after which they paused several times, before continuing burrowing. Most of the large individuals paused for several minutes when re-burrowing in sediment containing seagrass.

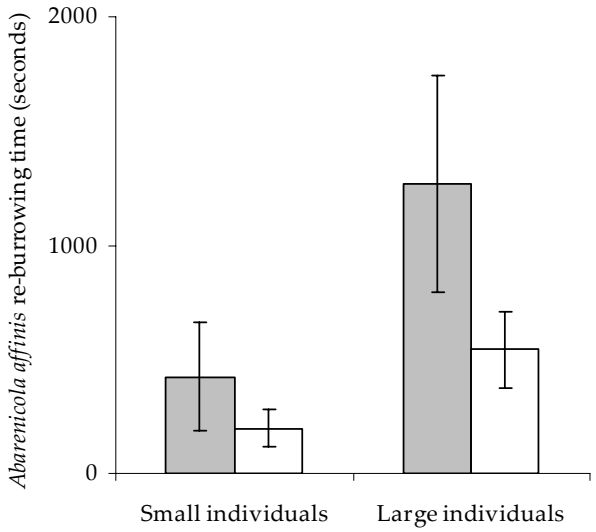


Fig. 25. *Abarenicola affinis* re-burrowing time for groups of small and large individuals (mean values ± SD, *n* = 8) in vegetated (*Zostera muelleri*) (shaded) and unvegetated sediment (open) in the laboratory (October 2009).

Table 18. Results of two-way crossed ANOVA (factors treatment, size group, and interactions) for *Abarenicola affinis* burrowing and sediment turnover parameters in the laboratory (October 2009) (significant values in bold).

Parameters	Treatment			Size group			Treatment x size group		
	df	*F*	*p*	*df*	*F*	*p*	*df*	*F*	*p*
Re-burrowing time (seconds)	1	22.10	**< 0.001**	1	44.05	**< 0.001**	1	0.82	0.372
Distance of burrow movement in 84 h (cm)	1	4.32	**0.047**	1	0.58	0.451	1	0.01	0.915
Defaecation rate (active h / 12 h)	1	0.19	0.668	1	7.07	**0.013**	1	1.10	0.302
Faecal amount (g dry weight / h)	1	0.49	0.490	1	3.39	0.076	1	1.28	0.267

Twenty-six of the 32 observed *Abarenicola affinis* moved their burrows at least once during 84 h of observation. Five of 6 lugworms that were spatially persistent were in unvegetated treatments. In bare sediment, lugworms moved mostly within the first 12 h of observation, after which they showed little or no movement until the end of the experiment (Fig. 26). In sediment containing seagrass, a greater number of lugworms moved their burrows during the experiment, compared with bare sediment (Fig. 26). In both size groups, lugworms moved more frequently (6-h intervals) in vegetated than in unvegetated treatments (Table 17). The distance over which burrows were moved in the 84-h period was greater in vegetated than in unvegetated treatments, but variation within size groups was high (Table 17). Treatment effects were more pronounced in large lugworms which moved twice the distance in the presence of seagrass compared with bare sediment. Two-way crossed ANOVA revealed that differences in movement distance between treatments were significant, whereas differences between size groups were not

(Table 18). No significant interactions of treatments and size groups were found, indicating that treatment effects were not size-related.

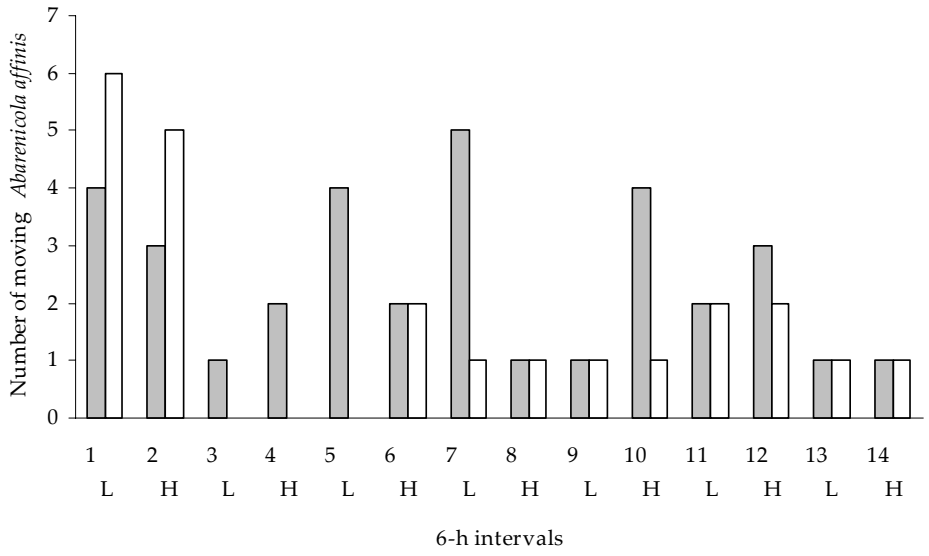


Fig. 26. Number of *Abarenicola affinis* moving in each 6-h interval in vegetated (*Zostera muelleri*) (shaded) and unvegetated sediment (open) in the laboratory (October 2009). Intervals coincided with simulated tidal stages of low (L) and high tides (H).

With the exception of one individual, all *Abarenicola affinis* in vegetated treatments burrowed through the seagrass matrix in the top 10 cm of sediment. Fewer small lugworms burrowed below 20 cm in sediment containing seagrass compared with bare sediment, whereas large lugworms burrowed below 20 cm in both treatments (Fig. 27).

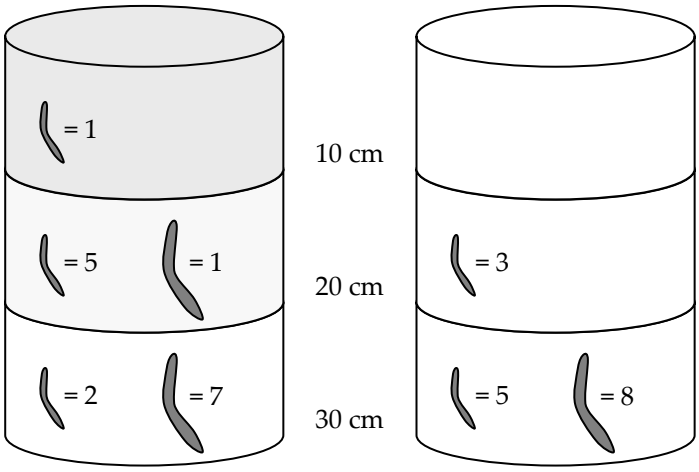


Fig. 27. Distribution of small and large *Abarenicola affinis* (each size group n = 8) at different burrow depth sections in vegetated (*Zostera muelleri*) (shaded) and unvegetated sediment in the laboratory (October 2009). The mean biomass of seagrass below-ground biomass was 19.363 (± 4.792) g dry weight in the upper 10 cm and 8.368 (± 2.535) g dry weight in the lower 10 cm depth section.

Sediment turnover by lugworms in sediments with and without seagrass

In both treatments, lugworm defaecation activity was relatively constant throughout the experiment (Fig. 28). A general pattern in relation to simulated tidal stage was observed, i.e., more lugworms were active at "high tide" compared with "low tide". There was a great range in activity among lugworms in each treatment, with individuals that defaecated in only few 6-h intervals and individuals that defaecated in each 6-h interval observed.

Defaecation rates of *Abarenicola affinis*, recorded at 1-h intervals over 12 h, were relatively similar between treatments (Table 17). On average, small lugworms defaecated slightly less often in vegetated than in unvegetated treatments. Large lugworms were generally less active than small ones with similar defaecation rates between treatments. Non-activity (defaecation rate = 0) was observed in the large size group in both treatments, whereas highly active

lugworms (defaecation rate > 0.75) were found only in the small size group, also in both treatments. Two-way crossed ANOVA showed no treatment effects on the defaecation rate, but a significant difference between size groups, independent of treatment (Table 18).

Small and large *Abarenicola affinis* responded differently to treatments in terms of faecal amount (Table 17). For small lugworms, faecal amounts were notably lower in sediment containing seagrass compared with bare sediment, whereas large individuals, which generally expelled larger amounts of sediment than small ones, showed relatively similar faecal amounts between treatments. However, the observed differences were not statistically significant (two-way crossed ANOVA, Table 18).

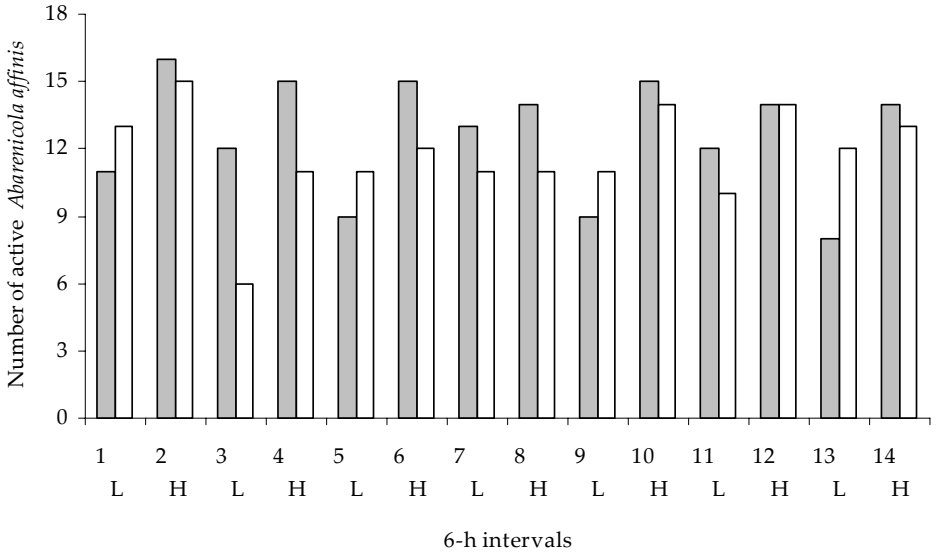


Fig. 28. Number of active *Abarenicola affinis* in each 6-h interval in vegetated (*Zostera muelleri*) (shaded) and unvegetated sediment (open) in the laboratory (October 2009). Intervals coincided with simulated tidal stages of low (L) and high tides (H).

Discussion

Burrowing ability and spatial persistence of lugworms in sediments with and without seagrass

The root-rhizome matrix of *Zostera muelleri* did not prevent burrowing by *Abarenicola affinis* as the lugworms were able to re-burrow and establish themselves in seagrass treatments. Soft-bodied burrowers such as lugworms may be less restricted in their burrowing activity than hard-bodied burrowers such as crustaceans or echinoids, probably because of their capability of changing body shape while moving through the seagrass matrix (Brenchley 1982). In comparison to *Abarenicola affinis*, which was able to reside in *Zostera muelleri* areas, bioturbating shrimps with hard bodies (*Callianassa filholi*) have been shown to be unable to establish themselves when transplanted in *Zostera muelleri* areas in Papanui Inlet, as they seemed incapable of penetrating or moving through the seagrass root-rhizome matrix (Berkenbusch *et al.* 2007). These and the present findings support the suggestion that in large bioturbators, body type may play a role in the establishment of the species in seagrass. Other studies, however, have shown that body type is of minor importance to the structure of infaunal communities in seagrass areas (Siebert & Branch 2005).

Despite establishment of burrows, *Abarenicola affinis* re-burrowed significantly more slowly in seagrass than in bare sediments. Re-burrowing took generally longer for large lugworms, which also seemed to have more difficulty penetrating the sediment containing seagrass, as they often paused while re-burrowing. These findings agreed with a previous study showing reduced burrowing abilities of the lugworms *Abarenicola pacifica* and *Abarenicola*

claparedii in seagrass, compared with bare sediment, with considerably longer re-burrowing times for the larger sized *Abarenicola claparedii* than for the smaller sized *Abarenicola pacifica* (Brenchley 1982).

The burrow restrictions imposed by seagrass may play a role in the distribution patterns of *Abarenicola affinis* in Papanui Inlet, as lugworm density has been shown to be adversely affected by *Zostera muelleri* below-ground biomass in this inlet (Chapter 3). Small lugworms seemed to be less inhibited in their burrowing ability than large individuals, which may have implications for the distribution of lugworm sizes on tidal flats with seagrass. It has been suggested previously that seagrass areas accommodate smaller individuals of burrowing organisms compared with bare sediment, due to a decrease in burrowing ability with increasing body size in the seagrass matrix (Brenchley 1982). The distribution of *Abarenicola affinis* in Papanui Inlet indicated such a pattern, i.e., small lugworms were highly abundant around the landward margin of the seagrass bed, whereas large lugworms occurred mostly in adjacent bare sediment (Chapter 3).

Re-burrowing seldom occurs in natural conditions as lugworms stay most of the time in their burrows to avoid the higher risk of predation at the sediment surface (Reise 1985). Re-burrowing would be necessary after surface migration, but such migration has been rarely documented, and has been linked mainly to freezing conditions in winter, forcing lugworms to migrate from intertidal into subtidal areas that are less severely affected (Lackschewitz & Reise 1998; Reise *et al.* 2001). Therefore, longer re-burrowing times in seagrass areas, as observed in the present study, may not have direct consequences for lugworms in tidal flats. However, in contrast to surface migration, movement of burrows occurs

frequently within days or weeks (Krager & Woodin 1993; Retraubun *et al.* 1996; this study), requiring the lugworm to establish new shafts by burrowing in the proximity of the surface. There, they are in the reach of predators, e.g., birds, flatfish and crabs, which exploit the upper sediment and use lugworms as an important food source (de Vlas 1979; Bergman 1988; Hulscher 1996). Burrowing restrictions imposed by seagrass may potentially extend the time that is needed to burrow in the top sediment layer and, therefore, may indirectly increase the risk of predation for lugworms in sediments containing seagrass.

Most *Abarenicola affinis* in unvegetated treatments moved their burrows within the first 12 h, after which they rarely relocated. In vegetated treatments, a greater number of lugworms moved their burrows throughout the 84-h observation period, and distance of burrow movements was significantly greater, particularly for large individuals. These findings indicated that in unvegetated treatments, lugworms established burrows of a more permanent character compared with vegetated treatments, whereas they may have attempted to emigrate from the sediment containing seagrass. It has been suggested in other studies that emigration of lugworms can be induced by decreasing food availability (Flach & Beukema 1994). As defaecation activity was relatively similar between treatments throughout the experimental period, it seemed unlikely that relocation of burrows was linked to food deficiency. Other factors that can cause relocation of burrows are the inability to maintain irrigation and access to the surface, which has been shown, e.g., for *Arenicola marina* in cohesive mud flats (Longbottom 1970). The maintenance of *Abarenicola affinis* burrows may have been impeded by the cohesive root-rhizome matrices of seagrass, which can significantly increase compactness of the sediment, and, thereby, create less permeable conditions (Brenchley 1982;

Siebert & Branch 2005; van Wesenbeeck *et al.* 2007). If permeability in the surrounding sediment is low, lugworms will require higher pumping pressures, i.e., increased energy costs, in order to maintain burrow water flow and, thereby, sufficient oxygen supply (Riisgard *et al.* 1996; Meysman *et al.* 2005). Lugworms in seagrass treatments may have been forced to increase their irrigation efforts to maintain burrow ventilation and, thus, a potential attempt to move towards less cohesive sediment is a plausible explanation for less spatial persistence and greater distance of burrow movements in seagrass treatments. However, the assessment of an emigration-response was limited by the small size of experimental buckets.

Whereas large lugworms burrowed to similar depths (> 20 cm) in both treatments, small individuals remained mostly within the seagrass root-rhizome matrix in vegetated treatments (above 20 cm depth), but burrowed to a greater depth in unvegetated sediment. Seagrass matrices extended to 20 cm sediment depth, which is common in the seagrass bed of Papanui Inlet (own unpubl. data). A generally shallower burrow depth was observed for the lugworm population in Papanui Inlet compared with the population in the neighbouring inlet without seagrass, Hoopers Inlet (Chapter 3). This was attributed to the smaller individual sizes of lugworms in Papanui Inlet, as individual size and burrow depth correlated in this study. The present findings suggest that seagrass additionally reduces the burrow depth of the lugworm population in Papanui Inlet.

Sediment turnover by lugworms in sediments with and without seagrass

Lugworm defaecation activity was similar between treatments in both extended (6-h interval) and more detailed (1-h interval) recordings. Similar to previous observations (Chapter 4), there was higher defaecation activity at simulated high tide compared with low tide. Small lugworms defaecated more frequently than large ones in both treatments, which agreed with reports on other lugworm species, e.g., *Arenicola marina, Abarenicola pacifica* (Wells 1953; Krager & Woodin 1993), and previous observations on *Abarenicola affinis* (Chapter 4). In unvegetated treatments, the higher defaecation rate in small lugworms resulted in relatively similar faecal amounts over time for both size groups, as it compensated for the lower faecal amounts of small individuals per single defaecation (Chapter 4). In vegetated treatments, small lugworms processed only 37% of the sediment that they processed in unvegetated treatments, whereas large individuals expelled only slightly less faecal amounts compared with bare sediment. There was, therefore, a considerable difference in faecal amounts between both size groups in vegetated treatments. This difference, however, was not significant, as there was also high variation of faecal amounts within each size group.

In previous lugworm studies, a lower faecal production has generally been linked to a decrease in food availability, as faecal amount and organic content of the sediment were positively correlated (Cadée 1976; de Wilde & Berghuis 1979; Hymel & Plante 2000). A decrease in faecal amounts, however, may also be related to high food availability (Taghon & Greene 1990). Taghon & Greene (1990) suggested that faecal amounts will correspondingly correlate with increasing food concentration only as long as sediment processing rates do not overwhelm maximum absorption rates of organic material by lugworms. If

food availability exceeds the peak of maximum absorption, less sediment will be processed. Such a pattern may be general in deposit-feeding sand swallowers ("compensatory intake model", Phillips 1984; Dade *et al.* 1990). In the present study, lugworms, particularly small individuals, produced less faecal amounts in vegetated treatments, but it seems unlikely that there was a lower organic concentration in these treatments, as measured field data from the collection site indicated similarly low organic content (1%) in both seagrass and bare intertidal areas (Chapter 3). On the contrary, it is possible that food availability in seagrass was locally enhanced, and that lugworms needed to process less sediment to gain maximum absorption rates. Food availability could have been substantially enhanced by addition of seagrass detritus which, depending on the stage of break down, contributes to organic material available to deposit-feeding organisms in sediments (Miyajima *et al.* 1998; Vizzini *et al.* 2002), and facilitates bacterial and meiofaunal growth (Danovaro 1996), both of which constitute a food source for lugworms (Riisgard & Banta 1998). In particular, detritus of *Zostera muelleri* has been found to significantly contribute to the diet of *Abarenicola affinis* in seagrass areas, especially in winter, when other food sources such as microphytobenthos are reduced (Leduc *et al.* 2006). The results of the present study suggest that if lugworms exploit a potentially higher food availability through seagrass detritus in otherwise low-organic sediment, small individuals may be more capable of doing so than large ones. Small individuals seemed less inhibited in their burrowing ability by the root-rhizome matrix, hence, their higher vertical and lateral persistence within the seagrass matrix.

Conclusions

In the laboratory experiment, *Abarenicola affinis* were able to establish burrows and feed in sediment containing the intertidal seagrass *Zostera muelleri*. In comparison with other large bioturbators, lugworms may be advantaged by their soft body when moving in the seagrass root-rhizome matrix. Nevertheless, the burrowing ability of *Abarenicola affinis* was significantly reduced by seagrass which may have implications for the distribution of lugworms on tidal flats, i.e., inhibit and / or preclude them from sediments containing dense seagrass below-ground matrices (Chapter 3). The study suggests that small lugworms seemed to be less inhibited in their burrowing activity as they stayed within the root-rhizome matrix in vegetated treatments, possibly exploiting a better food source by increased input of seagrass detritus into their diet. A potential interaction between decreased burrowing ability and increased food availability may balance functional responses of lugworms to seagrass, and seems to support smaller individuals in seagrass areas. These factors can play a role for the distribution patterns of *Abarenicola affinis* in Papanui Inlet, where the fragmented seagrass areas at the margins of the seagrass bed contain mostly small lugworms, whereas large lugworms occur in adjacent bare sediment (Chapter 3). The experiment showed limitations of a laboratory approach. The greater distance over which lugworms, particularly large individuals, moved their burrows in seagrass treatments suggested a possible attempt to migrate from the area. This aspect needs to be explored under field conditions to examine lateral directions of burrow movements, and whether distance of movement is increased when lugworms are introduced into potentially less suitable habitats.

Chapter 7 - General conclusions

Lugworm populations in southern New Zealand

The endemic lugworm *Abarenicola affinis* is sparsely distributed around New Zealand but is common in tidal inlets on the southeastern coast of the South Island (Wells 1963; Glasby *et al.* 2009; Chapter 2). The Otago coast, where the species has been known for more than a century (Ashworth 1903), represents perhaps the lugworm-richest region of New Zealand to date, with populations known from at least five tidal inlets (Wells 1963; Leduc *et al.* 2006; Chapter 2). Across four of these tidal inlets, lugworms are present at an overall density of 11 individuals per m^2, with local densities occasionally exceeding 100 individuals per m^2 (Chapter 2). The distribution of lugworms is characterised by patchiness across different spatial scales, i.e., across tidal inlets, intertidal zones and lateral parts of tidal flats, and within metres (Chapter 2). In contrast to this spatial variation, lugworm populations were found to be relatively stable throughout the year (Chapter 3), and seemed not to undergo drastic changes in their overall distribution patterns in 3 years of study at 3 intertidal sites (Papanui and Hoopers inlets, Harwood, Otago Harbour, pers. obs.). Thus, *Abarenicola affinis* is a relatively common and persistent member of intertidal benthic communities on the Otago coast.

Across tidal inlets, *Abarenicola affinis* populations differ in their characteristics, i.e., individual size, biomass and burrow depth (Chapter 3). Such variation pointed at some differences in recruitment, growth, and / or mortality across local populations, but also abiotic and biotic habitat factors are likely to contribute to these patterns (Chapter 3). It remains difficult to elucidate the

exact mechanisms responsible for the differentiation and maintenance of local populations without information on the connectivity of those populations through larval dispersal. In Otago tidal inlets, lugworm populations could be isolated from each other, i.e., recruit from different larval pools, as those inlets have constricted and shallow openings to the sea (Albrecht & Vennell 2007) which are likely to limit larval emigration and dispersal through the coastal current regime. Such restrictions would support isolation and patchiness of populations, and also potentially increase the importance of habitat characteristics in influencing the distribution and structure of local populations (Chapter 3).

Seagrass effects on lugworms - biotic interactions between antagonistic habitat-modifiers

Across tidal inlets, *Abarenicola affinis* distribution seemed to follow a pattern related to sediment characteristics, i.e., finer sediment supported higher lugworm abundances (Chapter 2). Within inlets, however, seagrass (*Zostera muelleri*) below-ground biomass was found to have a significant negative influence on lugworm abundance and biomass (Chapter 3). Thus, the presence of seagrass can play an important role in the distribution of *Abarenicola affinis* on tidal flats. In laboratory experiments, burrow restrictions imposed by seagrass root-rhizome matrices were evident, but did not prevent the establishment of burrows and feeding by *Abarenicola affinis* (Chapter 6). Small lugworms appeared more capable of staying within and moving through the seagrass matrix (Chapter 6). These laboratory findings reflected to some extent observations in the field: in a tidal inlet with an established seagrass bed,

Abarenicola affinis was restricted to the periphery of the inlet with small lugworms being relatively abundant in- and outside seagrass areas along the seagrass-bare sediment interface, whereas large individuals occurred mainly in adjacent bare sediment (Chapter 3). The findings emphasise the role of antagonistic habitat modification, i.e., destabilisation and stabilisation of the sediment, as a mechanism of negative interactions between organisms, likely resulting in inhibition and / or exclusion of one type of organism by another (Suchanek 1983; Phillipart 1994; Berkenbusch *et al.* 2007; van Wesenbeeck *et al.* 2007; Bouma *et al.* 2009). As indicated in other studies (Brenchley 1982; Harrison 1987), the present study shows that such interactions may influence the distribution and structure of populations in intertidal habitats, i.e., operate on larger ecosystem scales (Crooks 2002).

Negative interactions via habitat modification can be seen as similar to competition for space, particularly in small and enclosed habitats. A dominance of seagrass could generally decrease the potential for lugworms to expand into otherwise suitable habitats. Such patterns may be governed by priority effects, i.e., the first organism to arrive dominates the locality (van Wesenbeeck *et al.* 2007). In the present study, lugworms appeared to be restricted by predominant seagrass, but other studies have shown, conversely, that lugworms can prevent the establishment of seagrass, most likely linked to permanent burial of seeds and plants within the reworked sediment matrix (Phillipart 1994; van Weesenbeck *et al.* 2007).

In contrast to other studies that showed negative interactions between lugworms and seagrass (Brenchley 1982; Phillipart 1994; van Wesenbeeck *et al.* 2007), the present findings indicate that seagrass may support small lugworms

which are able to burrow within the root-rhizome matrix (Chapter 6) and were more prevalent than large individuals in seagrass areas in the field (Chapter 3). *Abarenicola affinis* could benefit from the use of seagrass detritus as an additional food source in otherwise low-organic sediment (Leduc *et al.* 2006), as suggested by smaller amounts of sediment processed by lugworms during feeding in seagrass areas compared with bare sediment (Chapter 6). The findings indicated some compatibility between both types of organisms, and suggested, furthermore, that apart from physical habitat modification other factors such as trophic relations could have an influence on lugworm-seagrass interactions. Such linking between habitat-mediated and trophic interactions occurs more directly, for example, when predation affects populations of habitat-modifying organisms (Reise 2002). The spatial persistence and more effective feeding of small lugworms within the seagrass matrix point to the possibility that factors not directly related to the antagonistic processes of habitat modification could become more relevant when intensity of engineering, e.g., stabilisation or destabilisation, is low (Norkko *et al.* 2006), allowing for the co-existence of both types of organisms.

Bioturbation and influence on other macrofauna - assessing aspects of ecosystem engineering by *Abarenicola affinis*

The distribution and abundance of intertidal soft-bottom infauna depends on physical, chemical and biological sediment properties (Reise 1985; Raffaelli & Hawkins 1996; Bertness 2007). The sedimentary environment is modified by benthic organisms themselves, and bioturbation is one major process of habitat alteration in sediments (Levinton 1995). Worldwide, intertidal habitats are often

dominated by bioturbators such as lugworms (Beukema 1976; Reise *et al*. 2010) or thalassinid shrimps (Suchanek 1983; Posey 1986). The marine coastal sediments are among the most biologically and geochemically active areas of the biosphere (Gattuso *et al.* 1998), and the identification of mechanisms that alter the functioning of such systems is critical to understand the relationship between diversity and functioning of organisms and the maintaining of living resources (Levin *et al*. 2001).

Bioturbation represents an example within the concept of ecosystem engineering, which can be generally understood as the physical alteration of habitat and resource flow through biotic activity, resulting in the generation, modification and maintenance of distinct habitats, with significant effects on species diversity, abundance, and ecosystem stability (Jones *et al.* 1994; Hastings *et al.* 2007). Studies on bioturbators have increasingly focussed on the importance of factors such as species-specific behaviour and activity rates (Boudreau & Marinelli 1994; Botto & Iribarne 2000), architecture and longevity of structures (Krager & Woodin 1993), distribution and biomass (Sandnes *et al.* 2000), habitat type (Volkenborn & Reise 2007; Volkenborn *et al.* 2007b), and interspecific differences (Berkenbusch & Rowden 2007) in explaining variation in their engineering impacts. Lugworms have been recognised as ecosystem engineers, mostly based on the European species *Arenicola marina* (e.g. Riisgard & Banta 1998; Reise 2002; Meysman *et al.* 2005; see also Chapter 1). The present study quantified the distribution and sediment turnover by another lugworm species, *Abarenicola affinis*, and investigated small-scale effects of this species on macrofaunal assemblages in tidal flats (Chapters 2, 4 & 5). The findings of these investigations represent aspects of the ecosystem engineering capacity of *Abarenicola affinis*, as they provide information on some important criteria in the

assessment of significant engineering species: density and spatial distribution of the engineers' population, type of resource flow that is modulated by the engineer, and consequences of resource flow modulation for other biota (Jones *et al.* 1994; Berkenbusch & Rowden 2003). In view of the recognition of *Arenicola marina* as an important ecosystem engineer, the study allowed for a comparison of *Abarenicola affinis* with its prominent European counterpart (Table 19).

Table 19. Comparison of ecological information representing aspects of the engineering impacts of *Abarenicola affinis* (New Zealand) and *Arenicola marina* (northern Europe).

Lugworm species	*Occupied habitat*	*Population distribution*	*Sediment turnover*	*Small-scale effects on macrofauna*
Abarenicola affinis	Tidal inlets of southern New Zealand (< 10 km²); Fine and muddy sediment (Chapter 2)	Patchily distributed (11 individuals per m²); relatively stable populations (Chapters 2 & 3)	Sediment turnover equivalent to 2 cm depth at 17 individuals per m²; relatively similar over seasons, variable with tidal stage and individual size (Chapter 4)	No significant effects, subtle promotional effects on surface tube-building corophiid amphipods (Chapter 5)
Arenicola marina	Vast coherent tidal flats of the North European Atlantic coast (~4700 km²); Medium sized, fine, and muddy sediment (Beukema 1976; Reise 1985; Reise *et al.* 2010)	Extensively distributed (20 - 40 individuals per m²); often dominating macrofaunal biomass; stable populations (Beukema 1976, 1992; Reise *et al.* 1994, 2010)	Sediment turnover equivalent to 6 cm depth at 17 individuals per m²; variable with season, tidal stage and individual size (Cadée 1976; Retraubun *et al.* 1996)	Significant negative effects on sedentary and mobile fauna living near the surface such as corophiid amphipods, small bivalves, and polychaetes; promotional effects on small subsurface infauna (Reise 1983; Brey 1991; Flach 1992, 1993)

The sediment turnover by *Abarenicola affinis* was relatively constant over seasons throughout one year, with lugworm activity corresponding to semidiurnal tidal cycles, i.e., they were mostly active during high tides (Chapter 4). Based on these findings and distribution patterns of an intertidal *Abarenicola affinis* population (Chapter 2), an annual sediment turnover estimate was calculated at 24.4 kg dry weight of sediment per m², equivalent to a reworked depth of approximately 2 cm (Chapter 4). This estimate appears low in comparison with *Arenicola marina*, which reworks sediment equivalent to a depth of approximately 6 cm at a comparable mean density (Cadée 1976). At the same time, *Arenicola marina* shows a widespread and dominant occurrence with mean densities of 20 - 40 individuals per m² over thousands of km² in European tidal flats (Beukema 1976; Reise *et al.* 2010), whereas *Abarenicola affinis* occupies smaller habitats, is more patchily distributed, and occurs at relatively lower abundances (Chapter 2). Thus, the bioturbative impact of *Abarenicola affinis* on its sedimentary environment is lower and less universal compared with *Arenicola marina*.

Abarenicola affinis did not play an influential role in macrofaunal distribution on a tidal flat of Otago (Chapter 5). Instead, physical factors such as tidal exposure and proportion of sediment fines had high explanatory power, indicating a pattern of macrofauna according to the variable conditions across intertidal zones and a general adaptation to lugworm bioturbation (Chapter 5). Small-scale exclusions of *Abarenicola affinis* did not result in significant changes in macrofaunal assemblage composition, but showed a subtle shift in macrofaunal abundance, created by patterns of the dominant corophiid amphipod *Paracorophium excavatum*: abundances were lower in exclusion plots compared with plots containing lugworms (Chapter 5). These observations, however,

were made on only one of two sampling occasions, when macrofauna was relatively homogeneously distributed across the experimental site, whereas this pattern was not evident on the other sampling occasion, when macrofauna showed high spatial variation. Thus, lugworm effects were variable over space and time and dependent on population dynamics of the associated macrofauna.

The findings indicated that bioturbation by *Abarenicola affinis* did not negatively influence sedentary macrofauna such as *Paracorophium excavatum*, although this amphipod has been shown to be susceptible to sediment disturbance by other intertidal burrowers, i.e., ghost shrimps (Berkenbusch *et al.* 2000). In contrast, the lower abundances of *Paracorophium excavatum* in exclusion plots pointed to the possibility that lugworms ameliorate the habitat for this amphipod, e.g., by increasing oxygen and decreasing toxic metabolites (sulphide) in the sediment through irrigation activities (Riisgard *et al.* 1996; Banta *et al.* 1999; Kristensen 2001). Compared with *Abarenicola affinis*, bioturbation and bioirrigation by *Arenicola marina* has been shown to have substantial negative or positive effects on abundances of surface and subsurface macrofauna in the proximity of burrows, including amphipods, polychaetes, and bivalves (Reise 1983; Brey 1991; Flach 1992; Flach & de Bruin 1993). These small-scale effects are likely to become important for overall ecosystem processes when lugworms are widespread and dominant, as was shown by long-term and large-scale exclusion experiments with *Arenicola marina* (plot size 400 m^2), revealing effects of its bioturbation and bioirrigation on the entire sedimentary habitat and community (Volkenborn *et al.* 2007a, Volkenborn & Reise 2007; Kuhnert *et al.* 2010). In comparison, *Abarenicola affinis* does not reach the dominance and ecological importance of *Arenicola marina*, which is reflected in smaller and patchier populations, relatively lower sediment turnover rates, and lack of a

small-scale impact on associated macrofauna. Thus, there is variability in the role that lugworms play as engineering species in different coastal ecosystems around the world, based on their species-specific population biology and environmental settings of their habitats. Furthermore, the presence of lugworms may have variable effects on macrofauna as a result of their bioturbating intensity and other mechanisms by which lugworms modify the sediment matrix.

Outlook

The study revealed aspects of the biology and ecology of *Abarenicola affinis* and considered the role that these organisms play in the sedimentary environment of tidal inlets of southern New Zealand. Further research is needed to specify species-habitat interactions of *Abarenicola affinis*. For example, aspects of reproductive biology such as spawning and larval dispersion require resolution to assess the degree of isolation among local populations, and to understand their linkage with the different habitats.

In this sense, biotic interactions such as those between lugworms and seagrass need further descriptive and experimental studies to reveal effects of both species, and to test whether there is the potential of mutual exclusion through mechanisms of habitat modification. In Otago, the opportunity exists to study population-level interactions between both organisms at multiple spatial and temporal scales. Experimental studies, e.g., mutual transplantation experiments, could be used to test the generality of the descriptive findings of the present

study, and to elucidate mechanisms and dynamics that have an influence on the relationship between lugworms and seagrass.

The current study revealed that biotic and abiotic factors can have an influence on *Abarenicola affinis* populations in different habitats. Future studies could compare lugworm impacts on sediment and associated biota across different tidal inlets of southern New Zealand and, thereby, assess the potential for variation in habitat conditions to modify the outcome and strength of lugworm effects.

Although *Abarenicola affinis* appears to have a lower impact on associated biota compared with *Arenicola marina*, there is some generality in fundamental implications of lugworm bioturbation and bioirrigation for the abiotic and biotic environments, e.g., particle and porewater transport through the sediment matrix (Fig. 1). On a small-scale, these activities provide micro-habitats (e.g. burrow shafts, faecal casts, feeding funnels), which could be the subject of future research in order to gain information on mechanisms by which *Abarenicola affinis* modifies the habitat, and illuminate their relative importance for the abiotic and biotic environment.

The present study has pointed out differences in engineering impacts among lugworm species around the world (e.g. *Abarenicola affinis*, *Arenicola marina*). It raises the need for comparative work based on standardised methods across species and habitats to better understand general and specific aspects of ecosystem engineering by lugworms.

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Appendix

Chapter 2 - *Abarenicola affinis* faecal cast density and sediment parameters across different intertidal zones in tidal inlets of southern New Zealand, sampled in September 2007.

Study site	Intertidal zone	Block	*Abarenicola affinis* fecal casts per m²	Mean grain size (μm)	Fines fraction (%)	Total organic matter (%)	Chlorophyll *a* (μg / g sediment dry weight)
Papanui Inlet	High	1	1.5	148	3.0	0.88	9.0
		2	44.3	147	3.8	0.77	3.1
		3	45.0	129	8.9	0.81	4.9
		4	65.3	146	4.2	0.57	1.9
		5	42.1	118	10.2	0.93	5.0
		6	29.8	146	5.0	0.91	3.6
	Mid	1	0.0	148	1.7	0.70	5.0
		2	1.5	148	3.8	0.86	4.5
		3	7.3	148	2.9	0.53	2.4
		4	0.0	146	4.4	0.60	3.0
		5	38.5	126	7.4	0.85	2.8
		6	11.6	146	1.9	0.50	2.1
	Low	1	0.0	148	4.9	0.73	2.5
		2	0.0	148	1.9	0.56	2.2
		3	0.0	146	6.7	0.64	2.2
		4	0.0	148	4.8	0.76	3.3
		5	16.7	145	7.4	0.75	2.8
		6	5.1	145	4.0	0.69	3.1
Hoopers Inlet	High	1	25.4	148	2.8	0.83	4.5
		2	19.6	148	2.3	0.56	3.8
		3	31.2	126	2.9	0.66	4.1
		4	0.0	66	66.2	2.16	17.6
		5	3.6	82	39.6	1.11	7.3
		6	0.7	109	20.3	1.58	12.2
	Mid	1	32.7	233	2.3	0.52	3.4
		2	10.9	147	2.4	0.52	2.0
		3	16.7	147	2.0	0.59	4.0
		4	8.0	55	64.4	1.46	11.4
		5	26.8	112	17.1	0.89	2.6
		6	54.4	146	5.6	0.76	2.9
	Low	1	24.7	147	3.2	0.58	2.3
		2	16.7	149	2.9	0.56	2.5
		3	5.8	148	1.6	0.45	2.6
		4	23.9	80	43.2	1.14	4.2
		5	67.5	145	9.4	0.65	2.0
		6	72.6	148	3.2	0.76	1.5
Harwood / Otago Harbour	High	1	29.0	150	1.5	0.50	2.5
		2	0.7	152	0.6	0.38	1.4
		3	22.5	150	2.5	0.65	6.1
		4	44.3	149	1.1	0.74	2.4
		5	0.0	152	1.3	0.53	2.9
		6	4.4	152	1.8	0.58	4.1
	Mid	1	0.0	150	0.7	0.43	1.5
		2	2.9	150	0.5	0.39	2.9
		3	10.9	149	0.7	0.68	3.0
		4	19.6	152	1.2	0.43	2.3
		5	2.9	182	1.6	0.89	2.5
		6	1.5	181	1.0	0.45	3.4
	Low	1	0.0	192	0.7	0.49	3.2

	2	19.6	149	1.1	0.39	3.4
	3	8.0	149	0.9	0.45	3.2
	4	0.0	150	1.3	0.46	2.5
	5	0.0	150	1.7	0.46	5.1
	6	16.7	152	1.3	0.49	3.7

Chapter 3 - *Abarenicola affinis*, sediment and seagrass parameters across different seasons in Papanui and Hoopers inlets, southern New Zealand, sampled between summer 2007 and spring 2008.

Study site	Month	No.	*Abarenicola affinis* Ind. per 314 cm²	*Abarenicola affinis* AFDW g per 314 cm²	Mean grain size (μm)	Fines fraction (%)	Total organic matter (%)	Chlorophyll *a* (μg / g sediment dry weight)	Distance from the shore (m)	*Zostera muelleri* above-ground biomass (g dry weight)	*Zostera muelleri* below-ground biomass (g dry weight)
Papanui Inlet	Dec	1	2	0.0393	147	4.0	0.70	4.2	24	0.141	4.163
		2	0	0.0000	147	2.0	0.59	2.5	340	0.381	7.107
		3	3	0.0326	148	2.6	0.81	3.9	200	0.072	6.815
		4	0	0.0000	148	1.9	0.66	2.0	455	0.064	8.958
		5	1	0.0208	146	2.3	1.01	6.0	120	0.065	5.958
		6	2	0.0416	147	2.2	0.64	2.5	315	0.251	9.433
		7	1	0.0302	147	2.4	0.50	2.0	464	0.010	5.230
		8	4	0.1721	146	6.7	0.93	2.7	20	0.000	0.000
		9	0	0.0000	148	3.1	0.73	3.4	347	0.316	5.447
		10	0	0.0000	147	3.8	0.90	2.7	616	0.235	4.840
		11	3	0.1030	145	7.9	0.71	2.4	48	0.000	0.000
		12	2	0.0262	147	3.0	0.68	3.1	380	0.050	3.592
		13	0	0.0000	147	3.6	0.61	2.1	454	0.293	5.253
		14	3	0.0273	146	7.2	0.80	2.9	104	0.044	2.878
		15	0	0.0000	148	3.1	0.76	2.6	299	0.262	7.478
	Mar	1	3	0.1513	146	4.4	0.72	5.5	29	0.034	3.925
		2	1	0.0078	148	2.3	0.72	5.4	200	0.096	3.031
		3	0	0.0000	149	1.9	0.50	3.7	455	0.161	2.125
		4	0	0.0000	147	3.4	0.57	2.0	653	0.400	5.667
		5	5	0.1512	145	6.3	0.80	7.3	33	0.000	0.000
		6	0	0.0000	147	2.1	0.56	7.7	195	0.620	4.679
		7	2	0.0505	148	2.7	0.59	4.0	438	0.091	3.334
		8	5	0.0749	147	3.0	0.65	4.4	64	0.133	2.069
		9	1	0.0125	148	2.5	0.58	4.4	243	0.246	5.357
		10	0	0.0000	148	3.2	0.72	2.3	612	0.000	0.000
		11	0	0.0000	147	2.9	0.75	3.5	410	0.175	6.915
		12	4	0.1370	145	4.4	0.63	4.0	123	0.000	0.000
		13	0	0.0000	147	3.9	0.59	3.7	454	0.226	5.069
		14	0	0.0000	148	4.2	0.76	5.4	293	0.446	9.058
		15	8	0.1253	144	9.5	0.74	2.9	35	0.000	0.000
	Jun	1	0	0.0000	148	2.6	0.55	3.0	260	0.230	5.027
		2	0	0.0000	148	1.3	0.59	2.1	418	0.000	0.000
		3	4	0.0743	145	5.0	0.59	4.6	34	0.000	0.000
		4	0	0.0000	147	2.8	0.57	3.8	302	0.214	4.689
		5	0	0.0000	148	2.7	0.55	2.4	485	0.174	3.700
		6	2	0.0330	147	2.8	0.56	7.9	131	0.130	6.116
		7	5	0.1401	145	5.8	0.45	2.5	33	0.000	0.000
		8	1	0.0265	148	2.2	0.52	3.4	280	0.069	4.549
		9	1	0.0118	147	2.7	0.58	3.9	153	0.057	3.637
		10	0	0.0000	147	2.8	0.50	3.3	555	0.180	4.972
		11	0	0.0000	147	2.8	0.45	2.3	405	0.137	3.944
		12	0	0.0000	147	4.1	0.47	3.3	567	0.000	0.000

		13	5	0.1439	123	10.6	0.47	5.1	30	0.000	0.000
		14	0	0.0000	147	3.8	0.49	2.8	396	0.398	4.392
		15	2	0.0574	125	8.7	0.51	3.1	104	0.000	0.000
	Sep	1	3	0.0999	146	4.0	0.53	2.9	24	0.035	2.356
		2	0	0.0000	147	2.9	0.58	2.8	533	0.062	2.013
		3	3	0.0866	146	4.2	0.63	3.0	34	0.019	1.552
		4	1	0.0129	147	3.2	0.77	3.2	302	0.058	4.546
		5	0	0.0000	147	2.6	0.55	3.0	131	0.030	3.482
		6	0	0.0000	147	2.9	0.56	1.9	280	0.257	7.437
		7	0	0.0000	148	4.7	0.64	3.2	666	0.382	4.563
		8	2	0.1074	146	7.7	0.90	5.4	20	0.000	0.000
		9	1	0.0215	147	3.1	0.59	2.6	153	0.150	3.092
		10	1	0.0075	147	3.1	0.52	3.3	330	0.274	3.675
		11	1	0.0135	147	3.6	0.54	4.5	380	0.118	4.838
		12	3	0.0895	119	12.2	0.85	5.0	25	0.000	0.000
		13	0	0.0000	148	3.9	0.57	3.3	409	0.332	2.987
		14	0	0.0000	147	4.3	0.67	6.1	195	0.443	7.276
		15	4	0.2396	121	13.2	0.83	4.2	81	0.000	0.000
Hoopers	Dec	1	3	0.2333	147	1.8	0.66	7.2	134	-	-
Inlet		2	3	0.4739	148	1.9	0.64	6.3	22	-	-
		3	1	0.0077	148	1.3	0.62	5.5	137	-	-
		4	2	0.0814	149	2.0	0.57	3.0	267	-	-
		5	1	0.0500	147	1.7	0.49	3.2	394	-	-
		6	1	0.0201	149	1.3	0.51	5.2	62	-	-
		7	2	0.0661	148	1.2	0.56	4.0	121	-	-
		8	1	0.0492	149	1.8	0.51	2.6	313	-	-
		9	2	0.1901	148	1.9	0.57	2.5	362	-	-
		10	1	0.0508	148	1.4	0.53	2.2	148	-	-
		11	1	0.0237	149	1.7	0.49	4.5	309	-	-
		12	5	0.1079	148	1.5	0.44	3.9	86	-	-
		13	3	0.1002	148	1.7	0.57	4.4	131	-	-
		14	0	0.0000	148	2.1	0.64	4.7	27	-	-
		15	5	0.1466	148	1.9	0.56	3.2	27	-	-
	Mar	1	2	0.1209	146	2.5	0.45	7.1	191	-	-
		2	2	0.1443	148	2.8	0.53	6.7	455	-	-
		3	2	0.2150	148	1.6	0.52	8.9	21	-	-
		4	1	0.1106	148	1.6	0.55	10.7	137	-	-
		5	1	0.2456	147	2.8	0.51	4.5	589	-	-
		6	1	0.0733	147	2.1	0.47	4.1	379	-	-
		7	3	0.1512	148	1.7	0.49	8.2	121	-	-
		8	4	0.3110	147	2.7	0.54	4.0	249	-	-
		9	1	0.1062	148	1.9	0.53	3.4	362	-	-
		10	0	0.0000	148	1.7	0.49	6.0	51	-	-
		11	0	0.0000	149	1.8	0.44	11.2	179	-	-
		12	1	0.2081	148	1.6	0.50	5.8	30	-	-
		13	1	0.3982	147	1.3	0.51	13.9	118	-	-
		14	2	0.3144	148	2.2	0.62	5.1	44	-	-
		15	1	0.0438	147	1.8	0.48	3.3	60	-	-
	Jun	1	1	0.1018	147	2.9	0.55	6.5	72	-	-
		2	3	0.1286	147	2.4	0.50	3.5	328	-	-
		3	1	0.0349	148	2.5	0.66	8.2	137	-	-
		4	1	0.0961	148	2.1	0.69	5.6	228	-	-
		5	1	0.0287	148	1.8	0.69	3.9	328	-	-
		6	1	0.0113	147	2.3	0.55	6.9	121	-	-
		7	4	0.2286	148	2.5	0.64	2.8	407	-	-
		8	1	0.1219	147	1.9	0.49	4.7	308	-	-
		9	1	0.0696	148	1.7	0.58	6.7	148	-	-
		10	1	0.1786	148	1.9	0.68	4.0	326	-	-
		11	3	0.1102	148	1.6	0.51	5.4	161	-	-
		12	2	0.3027	148	1.6	0.65	6.0	295	-	-
		13	0	0.0000	147	1.9	0.80	4.7	81	-	-
		14	1	0.1032	147	1.6	0.69	3.7	123	-	-

	15	0	0.0000	147	1.9	0.80	7.1	20	-	-
Sep	1	1	0.1789	148	3.0	0.59	4.6	74	-	-
	2	2	0.1674	147	3.4	0.46	3.1	525	-	-
	3	1	0.0381	148	2.1	0.55	5.3	201	-	-
	4	2	0.1737	147	3.5	0.49	2.6	461	-	-
	5	1	0.0201	148	2.3	0.58	3.3	285	-	-
	6	1	0.0221	147	2.3	0.41	2.7	313	-	-
	7	2	0.2271	148	3.5	0.50	2.7	407	-	-
	8	1	0.0958	148	1.8	0.44	1.8	68	-	-
	9	2	0.1005	147	2.7	0.49	3.4	203	-	-
	10	1	0.0366	148	3.1	0.62	3.4	326	-	-
	11	0	0.0000	148	2.5	0.48	7.4	51	-	-
	12	2	0.0909	148	2.2	0.41	3.5	369	-	-
	13	0	0.0000	148	2.7	0.56	3.5	86	-	-
	14	1	0.1761	148	2.6	0.56	2.6	30	-	-
	15	5	0.1691	147	3.0	0.56	4.6	41	-	-

Chapter 3 - Body measurements, burrow depth and sex of *Abarenicola affinis* individuals in Papanui and Hoopers inlets, southern New Zealand, sampled between summer 2007 and spring 2008.

Study site	Month	Total length (mm)	Thorax length (mm)	AFDW g	Burrow depth cm	Sex
Papanui Inlet	December	53	32	0.0165	20	-
		62	33	0.0228	30	m
		32	19	0.0056	10	-
		35	20	0.0098	10	f
		41	20	0.0172	10	-
		59	35	0.0208	20	f
		55	28	0.0219	10	-
		53	37	0.0197	30	f
		47	34	0.0302	20	m
		83	43	0.0442	20	f
		82	43	0.0467	20	m
		79	36	0.0417	30	f
		82	45	0.0395	30	f
		57	32	0.0232	20	f
		71	36	0.0284	20	f
		81	40	0.0514	30	m
		24	17	0.0054	10	-
		73	34	0.0208	30	-
		29	19	0.0037	20	-
		45	24	0.0088	20	f
		47	28	0.0148	20	m
	March	78	33	0.0749	30	f
		44	24	0.0451	30	m
		50	27	0.0313	30	m
		34	22	0.0078	20	f
		43	23	0.0123	30	m
		45	27	0.0201	30	m
		61	27	0.0193	30	m
		65	37	0.0300	30	m
		89	43	0.0695	30	m
		39	32	0.0137	10	-
		66	34	0.0368	30	f
		45	27	0.0148	20	-
		42	25	0.0104	20	-
		53	28	0.0247	30	f

		39	25	0.0124	30	f
		29	24	0.0126	30	-
		52	24	0.0125	30	f
		52	34	0.0503	30	m
		54	38	0.0376	30	m
		48	23	0.0222	30	f
		42	24	0.0269	30	f
		32	21	0.0069	20	-
		57	24	0.0194	30	m
		49	24	0.0101	30	ne
		62	26	0.0299	30	m
		50	25	0.0081	30	-
		62	27	0.0145	30	m
		63	24	0.0263	30	m
		40	23	0.0101	30	m
	June	54	34	0.0212	20	-
		39	23	0.0110	20	-
		57	30	0.0170	30	m
		55	30	0.0251	30	m
		29	19	0.0177	10	-
		46	26	0.0153	20	-
		69	33	0.0321	20	m
		57	35	0.0283	20	f
		63	34	0.0191	30	f
		70	37	0.0288	30	-
		59	27	0.0318	30	f
		71	31	0.0265	20	-
		40	19	0.0118	10	-
		36	21	0.0088	20	-
		24	22	0.0101	20	-
		62	34	0.0300	20	m
		73	35	0.0445	20	m
		57	35	0.0505	30	f
		60	38	0.0295	30	f
		57	36	0.0279	30	f
	September	31	19	0.0049	10	-
		63	34	0.0372	30	-
		74	37	0.0578	30	f
		45	28	0.0177	20	f
		78	33	0.0312	20	f
		70	33	0.0377	20	f
		35	21	0.0129	10	-
		52	27	0.0282	20	m
		73	37	0.0792	30	-
		47	25	0.0215	20	f
		36	23	0.0075	10	-
		30	22	0.0135	20	-
		60	30	0.0187	20	m
		67	38	0.0483	20	-
		34	34	0.0225	30	-
		52	27	0.0310	20	f
		64	35	0.0640	20	f
		66	37	0.0475	20	f
		110	49	0.0971	30	m
Hoopers Inlet	December	62	37	0.0859	40	m
		91	47	0.0770	40	-
		49	42	0.0704	40	m
		149	74	0.2008	40	m
		81	47	0.1144	40	m
		109	56	0.1587	40	m
		36	21	0.0077	10	-
		79	51	0.0347	40	-

	118	66	0.0467	40	f
	84	43	0.0500	40	f
	89	39	0.0201	30	-
	117	49	0.0361	30	m
	97	44	0.0300	40	m
	80	41	0.0492	40	f
	78	44	0.0922	40	m
	91	48	0.0979	40	f
	102	46	0.0508	40	f
	70	34	0.0237	30	-
	50	29	0.0153	30	-
	63	42	0.0245	30	f
	76	35	0.0289	30	f
	52	34	0.0201	30	m
	46	35	0.0191	40	-
	62	28	0.0234	30	-
	93	56	0.0316	30	-
	94	41	0.0452	40	m
	56	36	0.0352	30	f
	81	42	0.0317	30	f
	92	46	0.0223	30	f
	95	46	0.0326	30	f
	45	45	0.0248	40	f
March	69	47	0.0635	30	m
	103	51	0.0574	40	f
	86	33	0.0996	30	m
	92	54	0.0447	40	f
	95	47	0.1235	30	m
	87	50	0.0915	40	f
	87	45	0.1106	30	f
	131	72	0.2456	40	f
	95	48	0.0733	40	m
	39	23	0.0080	20	f
	84	48	0.0828	30	f
	86	38	0.0604	30	f
	49	33	0.0248	20	f
	66	34	0.0514	20	f
	79	37	0.0864	30	f
	116	58	0.1484	40	m
	84	43	0.1062	40	m
	154	64	0.2081	40	m
	128	83	0.3982	40	m
	83	47	0.1198	40	f
	175	57	0.1946	40	m
	73	34	0.0438	40	m
June	96	49	0.1018	40	f
	39	19	0.0089	30	-
	94	46	0.0627	40	f
	84	47	0.0570	40	f
	72	42	0.0349	30	f
	87	48	0.0961	40	m
	53	32	0.0287	30	f
	51	32	0.0113	30	-
	36	23	0.0215	20	f
	87	43	0.0717	30	m
	53	30	0.0069	30	-
	92	48	0.1285	40	m
	111	55	0.1219	40	m
	70	44	0.0696	20	-
	97	61	0.1786	40	f
	45	33	0.0240	30	f
	69	31	0.0369	30	f

		76	33	0.0493	30	f
		135	61	0.2374	40	f
		119	47	0.0653	40	-
		120	55	0.1032	40	f
	September	134	90	0.1789	40	f
		74	35	0.0281	20	f
		147	58	0.1393	40	f
		86	36	0.0381	30	f
		68	36	0.0640	20	f
		94	47	0.1097	40	m
		57	31	0.0201	20	f
		64	33	0.0221	30	-
		55	34	0.0601	30	f
		99	63	0.1670	30	m
		105	43	0.0958	30	f
		49	35	0.0343	30	-
		85	49	0.0662	30	m
		97	41	0.0366	30	m
		47	33	0.0354	20	m
		100	51	0.0555	30	m
		141	68	0.1761	40	m
		40	34	0.0200	10	-
		48	34	0.0266	10	-
		52	35	0.0341	20	f
		66	37	0.0336	20	-
		81	37	0.0548	30	m

Chapter 4 - *Abarenicola affinis* sediment turnover parameters during low and high tides in Papanui Inlet, southern New Zealand, sampled between summer and spring 2008.

Tide	Month	Cast no.	Defecation rate (active h / total h)	Faecal amount (g dry weight)	Tide	Month	Cast no.	Defecation rate (active h / total h)	Faecal amount (g dry weight) / *Fecal volume mm³*
Low	February	1	0.83	0.375	Low	November	1	0.50	0.221
		2	0.00	0.000			2	0.67	0.233
		3	0.17	0.041			3	0.33	0.069
		4	0.83	0.631			4	0.83	0.458
		5	0.67	0.101			5	1.00	0.749
		6	0.17	0.054			6	0.17	0.084
		7	0.50	0.196			7	0.50	0.090
		8	0.33	0.051			8	0.67	0.296
		9	0.33	0.053			9	0.00	0.000
		10	0.50	0.238			10	0.00	0.000
		11	0.00	0.000			11	0.83	0.318
		12	0.67	0.246			12	0.67	0.254
		13	0.17	0.040			13	0.83	0.400
		14	0.33	0.039			14	0.83	0.331
		15	0.00	0.000			15	0.17	0.033
		16	0.33	0.149			16	0.83	0.237
		17	0.00	0.000			17	0.67	0.211
		18	0.00	0.000			18	0.33	0.052
		19	0.00	0.000			19	0.50	0.413
		20	0.17	0.016			20	0.50	0.141
		21	0.00	0.000			21	0.33	0.044
		22	0.00	0.000			22	0.33	0.067
		23	0.17	0.146			23	0.17	0.122
		24	0.00	0.000			24	0.33	0.138
		25	0.25	0.018			25	0.00	0.000

	26	0.75	0.130			26	0.75	0.071
	27	1.00	0.334			27	0.25	0.019
	28	0.25	0.018			28	0.00	0.000
	29	0.75	0.102			29	0.50	0.114
	30	0.00	0.000			30	0.50	0.054
	31	0.50	0.049			31	0.00	0.000
	32	0.00	0.000			32	0.50	0.054
	33	0.25	0.075			33	0.00	0.000
	34	0.50	0.064			34	0.25	0.057
	35	0.25	0.056			35	0.25	0.018
	36	0.50	0.093			36	0.00	0.000
	37	0.75	0.139			37	0.50	0.057
	38	0.75	0.259			38	0.50	0.026
	39	0.25	0.063			39	0.50	0.035
	40	0.25	0.050			40	0.25	0.059
	41	0.00	0.000			41	0.25	0.039
	42	0.00	0.000			42	0.50	0.144
	43	0.50	0.060			43	0.25	0.148
	44	0.75	0.198			44	0.00	0.000
	45	0.00	0.000			45	0.75	0.241
	46	0.00	0.000			46	0.25	0.067
	47	0.50	0.100			47	0.25	0.033
	48	0.25	0.151			48	0.50	0.049
May	1	0.50	0.059	High	August	1	0.75	
	2	0.00	0.000			2	0.50	
	3	0.00	0.000			3	0.50	
	4	0.17	0.029			4	0.50	
	5	0.67	0.610			5	0.75	
	6	0.33	0.289			6	0.50	
	7	0.17	0.024			7	1.00	
	8	0.00	0.000			8	0.75	
	9	0.33	0.025			9	0.50	
	10	0.33	0.024			10	0.50	
	11	0.17	0.040			11	0.00	
	12	0.00	0.000			12	0.50	
	13	0.33	0.129			13	1.00	*404.8*
	14	0.33	0.035			14	0.75	*498.8*
	15	0.33	0.044			15	1.00	*534.6*
	16	0.83	0.120			16	0.75	*795.6*
	17	0.00	0.000			17	1.00	*219.5*
	18	0.17	0.043			18	1.00	*613.9*
	19	0.33	0.031			19	0.75	*144.7*
	20	0.67	0.049			20	0.25	*57.2*
	21	0.33	0.032			21	0.75	*67.8*
	22	0.17	0.033			22	0.50	*417.5*
	23	0.83	0.434			23	1.00	*403.3*
	24	0.00	0.000			24	0.75	*473.2*
	25	0.50	0.046			25	0.67	
	26	0.75	0.083			26	0.33	
	27	0.75	0.043			27	0.00	
	28	0.75	0.153			28	0.67	
	29	0.75	0.064			29	0.50	
	30	0.75	0.130			30	0.83	
	31	0.25	0.034			31	0.83	
	32	0.25	0.095			32	0.00	
	33	0.25	0.052			33	0.50	
	34	0.75	0.110			34	0.50	
	35	0.75	0.060			35	0.83	
	36	0.50	0.141			36	0.33	
	37	0.25	0.034			37	1.00	*222.5*
	38	1.00	0.239			38	0.67	*117.4*
	39	0.75	0.117			39	0.83	*259.1*

	40	0.75	0.149		40	0.83	*197.2*
	41	0.25	0.041		41	0.67	*132.3*
	42	0.00	0.000		42	0.67	*28.3*
	43	0.00	0.000		43	1.00	*90.2*
	44	1.00	0.204		44	0.67	*205.2*
	45	1.00	0.217		45	0.67	*78.6*
	46	0.25	0.036		46	1.00	*227.4*
	47	0.00	0.000		47	0.83	*175.7*
	48	1.00	0.094		48	1.00	*296.9*
August	1	0.17	0.027	November	1	0.00	*0.0*
	2	0.00	0.000		2	0.00	*0.0*
	3	0.50	0.055		3	0.50	*99.5*
	4	0.00	0.000		4	0.00	*0.0*
	5	0.33	0.034		5	0.25	*81.2*
	6	0.50	0.155		6	0.75	*76.9*
	7	0.33	0.076		7	0.00	*0.0*
	8	0.17	0.013		8	0.50	*72.6*
	9	0.50	0.048		9	0.75	*198.9*
	10	0.33	0.141		10	0.50	*243.5*
	11	0.67	0.289		11	0.50	*63.0*
	12	0.17	0.043		12	0.75	*289.2*
	13	0.67	0.089		13	0.75	
	14	0.00	0.000		14	0.50	
	15	0.17	0.031		15	0.00	
	16	0.00	0.000		16	0.25	
	17	0.33	0.192		17	0.50	
	18	0.17	0.199		18	0.25	
	19	0.00	0.000		19	1.00	
	20	0.17	0.017		20	1.00	
	21	0.17	0.017		21	1.00	
	22	0.17	0.018		22	0.00	
	23	0.17	0.131		23	1.00	
	24	0.00	0.000		24	0.75	
	25	1.00	0.135		25	1.00	*131.9*
	26	1.00	0.147		26	0.17	*3.4*
	27	0.75	0.133		27	0.83	*138.1*
	28	0.25	0.027		28	0.33	*5.3*
	29	0.25	0.032		29	0.83	*172.0*
	30	0.00	0.000		30	1.00	*143.1*
	31	0.50	0.137		31	1.00	*190.2*
	32	0.75	0.109		32	0.83	*87.0*
	33	0.25	0.018		33	1.00	*114.0*
	34	0.50	0.047		34	0.67	*100.1*
	35	0.00	0.000		35	1.00	*176.7*
	36	0.25	0.013		36	1.00	*231.3*
	37	0.00	0.000		37	0.17	
	38	0.25	0.036		38	0.67	
	39	0.25	0.032		39	0.33	
	40	0.00	0.000		40	0.83	
	41	0.50	0.074		41	0.17	
	42	0.75	0.118		42	0.67	
	43	0.00	0.000		43	0.83	
	44	0.75	0.057		44	1.00	
	45	1.00	0.282		45	0.33	
	46	0.25	0.016		46	0.33	
	47	0.75	0.079		47	1.00	
	48	0.00	0.000		48	1.00	

Chapter 4 - Body measurements and sediment turnover parameters of *Abarenicola affinis* individuals of different size groups in laboratory experiments conducted in summer and winter 2009.

Month	Size group	Thorax length (mm)	AFDW g	Defecation rate (active h / total h)	Fecal amount g dry weight	Fecal amount per single defecation (g dry weight)	Defecation frequency over 12 h (minutes)
February	Small	21	0.0124	0.46	0.075	-	30
		28	0.0201	0.69	0.259	0.333	40
		28	0.0258	0.33	0.146	0.181	60
		29	0.0222	0.63	0.360	-	42
	Large	36	0.0325	0.58	0.233	-	51
		38	0.0821	0.52	0.327	-	55
		42	0.1250	0.56	0.526	-	40
		46	0.0703	0.38	0.492	0.588	34
August	Small	21	0.0140	0.48	0.082	0.131	42
		23	0.0162	0.44	0.123	0.179	55
		24	0.0235	0.60	0.331	0.234	34
	Large	38	0.0453	0.67	0.437	0.363	55
		40	0.0564	0.67	0.438	0.477	45
		46	0.1347	0.63	0.685	0.614	65
		50	0.1318	0.50	0.482	0.670	144

Chapter 5 - Abundances of taxa across different intertidal zones in Papanui Inlet, southern New Zealand, sampled between summer 2007 and spring 2008.

Taxa	High intertidal zone									Mid intertidal zone										Low intertidal zone								
Oligochaeta	0	0	410	94	69	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	2	0	0	0	0	0	0	0
Nereididae	1	1	2	1	2	1	0	1	0	0	1	0	0	1	2	0	0	0	3	1	1	0	1	0	0	0	0	0
Exogone sp.	0	0	0	0	0	0	0	0	0	3	0	0	0	1	0	0	0	1	2	2	2	1	0	1	3	0	1	0
Typosyllis sp.	0	0	0	0	0	0	0	0	0	0	1	0	0	2	0	2	0	0	0	0	0	0	0	0	1	0	0	0
Aquillaspio aucklandica	0	0	0	0	0	0	0	0	0	2	1	1	0	0	0	0	0	0	0	1	5	1	2	0	4	4	1	0
Boccardia polybranchia	2	0	2	3	4	1	1	1	1	1	1	1	0	0	0	1	1	2	4	0	0	1	0	1	2	2	0	0
Scolecolepides benhami	18	21	24	8	21	19	16	15	11	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Abarenicola affinis	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Capitella sp.	0	1	124	89	86	25	7	13	4	0	0	0	3	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Macroclymenella stewartensis	0	0	0	0	0	0	0	1	0	9	7	3	2	5	1	2	0	3	10	1	10	0	1	3	3	7	3	1
Scoloplos cylindrifer	0	0	0	0	0	1	0	0	0	1	0	2	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Paraonidae	0	0	0	0	0	0	0	0	0	0	1	1	1	2	3	8	0	18	70	0	4	0	2	4	9	0	12	0
Paracalliope novizealandiae	0	0	0	0	23	17	41	0	0	2	2	8	50	37	57	7	13	0	0	2	23	25	13	31	40	23	26	8
Paracorophium excavatum	198	235	270	447	542	223	44	98	56	0	0	0	2	1	7	8	8	0	1	3	0	7	0	0	0	0	1	0
Liljeborgiidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	8	1	0	0	0	0	0	0
Parawaldeckia thomsoni	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0

Parawaldeckia karaka	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
Torridoharpinia hurleyi	0	7	0	0	0	7	0	0	0	15	9	17	1	2	2	19	4	4	2	4	28	5	9	7	3	4	8	6
Phoxocephalidae 1	0	0	0	0	0	0	0	0	0	30	13	2	0	0	0	1	1	1	0	4	3	1	5	3	12	9	1	1
Phoxocephalidae 2	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	1	0	0	1	0	0	0	0
Waitangi sp.	0	0	0	0	0	0	0	0	0	4	1	1	0	0	0	0	0	0	0	9	0	4	7	0	1	2	2	14
Cumacea	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Macrophthalmus hirtipes	1	2	0	0	0	1	1	1	1	0	1	0	1	0	0	0	0	0	0	1	3	0	0	0	0	0	0	0
Zeuxo novazealandiae	0	0	0	0	0	0	0	0	0	31	8	8	0	0	0	0	0	0	2	65	18	6	0	1	8	2	10	1
Heterosquilla tricarinata	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Harpacticoida	0	0	0	1	2	0	0	3	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0	1	0	1	0
Copepoda	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0
Ostracoda	0	0	0	0	0	0	0	0	0	2	0	6	0	1	0	0	0	4	0	0	0	1	2	5	15	1	1	0
Edwardsia neozelanica	5	0	4	1	0	1	0	1	0	1	3	0	2	0	1	1	3	2	1	0	0	1	0	0	0	0	0	5
Perrierina turneri	3	5	0	1	0	6	0	2	0	86	144	127	6	1	6	243	112	62	1	47	0	37	44	79	25	0	90	24
Arthritica bifurca	17	6	11	32	23	40	15	22	13	2	0	0	3	0	2	15	16	7	14	0	0	10	22	32	61	0	73	4
Nucula hartvigiana	2	0	0	0	0	0	0	0	0	38	63	38	1	22	0	51	18	95	14	9	72	1	18	15	38	37	80	0
Cominella glandiformis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	1	0	0	1	2	0	1	0	1	1
Nemertea	0	0	2	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	1	1	0	0	0

Chapter 5 - Abundances of taxa across different experimental treatments in Papanui Inlet, southern New Zealand, sampled in autumn (1-month) and spring (8-month) 2008.

Taxa	1-month sampling																	
	Exclusion						Control						Ambient					
	1	2	3	4	5	6	1	2	3	4	5	6	1	2	3	4	5	6
Oligochaeta	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0
Microphthalmus sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Aglaophamus macroura	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Nereididae	4	2	2	2	1	0	3	1	1	1	0	0	1	1	1	0	0	0
Typosyllis sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Aquillaspio aucklandica	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Boccardia polybranchia	2	0	2	0	0	2	8	3	0	0	1	0	2	2	0	0	0	2
Scolecolepides benhami	9	15	14	14	19	6	13	12	12	11	11	9	17	20	14	11	14	17
Abarenicola affinis	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Capitella sp.	18	18	21	8	2	1	11	17	2	4	7	0	5	20	6	3	4	0

Macroclymenella stewartensis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Scoloplos cylindrifer	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Paracalliope novizealandiae	65	11	23	58	0	5	30	12	46	89	9	15	31	18	4	4	0	8
Paracorophium excavatum	417	351	69	52	7	23	460	253	25	12	5	8	387	438	7	12	4	2
Torridoharpinia hurleyi	3	4	4	9	20	12	1	4	10	8	9	17	3	1	14	12	11	20
Phoxocephalidae 1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Phoxocephalidae 2	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0
Macrophthalmus hirtipes	0	0	0	1	0	0	0	0	0	2	1	1	0	0	0	2	0	1
Mysidae	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Harpacticoida	9	28	0	1	0	0	3	11	1	0	0	0	64	2	0	0	0	0
Ostracoda	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0
Pleuronectiformes	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Edwardsia neozelanica	0	0	0	2	1	0	2	0	0	0	3	0	3	4	1	0	1	0
Perrierina turneri	0	0	2	0	2	0	0	2	13	0	0	2	0	1	3	2	1	1
Arthritica bifurca	8	19	22	21	15	6	19	22	30	37	26	21	26	24	13	30	17	15
Cominella glandiformis	0	0	0	0	0	0	0	0	0	0	0	1	0	1	1	0	0	0
Nemertea	2	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
									8-month sampling									
Oligochaeta	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Microphthalmus sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Aglaophamus macroura	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Nereididae	0	2	3	0	0	0	1	0	3	0	1	0	0	0	2	0	5	1
Typosyllis sp.	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Aquillaspio aucklandica	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Boccardia polybranchia	4	5	0	0	1	1	3	4	1	0	1	1	1	3	0	1	7	4
Scolecolepides benhami	22	14	12	9	12	4	19	7	7	4	15	4	26	24	13	7	13	14
Abarenicola affinis	0	0	0	0	1	1	0	0	0	1	0	0	0	0	0	0	0	7
Capitella sp.	18	19	11	5	4	4	9	6	3	4	6	1	6	13	9	5	2	2
Macroclymenella stewartensis	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Scoloplos cylindrifer	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Paracalliope novizealandiae	9	1	0	0	0	2	1	21	1	0	0	5	3	3	0	0	0	2
Paracorophium excavatum	202	192	154	144	187	188	266	186	386	125	238	131	208	262	326	220	250	227
Torridoharpinia hurleyi	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	1
Phoxocephalidae 1	0	0	0	0	0	0	0	0	1	1	0	1	0	0	0	0	2	0
Phoxocephalidae 2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Macrophthalmus hirtipes	0	0	1	1	0	1	0	1	0	1	0	2	1	0	0	0	1	0
Mysidae	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Harpacticoida	3	1	0	0	0	0	6	0	1	0	0	0	2	2	0	0	0	0
Ostracoda	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Pleuronectiformes	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Edwardsia neozelanica	2	1	0	0	0	0	5	0	0	0	0	0	5	3	1	0	1	5
Perrierina turneri	0	0	0	0	0	0	0	0	1	0	0	0	1	0	1	1	0	0
Arthritica bifurca	18	21	27	25	31	42	21	27	40	34	27	33	14	24	31	18	23	16
Cominella glandiformis	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	1
Nemertea	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Chapter 6 - Body measurements, burrowing and sediment turnover parameters of *Abarenicola affinis* individuals of different size groups in vegetated and unvegetated treatments in laboratory experiments conducted in October 2009.

Treatment	Size group	Thorax length (mm)	AFDW g	Burrow depth (cm)	Re-burrowing time (seconds)	Burrow movement (active 6-h intervals in 84 h)	Distance of burrow movement in 84 h (cm)	Defecation activity (active 6-h intervals in 84 h)	Defecation rate (active h / 12 h)	Fecal amount (g dry weight)
Vegetated	Small	25	0.0497	30	693	3	7.3	13	0.58	0.184
		18	0.0197	20	602	3	4.8	13	0.83	0.195
		22	0.0149	20	305	2	2.7	11	0.58	0.071
		21	0.0279	30	149	2	4.6	6	0.17	0.044
		17	0.0099	20	198	1	0.9	11	0.42	0.086
		20	0.0257	20	791	1	2.6	12	0.83	0.184
		18	0.0136	10	354	3	6.2	12	0.25	0.065
		20	0.0193	20	300	5	12.8	10	0.50	0.107
	Large	41	0.1647	30	1738	1	12.5	14	0.42	0.273
		44	0.1612	30	999	2	12.1	11	0.50	0.527
		32	0.0581	30	1622	1	3.7	10	0.00	0.000
		39	0.1199	20	393	0	0.0	1	0.00	0.000
		51	0.2488	30	1488	1	2.8	7	0.50	0.466
		41	0.1342	30	1771	4	27.7	13	0.58	0.442
		46	0.2264	30	1023	3	17.4	8	0.50	0.293
		33	0.0680	30	1109	2	18.9	12	0.58	0.516
Un-vegetated	Small	20	0.0182	30	217	0	0.0	13	0.42	0.080
		24	0.0387	30	190	2	6.0	13	1.00	0.445
		23	0.0333	30	314	3	4.5	14	0.75	0.446
		20	0.0218	20	293	1	2.0	14	0.75	0.300
		17	0.0112	20	143	2	4.4	13	0.42	0.090
		24	0.0331	30	80	5	8.7	11	0.58	0.174
		19	0.0187	20	113	0	0.0	10	0.58	0.163
		23	0.0232	30	214	0	0.0	10	0.67	0.212
	Large	46	0.2459	30	776	2	16.4	12	0.42	0.487
		32	0.0850	30	421	1	2.6	12	0.50	0.237
		42	0.1393	30	520	2	9.7	14	0.42	0.351
		38	0.1059	30	329	1	1.2	9	0.08	0.040
		40	0.1712	30	437	0	0.0	1	0.00	0.000
		47	0.2459	30	734	3	14.0	12	0.58	0.729
		32	0.0644	30	688	0	0.0	11	0.67	0.443
		40	0.1537	30	436	1	1.1	8	0.00	0.000

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