# Sedimentation effects on the benthos of streams and estuaries: a cross-ecosystem comparison

*David J. Reid*[A,D], *Luca D. Chiaroni*[A], *Judi E. Hewitt*[A], *Drew M. Lohrer*[A],
*Christoph D. Matthaei*[B], *Ngaire R. Phillips*[A], *Mike R. Scarsbrook*[C],
*Brian J. Smith*[A], *Simon F. Thrush*[A], *Colin R. Townsend*[B],
*Kristel S. S. van Houte-Howes*[A] and *Aslan E. Wright-Stow*[A]

[A]National Institute of Water and Atmospheric Research, PO Box 11-115, Hamilton, New Zealand.
[B]Department of Zoology, University of Otago, PO Box 56, Dunedin, New Zealand.
[C]DairyNZ Ltd, Private Bag 3221, Hamilton, New Zealand.
[D]Corresponding author. Email: davidjonreid@hotmail.com

**Abstract.**    Connected ecosystems can be detrimentally affected by the same stressor, such as occurs when excess fine sediment moves from streams into estuaries. However, no previous study has directly compared sedimentation effects across these ecosystems. Responses of benthic macroinvertebrate communities to sedimentation were predicted to vary between streams and estuaries, because of intersystem differences in the physical environment and representation of species traits. To compare these responses, fine terrigenous sediment was added simultaneously to replicated plots in stream-run habitats and the adjacent estuary. Although sediment addition to streams caused reduced invertebrate densities after 1 week, no changes in taxon richness or consistent changes in community structure were detected, and densities had recovered another week later. In contrast, sediment addition to estuarine sites caused large declines in invertebrate densities and changes in community structure, which remained evident at the innermost sites 16 days after addition. Across both systems, sedimentation effects were detectable only for some of the common taxa, and biological traits were not predictive of effects. The potential for more severe effects in estuaries should be considered when predicting the implications of land-use changes that may increase sedimentation, and when setting guidelines for maintaining stream and estuarine condition.

## Introduction

Fine sediment (inorganic particles with diameter $<2$ mm) and other materials may be transported down slopes into water-bodies as loose particles that are entrained in overland flow; however, much of the sedimentation of streams occurs as pulsed inputs via landslides of unconsolidated banks (Owens *et al.* 2005; Marden *et al.* 2006). Increased sedimentation of streams and rivers has been shown to have detrimental effects on their structure and function (e.g. Quinn *et al.* 1997; Dolédec *et al.* 2006; Matthaei *et al.* 2006). Depending on the flow regime, slope and local bed composition, fine sediments can be flushed downstream during high flows (Petticrew *et al.* 2007). From coastal catchments, this sediment is then discharged into estuaries or directly onto the continental shelf, where further ecological impacts may occur (Thrush *et al.* 2004). Fine sediment may flocculate in marine environments (Xu *et al.* 2008) and persist for some time before being redistributed or buried by waves and tidal action (Cummings *et al.* 2003; Hewitt *et al.* 2003). The capacity for dispersal of excess fine sediment in estuaries depends on local hydrodynamics (Norkko *et al.* 2002; Hewitt *et al.* 2003) and the communities in both hard- and soft-bottomed estuaries have been shown to be detrimentally affected by pulses of high sediment loads (e.g. Airoldi 2003; Hewitt *et al.* 2003; Thrush *et al.* 2003; Lohrer *et al.* 2004).

It is widely accepted that the ecosystems within catchments and their adjacent coast should be treated as interconnected units for effective management (e.g. Gordon 2007; Mercer Clarke *et al.* 2008; Tallis *et al.* 2008). The amount of sediment contributed to waterbodies from their surrounding catchments depends on many natural factors, including climate, topography and soils (Hicks *et al.* 2004; Owens *et al.* 2005). Changes in land use can also result in significantly increased sediment delivery to aquatic ecosystems. For example, agriculture, forestry, mining, urbanisation and road construction all increase the amount of exposed soil, as well as potentially reducing the stability of stream banks and altering hydrologic cycles (e.g. Collier and Winterbourn 2000; Thrush *et al.* 2004; Owens *et al.* 2005). Assessment of sedimentation impacts across catchments

**Table 1.  Functional species trait categories which were expected to be most affected by pulsed sedimentation and the predicted mechanisms for effects on particular trait modalities**
See Table S1 in Accessory Publication for full list of trait modalities within each trait category

| Trait category | Possible mechanisms for any observed sedimentation effect |
|---|---|
| Relative size | Smaller animals may be more able to take advantage of refugia from sedimentation at microhabitat scales. |
| Body form | Spherical animals may be least able to avoid smothering, whereas cylindrical animals (e.g. worms) may be able to burrow into sediment. |
| Habitat preference | Near surface-dwelling taxa are likely to be more affected than deeper-burrowing taxa. Animals needing attachment sites are likely to be most affected by coating of stable surfaces in unstable fine sediments. |
| Feeding habits | Filter-feeders are likely to be most affected by increased suspended sediment, which may clog their feeding structures. Grazers and deposit-feeders may be most affected by smothering of their food sources. Predators and scavengers may benefit from decreased fitness of prey, although prey may be harder to find as a result of higher turbidity. |
| Dietary specificity | Dietary specialists are most likely to be affected by reductions in their specific food sources. |
| Mobility | More mobile animals are able to move away initially and move back quickly (likely to reduce densities of these animals initially, followed by rapid recovery as fine sediment is dispersed). |

requires identification of both the links between ecosystems and determination of thresholds for occurrence of ecologically significant changes, such as alteration of the structure and functioning of benthic communities. However, very few studies have assessed the effects of human-induced changes across ecosystems within a catchment (see Wall *et al.* 2005).

The aim of the present study was to determine the effects of sediment addition on invertebrate communities in connected streams and a soft-bottomed estuary, with the focus on effects on benthic organisms, because these are most likely to be affected by deposited sediment. In addition to measures that have traditionally been used to assess effects of sedimentation on invertebrate community structure (i.e. abundance, diversity and multivariate ordination of community composition), we also used a complementary approach of assessing changes in the representation of different biological traits in each community. Trait analysis combines structural (community composition) and functional (trait) information by aggregating individuals according to their biological traits, and has proven to be sensitive to impacts of land-use change, including sedimentation of streams (e.g. Richards *et al.* 1997; Dolédec *et al.* 2006; Townsend *et al.* 2008; Thompson *et al.* 2009). Depending on their suite of traits, sedimentation may detrimentally affect aquatic invertebrates via direct smothering, reduced surface-habitat heterogeneity, changes in fluxes of oxygen and nutrients, reduced autotrophic production, and/or impaired feeding and growth (Ryan 1991; Wood and Armitage 1997; Molinos and Donohue 2009). Some benthic organisms benefit from increases in the amount of fine sediment (e.g. Shaw and Richardson 2001; Norkko *et al.* 2002; Matthaei *et al.* 2006). Changes in the proportions of different taxa in communities may result in a shift in the functioning of the ecosystem. Identification of species traits that are particularly sensitive to environmental stressors provides information about changes in ecosystem function and may facilitate the exploration of underlying causal mechanisms for those stressors that potentially exert multiple effects on communities (Poff 1997; Richards *et al.* 1997), such as excess sediment. A further advantage of species trait analysis is that it can be used to compare changes in functional integrity across systems that differ in their taxonomic composition.

To our knowledge, no previous study has assessed the relative influence of sedimentation impacts on a wide suite of traits across stream and estuarine communities.

We conducted a field experiment where layers of fine sediment of the same type and thickness were added to plots located in adjacent stream and estuarine sites (mimicking a small-scale pulsed sedimentation event) within the same catchment, so that responses of the systems could be directly compared. Sediment addition was predicted to cause disturbances to benthic communities and be reflected in reductions in both invertebrate abundances and richness, as well as changes in the representation of certain biological traits (Table 1). Invertebrate communities in sediment-addition plots were predicted to recover as the sediment was dispersed, with their structure growing increasingly similar to that occurring in control plots.

## Materials and methods

### Site descriptions

Our study was conducted in Whangapoua Harbour and streams in the surrounding catchment, on the eastern side of the Coromandel Peninsula, North Island, New Zealand (Fig. 1). The catchment covers ~42 km$^2$ and is dominated by steep topography with surface and subsurface soils of clay and yellow–brown earths (Wright-Stow and Quinn 2009). The region is frequently exposed to cyclonic storms, with high mean annual rainfall (from ~2400 mm at ridge tops to ~1700 mm in the lower catchment) and highly variable stream flows (Boothroyd *et al.* 2004; Wright-Stow and Quinn 2009). Whangapoua Harbour covers an area of ~13 km$^2$, enclosed by a sandspit, with wind and wave action predominantly from the north-east (Hewitt *et al.* 2003). It experiences semi-diurnal tidal cycles, with an average range of 3 m, such that a large portion of the harbour is exposed during low tides (Hewitt *et al.* 2003).

Three third-order stream sites and three estuary sites were chosen for study. Two of the stream sites were located in the Opitonui River, and one in the Awaroa Stream (Fig. 1). The headwaters of the Opitonui River flow through native forest, whereas those of the Awaroa Stream are in pine plantation forest. Forest (either native or pine) occurs adjacent to all study reaches.
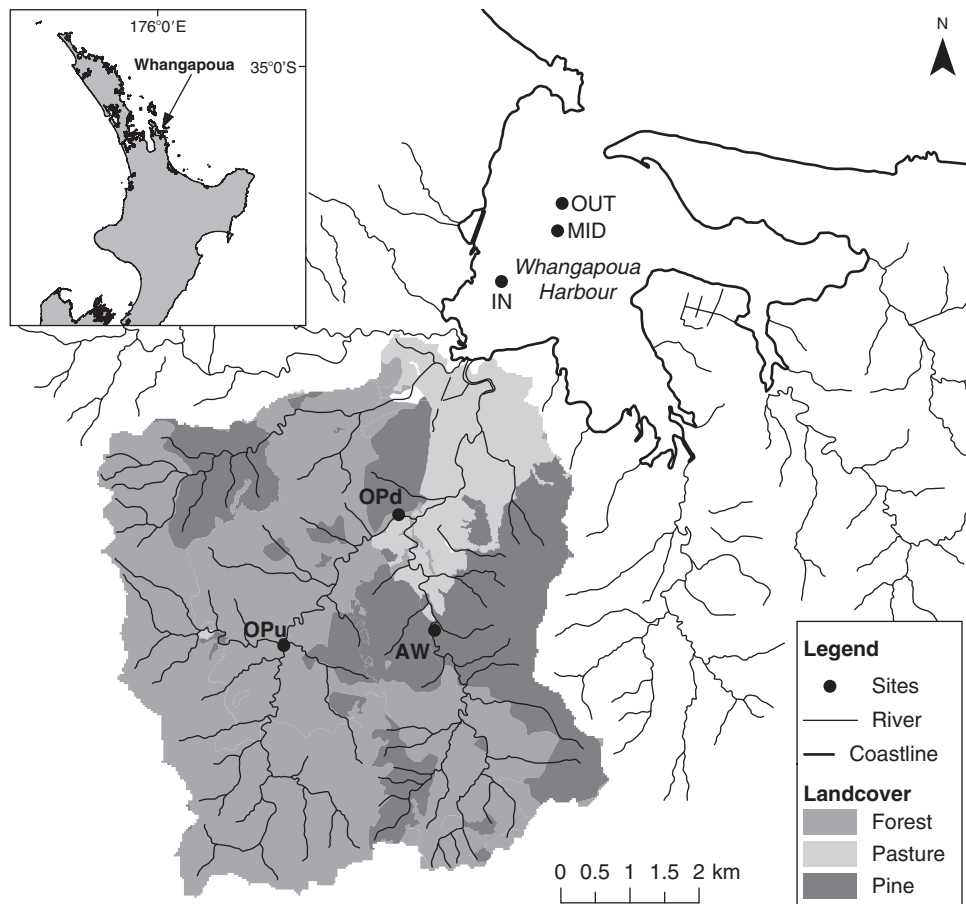
**Fig. 1.** Location of study sites on the eastern side of the Coromandel Peninsula, North Island, New Zealand. Stream sites were in the Opitonui River (OPu, upstream, and OPd, downstream) and Awaroa Stream (AW), and estuarine sites were located across a hydrodynamic gradient from inner to outer portions of the Whangapoua Harbour. Only those streams discharging to the harbour are shown, and land-cover shading is only shown for the study catchment.

The estuary sites were in the inner, middle and outer harbour, across a gradient from relatively low to relatively high tidal and wave-induced hydrodynamic energy (Hewitt *et al.* 2003). All estuary sites were located on the mid-intertidal sandflats and experienced similar inundation periods of 3–4 h in a tidal cycle (Hewitt *et al.* 2003; van Houte-Howes *et al.* 2004).

*Sediment addition*

In the recent past, large amounts of terrigenous sediment have been observed entering the aquatic environment during storms in the region (Quinn *et al.* 1995; Marden *et al.* 2006; J. Hewitt and S. Thrush, pers. obs.). Sediment was added to experimental plots to mimic the type and deposit thickness that frequently occur in these ecosystems as a result of landslides and runoff during such large storms.

The experiment was conducted over 16 days in austral spring (from mid-November 2006). The terrigenous sediment was predominantly composed of fine particles (diameter <2 mm, see Zweig and Rabení 2001) at the point of collection from land within the catchment and comprised 7% small gravel (2–8 mm), 14% coarse sand (500 µm – 2 mm), 10% medium sand (250–500 µm), 20% fine sand (63–250 µm), 39% silt (3.9–63 µm) and 10% clay (<3.9 µm). Within each site across both systems, this sediment was deposited onto five experimental plots to provide a layer ∼5 mm thick. Manipulated plots were selected randomly from amongst 10 plots, each ∼5 m$^2$ and at least 5 m apart. The remaining plots served as controls.

In streams, all manipulated plots were located in the middle of the channel in 'run' habitats (representative of the most common habitats for streams in the region, and with hydraulic conditions between those occurring in 'riffles' and 'pools'). A wooden diversion fence was erected on the upstream side of each plot to reduce current velocity while adding sediment, and removed after the sediment had settled onto the stream bed. At estuary sites, sediment was added to plots during low tide. Prior to addition, the sediment was mixed with seawater and buffered to restore the pH of the mixture to that of seawater. A metal ring (250-cm diameter, 5 cm high, pushed to a depth of ∼2 cm into the substratum) was deployed around the boundaries of each estuary plot to contain the added sediment. These rings were also deployed around control plots, left in place over one tidal cycle and then removed carefully.

## Physicochemical parameters

At the beginning of the experiment (Day 0), wetted channel widths of stream reaches were measured across 10 equidistant transects, and streambed surficial sediment particle sizes were determined following Wolman (1954) by classifying Wentworth scale sizes of 20 random particles per plot. At each stream plot, near-bed velocity (Model PVM-2A Flow Velocity Meter, Montedoro Whitney Inc., San Luis Obispo, CA, USA), electrical conductivity, pH and water temperature (water quality meter, Horiba, Kyoto, Japan) were measured on Days 0, 7 and 14. On the same days, the amounts of suspendable inorganic sediment within each plot were determined from a water sample collected after vigorously disturbing the streambed to a depth of ~5 cm within a 0.045-m$^2$ corer (Quinn *et al.* 1997). The inorganic fractions were determined by first measuring the weight of samples dried at 60°C, then ashing the samples at 400°C and reweighing. Masses of suspendable inorganic sediment per unit area of streambed were calculated.

Within each estuarine plot, three small cores of surface sediment (4.5 cm$^2$ × 2 cm deep) were randomly collected and pooled for analyses of particle size (Days 0, 7 and 15). A representative 5-g subsample of this sediment was wet-sieved into different-sized fractions (using mesh sizes of 2000, 500, 250, 150 and 63 μm), after digestion in 9% hydrogen peroxide to remove organics and disperse small particles. Pipette analysis was then used to separate the <63-μm fraction into silt (>9–63 μm) and clay (<9 μm) (Gatehouse 1971).

## Invertebrate community structure

Invertebrates were collected after 1 week (7 days), to assess the effect of sedimentation on community structure (relative short-term resistance of each site), and after ~2 weeks (14 days for streams and 16 days for estuary), to determine the relative rates of recovery towards control structure at each site. Across both systems, two samples were collected from each plot on each sampling occasion. A corer (0.045-m$^2$ area) and a 500-μm hand net were employed to collect invertebrate samples from streams, by first collecting and washing the upper layer of stones within the corer into the net and then agitating the stream bed contained within the corer and using the net to collect all animals in the water column, which were then preserved with 70% iso-propyl alcohol.

At estuarine sites, invertebrate samples were collected using sediment corers (0.013 m$^2$ × 15 cm deep). These samples were sieved with a 500-μm-mesh screen, and all macrofauna was preserved in 70% iso-propyl alcohol and stained with 0.2% Rose Bengal. Core holes were filled with sieved, defaunated azoic sand to prevent slumping by the surrounding sediment after each sampling event. During all sampling, care was taken to avoid previously sampled areas, and the cores were taken at least 30 cm from the boundaries of the plots to minimise edge effects. Less than 5% of each experimental plot was directly affected by sampling over the duration of the experiments. For both systems, invertebrates were identified to the lowest practical level of taxonomic resolution (usually species) and counted.

Although we did not collect any invertebrate samples before sediment addition, we randomly assigned our replicated experimental plots to the different treatments (sediment addition or control). Consequently, our statistical analyses provide assessments of the probability that differences in response variables between sediment addition and control plots were greater than any pre-existing differences between experimental plots (Quinn and Keough 2002).

## Statistical analyses

Data from stream and estuarine systems were analysed separately, with partial eta squares ($\eta^2$) calculated for all main and interaction terms in each analysis to allow comparisons of effect sizes between systems. The effect size indicates the relative importance of each main or interaction effect, with partial $\eta^2$ being the proportion (within a range of 0–1) of total variance in the response variable accounted for by the variance between predictor groups, after controlling for other variables in the model (Cohen 1988). Repeated-measures analysis of variance (ANOVA) was used to test for the effects of factors (with sediment addition and site as the fixed between-subjects factors, and time as the fixed within-subjects factor, and by using Pillai's Trace values to assess significance) on the total densities and taxon richness of invertebrate communities in each system. Densities and taxon richness counted from the two cores taken from within each plot at each collection time were averaged before conducting analyses of invertebrate data. Box plots and Levene's tests were used to examine data for normality and homogeneity of variance and log-transformations were applied before analyses where required. *Post hoc* Tukey's tests were conducted to determine where differences occurred within those factors that had a significant main effect.

Repeated-measures multivariate analysis of variance (MANOVA) was used to test for differences in community structure as a result of the same factors as used in repeated-measures ANOVAs (i.e. site × sediment addition × time). For estuarine community structure, separate MANOVAs (site × sediment addition) were also conducted for each time to facilitate interpretation, as the site × sediment addition × time interaction was highly significant in the initial repeated-measures MANOVA. Only taxa contributing at least 1% to the total abundances within either system and/or occurring in at least 50% of all samples within each system were included in the MANOVAs (adding up to >90% of the total counts within both systems), because these common taxa have the strongest effects on patterns in community structure. We further explored which common taxa contributed most to any overall significant sediment effects by examining the between-subjects effects (for sediment addition and site × sediment addition terms) and within-subjects contrasts (for site × sediment addition × time interaction) in the MANOVA (e.g. Matthaei *et al.* 2010). Non-metric multidimensional scaling (nMDS) was used to graphically display the differences in community structure as a result of sediment addition, and between sites and times, within each system. Here, log-transformations were employed to reduce the influence of the most abundant taxa (Clarke and Warwick 1994) before calculating Bray–Curtis dissimilarities among simplified community datasets.

Those traits of invertebrates that were most likely to be influenced by pulsed sediment additions were analysed (Table 1). Traits were assigned to taxa on the basis of an extensive review of relevant literature and the authors' expert
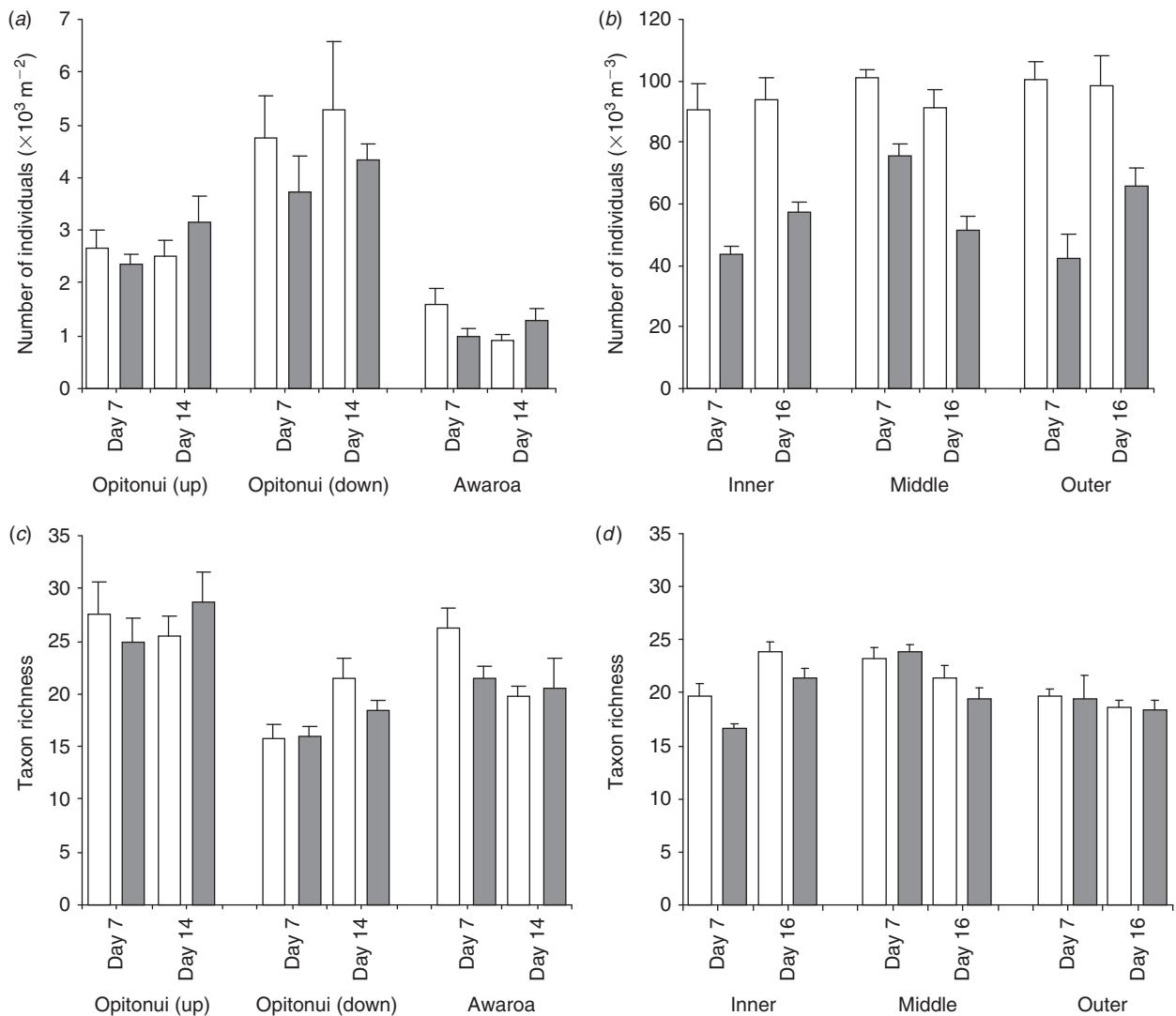
**Fig. 2.** Densities of invertebrates at (*a*) stream sites and (*b*) estuarine sites, and taxon richness at (*c*) stream sites and (*d*) estuarine sites. Mean values plus s.e. (*n* = 5 plots) are shown over time. Bars representing sediment treatment are shaded and controls unshaded. Note the intersystem differences in units of measurement for densities.

opinions. Several modalities were derived for each trait category (e.g. the trait category 'relative size' was divided into three ranges within each system). A 'fuzzy coding' approach was used to quantify the affinity for each taxon for each trait modality (Chevenet *et al.* 1994). Within each plot and time, the proportional representation of traits was calculated by multiplying the average abundance of each taxon by the affinity of that taxon for each trait modality, then summing the derived values across all taxa to obtain abundance-weighted relative trait frequencies for each trait modality, using ADE-4 2001 Release (http://pbil.univ-lyon1.fr/ADE-4/ADE-4.html, accessed 6 July 2010).

Differences in the representation of traits between the communities within plots were tested in two ways. First, repeated-measures MANOVAs and *post hoc* tests were conducted, as for community-structure data. Second, because most of the same trait modalities occurred in both systems, trait analyses allowed us to test whether the direction of the sedimentation effect on these modalities was consistent across these systems (as well as

across sites and times within each system), using univariate Wilcoxons signed-rank tests. Although this required a large number of statistical tests and the results should be interpreted with some caution, these non-parametric tests were conservative and no Bonferroni corrections were applied to adjust significance levels (Perneger 1998; Nakagawa 2004). All univariate analyses and MANOVAs were conducted using SPSS version 16.0 (IBM, Armonk, NY, USA), and nMDS analysis was conducted using PRIMER version 6 (PRIMER-E Ltd., Plymouth, UK).

## Results

### Abiotic environment

In streams, current velocities up to $0.58\ \mathrm{m\ s^{-1}}$ were recorded and wetted channel widths ranged from 3.2 to 10.1 m. Prior to experimental sediment addition, the streambed surficial sediment particle sizes in all stream plots were predominantly small

**Table 2. Summary of results for repeated-measures ANOVAs examining effects of site, sediment addition and time on the (log-transformed) total density and taxonomic richness of invertebrate communities within streams and the estuary**

Significant *P*-values (<0.05) are shown in bold

| System and source | d.f. | Density | | | Taxon richness | | |
|---|---|---|---|---|---|---|---|
| | | *F*-ratio | *P*-value | Partial $\eta^2$ | *F*-ratio | *P*-value | Partial $\eta^2$ |
| Streams | | | | | | | |
| Between subjects | | | | | | | |
| Site | 2 | 53.296 | **<0.001** | 0.816 | 16.520 | **<0.001** | 0.579 |
| Sediment addition | 1 | 0.439 | 0.514 | 0.018 | 0.639 | 0.432 | 0.026 |
| Site × sediment addition | 2 | 0.373 | 0.693 | 0.030 | 0.332 | 0.721 | 0.027 |
| Within subjects | | | | | | | |
| Time | 1 | 0.207 | 0.653 | 0.009 | 0.148 | 0.704 | 0.006 |
| Site × time | 2 | 1.473 | 0.249 | 0.109 | 4.492 | **0.022** | 0.272 |
| Sediment addition × time | 1 | 7.889 | **0.010** | 0.247 | 1.814 | 0.191 | 0.070 |
| Site × sediment addition × time | 2 | 1.576 | 0.228 | 0.116 | 2.085 | 0.146 | 0.148 |
| Estuary | | | | | | | |
| Between subjects | | | | | | | |
| Site | 2 | 1.818 | 0.184 | 0.132 | 5.121 | **0.014** | 0.299 |
| Sediment addition | 1 | 89.710 | **<0.001** | 0.789 | 2.536 | 0.124 | 0.096 |
| Site × sediment addition | 2 | 1.316 | 0.287 | 0.099 | 1.027 | 0.373 | 0.079 |
| Within subjects | | | | | | | |
| Time | 1 | 1.051 | 0.316 | 0.042 | 0.075 | 0.786 | 0.003 |
| Site × time | 2 | 10.288 | **0.001** | 0.462 | 21.797 | **<0.001** | 0.645 |
| Sediment addition × time | 1 | 2.971 | 0.098 | 0.110 | 0.472 | 0.499 | 0.019 |
| Site × sediment addition × time | 2 | 6.479 | **0.006** | 0.351 | 1.024 | 0.374 | 0.079 |

to large gravels, with some cobbles and minimal fine sediment. The predominantly fine terrigenous sediment added to stream plots visibly filled in interstitial spaces and coated upper surfaces of larger substrates. At the end of the experiment, this sediment was still visible within interstitial spaces, but had largely been washed from protruding substrates. The mean suspendable-sediment concentration in treated plots was $3620\,\mathrm{g\,m^{-2}}$ after 7 days, which had declined to $1940\,\mathrm{g\,m^{-2}}$ after 14 days, compared with $750\,\mathrm{g\,m^{-2}}$ in control plots over the duration of the experiment. The values of pH (ranging from 7.0 to 7.8) and electrical conductivity (ranging from 100 to $124\,\mu\mathrm{S\,cm^{-1}}$) were similar among sites, and between control and sediment-addition plots within sites. During the experiment, the spot water temperatures were consistently lower at the downstream Opitonui site (15.0–16.7°C) than at both the upstream Opitonui site (17.3–19.5°C) and the Awaroa site (15.4–20.3°C).

The terrigenous sediment added to estuarine plots formed layers that smothered the underlying natural substrates, which were predominantly fine to medium sands at all estuarine sites. During the experiment, these sediment layers were broken apart, by the action of tides and waves and bioturbation by resident invertebrate fauna, and buried by the movement of surrounding sediment into plots. The fine sediment was broken up and buried most rapidly at the outer site. Across all estuarine sites, the added sediment was sometimes visible, as an intact layer covered by ~5 mm of sand, within the cores used to collect invertebrates at the end of the experiment.

*Invertebrate community structure*

Across all stream sites, sediment addition resulted in lower invertebrate densities in treated plots than in controls after

7 days, but not after 14 days (Fig. 2*a*, Table 2). Reductions in invertebrate densities as a result of sediment addition were much more pronounced at estuarine sites than at stream sites, with highly significant differences between treated and control plots after both 7 and 16 days (Fig. 2*b*, Table 2). The effect size of sediment addition on invertebrate densities across both times was much smaller in the streams than in the estuary. Within both streams and the estuary, there were no detectable changes in taxon richness as a result of the addition of sediment, with very small effect sizes for sediment addition in both systems (Fig. 2*c*, *d*, Table 2).

In total, 111 taxa were identified from stream sites, and 73 taxa from estuarine sites, during the experiment. Of these, 21 stream taxa and 18 estuarine taxa were relatively abundant and/or common (cumulatively contributing >90% of the overall abundances in either system), so these taxa were used in the analyses of community structures.

The structures of macroinvertebrate communities in streams were highly variable, both spatially and temporally (Fig. 3*a*, Table 3). Despite a large overall effect size for sediment addition, the differences between communities in control and sediment-addition plots were significant ($P < 0.05$) only at the upstream Opitonui River site. The overall effects of sediment addition on stream communities did not change between 7 and 14 days. Sediment addition had a significant main effect on 8 of the 21 taxa in the simplified stream-community dataset; however, for most of these taxa, the effects were not consistent between sites and times (as reflected in the relatively high number of significant interactions between sediment addition and these two factors in the between-subjects effects or within-subjects contrasts for these taxa; see Table 3). The only exceptions were that consistently lower densities of the mayfly
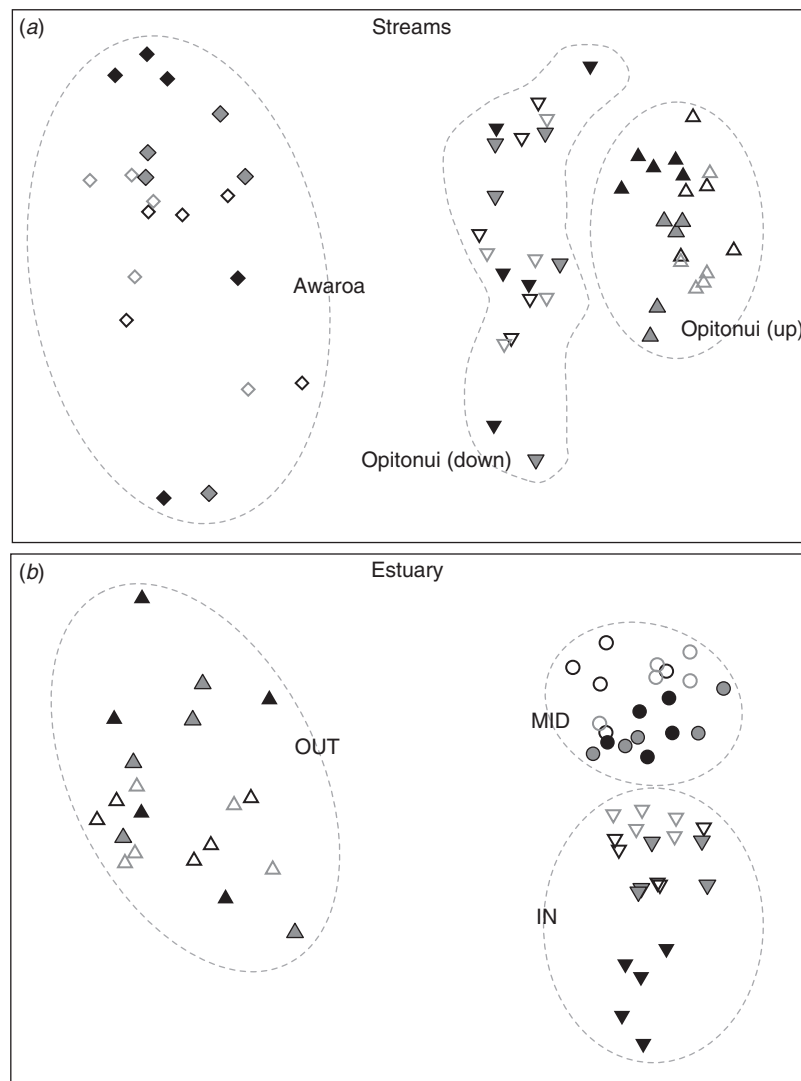
**Fig. 3.** Multidimensional ordinations (nMDS) of (*a*) stream communities (stress = 0.11) and (*b*) estuarine communities (stress = 0.09) 1 week (black symbols) or 2 weeks (14 days in streams and 16 days in estuary, grey symbols) after sediment addition. Symbols representing each site are grouped within the labelled ellipses; sediment treatment symbols are shaded and control symbols unshaded.

*Zephlebia* spp. and caddisfly *Pycnocentrodes* spp., and higher densities of the mayfly *Rallidens mcfarlanei*, occurred in treated plots than in controls.

As for streams, the structures of invertebrate communities at the three estuarine sites all significantly differed from each other (Fig. 3*b*, Table 3). Of particular note were the following patterns: most Lumberineridae worms occurred at the inner site, most of the amphipod *Parawaldeckia* spp. and the bivalve *Nucula hartvigiana* were found at the middle site, and comparatively low densities of the spionid worms *Prionospio aucklandica* and the bivalve *Macomona liliana*, and comparatively high densities of the bivalve *Paphies australis*, the isopod *Exosphaeroma falcatum* and the amphipod *Waitangi brevirostris* occurred at the outer site. Also similar to streams, the overall

effect size of sediment addition was large at the estuary sites. However, in contrast to streams, on Day 7, the differences in the structure of invertebrate communities as a result of sediment addition were significant ($P \leq 0.009$) at all sites. After 16 days, the communities in plots to which sediment had been added in the outer harbour were similar to those in controls ($P = 0.108$), although there were still significant effects as a result of sediment addition for the communities at the inner and middle sites ($P = 0.002$ in both cases; Fig. 3*b*). Although tests for between-subjects effects indicated that there were significant overall effects of sediment addition for 9 of the 18 taxa in the simplified community dataset, this effect was consistent across sites for only three of these taxa (*E. falcatum*, *N. hartvigiana* and *P. australis*), which were all negatively influenced by sediment.

**Table 3. Summary of results of repeated-measures MANOVAs examining effects of site, sediment addition and time on invertebrate community structure within streams and the estuary**

Significant *P*-values (<0.05) are shown in bold. Also shown are the number of taxa from simplified datasets (of a total of 21 taxa in streams, 18 taxa in estuary) for which each main and interaction term was significant, from either within-subjects contrasts or between-subjects effects

| System and source | d.f. | *F*-ratio | *P*-value | Partial $\eta^2$ | No. of taxa |
|---|---|---|---|---|---|
| Streams | | | | | |
| Between subjects | | | | | |
| Site | 42 | 18.341 | **<0.001** | 0.987 | 20/21 |
| Sediment addition | 21 | 3.341 | 0.125 | 0.946 | 8/21 |
| Site × sediment addition | 42 | 2.763 | **0.044** | 0.921 | 5/21 |
| Within subjects | | | | | |
| Time | 21 | 16.118 | **0.008** | 0.988 | 9/21 |
| Site × time | 10 | 9.072 | **<0.001** | 0.974 | 6/21 |
| Sediment addition × time | 21 | 0.715 | 0.732 | 0.790 | 5/21 |
| Site × sediment addition × time | 10 | 0.763 | 0.744 | 0.762 | 0/21 |
| Estuary | | | | | |
| Between subjects | | | | | |
| Site | 36 | 63.035 | **<0.001** | 0.993 | 18/18 |
| Sediment addition | 18 | 17.062 | **<0.001** | 0.978 | 9/18 |
| Site × sediment addition | 36 | 12.617 | **<0.001** | 0.966 | 5/18 |
| Within subjects | | | | | |
| Time | 18 | 12.719 | **0.001** | 0.970 | 5/18 |
| Site × time | 36 | 10.050 | **<0.001** | 0.958 | 7/18 |
| Sediment addition × time | 18 | 3.822 | **0.039** | 0.908 | 3/18 |
| Site × sediment addition × time | 36 | 3.573 | **0.004** | 0.889 | 8/18 |

*Biological traits*

Even though the overall effect sizes of sediment addition on representation of species traits in benthic macroinvertebrate communities were large in both systems, trait analyses were less sensitive than community-structure analyses for detecting effects of sediment addition, because of the high spatial and temporal variability of effects on traits, particularly in the estuary (Table 4, see Table S1 available as an Accessory Publication to this paper). The results of univariate analyses showed that in both systems, there were few consistent declines or increases in the proportions of taxa possessing each trait modality as a result of sediment addition, and across the estuary there were contrasting responses to sedimentation among sites for some trait modalities (see Table S1). In streams, the only consistent exception from this rule was the presence of lower abundances of animals that inhabit the water column in treated plots than in controls after 7 days, whereas across all treated estuarine plots, there were lower abundances of deposit feeders and higher abundances of scavengers than in controls after either 7 or 16 days.

**Discussion**

No previously published study has simultaneously examined the impacts of sedimentation on benthic invertebrate communities in streams and estuaries. Further, no previous study has compared the impacts of a common stressor on a suite of invertebrate species trait modalities between these two linked ecosystems. The communities in relatively fast-flowing runs of streams were less sensitive to pulsed inputs of terrigenous sediment than those in the adjacent estuary, at least in the short-term, when subjected to a similar-magnitude disturbance. In streams, the addition of

sediment did not result in the predicted changes in the overall community structure. Invertebrate densities were reduced by the addition of sediment to stream plots after 1 week, but had recovered to levels similar to control plots another week later. In contrast, sediment addition caused large reductions in invertebrate densities and changes in overall invertebrate community structure at all estuarine sites 7 days after additions. After 16 days, recovery from these impacts was evident only at the outer estuarine sites, although the invertebrate densities in treated plots remained low across all estuarine sites at this time. Contrary to predictions, there were no reductions in taxon richness as a result of sediment addition in either streams or the estuary, and only a relatively low proportion of the common taxa present within either system had consistently lower densities in plots with sediment added than in control plots. In most cases, the particular traits that benthic invertebrates possessed were not useful for predicting impacts from the small-scale pulsed sediment inputs.

Disturbance exerts significant influence on the communities in both streams and estuaries (see Lake 1990; Wall *et al.* 2005), and numerous studies have shown that benthic communities in both of these ecosystems are detrimentally affected by pulsed inputs of fine terrigenous sediment (e.g. Thrush *et al.* 2003; Lohrer *et al.* 2006*b*; Matthaei *et al.* 2006; Townsend *et al.* 2008). However, ecosystem responses to disturbance are controlled by the magnitude, timing, frequency and duration of the disturbance, as well as the physical, chemical and biological conditions that exist before and after the disturbance (Lake 2000; Molinos and Donohue 2009). The magnitude of response to similar sedimentation events may vary even within types of ecosystem. Previous studies in streams have demonstrated that communities that were largely algal-based were more

**Table 4.   Summary of results of repeated-measures MANOVAs examining effects of site, sediment addition and time on representation of trait modalities within streams and the estuary**

Significant *P*-values (<0.05) are shown in bold. Also shown are the number of trait modalities (of a total of 23 in the streams, 21 in the estuary) for which each main and interaction term was significant, from either within-subjects contrasts or between-subjects effects. See Table S1 in Accessory Publication for those modalities for which sediment addition had significant main or interaction effects

| System and source | d.f. | *F*-ratio | *P*-value | Partial $\eta^2$ | No. of modalities |
|---|---|---|---|---|---|
| Streams | | | | | |
|  Between subjects | | | | | |
|   Site | 46 | 1.053 | 0.530 | 0.890 | 16/23 |
|   Sediment addition | 23 | 9.033 | 0.104 | 0.990 | 6/23 |
|   Site × sediment addition | 46 | 2.295 | 0.149 | 0.946 | 0/23 |
|  Within subjects | | | | | |
|   Time | 23 | 1.522 | 0.472 | 0.946 | 11/23 |
|   Site × time | 46 | 2.767 | 0.101 | 0.955 | 9/23 |
|   Sediment addition × time | 23 | 0.467 | 0.860 | 0.843 | 0/23 |
|   Site × sediment addition × time | 46 | 0.661 | 0.804 | 0.835 | 1/23 |
| Estuary | | | | | |
|  Between subjects | | | | | |
|   Site | 42 | 27.750 | **<0.001** | 0.991 | 20/21 |
|   Sediment addition | 21 | 2.023 | 0.260 | 0.914 | 8/21 |
|   Site × sediment addition | 42 | 7.080 | **0.001** | 0.967 | 12/21 |
|  Within subjects | | | | | |
|   Time | 21 | 4.927 | 0.066 | 0.963 | 0/21 |
|   Site × time | 42 | 0.855 | 0.663 | 0.782 | 9/21 |
|   Sediment addition × time | 21 | 1.322 | 0.435 | 0.874 | 2/21 |
|   Site × sediment addition × time | 42 | 1.823 | 0.155 | 0.884 | 7/21 |

significantly affected by sedimentation than were those with a detritus base (Schofield *et al.* 2004), and the greatest impacts of fine-sediment addition on macroinvertebrate communities occurred where pre-existing fine-sediment cover was comparatively low and richness and diversity of the community were comparatively high (Matthaei *et al.* 2006). Lohrer *et al.* (2006*b*) found that invertebrate communities in coarse sand outside of an estuary were more sensitive to fine-sediment additions than those which lived in muddier sediments within the estuary, whereas Norkko *et al.* (2002) concluded that the impacts of sediment addition on invertebrate communities within an estuary persisted longer at sheltered muddy sites than at exposed sandy sites where a storm acted to rapidly disperse the sediment.

Given the fundamental differences in structure and function of invertebrate communities in streams and soft-bottomed estuaries, it was not unexpected that there would be some differences in community response to the same disturbance between these two ecosystems. Factors that contribute to the intersystem differences in antecedent communities, rates of removal of added sediment from treated plots, and responses of communities to the added sediment include differences in hydrodynamics (cf. Norkko *et al.* 2002; Hewitt *et al.* 2003; Thrush *et al.* 2003), composition of underlying substrate (cf. Hewitt *et al.* 2003; Lohrer *et al.* 2006*b*; Matthaei *et al.* 2006) and the behaviour of the added sediment (Xu *et al.* 2008).

*Invertebrate community structure*

Invertebrate communities in streams of New Zealand are generally dominated by mobile insect larvae living among relatively heterogenous streambed substrates (Collier and Winterbourn 2000). The macroinvertebrate communities at the partially shaded stream sites used for our experiment are likely to depend on a mix of both allochthonous detritus and autotrophic production (Hicks 1997), with grazers being most abundant and few dietary specialists being present. In contrast, estuarine invertebrate communities were dominated by infauna, mainly polychaetes, crustaceans and molluscs living in relatively uniform marine sediments (*sensu* Wall *et al.* 2005; Dittman 2007). Estuarine food webs are primarily driven by benthic microalgae and pelagic inputs (Middelburg *et al.* 2000; Countway *et al.* 2007), with filter- and deposit-feeders being dominant and more dietary specialists being present than in streams. Mesoscale dispersal in streams occurs largely by larval drift, and adult flight and oviposition between reaches, whereas in estuaries diminutive larvae may disperse large distances on currents and tides. However, at the spatial and temporal scales of our experiment, resident macrofauna may have actively moved between plots and the surrounding habitat patches in response to sediment addition in both systems (Downes and Keough 1998).

The apparent low sensitivity of stream communities to sediment addition contrasts with the results of most previously published studies conducted at various spatial scales (see Ryan 1991; Wood and Armitage 1997; and references therein, for examples). High loads of fine sediment, as a result of increased contributions from large-scale land-use changes over long periods of time, have frequently and consistently been implicated with large changes in the structure of benthic communities in streams (e.g. Cline *et al.* 1982; Quinn and Hickey 1990; Kaller and Hartman 2004; Niyogi *et al.* 2007). However, synergistic interactions between excess sediment and other ecosystem stressors caused by land-use changes (Lemly 1982; Townsend *et al.* 2008) make it difficult to disentangle other impacts from

those caused by sedimentation, using correlative field studies across land-use gradients. Manipulative sediment-addition experiments, with appropriate controls, are required to directly test sedimentation effects.

Most manipulative experiments that have directly examined the effects of sedimentation on stream invertebrate communities were performed in artificial channels in the field. This allowed sediment to be uniformly added to the entire channel, and precluded the presence of refuges that were free from sedimentation, typically resulting in large changes to invertebrate community structure (e.g. Shaw and Richardson 2001; Suren and Jowett 2001; Connolly and Pearson 2007; Molinos and Donohue 2009). These experimental studies are useful in assessing patterns of response to sedimentation, because they closely approximate natural conditions and allow control of both the magnitude of the disturbance and potentially confounding variables. However, the results from experiments in artificial channels cannot be directly extrapolated to natural stream reaches (Lamberti and Steinman 1993; Matthaei *et al.* 2006) and experiments within streams are also required to assess sedimentation effects under more natural conditions.

Similar to the present experiment, sediment was added to small plots within natural streams by Schofield *et al.* (2004) and de Castro Vasconcelos and Melo (2008). This sediment adversely affected invertebrate communities, but the magnitude of effect varied depending on food-web structure (Schofield *et al.* 2004) and the size class of the added sediment (de Castro Vasconcelos and Melo 2008). Matthaei *et al.* (2006) conducted a larger-scale experiment where sediment was added to the entire length of 50-m stream reaches in New Zealand. These additions caused significant reductions in overall invertebrate taxon richness; however, the reductions were not as pronounced as most of those for experiments conducted using artificial channels. This may have been because of the existence of refugia within each reach that were largely unaffected by the added sediment (Matthaei *et al.* 2006). In the present study, only a minor portion of the stream beds were covered by the added sediment, and unaffected refugia were readily available immediately outside of experimental plots. We acknowledge that the processes involved in impact and recovery are likely to change as larger areas are covered by sediment. Pulsed inputs of sediment of varying sizes, up to large landslides, occur frequently in the study streams (Quinn *et al.* 1995; Marden *et al.* 2006) and the benthos had most likely adapted to cope with this type of disturbance, via the use of refuges (Matthaei *et al.* 2006) and physiological adaptations (Ryan 1991; Farnsworth and Milliman 2003).

Although some estuarine species also have mechanical and physiological adaptations that allow them to survive sedimentation of the magnitude commonly encountered in their environment (Hinchey *et al.* 2006), we speculate that this may be less of a selective pressure in estuaries than in streams. In estuaries, changes in the structure of invertebrate communities have been observed in several studies where terrigenous sediment has been added to experimental plots (e.g. Norkko *et al.* 2002; Thrush *et al.* 2003; Lohrer *et al.* 2004). There are several possible reasons for estuarine communities being more sensitive to pulsed fine-sediment input than were communities in stream runs during the present study. In all treated estuarine plots, the

fine terrigenous sediment layer effectively blanketed the entire area of the underlying sandy substrate. Even thin layers of terrigenous sediment can reduce interstitial water circulation and the supply of oxygen to underlying estuarine sediments (Sarriquet *et al.* 2007; Cummings *et al.* 2009), which is likely to have contributed to the observed effects on estuarine communities. In contrast, although the sediment added to streams filled interstitial spaces around gravels, larger particles were able to protrude above this layer and therefore continued to provide some oxygenated habitat heterogeneity in treated stream plots. There was less hydrodynamic power to move the added sediment because of tides and waves in the estuary than from stream flow, which was further hindered by both the coagulation that occurred when the fine sediment mixed with seawater (Xu *et al.* 2008) and the periodic emersion of sites during low tides. In the estuary, much of the fine-sediment layer was not removed from treated plots, instead persisting and being buried by bed-load movement of surrounding sand when immersed (see Hewitt *et al.* 2003).

Conversely, in the manipulated stream runs, the fine sediment was washed downstream by the constant and unidirectional flow of water. This sediment is likely to accumulate and persist for longer in slow-flowing pools than in runs, and the impacts on invertebrate communities and community recovery are likely to differ between pools and runs. The unidirectional stream flow would have also provided a constant supply of new colonists to stream plots from upstream areas unaffected by sedimentation. Increased sedimentation has been shown to promote drift of stream invertebrates (Culp *et al.* 1986; Suren and Jowett 2001; Molinos and Donohue 2009); however, in small plots, emigrants may be continually replaced by animals from upstream sources (Townsend *et al.* 1997).

In addition to the differences in the responses of stream and estuarine invertebrate communities to sediment addition, there were also differences in community response and recovery among estuarine sites, associated with the increase in hydrodynamic energy from the inner to outer site (Hewitt *et al.* 2003). Although all of the estuarine sites had similar sandy substrates and were immersed for similar amounts of time during each tidal cycle, there were changes in species dominance across the hydrodynamic gradient. These changes resulted in differences in benthic community response to sediment addition, because the dominant species within each community were usually among those most obviously affected by sediment. However, hydrodynamic energy primarily influences the degree to which estuarine communities are affected by sedimentation via its ability to aid recovery by moving sediments and transporting colonists (Hewitt *et al.* 2003; Thrush *et al.* 2003). Ours was only a relatively short-term experiment; however, the dispersal and/or burial of added sediment, and recovery of invertebrate communities from sedimentation, were more rapid at the outer site than at more inner sites. This finding is consistent with the patterns observed in longer-term experiments conducted at estuarine sites across hydrodynamic gradients (see Norkko *et al.* 2002; Hewitt *et al.* 2003; Thrush *et al.* 2003).

### Biological traits

In both systems, the use of species trait analyses was less sensitive than the use of community-structure analyses for

distinguishing the effects of sediment addition, because there were few consistent effects on any particular trait modality. Our results contrast with previous studies in streams, which found that the representations of certain species trait modalities were significantly correlated with fine-sediment cover and that analysing a suite of traits was equally sensitive as, or more sensitive than community-structure analyses, for detecting sediment impacts (e.g. Richards *et al.* 1997; Rabení *et al.* 2005; Dolédec *et al.* 2006; Townsend *et al.* 2008). Susceptibility of estuarine macrofauna to sedimentation has also been shown to be related to specific traits, including mobility (e.g. Norkko *et al.* 2002), animal size and habitat preference (e.g. Lohrer *et al.* 2004), and feeding groups (e.g. Lohrer *et al.* 2006*a*). However, no previous study has assessed the relative influence of sedimentation effects on a wide suite of traits in estuarine communities. In some streams, sediment cover has been demonstrated to be predictive of certain behavioural and physiological traits of resident fauna (Rabení *et al.* 2005; Townsend *et al.* 2008), whereas in other streams, life-history traits were found to be most sensitive to sedimentation (Richards *et al.* 1997; Dolédec *et al.* 2006). In these correlative field studies, the impacts of sedimentation on stream fauna occurred at reach- to catchment-scales and over relatively long periods of time (i.e. after several years to decades of land-use intensification). Reductions in the representation of invertebrates possessing particular traits, especially life-history traits, are most likely to occur owing to press disturbances at relatively broad spatial scales and over intergenerational timescales. However, there is limited information about the spatial and temporal thresholds for sedimentation effects on populations and communities in different aquatic systems (but see Norkko *et al.* 2002; Kaller and Hartman 2004; Lohrer *et al.* 2006*b*; Larsen *et al.* 2009). Larger-scale studies would be required to assess how more widespread sedimentation pulses affect aquatic communities.

### Implications for future research and management

It is widely acknowledged that excessive sedimentation owing to human activities is a major contributor to declines in the condition of aquatic ecosystems (GESAMP 1994; Henley *et al.* 2000; Owens *et al.* 2005). Globally, rivers discharge more than 20 billion tonnes of suspended and dissolved solids annually and human activity may be directly or indirectly responsible for 80–90% of the sediment delivered to the coast (Farnsworth and Milliman 2003). However, there are only relatively few legislation and management guidelines that relate to sediment discharged into waterbodies, with many countries having little or no specific legislation (Köthe 2003; Owens *et al.* 2005). More research on sediment thresholds for taxa in different ecosystems is required to develop sediment-quantity guidelines for protection of the values and ecological condition of aquatic ecosystems. Management guidelines are often set to protect freshwater values and ecology, with the implicit assumption that these guidelines will be stringent enough to ensure that downstream marine ecosystems will also be adequately protected. Our results have demonstrated that this assumption is incorrect for sedimentation impacts. In those cases where human activities are likely to cause impacts across multiple ecosystems, guidelines should be set to protect the most sensitive systems. Linkages between ecosystems must also be considered when developing management options, and controlling the source of sedimentation is usually preferable and less costly than on-going management of downstream impacts (Reid and Page 2003; Quinn *et al.* 2004; Owens *et al.* 2005). We echo the call of others for more research recognising the interconnectedness of neighbouring freshwater and estuarine ecosystems, which have historically been studied independently of each other.

### References

Airoldi, L. (2003). The effects of sedimentation on rocky coastal assemblages. *Oceanography and Marine Biology* **41**, 161–236.

Boothroyd, I. K. G., Quinn, J. M., Langer, E. R., Costley, K. J., and Steward, G. (2004). Riparian buffers mitigate effects of pine plantation logging on New Zealand streams: 1. Riparian vegetation structure, stream geomorphology and periphyton. *Forest Ecology and Management* **194**, 199–213. doi:10.1016/J.FORECO.2004.02.018

Chevenet, F., Dolédec, S., and Chessel, D. (1994). A fuzzy coding approach for the analysis of long-term ecological data. *Freshwater Biology* **31**, 295–309. doi:10.1111/J.1365-2427.1994.TB01742.X

Clarke, K. R., and Warwick, R. M. (1994). 'Change in Marine Communities: an Approach to Statistical Analysis and Interpretation.' (PRIMER-E Ltd.: Plymouth, UK.)

Cline, L. D., Short, R. A., and Ward, J. V. (1982). The influence of highway construction on the macroinvertebrates and epilithic algae of a high mountain stream. *Hydrobiologia* **96**, 149–159. doi:10.1007/BF02185430

Cohen, J. (1988). 'Statistical Power Analysis for the Behavioural Sciences.' 2nd edn. (Lawrence Erlbaum Associates: Hillsdale, NJ.)

Collier, K. J., and Winterbourn, M. J. (Eds) (2000). 'New Zealand Stream Invertebrates: Ecology and Implications for Management.' (The Caxton Press: Christchurch.)

Connolly, N. M., and Pearson, R. G. (2007). The effect of fine sedimentation on tropical stream macroinvertebrate assemblages: a comparison using flow-through artificial stream channels and recirculating mesocosms. *Hydrobiologia* **592**, 423–438. doi:10.1007/S10750-007-0774-7

Countway, R. E., Canuel, E. A., and Dickhut, R. M. (2007). Sources of particulate organic matter in surface waters of the York River, VA estuary. *Organic Geochemistry* **38**, 365–379. doi:10.1016/J.ORGGEOCHEM.2006.06.004

Culp, J. M., Wrona, F. J., and Davies, R. W. (1986). Response of stream benthos and drift to fine sediment deposition versus transport. *Canadian Journal of Zoology* **64**, 1345–1351. doi:10.1139/Z86-200

Cummings, V., Thrush, S., Hewitt, J., Norkko, A., and Pickmere, S. (2003). Terrestrial deposits on intertidal sandflats: sediment characteristics as indicators of habitat suitability for recolonising macrofauna. *Marine Ecology Progress Series* **253**, 39–54. doi:10.3354/MEPS253039

Cummings, V., Vopel, K., and Thrush, S. (2009). Terrigenous deposits in coastal marine habitats: influences on sediment geochemistry and behaviour of post-settlement bivalves. *Marine Ecology Progress Series* **383**, 173–185. doi:10.3354/MEPS07983

de Castro Vasconcelos, M., and Melo, A. S. (2008). An experimental test of the effects of inorganic sediment addition on benthic macroinvertebrates of a subtropical stream. *Hydrobiologia* **610**, 321–329. doi:10.1007/S10750-008-9447-4

Dittman, S. (2007). Soft sediments. In 'Marine Ecology'. (Eds S. D. Connell and B. M. Gillanders.) pp. 428–456. (Oxford University Press: Melbourne.)

Dolédec, S., Phillips, N., Scarsbrook, M., Riley, R. H., and Townsend, C. R. (2006). Comparison of structural and functional approaches to determining landuse effects on grassland stream invertebrate communities. *Journal of the North American Benthological Society* **25**, 44–60. doi:10.1899/0887-3593(2006)25[44:COSAFA]2.0.CO;2

Downes, B. J., and Keough, M. J. (1998). Scaling of colonization processes in streams: parallels and lessons from marine hard substrata. *Australian Journal of Ecology* **23**, 8–26. doi:10.1111/J.1442-9993.1998.TB00702.X

Farnsworth, K. L., and Milliman, J. D. (2003). Effects of climatic and anthropogenic change on small mountainous rivers: the Salinas River example. *Global and Planetary Change* **39**, 53–64. doi:10.1016/S0921-8181(03)00017-1

Gatehouse, J. S. I. (1971). Sedimentary analysis. In 'Procedures in Sedimentology and Petrology'. (Ed. R. E. Carver.) pp. 59–94. (Wiley Interscience: New York.)

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.)

Gordon, I. J. (2007). Linking land to ocean: feedbacks in the management of socio-ecological systems in the Great Barrier Reef catchments. *Hydrobiologia* **591**, 25–33. doi:10.1007/S10750-007-0781-8

Henley, W. F., Patterson, M. A., Neves, R. J., and Lemly, A. D. (2000). Effects of sedimentation and turbidity on lotic food webs: a concise review for natural resource managers. *Reviews in Fisheries Science* **8**, 125–139. doi:10.1080/10641260091129198

Hewitt, J. E., Cummings, V. J., Ellis, J. I., Funnell, G., Norkko, A., Talley, T. S., and Thrush, S. F. (2003). The role of waves in the colonisation of terrestrial sediments deposited in the marine environment. *Journal of Experimental Marine Biology and Ecology* **290**, 19–47. doi:10.1016/S0022-0981(03)00051-0

Hicks, B. J. (1997). Food webs in forest and pasture streams in the Waikato region, New Zealand: a study based on analyses of stable isotopes of carbon and nitrogen, and fish gut contents. *New Zealand Journal of Marine and Freshwater Research* **31**, 651–664. doi:10.1080/00288330.1997.9516796

Hicks, D. M., Quinn, J. M., and Trustrum, N. A. (2004). Stream sediment load and organic matter. In 'Freshwaters of New Zealand'. (Eds J. S. Harding, M. P. Mosley, C. P. Pearson and B. K. Sorrell.) pp. 12.1–12.16. (The Caxton Press: Christchurch, New Zealand.)

Hinchey, E. K., Schaffner, L. C., Hoar, C. C., Vogt, B. W., and Batte, L. P. (2006). Responses of estuarine benthic invertebrates to sediment burial: the importance of mobility and adaptation. *Hydrobiologia* **556**, 85–98. doi:10.1007/S10750-005-1029-0

Kaller, M. D., and Hartman, K. J. (2004). Evidence of a threshold level of fine sediment accumulation for altering benthic invertebrate communities. *Hydrobiologia* **518**, 95–104. doi:10.1023/B:HYDR.0000025059.82197.35

Köthe, H. (2003). Existing sediment management guidelines: an overview. *Journal of Soils and Sediments* **3**, 139–143. doi:10.1065/JSS2003.08.082

Lake, P. S. (1990). Disturbing hard and soft bottom communities – a comparison of marine and freshwater environments. *Australian Journal of Ecology* **15**, 477–488. doi:10.1111/J.1442-9993.1990.TB01472.X

Lake, P. S. (2000). Disturbance, patchiness, and diversity in streams. *Journal of the North American Benthological Society* **19**, 573–592. doi:10.2307/1468118

Lamberti, G. A., and Steinman, A. D. (1993). Research in artificial streams: applications, uses and abuses. *Journal of the North American Benthological Society* **12**, 313–384. doi:10.2307/1467618

Larsen, S., Vaughan, I. P., and Ormerod, S. J. (2009). Scale-dependent effects of fine sediments on temperate headwater invertebrates. *Freshwater Biology* **54**, 203–219. doi:10.1111/J.1365-2427.2008.02093.X

Lemly, A. D. (1982). Modification of benthic insect communities in polluted streams: combined effects of sedimentation and nutrient enrichment. *Hydrobiologia* **87**, 229–245. doi:10.1007/BF00007232

Lohrer, A. M., Thrush, S. F., Hewitt, J. E., Berkenbusch, K., Ahrens, M., and Cummings, V. J. (2004). Terrestrially derived sediment: response of marine macrobenthic communities to thin terrigenous deposits. *Marine Ecology Progress Series* **273**, 121–138. doi:10.3354/MEPS273121

Lohrer, A. M., Hewitt, J. E., and Thrush, S. F. (2006a). Assessing far-field effects of terrigenous sediment loading in the coastal marine environment. *Marine Ecology Progress Series* **315**, 13–18. doi:10.3354/MEPS315013

Lohrer, A. M., Thrush, S. F., Lundquist, C. J., Vopel, K., Hewitt, J. E., and Nicholls, P. E. (2006b). Deposition of terrigenous sediment on subtidal marine macrobenthos: response of two contrasting community types. *Marine Ecology Progress Series* **307**, 115–125. doi:10.3354/MEPS307115

Marden, M., Rowan, D., and Phillips, C. (2006). Sediment sources and delivery following plantation harvesting in a weathered volcanic terrain, Coromandel Peninsula, North Island, New Zealand. *Australian Journal of Soil Research* **44**, 219–232. doi:10.1071/SR05092

Matthaei, C. D., Weller, F., Kelly, D. W., and Townsend, C. R. (2006). Impacts of fine sediment addition to tussock, pasture, dairy and deer farming streams in New Zealand. *Freshwater Biology* **51**, 2154–2172. doi:10.1111/J.1365-2427.2006.01643.X

Matthaei, C. D., Piggott, J. J., and Townsend, C. R. (2010). Multiple stressors in agricultural streams: interactions among sediment addition, nutrient enrichment and water abstraction. *Journal of Applied Ecology* **47**, 639–649. doi:10.1111/J.1365-2664.2010.01809.X

Mercer Clarke, C. S. L., Roff, J. C., and Bard, S. M. (2008). Back to the future: using landscape ecology to understand changing patterns of land use in Canada, and its effects on the sustainability of coastal ecosystems. *ICES Journal of Marine Science* **65**, 1534–1539. doi:10.1093/ICESJMS/FSN107

Middelburg, J. J., Barranguet, C., Boschker, H. T. S., Herman, P. M. J., Moens, T., and Heip, C. H. R. (2000). The fate of intertidal microphytobenthos carbon: an in situ $^{13}$C-labeling study. *Limnology and Oceanography* **45**, 1224–1234. doi:10.4319/LO.2000.45.6.1224

Molinos, J. G., and Donohue, I. (2009). Differential contribution of concentration and exposure time to sediment dose effects on stream biota. *Journal of the North American Benthological Society* **28**, 110–121. doi:10.1899/08-046.1

Nakagawa, S. (2004). A farewell to Bonferroni: the problems of low statistical power and publication bias. *Behavioral Ecology* **15**, 1044–1045. doi:10.1093/BEHECO/ARH107

Niyogi, D. K., Koren, M., Arbuckle, C. J., and Townsend, C. R. (2007). Longitudinal changes in biota along four New Zealand streams: declines and improvements in stream health related to land use. *New Zealand Journal of Marine and Freshwater Research* **41**, 63–75. doi:10.1080/00288330709509896

Norkko, A., Thrush, S. F., Hewitt, J. E., Cummings, V. J., Norkko, J., Ellis, J. I., Funnell, G. A., Schultz, D., and MacDonald, I. (2002). Smothering of estuarine sandflats by terrigenous clay: the role of wind-wave disturbance and bioturbation in site-dependent macrofaunal recovery. *Marine Ecology Progress Series* **234**, 23–42. doi:10.3354/MEPS234023

Owens, P. N., Batalla, R. J., Collins, A. J., Gomez, B., Hicks, D. M., Horowitz, A. J., Kondolf, G. M., Marden, M., Page, M. J., Peacock, D. H., Petticrew, E. L., Salomons, W., and Trustrum, F. (2005). Fine-grained sediment in river systems: environmental significance and management issues. *River Research and Applications* **21**, 693–717. doi:10.1002/RRA.878

Perneger, T. V. (1998). What's wrong with Bonferroni adjustments. *British Medical Journal* **316**, 1236–1238.

Petticrew, E. L., Krein, A., and Walling, D. E. (2007). Evaluating fine sediment mobilization and storage in a gravel-bed river using controlled reservoir releases. *Hydrological Processes* **21**, 198–210. doi:10.1002/HYP.6183

Poff, N. L. (1997). Landscape filters and species traits: towards mechanistic understanding and prediction in stream ecology. *Journal of the North American Benthological Society* **16**, 391–409. doi:10.2307/1468026

Quinn, J. M., and Hickey, C. W. (1990). Characterisation and classification of benthic invertebrate communities in 88 New Zealand rivers in relation to environmental factors. *New Zealand Journal of Marine and Freshwater Research* **24**, 387–409. doi:10.1080/00288330.1990.9516432

Quinn, G. P., and Keough, M. J. (2002). 'Experimental Design and Data Analysis for Biologists.' (Cambridge University Press: Cambridge, UK.)

Quinn, J. M., Stroud, M. J., Parkyn, S. M., and Burrell, G. P. (1995). Impacts of an intense rainstorm on 3–4 March 1995 on Whangapoua Forest landscape and streams. NIWA consultancy report ERN301/1. National Institute of Water and Atmospheric Research, Hamilton, New Zealand.

Quinn, J. M., Cooper, A. B., Davies-Colley, R. J., Rutherford, J. C., and Williamson, R. B. (1997). Land use effects on habitat, water quality, periphyton, and benthic invertebrates in Waikato, New Zealand, hill-country streams. *New Zealand Journal of Marine and Freshwater Research* **31**, 579–597. doi:10.1080/00288330.1997.9516791

Quinn, J. M., Boothroyd, I. K. G., and Smith, B. J. (2004). Riparian buffers mitigate effects of pine plantation logging on New Zealand streams. 2. Invertebrate communities. *Forest Ecology and Management* **191**, 129–146. doi:10.1016/J.FORECO.2003.11.013

Rabení, C. F., Doisy, K. E., and Zweig, L. D. (2005). Stream invertebrate community functional responses to deposited sediment. *Aquatic Sciences* **67**, 395–402.

Reid, L. M., and Page, M. J. (2003). Magnitude and frequency of landsliding in a large New Zealand catchment. *Geomorphology* **49**, 71–88. doi:10.1016/S0169-555X(02)00164-2

Richards, C., Haro, R. J., Johnson, L. B., and Host, G. E. (1997). Catchment and reach-scale properties as indicators of macroinvertebrate species traits. *Freshwater Biology* **37**, 219–230. doi:10.1046/J.1365-2427.1997.D01-540.X

Ryan, P. A. (1991). Environmental effects of sediment on New Zealand streams: a review. *New Zealand Journal of Marine and Freshwater Research* **25**, 207–221. doi:10.1080/00288330.1991.9516472

Sarriquet, P. E., Bordenave, P., and Marmonier, P. (2007). Effects of bottom sediment restoration on interstitial habitat characteristics and benthic macroinvertebrate assemblages in a headwater stream. *River Research and Applications* **23**, 815–828. doi:10.1002/RRA.1013

Schofield, K. A., Pringle, C. M., and Meyer, J. L. (2004). Effects of increased bedload on algal- and detrital-based stream food webs: experimental manipulation of sediment and macroconsumers. *Limnology and Oceanography* **49**, 900–909. doi:10.4319/LO.2004.49.4.0900

Shaw, E. A., and Richardson, J. S. (2001). Direct and indirect effects of sediment pulse duration on stream invertebrate assemblages and rainbow trout (*Oncorhynchus mykiss*) growth and survival. *Canadian Journal of Fisheries and Aquatic Sciences* **58**, 2213–2221. doi:10.1139/F01-160

Suren, A. M., and Jowett, I. A. (2001). Effects of deposited sediment on invertebrate drift: an experimental study. *New Zealand Journal of Marine and Freshwater Research* **35**, 725–737. doi:10.1080/00288330.2001.9517038

Tallis, H., Ferdaña, Z., and Gray, E. (2008). Linking terrestrial and marine conservation planning and threats analysis. *Conservation Biology* **22**, 120–130. doi:10.1111/J.1523-1739.2007.00861.X

Thompson, R. M., Phillips, N. R., and Townsend, C. R. (2009). Biological consequences of clear-cut logging around streams – moderating effects of management. *Forest Ecology and Management* **257**, 931–940. doi:10.1016/J.FORECO.2008.10.025

Thrush, S. F., Hewitt, J. E., Norkko, A., Cummings, V. J., and Funnell, G. A. (2003). Macrobenthic recovery processes following catastrophic sedimentation on estuarine sandflats. *Ecological Applications* **13**, 1433–1455. doi:10.1890/02-5198

Thrush, S. F., Hewitt, J. E., Cummings, V. J., Ellis, J. I., Hatton, C., Lohrer, A., and Norkko, A. (2004). Muddy waters: elevating sediment input to coastal and estuarine habitats. *Frontiers in Ecology and Evolution* **2**, 299–306. doi:10.1890/1540-9295(2004)002[0299:MWESIT]2.0.CO;2

Townsend, C. R., Scarsbrook, M. R., and Dolédec, S. (1997). The intermediate disturbance hypothesis, refugia, and biodiversity in streams. *Limnology and Oceanography* **42**, 938–949. doi:10.4319/LO.1997.42.5.0938

Townsend, C. R., Uhlmann, S. S., and Matthaei, C. D. (2008). Individual and combined responses of stream ecosystems to multiple stressors. *Journal of Applied Ecology* **45**, 1810–1819. doi:10.1111/J.1365-2664.2008.01548.X

van Houte-Howes, K. S. S., Turner, S. J., and Pilditch, C. A. (2004). Spatial differences in macroinvertebrate communities in intertidal seagrass habitats and unvegetated sediment in three New Zealand estuaries. *Estuaries* **27**, 945–957. doi:10.1007/BF02803421

Wall, D. H., Ayres, E., Behan-Pelletier, V., Covich, A. P., and Snelgrove, P. V. R. (2005). Soils, freshwater and marine sediments: the need for integrative landscape science. *Marine Ecology Progress Series* **304**, 271–307.

Wolman, M. G. (1954). A new method of sampling coarse river-bed. *Transactions – American Geophysical Union* **35**, 951–956.

Wood, P. J., and Armitage, P. D. (1997). Biological effects of fine sediment in the lotic environment. *Environmental Management* **21**, 203–217. doi:10.1007/S002679900019

Wright-Stow, A., and Quinn, J. (2009). Effects of progressive catchment harvesting on stream clarity, temperature, habitat and invertebrates in Whangapoua Forest. Seventeenth annual report incorporating results from 1992–2009. National Institute of Water and Atmospheric Research Ltd (NIWA) report to Ernslaw One Ltd., Hamilton, New Zealand.

Xu, F. H., Wang, D. P., and Riemer, N. (2008). Modelling flocculation processes of fine-grained particles using a size-resolved method: comparison with published laboratory experiments. *Continental Shelf Research* **28**, 2668–2677. doi:10.1016/J.CSR.2008.09.001

Zweig, L. D., and Rabení, C. F. (2001). Biomonitoring for deposited sediment using benthic invertebrates: a test on four Missouri streams. *Journal of the North American Benthological Society* **20**, 643–657. doi:10.2307/1468094