



The role of waves in the colonisation of terrestrial sediments deposited in the marine environment

J.E. Hewitt^{a,*}, V.J. Cummings^a, J.I. Ellis^a, G. Funnell^a,
A. Norkko^a, T.S. Talley^b, S.F. Thrush^a

^a*NIWA, P.O. Box 11-115, Hamilton, New Zealand*

^b*Department of Environmental Science and Policy, University of California, One Shields Ave,
Davis, CA 95616, USA*

Received 3 July 2002; received in revised form 23 January 2003; accepted 30 January 2003

Abstract

Elevated rates of sediment run-off, as a result of changes in land-use and climate, are a significant threat to marine coastal communities, with a potential to cause broad-scale, long-term alteration of habitats. Individual sedimentation events can smother estuarine flats with terrigenous sediments, creating a significant disturbance to local benthic communities. Variations in the degree to which a habitat is altered, the rate at which mixing occurs, and species-specific dispersal and responses to the altered habitat, suggest that colonisation of terrestrial sediment depositions will vary with location, both between and within estuaries. This study was designed to explore the effect that variations in wave-induced hydrodynamics would have on long-term colonisation of terrestrial sediment depositions on intertidal flats. Sites for the experimental deposition of terrestrial sediment were located along a gradient in wave exposure, with only limited variation in immersion times (30 min) and ambient sediment particle sizes (predominantly fine sand). Over 20 months, periodic measurements were made of factors predicted to affect colonisation: the sediment characteristics of the deposited sediment; local-scale wave climate; bioturbation of the deposited sediment; and local populations of benthic invertebrates. Neither opportunistic use of the new resource, progressive recovery or facilitation by colonising macrofauna was observed. Little vertical mixing of the deposited and existing sediment by either waves or bioturbators occurred; instead bedload transport was the dominant process. Local differences in hydrodynamic conditions and macrobenthic communities resulted in site-specific colonisation of the experimental plots. The strength and duration of the macrofaunal response to deposited sediment observed in this study suggest that chronic small-scale (*m*'s) patchy

* Corresponding author. Tel.: +64-7-8567026; fax: +64-7-85670151.

E-mail address: j.hewitt@niwa.cri.nz (J.E. Hewitt).

deposition of terrestrial sediment in the intertidal marine environment has a strong potential to alter both habitats and communities.

© 2003 Elsevier Science B.V. All rights reserved.

Keywords: Bioturbation; Macrobenthic recovery dynamics; Sedimentation; Terrestrial impacts; Wind waves; Bedload transport

1. Introduction

Disturbance events contribute to species distribution patterns by removing established individuals and allowing colonisation of new individuals. Mechanisms controlling colonisation are often unclear but important, given the potential for increased habitat isolation and widespread disturbance of estuarine and coastal environments. Sediment run-off from land has recently been recognised as a significant threat to marine coastal communities (GESAMP, 1994; Gray, 1997), as changes in land-use and modification of coastlines have increased rates of sedimentation and changed the areal extent of depositional environments in estuaries (Edgar and Barrett, 2000). Catastrophic sedimentation events, depositing cm thick layers of fine terrigenous sediments in short time periods, can lead to mass mortality of benthic fauna (McKnight, 1969; Peterson, 1985; Norkko et al., 2002). Although, in the short-term, mortality is the most dramatic effect, perhaps more important is the potential for broad-scale, longer-term alteration of habitats (Huston and De Angelis, 1994; Ellis et al., 2000) and subsequent community changes. The potential for habitat alteration to occur will depend on characteristics of the deposited material, how this changes over time and macrobenthic colonisation processes. As gradients in physical and biological processes often occur in estuaries, the mechanisms driving colonisation may also vary (Thrush et al., 2000).

Terrestrial sediment depositions can result in altered habitats by changing sediment food quality (Cummings et al., *in press*) and sediment grain size; with the latter affecting sediment porosity and stability and biogeochemical fluxes (Rhoads and Young, 1970). The more the sediment particle size of the deposited sediment differs from that of the existing sediment, the greater the potential that the depositions will be unsuitable for colonisation by macrofauna from the surrounding sediment (Maurer et al., 1986). In this case, the spatial and temporal scale of both vertical and horizontal mixing of the deposited sediment with existing sediment may be critical for colonisation (Zajac et al., 1998; Norkko et al., 2002).

Large-scale horizontal mixing of sediments on intertidal sandflats by physical factors is most frequently driven by locally generated wind waves (Bell et al., 1997), making the relative importance of biological vs. physical mixing dependent on wave exposure. Important factors affecting this relationship include the length of time the intertidal flat is exposed to wave-induced turbulence, the amount of energy expended by the waves on the sediment, and the frequency with which wave-induced mixing occurs. The amount of mixing and erosion of sediment driven by waves will vary with both large- and small-

spatial changes in hydrodynamics. Similarly, bioturbation can also have significant effects at a variety of spatial scales (e.g., Thayer, 1993; Bertness and Leonard, 1997; Thrush and Whitlatch, 2001), with the amount of sediment mixing being dependent on density and activity of the resident burrowers (Cadee, 1979; Thayer, 1993). While bioturbation predominantly mixes particles through the sediment column, high turnover rates mediated by currents can result in significant horizontal transport (Rhoads and Young, 1970). Bioturbation can also influence microtopography; burrows and mounds often last longer than surface-sediment ripples, and can have both direct and indirect effects on other macrofauna (e.g., Thrush, 1986; Wolfrath, 1992; Tamaki and Ingle, 1993).

The colonisation of deposited sediment will occur via both active and passive migration from surrounding undisturbed areas, either as larval settlement, or post-settlement dispersal of adults and juveniles (e.g., Beukema and de Vlas, 1989; Emerson and Grant, 1991; Armonies, 1992). Hydrodynamic conditions often mediate the relative importance of active or passive movement (Commito et al., 1995). However, the scale at which hydrodynamic variability most affects colonisation is likely to be larger for larval migration than for post-settlement dispersal (e.g., broad-scale flow vs. smaller-scale bedload transport patterns). While net movement is likely to correlate with hydrodynamic regime and bedload transport, especially for passive movement (Miller and Sternberg, 1988; Emerson and Grant, 1991), significant movement of adult and juvenile fauna can occur under very low-energy wave conditions, dependent on dispersal mechanisms (Commito et al., 1995; Norkko et al., 2001). Different modes of living within the sediment will also affect the potential to be moved by waves (e.g., subsurface vs. surface dwellers (Tamaki, 1987)). Thus, a combination of factors results in species-dependent differences in colonisation.

Variations in the degree to which a habitat is altered, the rate at which sediment mixing occurs, and species-specific dispersal and responses to the altered habitat suggest that the colonisation of terrestrial sediment depositions will vary with location, both between and within estuaries. At two sites within Okura estuary in New Zealand, different processes drove the recovery of macrofaunal communities, over a 9-month period, from experimental addition of terrigenous clay (Norkko et al., 2002). Episodic wind-wave disturbance removed the terrigenous layers at one site, facilitating rapid recovery. At a more sheltered site, sediment transport and bioturbation by crabs were important in modifying the deposited sediment and allowing recovery. This study follows the Norkko et al. (2002) study and was designed to explore the effect that variations in wave-induced hydrodynamics would have on long-term colonisation of terrestrial sediment depositions. Sites for the experimental deposition of terrestrial sediment were located along a gradient in wave exposure, with only limited variation in immersion times and ambient sediment particle sizes. Over 20 months, periodic measurements were made of factors predicted to affect colonisation: the sediment characteristics of the deposited sediment; local-scale wave climate; bioturbation of the deposited sediment; and local populations of benthic invertebrates. This information allowed assessment of the relative importance to macrobenthic invertebrate colonisation of a number of naturally covarying factors (waves, bioturbation, local population densities and sediment characteristics).

2. Methods

2.1. Experimental design

Whangapoua Harbour (Fig. 1) is a medium-sized New Zealand harbour (13 km²), connecting to the Pacific Ocean and exposed to wind and wave action from the northeast. The harbour has three arms, each with a small freshwater input, and extensive intertidal sandflats dissected by numerous subtidal drainage channels. Tides are semi-diurnal with an average range of 3 m. Previous work in this harbour revealed strong differences in wave activity both in different arms of the harbour, and over relatively small distances within an arm (Thrush et al., 2000).

Due to the scale of the deposition and the need to simultaneously measure hydrodynamics at all sites, only three locations were selected for experimentation, all within the western arm (Fig. 1). The sites were situated just below mid-tide on a large intertidal sandflat, and were separated by small drainage channels (Fig. 1).

Terrigenous sediment for this experiment was taken from the hills above the harbour and mixed in a commercial concrete mixing truck, with 70% by volume saltwater from the harbour. At each of the three sites, a single 5-m-diameter aluminium ring was pushed into the sediment surface and filled with the sediment slurry (~ depth 4 cm) by helicopter. The ring was left in place over one tidal cycle and then removed, allowing the sediment slurry edges to run, forming a slight ramp to the sandflat surface. In this experiment, a large plot size was used to limit active migration by adults and to increase the horizontal transport

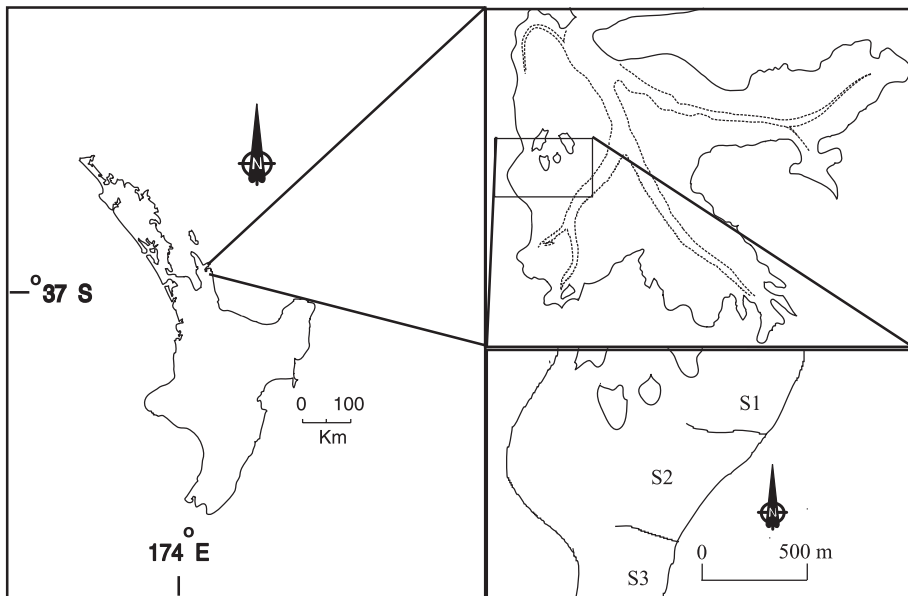


Fig. 1. The location of the three experimental sites (S1–S3) in Whangapoua Harbour, North Island, New Zealand.

needed to cover the plot, thus more closely mimicking the potential effect of sediment deposition over a large area. The experiment was set up over 2 fine days in summer (3rd–4th February, 1999); no rain fell; skies were 50–80% clear and maximum temperatures were 23 °C.

2.2. Sample collection

An initial sampling, 1 week after deposition, confirmed that no live macrofauna were left in the plots. Sampling was then carried out after 10, 12, 14, 16 and 20 months. On each of these sampling occasions, two samples were taken between 50 and 100 cm from the edge of the plot from diametrically opposite positions, with corresponding samples taken 1 m from the edge of the plot in the ambient sediment. The position for sampling was rotated clockwise by 30° each time. Overall sampling occasions, less than 1% of each plot was sampled.

Macrofauna were sampled to a depth of 15 cm, using a 10-cm-diameter corer. Cores were sectioned into two parts, the deposited terrestrial sediment and the natural marine sediment for the cores taken from the deposited sediment plots, and above and below 2 cm deep for cores taken from the surrounding sediment. After sieving (500- μ m mesh sieve), macrofauna were preserved in 70% Isopropyl alcohol and stained with 0.2% Rose Bengal.

Photos were taken of the sediment surface (0.25-m² quadrates), and the depth of the deposited sediment and any sand layer present on the surface as a result of bedload transport were measured. At one of the sampling positions (both inside the plot and outside in the ambient sediment), measurements were made of sediment firmness using a penetrometer with a 25-mm-diameter foot. From the same position, sediment shear strength was also measured using a shear vane with a 48-mm-diameter foot. Five measurements of each were made and an average value produced.

Sediment samples were also taken from the top 2 cm of sediment at each position, using a 2-cm corer, for chemical and particle size analysis. These samples were kept dark and cool until they could be frozen for later analysis.

Throughout the duration of the experiment, time series of data on hydrostatic pressure at the bed were made using a DOBIE wave gauge (see [Thrush et al., 2000](#), for a detailed description). Pressure was measured every 30 min in bursts, with each burst containing 2048 sampling points separated by 0.2 s.

2.3. Sample processing

Macrofauna were sorted, identified to the lowest practical level of taxonomic resolution and counted. For each core and core section, numbers of rare taxa (i.e., taxa with fewer than an average of one individual per core), total numbers of taxa and individuals, and the Shannon–Weiner diversity index were calculated. Numbers of burrows and holes present in the photo quadrats were counted to give an index of the level of bioturbation.

Samples taken for sediment particle size were digested in 9% hydrogen peroxide to remove organics. Wet sieving separated the sample into gravel (>2 mm, in this case, shell hash), coarse sand (500 μ m–2 mm), medium sand (250–500 μ m), fine sand (63–250 μ m)

and mud (<63 μm). Pipette analysis was then used to separate the mud fraction into silt (>3.9 μm) and clay (<3.9 μm). All fractions were dried at 60 °C, and percent volumes calculated. Organic content was measured as percentage loss on ignition after 5.5 h at 400 °C, after drying at 60 °C. Samples taken for chlorophyll *a* were freeze-dried and analysed within the month. Chlorophyll *a* was extracted by boiling freeze-dried sediment in 95% ethanol, and the extract processed using a spectrophotometer. An acidification step was used to separate degradation products from chlorophyll *a* (Sartory, 1982). Chlorophyll *a* concentrations per gram sediment dry weight were then calculated.

The time series pressure data were converted into estimates of wave orbital velocity at the bed (U_b) using significant wave height, H_{sig} , (average height of the highest 33.3% of the waves in a burst), wave period, \bar{T} , (estimated using the Longuet-Higgins (1975) definition and linear wave theory). Average immersion times were calculated for each site. Finally, statistics on the wave data were calculated for each period between sampling dates. Wave data used in the study are: the % time that waves were present at each site while the site was immersed (hereafter waves); maximum and mean U_b^3 (hereafter energy), and the % time that U_b exceeded the theoretical critical threshold for lifting a grain of sand sized 250 μm (the median grain size at the sites) while the site was immersed (hereafter sand transport).

2.4. Statistical analyses

Initially, means and ranges for each physical and chemical variable in the ambient sediment at each site were calculated. Differences between the sites were analysed using a

Table 1
Maximum, mean and minimum ambient conditions found over time at the sites

	Site contrast	Site 1	Site 2	Site 3
Immersion (%)	1>2 3	50.7, 48.9, 47.2	51, 45.5, 42.8	47.5, 44.5, 43.5
Waves (%)	1 2>3	69.6, 28.6, 7.5	41.8, 20.2, 7.4	30.3, 10.4, 3.8
Max energy (cm s^{-1})	1>2>3	6.0, 2.5, 0.3	4.0, 1.5, 0.6	1.0, 0.6, 0.3
Mean energy (cm s^{-1})		0.60, 0.19, 0.30	0.20, 0.10, 0.01	0.80, 0.04, 0.02
Sand transport (%)		88.3, 40.5, 17.5	62.5, 33.6, 6.4	22.7, 19.4, 14.6
Shell (%)	2>1>3	1.7, 1.0, 0.3	5.7, 2.6, 0.6	0.4, 0.1, 0.0
Coarse sand (%)		6.2, 5.1, 4.0	13.0, 7.6, 4.9	6.3, 5.9, 4.9
Medium sand (%)		52.0, 31.8, 23.2	37.4, 33.9, 29.0	36.5, 31.4, 27.6
Fine sand (%)	1 3>2	71.9, 61.2, 41.7	58.8, 54.4, 49.3	66.5, 61.7, 56.9
Silt (%)		0.7, 0.6, 0.5	1.3, 0.9, 0.5	1.0, 0.7, 0.5
Clay (%)		0.6, 0.2, 0.1	1.0, 0.3, 0.0	0.8, 0.3, 0.1
Firmness (kg cm^{-2})	3 2 2 1	3.9, 2.1, 1.2	4.5, 2.7, 1.4	5.0, 3.4, 1.6
Shear strength (kg cm^{-2})	3>2>1	1.5, 1.5, 0.6	1.9, 1.4, 1.1	2.4, 1.8, 1.4
Chlorophyll <i>a</i> ($\mu\text{g g}^{-1}$)	3 2 2 1	6.9, 5.4, 3.2	8.2, 5.3, 2.0	7.3, 6.3, 4.3
Organics (%)	3>2 1	0.90, 0.60, 0.50	0.85, 0.67, 0.52	0.90, 0.81, 0.60
No. of burrows (0.25 m^2)		2, 1, 0	2, 1, 0	2, 1, 1

Sites that were not significantly different from each other are connected by lines (see Appendix A for full statistical information). Waves=% time waves were present while the site was immersed. Max and mean energy = maximum and mean U_b^3 . Sand transport=% time exceeded the theoretical critical threshold for lifting a grain of sand sized 250 μm while the site was immersed.

Friedman's test. When a difference was observed ($p < 0.05$), a Tukey's rank sum test was used to determine which sites were different. Macrofaunal community composition in the ambient sediment at the three sites was assessed by nonmetric multidimensional scaling ordination on Bray Curtis similarities of untransformed data (Clarke, 1993) and correspondence analysis (CANOCO; ter Braak and Smilauer, 1998). The five most common taxa at each site on each time were determined, along with the other univariate macrofaunal variables (rare taxa, total numbers of taxa and individuals, and the Shannon–Weiner diversity index).

Differences between ambient and deposited sediment, in sediment characteristics and univariate macrofaunal variables, were then assessed using generalized linear models (GzLM) with site and location as fixed factors and time as a random variable. Differences between location (A=ambient vs. D=deposited sediment) were assessed using contrast statements. Overall differences in sediment characteristics between the deposited and marine sediment were investigated using redundancy analysis (CANOCO). The effect of the deposited sediment on macrofaunal community composition was assessed using canonical correspondence analysis (CCA; CANOCO, ter Braak, 1986, 1987).

The duration of the experiment, the variability in wave climate we measured at each site, and the lack of temporal autocorrelation in colonisation allowed us to assess the role

Table 2

The five most dominant taxa found in the ambient sediment at each site on each sampling occasion

Time	Site 1	Site 2	Site 3
10 Months	<i>Aquilaspio</i> (28.5 ± 0.5)	<i>Aquilaspio</i> (25.5 ± 5.5)	<i>Austrovenus</i> (4.5 ± 0.5)
	<i>Lumbrineris</i> (7 ± 3)	Lysianassidae (12 ± 1)	Lysianassidae (4 ± 3)
	<i>Colurostylis</i> (5 ± 5)	<i>Nucula</i> (6.5 ± 4.5)	<i>Nucula</i> (4 ± 2)
	Oligochaete (3 ± 3)	Phoxocephalidae (5.5 ± 2.5)	<i>Exosphaeroma</i> (3 ± 0)
	<i>Nucula</i> (2.5 ± 1.5)	<i>Lumbrineris</i> (4.5 ± 2.5)	Nereidae (2.5 ± 0.5)
12 Months	<i>Aquilaspio</i> (12.5 ± 2.5)	<i>Aquilaspio</i> (17 ± 4)	<i>Austrovenus</i> (5 ± 1)
	Lysianassidae (5 ± 1)	Lysianassidae (16 ± 2)	<i>Scoloplos</i> (5 ± 1)
	<i>Scoloplos</i> (3 ± 3)	<i>Aonides</i> (5 ± 1)	<i>Lumbrineris</i> (4 ± 1)
	<i>Lumbrineris</i> (2.5 ± 0.5)	<i>Scoloplos</i> (3 ± 3)	Lysianassidae (3.51.5)
	Nereidae (2.5 ± 0.5)	<i>Lumbrineris</i> (2.5 ± 1.5)	<i>Exosphaeroma</i> (2 ± 0)
14 Months	<i>Aquilaspio</i> (19 ± 7)	<i>Aquilaspio</i> (40 ± 12)	<i>Lumbrineris</i> (6 ± 0)
	Oligochaete (9.5 ± 7.5)	<i>Lumbrineris</i> (8 ± 3)	<i>Austrovenus</i> (5 ± 1)
	<i>Lumbrineris</i> (6 ± 4)	<i>Nucula</i> (4.5 ± 4.5)	<i>Nucula</i> (5 ± 5)
	<i>Nucula</i> (3.5 ± 1.5)	Lysianassidae (3.5 ± 1.5)	<i>Scoloplos</i> (3.5 ± 0.5)
16 Months	<i>Aquilaspio</i> (18 ± 9)	<i>Aquilaspio</i> (43 ± 8)	Nereidae (8.5 ± 3.5)
	Nereidae (16 ± 6)	Oligochaete (8.5 ± 6.5)	<i>Nucula</i> (6 ± 4)
	Oligochaete (10.5 ± 6.5)	<i>Lumbrineris</i> (6.5 ± 0.5)	<i>Scoloplos</i> (5 ± 1)
	Lysianassidae (5 ± 2)	Nereidae (5.5 ± 1.5)	<i>Lumbrineris</i> (4 ± 2)
	<i>Colurostylis</i> (4 ± 1)		<i>Capitella</i> (3.5 ± 2.5)
20 Months	<i>Aquilaspio</i> (15 ± 2)	<i>Aquilaspio</i> (13.5 ± 5.5)	<i>Nucula</i> (17 ± 5)
	<i>Nucula</i> (10 ± 2)	<i>Capitella</i> (10 ± 8)	<i>Lumbrineris</i> (7 ± 3)
	Phoxocephalidae (6.5 ± 0.5)	<i>Nucula</i> (9.5 ± 0.5)	<i>Austrovenus</i> (5 ± 1)
	<i>Capitella</i> (5.5 ± 3.5)	<i>Lumbrineris</i> (6 ± 1)	<i>Colurostylis</i> (4.5 ± 3.5)
	Oligochaete (5 ± 1)	Nereidae (6 ± 2)	Nereidae (4 ± 1)

Values in brackets are mean number per core ± S.E.

of hydrodynamics in affecting changes in sediment characteristics and macrobenthic colonisation of the deposited sediment in the plots. This was done in two steps.

- (1) The relationships between sediment characteristics in the plots and wave data were investigated using univariate generalized linear modelling (GzLM; McCullagh and Nelder, 1989) and multivariate redundancy analysis. A reduced set of sediment characteristics was used for this analysis: chlorophyll *a*; % mud (= % silt + % clay); % large particles (= % coarse + % shell hash); % organic content; sediment firmness; and sediment shear strength. Backwards elimination and an exit value of $\alpha = 0.15$ was used for the univariate analyses. Unfortunately, backward elimination is not yet available in the programme CANOCO, so for the multivariate analysis, redundancy analysis with forward selection was used, with the overall model tested for significance. The model was also checked for dependence on the initial choice of variable by using different starting variables. Colinearity diagnostics were examined (see Belsley et al., 1980) for all GzLM analyses, but no problems were observed with the reduced datasets.
- (2) The relationships between macrofauna in the deposited sediment and sediment characteristics, bioturbation and hydrodynamics were investigated using univariate GzLM's (on those taxa with sufficient abundances (>3 individuals per core on most occasions) at all sites) and CCA. The potential for local populations to affect colonisation was investigated by including ambient abundances as an explanatory

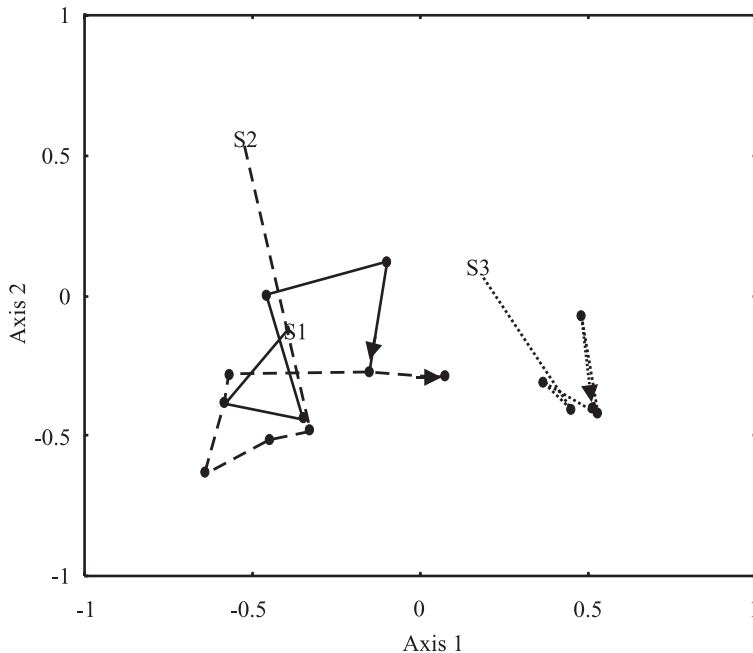


Fig. 2. Changes in communities found at the three sites over time using correspondence analysis. Only two axes are displayed as the amount explained by the 3rd ordination axis was less than half that of the 2nd axis. S1–S3 represents the 1st sampling date of each site, while the arrow represents the last sampling time.

variable. In order to achieve the same thing multivariately, a correspondence analysis was run. Sample scores along the first two axes (only 2 were used as the percent explained by the third was considerably less than that explained by the second) were then used as indicators of ambient community in a CCA. The CCA linked communities found in the deposited sediment with sediment characteristics, bioturbation, hydrodynamics and ambient communities.

3. Results

3.1. Site descriptions

The sites show slight but significant differences in immersion time (Table 1), with site 1 emerging from the water on average 37 min later than site 3. There was a clear gradient in wind-wave disturbance between the sites, with ripples on the sediment surface more common at site 1. Generally, site 2 was more similar to site 1 than site 3 in time immersed, amount of time waves was observed and the maximum amount of energy expended on the

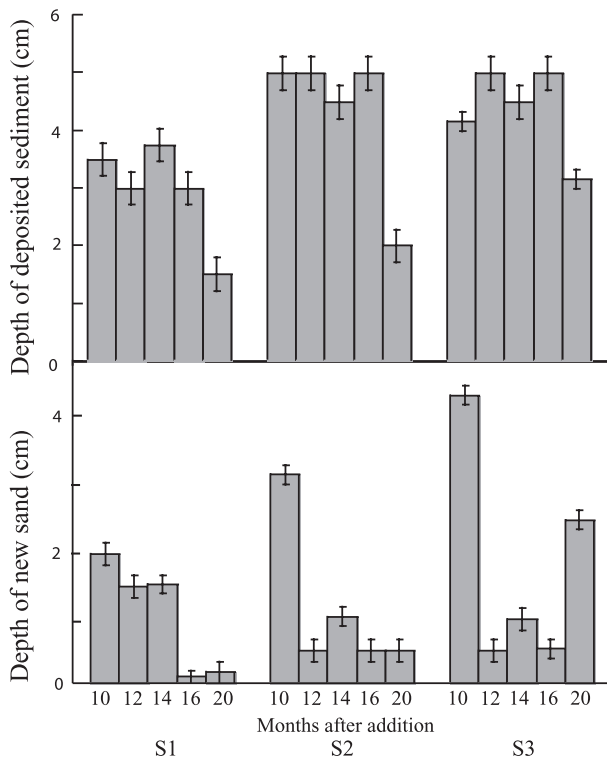


Fig. 3. Means \pm standard errors of depth of deposited sediment and depth of new sand at the three sites over time (as months after addition). Friedman's tests ($df=2$) on the differences, between sites, in both depth of deposited sediment and new sand had p -values of 0.0536 and 0.8224, respectively.

bed by waves (Table 1). Although significant differences in hydrodynamic conditions were observed between sites, these were not consistent over time; e.g., the mean energy expended on the bed was not highest at each site at the same time.

Sediments at all three sites were composed predominantly (50–60%) of fine sand with very little silt (~ 1%) or clay (<1%). Site 2 was most different, having higher levels of shell and less fine sand (Table 1). Conversely, mean sediment firmness, shear strength, chlorophyll *a* and organic content suggest a gradient from site 3 (highest) through to site 1. The amount of bioturbation (as measured by crab burrows) in the ambient sediment was low at all sites and not significantly different between sites.

Differences between sites in the composition of the ambient macrobenthic communities were also observed (Table 2). Although temporal changes were observed, sites 1 and 2 were always more similar to each other than to site 3 (Fig. 2). Site 1 was always dominated by the spionid polychaete, *Aquilaspio aucklandica*, with oligochaetes, the polychaete *Lumbrineris brevicirris*, and the bivalve *Nucula hartvigiana* also abundant. *Aquilaspio* also dominated at site 2, with Lysianassidae amphipods, Nereidae polychaetes and *Lumbrineris* frequently being abundant. In contrast to these two sites, site 3 had few *Aquilaspio* and instead was dominated by a number of taxa (*Nucula*, *Lumbrineris*, Nereidae and the cockle *Austrovenus stutchburyi*). Orbinid polychaetes, *Scoloplos* spp. (consisting of both *S. ohlini* and *S. cylindifer*), were frequently abundant. Strong differences were observed in the vertical distribution of species within the sediment. *Aquilaspio*, *Austrovenus*, *Nucula*, the cumacean *Colurostylis lemurum*, the polychaete *Capitella*, the isopod *Exosphaeroma* spp. (consisting of both *E. chilensis* and *E. falcatum*) and *Lumbrineris* were found only in the top 2 cm. The

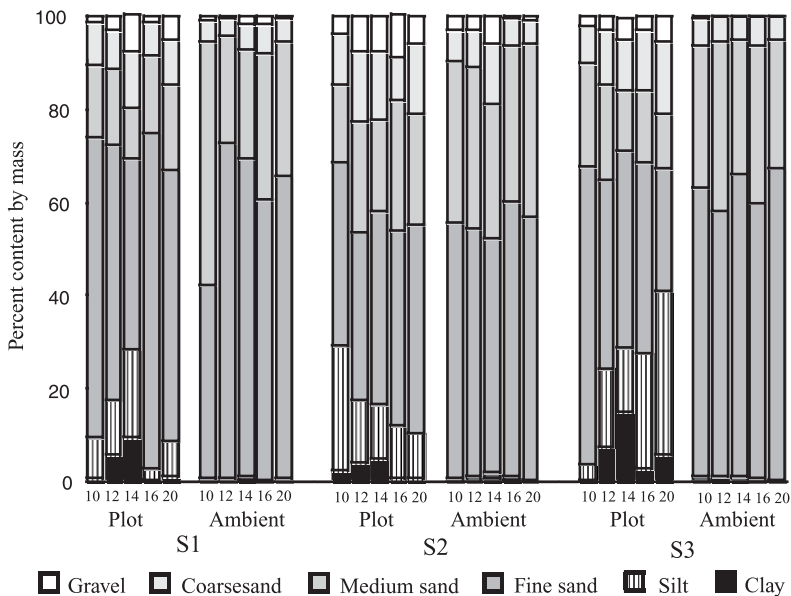


Fig. 4. Changes in particle size observed over time (as months after addition) in the plots and the surrounding sediment at the three sites.

polychaetes *Aonides oxycephala* and *Orbinia* sp. and the bivalve *Macomona liliana* were found deeper in the sediment. These strong differences meant that statistical results of analyses carried out on data from the top of the cores were similar to those carried out on data from the full core. Thus, only the full core results will be discussed.

3.2. Differences between ambient and deposited sediments

After 10 months, depth of the sediment deposited in the plots was still around 4 cm, although there were differences between the sites (Fig. 3). Site 1 (the site with the most wave action) had less deposited sediment remaining than the other sites. Although depth of the deposited sediment continued to change over the course of the sampling, this difference between the sites was maintained. The amount of new sand found on top of the deposited sediment at each site also varied with time, but more sand was generally found at site 3 (Fig. 3), presumably as at the other two sites, the sand was more likely to be scoured off. More silt and clay were consistently found in the plots than in adjacent sediments within each site (Fig. 4, Appendix B). Over time, some of the deposited sediment formed hard clumps >500 µm, resulting in higher proportions of larger particles in the plots than in the ambient sediment.

Numbers of burrows found in the deposited sediment were low (3.0 per 0.25 m²), but still significantly higher than in the ambient sediment (1.3 per 0.25 m²). A consistent, but

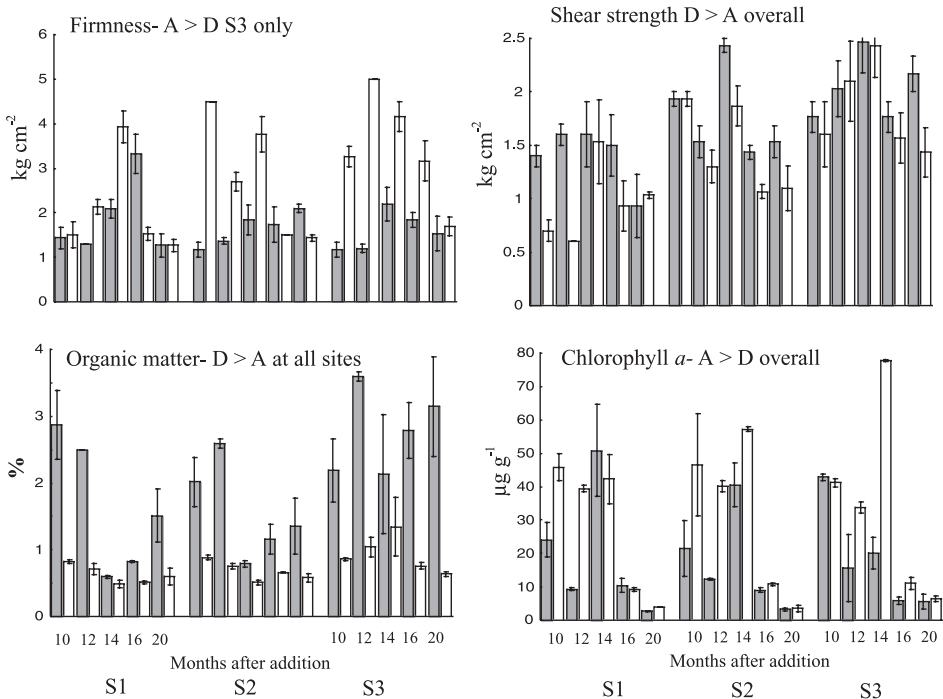


Fig. 5. Mean sediment characteristics (\pm standard errors) observed in the deposited sediment plots (D, shaded) and the ambient sediment (A, not shaded) observed over time (as months after addition) at the three sites.

Table 3

p-Values from (a) redundancy analysis on sediment characteristics and (b) canonical correspondence analysis on macrofauna using dummy variables to represent treatment, site and treatment*site interactions

	(a) Sediment characteristics	(b) Macrofauna
Treatment	0.0020	0.0020
Site	0.0040	0.0060
Treatment*Site	0.0379	0.0161

One thousand random permutations were used to calculate the *p*-values.

nonsignificant, variation between sites was observed with site 3 always having fewer burrows in the plots (means over time for sites 1, 2 and 3 were 3, 3.5 and 2.4, respectively). Although large numbers of juvenile crabs (*Helice crassa*) were observed at the sites on a few early occasions, these did not recruit to the plots or ambient sediment in any numbers.

Differences in other measured sediment characteristics were observed over the 10- to 20-month period of sampling (Fig. 5, Appendix B), however, these did not appear related

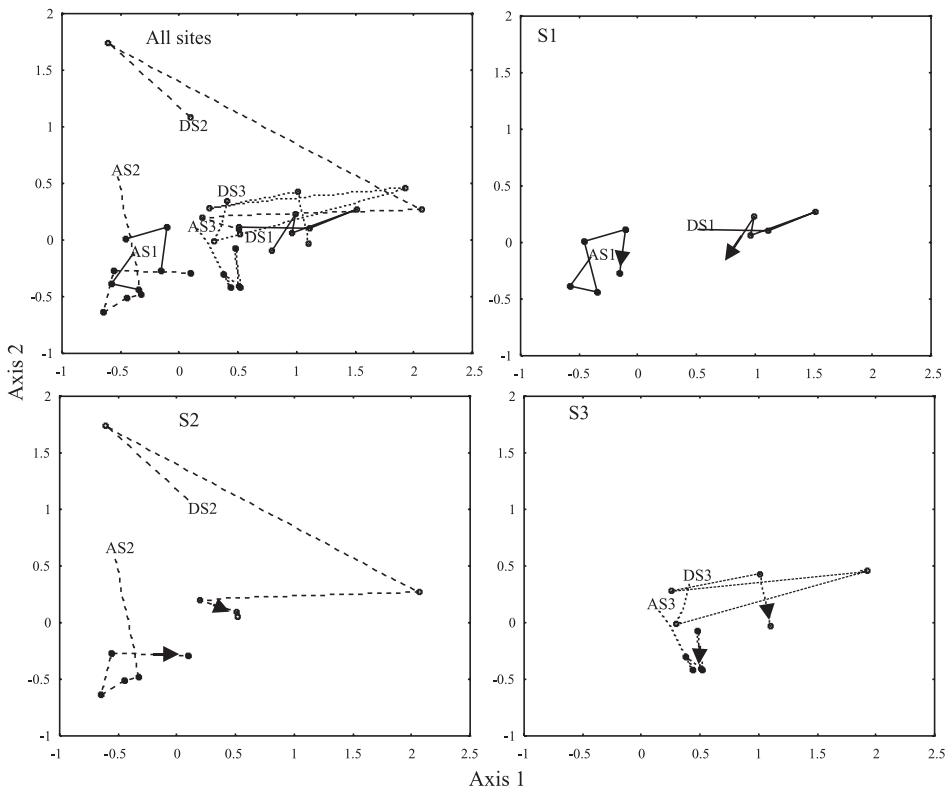


Fig. 6. Differences in communities found in the deposited sediment plots (DS1, DS2, DS3) and the surrounding sediment (AS1, AS2, AS3) at the three sites over time using correspondence analysis. Only two axes are displayed as the eigenvalue for the 3rd ordination axis was less than half that of the 2nd axis.

to time since deposition. Site differences were observed for sediment firmness; where higher values in the ambient than deposited sediment were significant at site 3 only. Higher sediment shear strength and organic content were found in the deposited sediment plots than in the ambient sediment, while chlorophyll *a* content was lower in the plots. Analysing all the sediment characteristics together, using redundancy analysis, identified significant treatment, site and site*treatment interaction terms (Table 3a).

Macrofaunal communities in the ambient sediment were less temporally variable than the communities in the deposited sediment plots (Fig. 6, Tables 2 and 4). Generally, the plot communities did not vary in a consistent way at all sites (Fig. 6), although, 14 months after sediment deposition, the plots were most dissimilar to the controls at all sites, and exhibited low macrofaunal density. Significant treatment, site and site*treatment interaction terms were observed (Table 3b). Taxa found more commonly (either in terms of abundance or frequency) in the plots than in the ambient sediment were the Cumacean *C. lemurum*, nereids (as juveniles), the crab *Macrophthalmus hirtipes*, capitellids, the isopods *Exosphaeroma* sp. and *Cirolana* sp. and corophid amphipods (Table 4).

Differences found for univariate macrofauna variables, between the deposited sediment plots and the ambient sediment, are summarised in Figs. 7 and 8 and Appendix C. Generally, significantly higher abundances were found in the ambient sediment at all sites,

Table 4

The five most dominant taxa found in the deposited terrestrial sediment at each site on each sampling occasion

Time	Site 1	Site 2	Site 3
10 Months	Nereidae (1.5 ± 0.5)	Oligochaete (47 ± 47)	<i>Macomona</i> (0.5 ± 0.5)
	<i>Austrovenus</i> (1 ± 0.2)	<i>Scoloplos</i> (6 ± 0.3)	<i>Colurostylis</i> (0.5 ± 0.5)
	<i>Macrophthalmus</i> (1 ± 0.1)	<i>Colurostylis</i> (3.5 ± 0.5)	<i>Exosphaeroma</i> (0.5 ± 0.5)
12 Months		<i>Aquilaspio</i> (3 ± 3)	<i>Aquilaspio</i> (0.5 ± 0.5)
			<i>Boccardia</i> (0.5 ± 0.5)
	<i>Orbinia</i> (2 ± 1.1)	<i>Austrovenus</i> (0.5 ± 0.5)	<i>Orbinia</i> (2 ± 0)
	<i>Lumbrineris</i> (1 ± 0.2)	<i>Macrophthalmus</i> (0.5 ± 0.5)	<i>Macrophthalmus</i> (1 ± 1)
			<i>Austrovenus</i> (0.5 ± 0.5)
14 Months			<i>Exosphaeroma</i> (0.5 ± 0.5)
			<i>Lumbrineris</i> (0.5 ± 0.5)
	<i>Nucula</i> (2.5 ± 1.5)	Nereidae (1.5 ± 0.5)	<i>Nucula</i> (0.5 ± 0.5)
	Nereidae (2.5 ± 0.5)	<i>Colurostylis</i> (0.5 ± 0.5)	
	<i>Colurostylis</i> (1.5 ± 1.5)	<i>Zeacumantus</i> (0.5 ± 0.5)	
16 Months	<i>Orbinia</i> (1.5 ± 0.5)	<i>Cirolanidae</i> (0.5 ± 0.5)	
		<i>Aquilaspio</i> (0.5 ± 0.5)	
	<i>Capitella</i> (34.5 ± 12.5)	<i>Capitella</i> (9.5 ± 8.5)	<i>Colurostylis</i> (4 ± 1)
	Nereidae (20 ± 1.1)	Nereidae (7 ± 3)	<i>Capitella</i> (3 ± 1)
	<i>Nucula</i> (7 ± 2.2)	<i>Aquilaspio</i> (4 ± 1)	<i>Orbinia</i> (3 ± 3)
20 Months	<i>Oligochaete</i> (6 ± 4.1)	<i>Scoloplos</i> (4 ± 2)	<i>Scoloplos</i> (3 ± 3)
		<i>Lysianassidae</i> (3.5 ± 2.5)	
	Nereidae (7.5 ± 3.5)	<i>Lysianassidae</i> (5 ± 1.1)	<i>Colurostylis</i> (9 ± 7)
	<i>Nucula</i> (7 ± 2)	<i>Capitella</i> (2.5 ± 0.5)	<i>Nucula</i> (6 ± 6)
	<i>Colurostylis</i> (4.5 ± 1.5)	Nereidae (2.5 ± 0.5)	<i>Exosphaeroma</i> (3.5 ± 3.5)
<i>Scoloplos</i> (3.5 ± 1.5)	<i>Scoloplos</i> (2.5 ± 2.5)	<i>Paracorophium</i> (3 ± 1)	
<i>Capitella</i> (2.5 ± 0.5)	<i>Nucula</i> (2 ± 2)	<i>Austrovenus</i> (2 ± 2)	

The mean abundance per core and standard error are given in brackets.

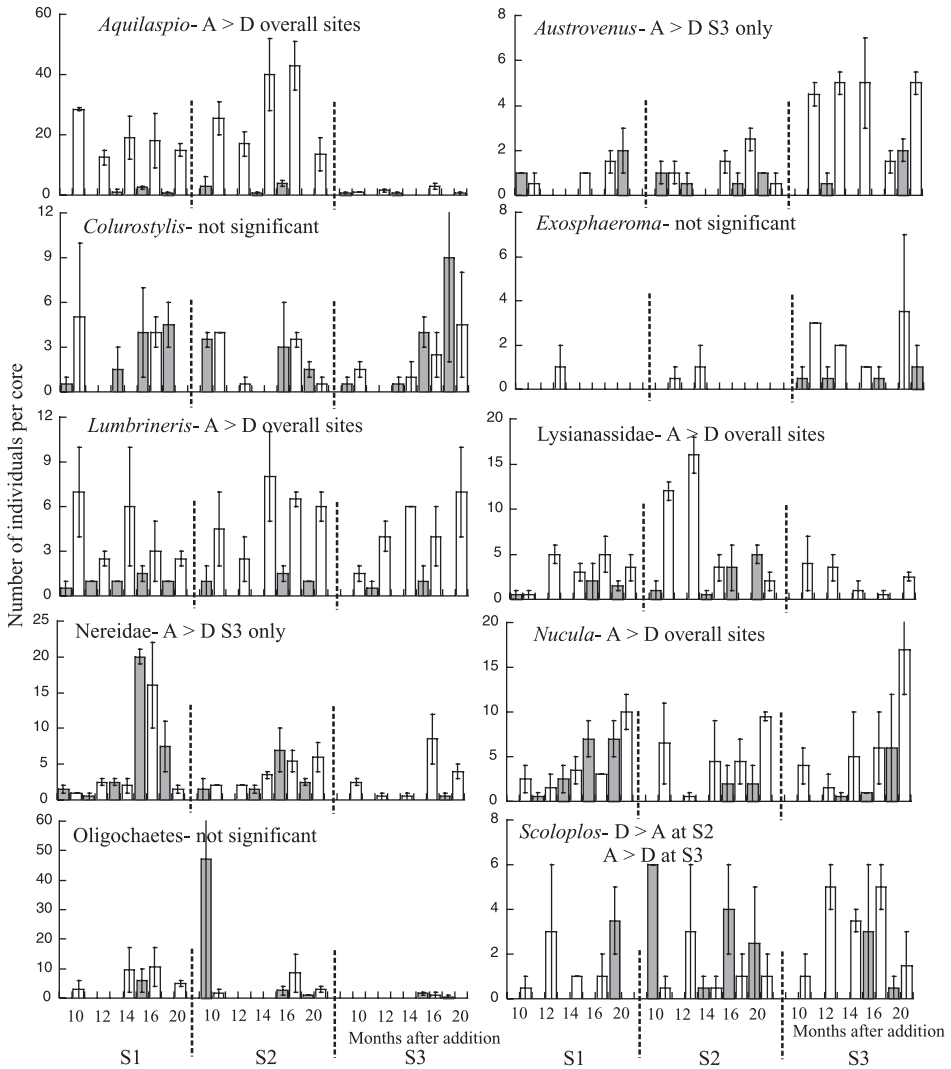


Fig. 7. Differences in abundances of taxa found in the plots (D, shaded) and the surrounding sediment (A, not shaded) at the three sites over time (as months after addition).

except for those sites where taxa had very low natural abundances (e.g., *Austrovenus* at sites 1 and 2). No significant treatment effects were found for *Colurostylis*, *Exosphaeroma* or oligochaetes and the treatment effects for *Scoloplos* were inconsistent between sites.

Both the total number of taxa and the number of rare taxa were significantly higher in the ambient sediment than in the deposited sediment plots, however, by 20 months, this effect was much diminished. The total number of individuals found in the ambient sediment was generally higher than in the plots, though this was significant only at sites 1 and 2. Surprisingly, these results were not reflected in the Shannon–Weiner diversity

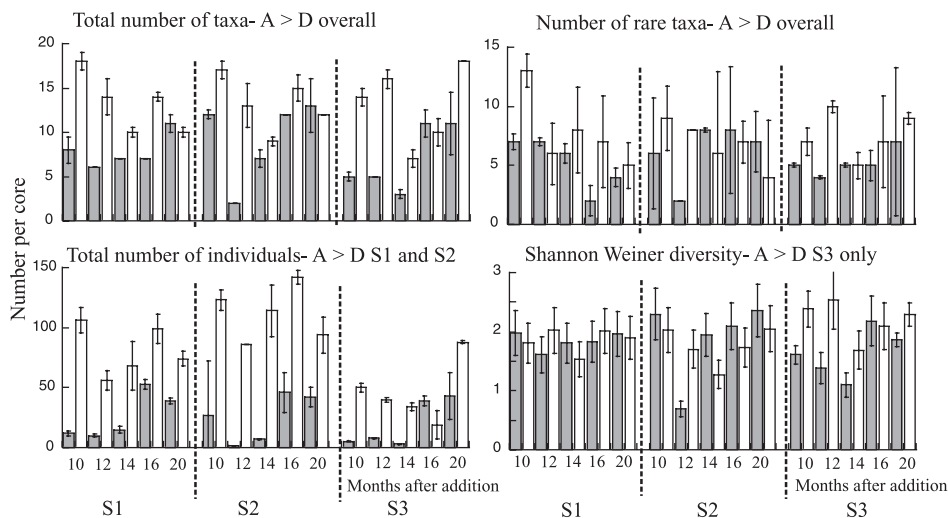


Fig. 8. Differences in abundances of different aggregate groups of taxa found in the plots (D, shaded) and the surrounding sediment (A, not shaded) at the three sites over time (as months after addition).

index, for which significantly higher diversity was only found in the ambient sediment at site 3.

3.3. The role of hydrodynamics, bioturbation and local populations in affecting colonisation

Variations in sediment characteristics found in the deposited sediment plots over time were generally well explained by wave data (>45% for all but chlorophyll *a*, see Table 5 and

Table 5
Results of multiple regression analysis on the sediment characteristics of the experimental plots using wave data as explanatory variables

	% Explained	Immersion time	Waves	Max energy	Mean energy	Sand transport
Deposited sediment depth	83	-0.31		-25.2	-991.6	-0.08
New sand depth	45	0.40			-	-
Chlorophyll <i>a</i>	<10					
% Organics	48	-0.24			+866.4	-0.06
% Mud	72	-0.33		96.5	-636.0	-0.02
% Large particles	59	-0.11		51.39	-500.8	
Firmness	49		+0.02			
Shear strength	50	-0.10				

% Explained=model sum of squares divided by total sum of squares. Direction of effect is given as + or - followed by the parameter estimate. Italicised results have *p*-values 0.05–0.1, all other *p*-values are <0.05. Waves=% time waves were present. Max and mean energy=maximum and mean U_b^3 . Sand transport=% time that U_b exceeded the theoretical critical threshold for lifting a grain of sand sized 250 μm .

Appendix D). Immersion was usually a significant explanatory variable, negatively affecting deposited sediment depth, firmness, shear strength, and amount of organics, mud and large particles while positively affecting new sand depth only. The length of time waves was over the sites, the maximum energy expended on the bed and the amount of time that sand was transported were less likely to be useful as explanatory variables, although they were all important for more than one sediment characteristic. The period when the highest maximum energy was recorded did correspond well with the time when fewest numbers of macrofauna were found at all sites (14-month sampling occasion).

Sediment characteristics, local populations, bioturbation and hydrodynamic conditions all affected the colonisation of the plots and explained high amounts of variation in most of the macrofaunal data (Table 6, Appendix E). Densities in the ambient

Table 6

Results of multiple regression and canonical correspondence analysis on macrofauna in the deposited sediment plots

	% Explained	Sediment characteristics	Ambient density	Number of burrows	Wave data
<i>Aquilaspio</i>	86.9	– % organics – large particles – firmness	+		– immersion + waves + max energy – sand transport
<i>Colurostylis</i>	81.5	+ chlorophyll <i>a</i> + mud – firmness			+ immersion + waves – max energy + mean energy
<i>Lumbrineris</i>	95.9	+ chlorophyll <i>a</i> + firmness – shear strength – large particles	+		– immersion + max energy – mean energy
<i>Nucula</i>	87.6	– chlorophyll <i>a</i> – % organics – firmness	+	–	+ waves + max energy
Nereidae	89.4	– % organics			+ waves + max energy – mean energy – sand transport
Total no. of taxa	56.8	+ chlorophyll <i>a</i>	na		+ max energy – mean energy
No. of rare taxa	76.1	+ chlorophyll <i>a</i> + shear strength	na	+	– waves + mean energy – sand transport
Total no. of individuals	59.5		na		+ waves
Community composition	96	chlorophyll <i>a</i> organics mud firmness	correspondence axis 1 correspondence axis 2		waves mean energy

Direction of effect is given as + or – for the univariate analyses and % explained = model sum of squares divided by total sum of squares. For the community composition, % explained = Σ canonical/ Σ unconstrained eigenvalues. na = not included in the model. Waves = % time waves were present. Max and mean energy = maximum and mean U_b^3 . Sand transport = % time that U_b exceeded the theoretical critical threshold for lifting a grain of sand sized 250 μ m.

Table 7

Summary of regression analysis on macrofauna found in the deposited sediment plots, showing the relative importance, as percentages of the model sum of squares, of hydrodynamic conditions, sediment characteristics, ambient densities and bioturbation

	Hydrodynamic conditions	Sediment characteristics	Ambient densities	Bioturbation (no. of crab burrows)
<i>Aquilaspio</i>	21	63	16	0
<i>Colurostylis</i>	46	64	0	0
<i>Lumbrineris</i>	43	54	3	0
<i>Nucula</i>	40	21	22	16
Nereidae	89	11	0	0
Total no. of taxa	88	12	0	0
No. of rare taxa	57	19	0	24
Total no. of individuals	100	0	0	0

sediment were important for three of the taxa (*Aquilaspio*, *Lumbrineris* and *Nucula*). Food content of the sediment, either as chlorophyll *a* or % organics, was always an important variable, except for total number of individuals. Sand transport was important for *Aquilaspio*, nereids (mainly juveniles) and the number of rare taxa found. The maximum energy expended on the bed was frequently important and usually resulted in increased densities. Occasionally, both the maximum and mean energy expended on the bed were important, although these usually operated in opposite directions. Although the number of burrows found in the deposited sediment over time showed little difference between sites, this variable was included in the analysis, it was rarely an important factor.

Finally, the relative importance of bioturbation, ambient densities of macrofauna, hydrodynamics and sediment characteristics on macrofaunal densities and community composition found within the deposited sediment plots was investigated using partial CCA and regressions. Around 15% of the variability in community composition was associated with interactions between hydrodynamic, sediment and ambient community characteristics. After these interactions were accounted for, hydrodynamic conditions, sediment characteristics and the ambient communities explained 30%, 36% and 15% of the variability in community composition, respectively. For specific taxa, the relative importance of ambient densities, bioturbation, hydrodynamics and sediment characteristics varied (Table 7), although generally bioturbation and ambient densities were least important. The exception to this was *Nucula*, a small surface-dwelling bivalve. Sediment characteristics were most important for *Aquilaspio*, *Colurostylis* and *Lumbrineris*, while hydrodynamic conditions explained over 80% of the variability in Nereidae, total number of taxa and total number of individuals.

4. Discussion

This study follows that of Norkko et al. (2002), and was designed to investigate the effects of wave-initiated sediment mixing and bedload transport on colonisation of

terrestrial sediment deposited on intertidal soft sediments. Dewatering of the sediment on the scale reported by Norkko et al. (2002) was not observed, however, the deposited sediment resulted in the death of all animals previously living in the smothered sediment, similar to Norkko et al. (2002). Sampling for macrofaunal recolonisation was not begun until 10 months after the sediment had been deposited, when the terrestrial sediments had been well weathered, but colonisation was still erratic. The deposited muddy sediment resulted in an altered habitat that was still obviously different from the ambient sediment at all sites after 20 months. Persistent differences between sites were observed in the communities found in the deposited sediment, even though all sites were located on one large intertidal sandflat.

Frequently, macrofaunal recovery is documented as being facilitated by animals remaining after the disturbance or by initial colonists (Rhoads and Young, 1970; Gallagher et al., 1983; Thrush, 1988; Warwick et al., 1990; Thrush et al., 1992; Aarnio et al., 1998; Norkko et al., 2002). In our study, facilitation by animals was limited; all animals died as a result of the deposition of terrestrial sediments. The different sediment was not utilised as a new resource providing a habitat for species different from those found in the adjacent sandflat (similar to the works of Bonsdorff, 1980; Levin, 1984; Zajac and Whitlatch, 1985; Savidge and Taghon, 1988; Thrush et al., 1996). Low densities of crab burrows were observed, and, occasionally, some rare individuals (e.g., Corophiidae, *Macrophthalmus* and Cirolanidae at site 1, *Callianassa* at site 2 and Cirolanidae at site 3) that did not occur in the ambient sediments were found; however, these did not persist.

While the temporal scale of our study (20 months) offers an opportunity for larval migration to be important, the relatively small-spatial scale (5 m) suggests that adult and juvenile dispersal is more likely (Thrush and Whitlatch, 2001); although this should be affected by sediment stability and habitat condition (Whitlatch et al., 2001). The hydrodynamic variables found to be important in the multiple regression analyses (sand transport and energy expended on the bed by waves) suggests bedload transport to be the dominant process by which animals moved into the deposited sediment, and thus that adult and juvenile colonisation is more likely to be important than larval migration. Three different dispersal mechanisms are suggested; active movement; active positioning to take advantage of bedload transport or wave suspension, and passive transport under extreme wave events. Maximum and mean energy expended on the bed influenced the abundance of some species in opposite directions suggesting two different dispersal mechanisms; animals which frequently rely on waves for moving them, or animals which are only moved by extreme events. Taxa that were found in similar or higher numbers in the deposited vs. ambient sediment (*Colurostylis*, capitellids, corophids and *Exosphaeroma*) are taxa that can be considered to be relatively mobile. For example, the capitellids and corophids were small and found in the new sand deposited on top of the plots as a result of bedload transport. In the previous studies, we have observed *Exosphaeroma* moving both in bedload and the water column (Cummings et al., 1995; Hewitt et al., 1997). Cumaceans are even more actively mobile, both as adults and juveniles, and are often considered to be semi-pelagic. However, we have observed *Austrovenus*, *Nucula* and *Macomona* juveniles moving both actively and passively in other intertidal areas (Pridmore et al., 1991; Commito et al., 1995), yet these were rarely found in the deposited sediment.

The communities found in the deposited sediment did not demonstrate a recovery towards ambient. Although recovery may not necessarily converge on to a community similar to the original (unlike, e.g., [Bonsdorff, 1989](#); [Thrush et al., 1996](#)), colonisation of a small patch would be anticipated to do so, unless high-density external migration occurred or the habitat had been significantly changed. Given the duration of our study, 20 months, lack of convergence is likely to reflect a significantly altered habitat. Sediment characteristics of the deposited sediment were markedly different and remained so, and most taxa were found in lower abundances in it compared to the surrounding sediment. Fewer total number of taxa and total numbers of individuals and, at one site, a lower Shannon–Weiner diversity were also found in the deposited sediment. Most of the taxa found in lower numbers in the deposited sediment (*Aquillaspio*, *Lumbrineris*, *Nucula*, *Austrovenus*) have all been demonstrated to be sensitive to depositions of terrestrial sediment in the laboratory (authors' unpublished data). These results support the modification of [Rhoads et al. \(1978\)](#) succession model by [Zajac \(2001\)](#) to include a variety of successional endpoints. In particular, [Zajac \(2001\)](#) suggests that changes to sediment characteristics in sandy habitats will result in variable successions due to species-specific sediment–organism relationships.

No progressive increase in abundances was observed. Permanent residents appeared to be few, with transients dominating. The community composition of the deposited sediment was, thus, more variable over time than that found in the ambient sediment, supporting the suggestion that increased variability is a sign of a disturbed community ([Warwick and Clarke, 1993](#)). Dominance by transients also occurred in response to the experimental removal of a stabilizing worm tube mat ([Thrush et al., 1996](#)). [Thrush et al. \(1996\)](#) found that recovery was driven by seasonal decreases in worm tube mats surrounding the experimental plots, rather than by a defined progressive recovery of the disturbed plots. However, the time period over which the disturbed plots were dominated by transients was not as long as in our study. In our study, the wave climate, the lack of vertical mixing of the deposited and existing sediment by either waves or bioturbators, and the sediment characteristics of the deposited sediment resulted in a lack of colonisation and establishment.

Variations in deposited sediment characteristics between sites were generally well explained by local hydrodynamics. Wind waves and tidal current generally facilitate recovery of localised disturbed patches by transporting benthic microphytes, detritus and different life-stages of macrofauna ([Yeo and Risk, 1979](#); [Miller et al., 1984](#); [Butman, 1987](#); [Delgado et al., 1991](#); [Gunther, 1992](#)). We found the amount of time that the critical threshold for erosion of sand particles was exceeded (i.e., sand transport) to be important. This factor represents the time available not only for the deposited sediment to be eroded, but also for transport of bedload and associated animals onto the deposited sediment. The maximum energy expended on the bed between each sampled occasion was also important, even though the maximum we recorded was much less than that recorded by [Norkko et al. \(2002\)](#) during a storm, which removed their deposited sediment completely. We also found immersion time to usually be a significant explanatory variable. In spite of the small range in immersion times, it was negatively correlated with depth of deposited sediment, the amount of new sand moved on to the deposited sediment surface, and the shear strength and organic content of the surface sediment. Immersion time is likely to control the drying of the sediment and thus its erodability.

Interactions were observed between the effects of local populations, bioturbation, local hydrodynamic conditions and sediment characteristics on colonisation by macrofauna. While all components, especially sediment characteristics, were important in explaining community composition, interactions between the three components explained a considerable proportion of the variance (15%). For taxa, the relative importance of bioturbation, local communities, hydrodynamics and sediment characteristics varied. In some cases, the relative importance clearly reflects functional characteristics of taxa (Pearson, 2001), suggesting that these results may be transferable to other locations. For example, the density of ambient populations, crab burrows and hydrodynamics were all important for *Nucula* (a surface-sediment dweller which is easily moved as bedload). Hydrodynamics and sediment characteristics were important for *Colurostylis* (a motile, semi-pelagic burrower). However, *Aquilaspio* (a free-living, small deposit-feeding spionid living in the surficial 2 cm) showed a response more species-specific than functionally related, with sediment characteristics explaining most of the variability. This species, more than other functionally similar spionids found in New Zealand intertidal soft-sediment habitats, has consistently shown a negative response to terrestrial sediment (see also Norkko et al., 2002; Thrush et al., in press).

5. Conclusions

Our study demonstrates persistent differences over 20 months between deposited terrestrial and existing marine sediment. Effects on macrofauna were extreme and the recovery dynamics were unusual. Little vertical mixing of the deposited and existing sediment by either waves or bioturbators occurred; instead bedload transport dominated. Colonisation of the deposited sediment appeared likely to be driven mainly by dispersal with bedload, and no facilitation was apparent. Progressive recovery to either the community living in the surrounding sediment or to a new stable state was also not observed. Instead, residents appeared to be few, and domination by transients resulted in communities that were variable over time. Within this framework, local differences in hydrodynamic conditions and populations resulted in differential colonisation into deposited sediment on one intertidal sandflat. Sediment characteristics, hydrodynamics and local community composition all affected colonisation with strong interactions occurring between these three components. The strength and duration of the response to deposited sediment observed in this study suggest that chronic small-scale patchy deposition of terrestrial sediment in the intertidal marine environment has a strong potential to alter both habitats and communities.

Acknowledgements

We thank Iain McDonald and Mal Green for the help in collecting and analysing the wave data. Drew Talley and Diane Schultz helped with the fieldwork. This research was funded by the New Zealand Foundation for Research, Science and Technology (CO1X0028). [RW]

Appendix A

Results of Friedman's tests ($df=2$) on the differences in sediment characteristics, wave climate and immersion time between sites.

	χ^2	p -value
% Gravel	9.62	0.0081
% Coarse sand	4.82	0.0898
% Medium sand	2.48	0.2894
% Fine sand	5.46	0.0652
% Silt	4.37	0.1124
% Clay	0.065	0.9679
Chlorophyll <i>a</i>	1.52	0.4677
% Organic content	5.11	0.0775
Sediment firmness	3.04	0.2187
Sediment shear strength	7.74	0.0209
Immersion time	5.54	0.0198
% Waves	4.16	0.1249
Maximum work	3.92	0.1404
Mean work	4.062	0.1312
Exceedence	3.38	0.1845
No. of burrows	2.94	0.0917

Appendix B

Results of generalized linear modelling on the effect of deposited sediment on sediment characteristics. Site and treatment were fixed factors, time was a random factor and a site*treatment interaction was included. Where a significant site*treatment interaction ($p < 0.15$) is reported, p -values for the effect of treatment at each site are given.

	Factor	df	Sum of squares	F -value	p -value	Site	Treatment p -value
Chlorophyll <i>a</i>	Model	9	89.37	6.11	0.0004		
	Error	20	32.48				
	Time	4	54.80	8.44	0.0004		
	Site	2	0.60	0.18	0.8340		
	Treatment	1	29.38	18.09	0.0004		
	Site*Treatment	2	4.60	1.42	0.2661		
Firmness	Model	9	20.20	2.75	0.0285	S1	0.7557
	Error	20	16.32			S2	0.1912
	Time	4	6.43	1.97	0.1380	S3	0.0338
	Site	2	1.50	0.92	0.4152		
	Treatment	1	8.69	10.66	0.0039		
	Site*Treatment	2	3.58	2.19	0.1378		

(continued on next page)

Appendix B (continued)

	Factor	<i>df</i>	Sum of squares	<i>F</i> -value	<i>p</i> -value	Site	Treatment <i>p</i> -value
Shear strength	Model	9	5.63	8.84	<0.0001		
	Error	20	1.41				
	Time	4	1.90	6.7	0.0014		
	Site	2	2.89	20.43	<0.0001		
	Treatment	1	0.78	11	0.0034		
	Site*Treatment	2	0.06	0.45	0.6438		
% Organics	Model	9	0.04	10.16	<0.0001	S1	0.0431
	Error	20	0.01			S2	0.0094
	Time	4	0.00	1.98	0.1364	S3	0.0034
	Site	2	0.01	8.61	0.0020		
	Treatment	1	0.02	58.67	<0.0001		
	Site*Treatment	2	0.00	3.81	0.0396		
% Mud	Model	9	0.90	8.86	<0.0001		
	Error	20	0.23				
	Time	4	0.04	0.83	0.5238		
	Site	2	0.03	1.4	0.2691		
	Treatment	1	0.80	71.45	<0.0001		
	Site*Treatment	2	0.02	1.09	0.3564		
% Large particles	Model	9	0.21	9.55	<0.0001		
	Error	20	0.05				
	Time	4	0.02	1.97	0.1378		
	Site	2	0.04	8.03	0.0028		
	Treatment	1	0.15	61.02	<0.0001		
	Site*Treatment	2	0.00	0.51	0.6090		

Appendix C

Results of generalized linear modelling on the effect of deposited sediment on the abundances of selected taxa and univariate indicators of community structure. Where a significant site*treatment interaction ($p < 0.15$) is reported, *p*-values for the effect of treatment at each site are given. A Poisson distribution with a log link was used for the taxa and a normal distribution with an identity link was used for the univariate indicators.

	Factor	<i>df</i>	Sum of squares or deviance	<i>F</i> - or χ^2 -value	<i>p</i> -value	Site	Treatment <i>p</i> -value
Total no. of taxa	Model	9	335.03	3.83	0.0059		
	Error	20	194.33				
	Treatment	1	197.63	20.34	0.0002		
	Site	2	7.27	0.37	0.6927		
	Time	4	124.87	3.21	0.0344		
	Site*Treatment	2	5.27	0.27	0.7654		
No. of rare taxa	Model	9	46.73	1.01	0.4636		
	Error	20	102.73				
	Treatment	1	26.13	5.09	0.0355		
	Site	2	0.07	0.01	0.9935		

Appendix C (continued)

	Factor	df	Sum of squares or deviance	F- or χ^2 -value	p-value	Site	Treatment p-value
No. of rare taxa	Time	4	14.47	0.7	0.5984		
	Site*Treatment	2	6.07	0.59	0.5634		
Total no. of individuals	Model	9	39381.67	14.03	<0.0001	S1	0.0372
	Error	20	6237.80			S2	0.0008
	Treatment	1	23632.13	75.77	<0.0001	S3	0.0916
	Site	2	6310.87	10.12	0.0009		
	Time	4	4871.80	3.91	0.0168		
Shannon–Weiner	Site*Treatment	2	4566.87	7.32	0.0041		
	Model	9	2.18	2.08	0.0823	S1	0.8958
	Error	20	2.33			S2	0.7033
	Treatment	1	0.18	1.56	0.2266	S3	0.0305
	Site	2	0.05	0.21	0.8134		
<i>Aquilaspio</i>	Time	4	1.29	2.77	0.0553		
	Site*Treatment	2	0.66	2.84	0.0821		
	Model	15	894.13				
	Error	14	35.82				
	Treatment	1		80.60	<0.0001		
<i>Austrovenus</i>	Site	2		35.30	<0.0001		
	Time	4		5.66	0.2257		
	Time*Site	8		7.89	0.4447		
	Model	9	64.86	64.86	<0.0001		
	Error	20	43.46	43.46			
<i>Colurostylis</i>	Treatment	1		9.18	0.0025	S1	0.9997
	Site	2		6.10	0.0474	S2	0.2324
	Time	4		3.54	0.4718	S3	0.0001
	Treatment*Site	2		9.27	0.0097		
	Model	15	117.09				
<i>Exosphaeroma</i>	Error	14	31.88				
	Treatment	1		0.45	0.5046		
	Site	2		0.00	1		
	Time	4		1.63	0.8031		
	Time*Site	8		9.55	0.2977		
<i>Lumbrineris</i>	Model	15	59.17	1.63	0.1827		
	Error	14	33.80				
	Treatment	1		1.12	0.3082		
	Site	2		6.39	0.0107		
	Time	4		1.08	0.4018		
Lysianassidae	Time*Site	8		0.78	0.6247		
	Model	15	127.59				
	Error	14	20.41				
	Treatment	1		46.19	<0.0001		
	Site	2		1.27	0.5308		
Lysianassidae	Time	4		5.98	0.2009		
	Time*Site	8		8.34	0.4011		
	Model	9	667.00	1.77	0.1375		
	Error	20	836.87				
	Treatment	1		7.34	0.0135		
	Site	2		2.58	0.1006		

(continued on next page)

Appendix C (continued)

	Factor	df	Sum of squares or deviance	F- or χ^2 -value	p-value	Site	Treatment p-value
Lysianassidae	Time	4		0.65	0.6306		
	Treatment*Site	2	34.20	0.41	0.67		
Nereidae	Model	15	214.59	214.59	<0.0001	S1	0.0876
	Error	14	59.69	59.69		S2	0.104
	Treatment	1		3.26	0.0708	S3	0.0006
	Site	2		12.87	0.0016		
	Time	4		84.84	<0.0001		
	Time*Site	8		15.69	0.047		
Nucula	Model	15	180.25	180.25	<0.0001		
	Error	14	49.71	49.71			
	Treatment	1		44.16	<0.0001		
	Site	2		1.50	0.4719		
	Time	4		83.60	<0.0001		
	Time*Site	8		11.58	0.1712		
Oligochaeta	Model	15	445.23				
	Error	14	163.87				
	Treatment	1		0.46	0.4982		
	Site	2		0.00	1		
	Time	4		0.83	0.9346		
	Time*Site	8		3.63	0.8885		
Scoloplos	Model	15	46.10	46.10	<0.0001	S1	0.3499
	Error	14	75.44	75.44		S2	0.0267
	Treatment	1		2.35	0.1254	S3	0.0003
	Site	2		5.92	0.0518		
	Time	4		7.02	0.1349		
	Time*Site	8		20.56	0.0084		

Appendix D

Results of multiple generalized linear modelling of sediment characteristics using hydrodynamic data. Binomial error distributions were used for the percentage data and a Poisson error was used for the number of burrows. For these variables, deviance rather than sum of squares are given.

	% Explained	Factor	df	Deviance/sum of squares	Parameter estimate	F or t-value	p-value	
Deposited sediment depth	82.8	Model	2	17.59		28.95	<0.0001	
		Error	12	3.65				
		Intercept	1			18.73	7.36	<0.0001
		Immersion	1			-0.31	-5.56	0.0001
		Max work	1			-25.19	-2.47	0.0297
New sand depth	44.7	Model	3	10.05		2.95	0.0755	
		Error	11	12.46				
		Intercept	1			-17.24	-2.43	0.0357

Appendix D (continued)

	% Explained	Factor	df	Deviance/sum of squares	Parameter estimate	F or t-value	p-value
New sand depth		Immersion	1		0.40	2.61	0.0259
		Mean work	1		−991.59	−1.86	0.0918
		Exceed	1		0.08	2.21	0.0517
Firmness	49.0	Model	1	2.30		12.49	0.0037
		Error	13	2.39			
		Intercept	1		1.25	7.50	<0.0001
Shear strength	49.4	Waves	1		0.02	3.53	0.0037
		Model	1	1.19		12.71	0.0035
		Error	13	1.22			
% Organics	47.5	Intercept	1		6.44	4.87	0.0003
		Immersion	1		−0.10	−3.57	0.0035
		Model	3	7.34		3.31	0.0609
% Mud	72.0	Error	11	8.12			
		Intercept	1		14.16	3.40	0.006
		Immersion	1		−0.24	−2.75	0.0188
% Large particles	59.0	Mean work	1		866.37	2.12	0.0573
		Exceed	1		−0.06	−2.31	0.0417
		Model	4	84.45			<0.0001
% Large particles	59.0	Error	10	32.84			
		Intercept	1		13.34	52.54	<0.0001
		Immersion	1		−0.33	62.43	<0.0001
% Large particles	59.0	Max work	1		96.53	27.10	<0.0001
		Mean work	1		−635.96	7.53	0.0061
		Exceed	1		−0.02	4.03	0.0446
% Large particles	59.0	Model	3	13.43			0.0038
		Error	11	9.34			
		Intercept	1		3.26	4.51	0.0337
% Large particles	59.0	Immersion	1		−0.11	10.41	0.0013
		Max work	1		51.39	9.88	0.0017
		Mean work	1		−500.75	9.02	0.0027

Appendix E

Results of multiple generalized linear modelling of biological data by sediment characteristics and hydrodynamic data. Poisson distributions were used for the number of burrows. For these variables, deviance rather than sum of squares are given. Where a species name appears as an independent variable, the densities used were from the surrounding sediment.

	% Explained	Factor	df	Deviance/sum of squares	Parameter estimate	F- or t-value	p-value
<i>Aquilaspio</i>	86.9	Model	8	86.19		12.57	0.0031
		Error	6	5.14			
		Intercept	1		76.67	6.61	0.0006

(continued on next page)

Appendix E (continued)

	% Explained	Factor	df	Deviance/sum of squares	Parameter estimate	F- or t-value	p-value
<i>Aquilaspio</i>		% Organics	1		-2.54	-5.29	0.0019
		% Coarse +	1		-0.40	-5.57	0.0014
		Firmness	1		-1.97	-2.68	0.0364
		Immersion	1		-1.30	-6.29	0.0008
		Waves	1		0.09	3.37	0.015
		Max work	1		197.06	4.88	0.0028
		Exceed	1		-0.17	-6.13	0.0009
<i>Colurostylis</i>	81.5	<i>Aquilaspio</i>	1		0.03	1.97	0.0959
		Model	7	324.33		9.83	0.0037
		Error	7	33.01			
		Intercept	1		-37.12	-1.80	0.1147
		Chlorophyll <i>a</i>	1		0.82	2.19	0.065
		% Mud	1		0.52	5.55	0.0009
		Firmness	1		-6.36	-4.01	0.0051
		Immersion	1		0.76	1.74	0.1253
		Waves	1		0.33	5.76	0.0007
		Max work	1		-349.65	-2.00	0.0852
<i>Lumbrineris</i>	95.9	Mean work	1		2956.9	1.71	0.1303
		Model	8	17.03		42.16	0.0001
		Error	6	0.30			
		Intercept	1		36.56	11.61	<0.0001
		Chlorophyll <i>a</i>	1		0.22	6.02	0.001
		% Coarse +	1		-0.24	-9.89	<0.0001
		Firmness	1		1.20	9.72	<0.0001
		Shear strength	1		-3.34	-12.43	<0.0001
		Immersion	1		-0.67	-11.11	<0.0001
		Mean work	1		-1830.8	-8.83	0.0001
Neridae	89.4	Max work	1		224.37	10.46	<0.0001
		<i>Lumbrineris</i>	1		0.09	4.33	0.0049
		Model	5	1453.1		24.49	<0.0001
		Error	9	106.82			
		Intercept	1		12.90	2.55	0.0311
		% Organics	1		-3.69	-3.32	0.009
		Waves	1		0.47	7.65	<0.0001
		Mean work	1		-11266.0	3.60	0.0058
		Max work	1		782.61	-4.10	0.0027
		Exceed	1		-0.28	-2.14	0.0608
<i>Nucula</i>	87.6	Model	7	358.68		15.12	0.001
		Error	7	23.72			
		Intercept	1		23.10	3.58	0.0089
		Chlorophyll <i>a</i>	1		-1.11	-2.62	0.0342
		% Organics	1		-3.24	-3.25	0.0141
		Firmness	1		-2.85	-1.99	0.0872
		<i>Nucula</i>	1		0.41	4.67	0.0023
		Waves	1		0.29	5.88	0.0006
		Max work	1		107.96	-2.35	0.0509
		No. of burrows	1		-2.03	-4.01	0.0051
Total no. of taxa	56.8	Model	3	96.57		4.82	0.0222
		Error	11	73.43			

Appendix E (continued)

	% Explained	Factor	df	Deviance/sum of squares	Parameter estimate	F- or t-value	p-value	
Total no. of taxa		Intercept	1		3.40	1.73	0.1114	
		Chlorophyll <i>a</i>	1		0.66	1.73	0.1109	
		Max work	1		442.62	3.58	0.0043	
		Mean work	1		−4340.4	−3.21	0.0083	
No. of rare taxa	76.1	Model	6	39.34		4.23	0.0323	
		Error	8	12.39				
Total no. of individuals	59.5	Intercept	1		−2.97	−1.15	0.2853	
		Chlorophyll <i>a</i>	1		0.45	2.31	0.05	
		Shear strength	1		2.18	2.30	0.0502	
		Mean work	1		2545.0	3.90	0.0045	
		Exceed	1		−0.13	−3.08	0.0151	
		Waves	1		−0.06	−2.69	0.0275	
		No. of burrows	1		0.93	3.68	0.0063	
		Model	1	2806.0			19.10	0.0008
		Error	13	1909.5				
		Intercept	1			8.03	1.70	0.1121
Waves	1			0.78	4.37	0.0008		

References

- Aarnio, K., Bonsdorff, E., Norkko, A., 1998. Role of *Halicryptus spinulosus* (Priapulida) in structuring meiofauna and settling macrofauna. Mar. Ecol. Prog. Ser. 163, 145–153.
- Armonies, W., 1992. Migratory rhythms of drifting juvenile molluscs in tidal waters of the Wadden Sea. Mar. Ecol. Prog. Ser. 83, 197–206.
- Bell, R.G., Hume, T.M., Dolphin, T.J., Green, M.O., Walters, R.A., 1997. Characterisation of physical factors on an intertidal sandflat, Manukau Harbour, New Zealand. J. Exp. Mar. Biol. Ecol. 216, 11–32.
- Belsley, D.A., Kuh, E., Welsch, R.E., 1980. Regression Diagnostics: Identifying Influential Data and Sources of Colinearity. Wiley, New York.
- Bertness, M.D., Leonard, G.H., 1997. The role of positive interactions in communities: lessons from intertidal habitats. Ecology 78, 1976–1989.
- Beukema, J.J., de Vlas, J., 1989. Tidal-current transport of thread-drifting postlarval juveniles of the bivalve *Macoma balthica* from the Wadden Sea to the North Sea. Mar. Ecol. Prog. Ser. 52, 193–200.
- Bonsdorff, E., 1980. Macrobenthic recolonisation of a dredged brackishwater bay in S.W. Finland. Ophelia, Suppl. 1, 145–155.
- Bonsdorff, E., 1989. Infaunal colonization and its dependence on environmental variation—experimental evidence from the northern Baltic Sea. In: Ryland, J.S., Tyler, P.A. (Eds.), Reproduction, Genetics and Distribution of Marine Organisms. Olsen and Olsen, Fredensborg, pp. 349–356.
- Butman, C.A., 1987. Larval settlement of soft-sediment invertebrates: the spatial scales of pattern explained by active habitat selection and the emerging role of hydrological processes. Oceanogr. Mar. Biol. Ann. Rev. 25, 113–165.
- Cadee, G.C., 1979. Sediment reworking by the polychaete *Heteromastus filiformis* on a tidal flat in the Dutch Wadden Sea. Neth. J. Sea Res. 13, 441–454.
- Clarke, K.R., 1993. Non-parametric multivariate analyses of changes in community structure. Aust. J. Ecol. 18, 117–143.
- Commito, J.A., Thrush, S.F., Pridmore, R.D., Hewitt, J.E., Cummings, V.J., 1995. Dispersal dynamics in a wind-driven benthic system. Limnol. Oceanogr. 40, 1513–1518.
- Cummings, V.J., Pridmore, R.D., Thrush, S.F., Hewitt, J.E., 1995. Post-settlement movement by intertidal benthic macroinvertebrates: do common New Zealand species drift in the water column? N.Z. J. Mar. Freshw. Res. 29, 59–67.

- Cummings, V., Thrush, S., Hewitt, J., Norkko, A., Pickmere, S., in press. Terrestrial sediment deposits in marine soft-sediments: sediment characteristics as indicators of habitat suitability for recolonising macrofauna. *Mar. Ecol. Prog. Ser.*
- Delgado, M., de Jonge, V.N., Peletier, H., 1991. Experiments on resuspension of natural microphytobenthos populations. *Mar. Biol.* 108, 321–328.
- Edgar, G.J., Barrett, N.S., 2000. Effects of catchment activities on macrofaunal assemblages in Tasmanian estuaries. *Estuar. Coast. Shelf Sci.* 50, 639–654.
- Ellis, J.I., Norkko, A., Thrush, S.F., 2000. Broad-scale disturbance of intertidal and shallow sublittoral soft-sediment habitats: effects on the benthic macrofauna. *J. Aquat. Ecosyst. Health* 7, 57–74.
- Emerson, C.W., Grant, J., 1991. The control of softshell clam (*Mya arenaria*) recruitment on intertidal sandflats by bedload sediment transport. *Limnol. Oceanogr.* 36, 1288–1300.
- Gallagher, E.D., Jumars, P.A., Truebold, D.D., 1983. Facilitation of soft-bottom benthic succession by tube builders. *Ecology* 64, 1200–1216.
- GESAMP, 1994. Group of Experts on the Scientific Aspects of Marine Environmental Protection: Anthropogenic Influences on Sediment Discharge to the Coastal Zone and Environmental Consequences. UNESCO-TOC, Paris.
- Gray, J.S., 1997. Marine biodiversity: patterns, threats and conservation needs. *Biodivers. Conserv.* 6, 153–175.
- Gunther, C., 1992. Dispersal of intertidal invertebrates: a strategy to react to disturbances of different scales? *Neth. J. Sea Res.* 30, 45–56.
- Hewitt, J.E., Pridmore, R.D., Thrush, S.F., Cummings, V.J., 1997. Assessing the short-term stability of spatial patterns of macrobenthos in a dynamic estuarine system. *Limnol. Oceanogr.* 42, 282–288.
- Huston, M.A., De Angelis, D.L., 1994. Competition and coexistence: the effects of resource transport and supply rates. *Am. Nat.* 144, 954–977.
- Levin, L.A., 1984. Life history and dispersal patterns in a dense infaunal polychaete assemblage: community structure and response to disturbance. *Ecology* 65, 1185–1200.
- Longuet-Higgins, M.S., 1975. On the joint distribution of the period and amplitudes of sea waves. *J. Geophys. Res.* 80, 2688–2694.
- Maurer, D., Keck, R.T., Tinsman, J.C., Leathem, W.A., Wethe, C., Lord, C., Church, T.M., 1986. Vertical migration and mortality of marine benthos in dredged material: a synthesis. *Int. Rev. Gesamten Hydrobiol.* 71, 49–63.
- McCullagh, P., Nelder, J.A., 1989. *Generalised Linear Models*. Chapman & Hall, London.
- McKnight, D.G., 1969. A recent, possibly catastrophic burial in a marine molluscan community. *N.Z. J. Mar. Freshw. Res.* 3, 177–179.
- Miller, D.C., Sternberg, R.W., 1988. Field measurements of the fluid and sediment-dynamic environment of a benthic deposit feeder. *J. Mar. Res.* 46, 771–796.
- Miller, D.C., Jumars, P.A., Nowell, A.R.M., 1984. Effects of sediment transport on deposit feeding: scaling arguments. *Limnol. Oceanogr.* 29, 1202–1217.
- Norkko, A., Cummings, V.J., Thrush, S.F., Hewitt, J.E., Hume, T.H., 2001. Local dispersal of juvenile bivalves: implications for sandflat ecology. *Mar. Ecol. Prog. Ser.* 212, 131–144.
- Norkko, A., Thrush, S.F., Hewitt, J.E., Cummings, V.J., Norkko, J., Ellis, J.I., Funnell, G.A., Schultz, D., MacDonald, I., 2002. Smothering of estuarine sandflats by terrigenous clay: the role of wind-wave disturbance and bioturbation in site-dependent macrofaunal recovery. *Mar. Ecol. Prog. Ser.* 234, 23–41.
- Pearson, T.H., 2001. Functional group ecology in soft-sediment marine benthos: the role of bioturbation. *Oceanogr. Mar. Biol. Ann. Rev.* 39, 233–267.
- Peterson, C.H., 1985. Patterns of lagoonal bivalve mortality after heavy sedimentation and their paleoecological significance. *Paleobiology* 11, 139–153.
- Pridmore, R.D., Thrush, S.F., Wilcock, R.J., Smith, T.J., Hewitt, J.E., Cummings, V.J., 1991. Effect of the organochlorine pesticide technical chlordane on the population structure of suspension and deposit feeding bivalves. *Mar. Ecol. Prog. Ser.* 76, 261–271.
- Rhoads, D.C., Young, D.K., 1970. The influence of deposit-feeding organisms on sediment stability and community trophic structure. *J. Mar. Res.* 28, 150–178.
- Rhoads, D.C., McCall, P.L., Yingst, J.Y., 1978. Production and disturbance on the estuarine seafloor. *Am. Sci.* 66, 577–586.

- Sartory, D.P., 1982. Spectrophotometric analysis of chlorophyll *a* in freshwater phytoplankton, Hydrological Research Institute Technical Report 115, Pretoria.
- Savidge, W.B., Taghon, G.L., 1988. Passive and active components of colonization following two types of disturbance on an intertidal sandflat. *J. Exp. Mar. Biol. Ecol.* 115, 137–155.
- Tamaki, A., 1987. Comparison of resistivity to transport by wave action in several polychaete species on an intertidal sand flat. *Mar. Ecol. Prog. Ser.* 37, 181–189.
- Tamaki, A., Ingole, B., 1993. Distribution of juvenile and adult ghost shrimps, *Callinassa japonica* Ortmann (Thalassinidea), on an intertidal sand flat: intraspecific facilitation as a possible pattern-generating factor. *J. Crustac. Biol.* 13, 175–183.
- ter Braak, C.J.F., 1986. Canonical correspondence analysis: a new eigenvector technique for multivariate direct gradient analysis. *Ecology* 67, 1167–1179.
- ter Braak, C.J.F., 1987. The analysis of vegetation–environment relationships by canonical correspondence analysis. *Vegetatio* 69, 69–77.
- ter Braak, C.J.F., Smilauer, P., 1998. CANOCO Release 4 Reference Manual and User's Guide to Canoco for Windows-Software for Canonocal Community Ordination. Microcomputer Power, Ithaca, NY.
- Thayer, C.W., 1993. Sediment-mediated biological disturbance and the evolution of marine benthos. In: Tevesz, M.J.S. (Ed.), *Biotic Interactions in Recent and Fossil Benthic Communities*. Plenum, New York, pp. 479–625.
- Thrush, S.F., 1986. Spatial heterogeneity in subtidal gravel generated by the pit-digging activity of cancer pagurus. *Mar. Ecol. Prog. Ser.* 30, 221–227.
- Thrush, S.F., 1988. The comparison of macrobenthic recolonization patterns near and away from crab burrows on a sublittoral sand flat. *J. Mar. Res.* 46, 669–681.
- Thrush, S.F., Whitlatch, R.B., 2001. Recovery dynamics in benthic communities: balancing detail with simplification. In: Reise, K. (Ed.), *Ecological Comparisons of Sedimentary Shores*. Springer, Berlin, pp. 297–316.
- Thrush, S.F., Pridmore, R.D., Hewitt, J.E., Cummings, V.J., 1992. Adult infauna as facilitators of colonization on intertidal sandflats. *J. Exp. Mar. Biol. Ecol.* 159, 253–265.
- Thrush, S.F., Whitlatch, R.B., Pridmore, R.D., Hewitt, J.E., Cummings, V.J., Maskery, M., 1996. Scale dependent recolonization: the role of sediment stability in a dynamic sandflat habitat. *Ecology* 77, 2472–2487.
- Thrush, S.F., Hewitt, J.E., Cummings, V.J., Green, M.O., Funnell, G.A., Wilkinson, M.R., 2000. Improving the generality of field experiments: the interaction of processes operating over different spatial scales on intertidal sandflats. *Ecology* 81, 399–415.
- Thrush, S.F., Hewitt, J.E., Norkko, A., Cummings, V.J., Funnell, G.A., in press. Macrobenthic recovery processes following catastrophic sedimentation on estuarine sandflats. *Ecol. Appl.*
- Warwick, R.M., Clarke, K.R., 1993. Increased variability as a symptom of stress in marine communities. *J. Exp. Mar. Biol. Ecol.* 172, 215–226.
- Warwick, R.M., Clarke, K.R., Gee, J.M., 1990. The effect of disturbance by soldier crabs *Mictyris platycheles* H. Milne Edwards on meiobenthic community structure. *J. Exp. Mar. Biol. Ecol.* 135, 19–33.
- Whitlatch, R.B., Lohrer, A.M., Thrush, S.F., 2001. Scale-dependent recovery of the benthos: effects of larval and post-larval life stages. In: Aller, J.Y., Woodin, S.A., Aller, R.C. (Eds.), *Organism–Sediment Interactions*. University of South Carolina Press, Columbia, pp. 181–198.
- Wolfrath, B., 1992. Burrowing of the fiddler crab *Uca tangeri* in the Rio Formosa in Portugal and its influence on sediment structure. *Mar. Ecol. Prog. Ser.* 85, 237–243.
- Yeo, R.K., Risk, M.J., 1979. Intertidal catastrophes: effect of storms and hurricanes on intertidal benthos of the Minas Basin, Bay of Fundy. *J. Fish. Res. Board Can.* 36, 667–669.
- Zajac, R.N., 2001. Organism–sediment relationships at multiple spatial scales: implications for community structure and successional dynamics. In: Aller, J.Y., Woodin, S.A., Aller, R.C. (Eds.), *Organism–Sediment Relationships*. University of South Carolina Press, Columbia, pp. 119–140.
- Zajac, R.N., Whitlatch, R.B., 1985. A hierarchical approach to modelling soft-bottom successional dynamics. In: Gibbs, P. (Ed.), *Proceedings of the 19th European Marine Biological Symposium*. Cambridge Univ. Press, Cambridge, England, pp. 265–276.
- Zajac, R.N., Whitlatch, R.B., Thrush, S.F., 1998. Recolonisation and succession in soft-sediment infaunal communities: the spatial scale of controlling factors. *Hydrobiologia* 376, 227–240.