



Auckland
Regional Council
TE RAUHITANGA TAIAO

Effects of Suspended Sediment Concentrations on Suspension and Deposit Feeding Marine Macrofauna

August 2003 Technical Publication 211

Auckland Regional Council
Technical Publication No. 211, August 2003
ISSN 1175 205X, ISBN 1877353159
www.arc.govt.nz

Printed on recycled paper

Effects of suspended sediment concentrations on suspension and deposit feeding marine macrofauna

P. Nicholls
J. Hewitt
J. Halliday

Prepared for

Auckland Regional Council

ARC Technical Publication
Auckland Regional Council

NIWA Client Report: ARC03267
National Institute of Water & Atmospheric Research Ltd
Hamilton

August 2003

CONTENTS

Executive Summary	iv
1. INTRODUCTION	6
1.1 Study species	7
1.2 Study rationale	10
2.1 Sediment	12
2.1.1 Turbidity and suspended sediment concentrations	13
2.1.2 Irradiance (PAR)	15
2.1.3 Benthic chlorophyll a	15
2.1.4 Organic content and total sugars	15
2.1.5 Water sampling	15
2.1.6 Suspended sediment concentrations (TPM)	15
2.1.7 Organic matter content	16
2.1.8 Chlorophyll a	16
2.2 Experimental set-up	16
2.2.1 Zeacumantus	17
2.2.2 Echinocardium	18
2.2.3 Boccardia	18
2.2.4 Macomona	19
2.2.5 Pecten	19
2.3 Statistical Analyses	20
3. RESULTS	22
3.1 Turbidity, Suspended Sediment Concentrations and Photosynthetically Active Radiation	22
3.2 Water sampling and settling fluxes	23
3.3 Zeacumantus	24
3.4 Echinocardium	26
3.5 Boccardia	28
3.6 Macomona	28
3.7 Pecten30	
4. CONCLUSIONS	34
5. REFERENCES	38

Executive Summary

This report is a continuation of research by NIWA and the Auckland Regional Council on the effects of increased sediment loading in estuaries. Here, we concentrate on the effects of increased suspended sediment concentrations. Increased suspended sediment concentrations can decrease light levels at the seafloor, affecting microphytes or benthic primary producers, an important food source for many macrofaunal species. Suspended sediments can also clog filter-feeding structures of animals, thus interfering with food intake and potentially affecting growth and condition. The deposition of suspended sediments onto the seafloor can adversely affect macrofauna by decreasing oxygen concentrations and changing sediment properties such as grain size, chlorophyll *a* and organic matter content.

We examined the behavioural responses of 4 common and widespread macrofauna; one surface grazer (the snail *Zeacumantus lutulentus*), three deposit-feeders (the heart urchin *Echinocardium australe* a tube building worm *Boccardia syrtis* and the wedge shell *Macomona liliana*), and one suspension feeder (the scallop *Pecten novaezelandiae*) to a range of suspended sediment concentrations in the laboratory. The sediment in suspension was terrestrial in origin to mimic storm-induced sediment run off events.

There was no consistent response in *Zeacumantus* behaviour to increased suspended sediment concentrations after 14 days. Feeding rates for *Boccardia* decreased over time, with the largest decreases occurring in treatments with the highest suspended sediment concentrations (750 mg L⁻¹). Burial times and death rates in *Echinocardium* increased with increasing exposure to suspended sediment. After 14 days of exposure to the highest suspended sediment concentrations, most of the *Macomona* had died or were lying exposed on the surface of the sediment. For *Pecten*, variation in clearance rates suggested that the highest suspended sediment concentrations we used exceeded the ability of *Pecten* to process the particles. By the end of the experiment, *Pecten* in the controls had higher condition than those in the other treatments.

These experiments emphasise the negative effects that suspended sediment concentrations may have on common macrofaunal species within the Auckland Region. *Pecten*, *Boccardia*, *Echinocardium* and *Macomona* all responded negatively to increased sediment concentrations while *Zeacumantus* was relatively robust in the short term.

All the animals used in these trials are at risk from increased suspended sediment concentrations in estuaries, because they are common and widespread throughout the Auckland Region. These trials have shown that *Boccardia*, *Echinocardium*, *Macomona* and *Pecten* react negatively to increased suspended sediment concentrations in the short term. As land-use changes associated with human population increases and intensify, the frequency and magnitude of terrigenous run-off events are likely to increase, imposing further stress on macrofaunal communities. These short term experiments help to identify species at risk from the indirect effects of elevated suspended sediment concentrations, helping in both the prediction and interpretation of long-term trends in those or similar species.

1. INTRODUCTION

There is growing recognition that terrigenous sediments pose a threat to the biodiversity of estuaries and coastal areas (Gray 1997). Episodic events such as landslides, extreme rain events and flooding can result in catastrophic deposition of sediments and may have a profound influence on the structure and function of macrobenthic communities (Ellis et al. 2000). Experiments investigating the effects of terrigenous sediments have shown that increased sediment deposition onto the seafloor can adversely affect macrofauna by decreasing oxygen concentrations and by changing sediment properties such as grain size, stable isotopes, chlorophyll *a* and organic matter content (Berkenbusch et al. 2001; Gibbs et al. 2001; Nicholls et al. 2000; Norkko et al. 2001b).

The effect on macrofauna of terrigenous sediment entering marine ecosystems, however, is not restricted to catastrophic sediment deposition events. It can also be the result of longer-term chronic effects of increased suspended sediment concentrations in the water. In 2001, Hewitt et al. investigated the effect of suspended sediment concentrations on common suspension-feeders (*Austrovenus stutchburyi* and *Paphies australis*) in Whitford's intertidal flats. They found that both the short and long-term growth of these animals was negatively affected by increased suspended sediment concentrations.

Suspension-feeders are the functional group most likely to be directly impacted by increased suspended sediment concentrations. They feed by extracting organic particles from the water column, thus high concentrations of inedible suspended sediment particles can directly interfere with food intake by clogging filter-feeding structures, potentially affecting growth and condition of these animals.

The work in this report extends the work of Hewitt et al. (2001) by including a number of other common and conspicuous taxa that occur in a broad array of habitats. It is an extension of a series of studies undertaken by NIWA to determine the risk of urban development to the receiving environment, and it is of regional concern because suspended sediment concentrations are considered to be a threat to the coastal ecology of many areas in the Auckland Region.

Many deposit-feeders and grazers feed by processing and grazing surface sediments to remove microphytobenthos and organic detritus. Animals from these feeding groups, while not directly affected by increased levels of suspended sediments, can be indirectly affected by food limitation when turbid water reduces the ability of the microphytobenthos to photosynthesize and grow. The dynamics of intertidal

microphytobenthos production are controlled by the night/day cycle and tidal hydrodynamic forcing, which determines changes in environmental conditions, such as light and nutrient availability and temperature (Guarini et al. 2000). In general, the contribution of microphytobenthos to the overall primary production in estuaries with relatively high turbidity is low, with fewer epiphytic grazers observed in areas with consistently high turbidities (Kromkamp et al. 1995). Kromkamp et al. (1995) also found that photosynthetic activity of the microphytobenthos declined dramatically after intertidal flats emerge from the water. Changes in pH and CO₂ concentrations appeared to be partially responsible for this decrease in activity along with diel rhythms, as the benthic algae migrate up and down in the surface layers during the day and during the flood and ebb of the tides. Microphytobenthos and microbial biofilms play critical roles in nutrient remineralization and in primary production in intertidal ecosystems (Decho 2000). Microbial biofilms of extracellular polymeric secretions from these micro-organisms may also bind and thus stabilize sediments against resuspension. As primary producers, these organisms also form the basis of the intertidal food chain (Gibbs et al. 2001)

This report specifically investigates the behavioural responses of the grazer *Zeacumantus lutulentus*; the deposit-feeders, *Echinocardium australe*, *Boccardia syrtis* and *Macomona liliana*, and the suspension-feeder, *Pecten novaezelandiae*, to a range of suspended (terrigenous) sediment concentrations in the laboratory. All the animals used in these trials are at risk from increased suspended sediment concentrations in estuaries, because they are common and widespread throughout the Auckland Region.

Boccardia, *Macomona* and *Zeacumantus* may be most at risk as they are highly abundant within harbours and estuaries; they are most likely to be exposed to high turbidity for extended periods of time. Risks to *Pecten* are more commonly associated with fishing pressure and changes in habitat complexity due to dredging. However, *Pecten* does occur in harbours, for example Mahurangi and Manukau. Also sediment run-off during substantive rainfall events can enter coastal embayments directly, as we observed in Kawau Bay. Increasing turbidity in harbours over the long term may also result in more extensive effects as turbid plumes of water extend out of the estuary into the less sheltered coastal areas.

1.1 Study species

Separating macrofauna into feeding guilds is not an easy exercise. We know little about many of the species and benthic species generally exhibit plasticity in feeding, switching from one mode to another as environmental conditions and food availability change. The species we have selected for experimentation are common, likely to be

important to the functioning of ecosystems, and their feeding habits are relatively well characterised.

1. The herbivorous gastropod, *Zeacumantus lutulentus*, can be found in high densities in the surface layers of intertidal sand and mud flats throughout the Auckland region. They are highly mobile and graze the muddy sediment – water interface, feeding on loose surficial detritus and benthic microphytes. Their faecal pellets are deposited on the sediment surface where they become food for organisms. *Zeacumantus* are found at all the monitored sites in the Waitemata, except Shoal Bay, which is relatively sandy. They are also common at Meola Reef. In Mahurangi and Manukau Harbours, *Zeacumantus* are relatively rare at the monitored sites and NIWA does not presently monitor trends in their abundance. *Zeacumantus* are likely to be indirectly affected by increasing water turbidity because they pass large quantities of surface sediment through their guts to extract microphytobenthos. Gibbs (*pers. obs.*) observed that the *Zeacumantus* crawling through terrigenous deposits would ingest some terrigenous sediment, but would then stop feeding.
2. The heart urchin *Echinocardium australe* is a large burrowing deposit feeder common in the subtidal zone in both sandy and muddy subtidal habitats. Their abundance, size and mobility means they mix a large volume of surficial sediment. Bioturbation by *Echinocardium* increases oxygen penetration and releases nutrients such as ammonium and phosphate into the overlying water (Lohrer et al. 2003).
3. The deposit-feeding polychaete, *Boccardia syrtis*, lives in tubes that protrude from the sediment surface in intertidal and subtidal habitats. In high numbers, the densely packed tube mats stabilise and bind the surface sediment (Thrush et al. 1996); because of its ecological importance, this species is monitored in the Manukau monitoring programme. Part of the polydorid species complex, this species is also common in Jamieson Bay, Mid Harbour and Hamilton Landing in the Mahurangi Harbour. Like many surface deposit-feeders, this species can switch feeding modes and can consume suspended particles from the water column. Nicholls et al. (2000) found that *Boccardia* were highly sensitive to terrigenous sediment deposition. There were significant mortalities after just 24 hours, when more than 3 cm of terrigenous sediment was deposited over the original marine sediment.
4. The wedge shell, *Macomona liliana*, is a common inhabitant of soft sediments, and often a numerically- dominant species in sandy to muddy-sand areas. In a survey of 90 sites in the Whitford embayment, Norkko et al.

(2001) found *Macomona* in sediments containing up to 40% silt/clay, but maximum densities occurred in sediments with 0-5 %. Adults live up to 10 cm below the sediment surface, and generally deposit feed (although under some conditions they may also suspension feed). While *Macomona* are known to move as juveniles (Cummings et al. 1995; Norkko et al. 2001a), adult movement is limited. Previous work suggests an adult *Macomona* is not likely to move out of a patch > 1 m in radius, even over a 5 month period (Hewitt et al. 1996, Thrush et al. 1994). *Macomona* adults have a strong influence on the composition of the surrounding benthic community: high densities of this bivalve have a negative effect on juvenile conspecifics and other members of the infaunal community (Thrush et al. 1992, 1996, Hewitt et al. 1997). They are very important food resources for shore birds and fish. To date, little work has been done to investigate the effect of sediment grain size, or suspended sediment concentrations, on *Macomona*. However, a recent experiment, in which *Macomona* was transplanted along a gradient of varying turbidity, has found a lower physiological condition of *Macomona* at sites with relatively high suspended sediment concentrations (Hewitt et al. unpublished data). In addition, there is some evidence of decline in natural *Macomona* populations in Mahurangi Harbour, which may be related to changes in sediment conditions in the estuary (Cummings et al. 2003). Norkko et al. (2001b) found that *Macomona* were sensitive to sediment with a clay/silt content greater than 25%. *Macomona* may be negatively affected by terrigenous sediment deposition because the fine particles bind to the surface sediments blocking the feeding of *Macomona* (Gibbs, pers. obs.)

5. The New Zealand scallop, *Pecten novaezealandiae*, is a suspension feeding bivalve. This species is found subtidally, generally in sandy coastal areas. *Pecten* are highly mobile, and rapid closure of their shell jets the water enabling the animal to move. *Pecten* also use this same clapping movement to expel sediment from within their mantle cavity. The effects of increased suspended sediments on *Pecten* populations are poorly known and need to be investigated, particularly to identify those areas in the Auckland Region where *Pecten* populations are most at risk.

1.2 Study rationale

Laboratory experiments were used to investigate short-term (0-14 days) behavioural changes occurring as a result of increases in suspended sediment concentrations. Laboratory experiments were used because they offer a controlled environment in which manipulative trials can be performed. However, when using short-term behavioural responses as an indication of longer-term effects on growth, reproduction or mortality, the aspect of behaviour and the duration of the experiment need to be carefully chosen. While studying suspension feeders, Hewitt et al. (2001) observed that changes in feeding rate, sustained for more than 10 days, resulted in changes in growth. Following this study, the behavioural response variable chosen for the suspension feeder *Pecten* was feeding rate. For the grazers and deposit feeders it is extremely difficult to measure feeding rates accurately, especially when visual observations are affected by the experimental treatments (i.e., increased suspended sediment concentrations reduces water clarity and thus vision.). Thus other behavioural responses were chosen.

Boccardia use the surface sediments not only as a source of food but also as a source of building material for their tubes. These polychaetes thrust out palps, which are waved around in the water and onto the surface sediments below. For this experiment, the proportion of *Boccardia* with their palps waving or “feeding” just after adding the clay, was used as the behavioural response. A failure to come out of their tubes and feed was counted as a negative effect, because a prolonged cessation of feeding would increase an individual’s chance of mortality.

Reburial rates were chosen to assess levels of stress for *Macomona* and *Echinocardium*, both infaunal species, because these have been used successfully in other studies. Reburial rates were used by Nicholls et al. (2000) with *Nucula hartvigiana* and *Alpheus* sp., and by Norkko et al. (1999) for *Macomona*, *Austrovenus stutchburyi* and *Paphies australis*. In 2001 Norkko et al. used them for *Austrovenus*, *Fellaster zelandiae* and *Nucula*, with some good results. When these animals are placed on the sediment surface they burrow immediately, which is considered predator avoidance. Sub-lethally stressed animals remaining on the sediment surface are more vulnerable to predators (Norkko & Bonsdorff 1996; Lohrer et al. 2003).

For the surface-dwelling mobile *Zeacumantus*, we decided to measure the speed of the animal to ‘right’ itself when placed with its dorsal side downwards. This is often used as an indicator of physiological status since healthy animals will try to reorient themselves as quickly as possible. Waves tumble the animals around flipping them on their backs; so any animal that cannot right itself quickly is exposed to predation, or is transported into potentially unfavourable conditions. Time taken to reorient was also used by Nicholls et al. (2000) for *Amphibola crenata*, and this proved very successful.

2. METHODS

2.1 Sediment

The terrestrial sediment used in these experiments was collected from roading developments near Warkworth. The dry sediment was broken apart, and then mixed with seawater. After thorough stirring and mixing, the slurry was passed through a 1-cm mesh screen to remove large lumps. The pH of the slurry was 2.9 just after mixing. To buffer the acidity, sodium hydroxide (NaOH) was dissolved in seawater and added to the slurry.

Particle analysis using the Galai particle analyser (Galai cis-100; Galai Productions Ltd, Migdal Haemek, Israel) indicate that 77 % of particles in the slurry were smaller than 63 μm (i.e., mud). Of this mud, 9 % was clay (<3.9 μm) and 20 % was medium silt (15-32 μm ; see Table 1).

Table 1: Grain size composition of terrestrial sediment used in this experiment and also by Lohrer et al. (2003).

Grain size description	Size class (μm)	% of sample by weight
Clay	0.0 - 3.9	8.9
Very fine silt	3.9 - 7.8	10.6
Fine silt	7.8 - 15.6	10.6
Medium silt	15.6 - 31.2	20.5
Coarse silt	31.2 - 62.5	20.4
Very fine sand	62.5 - 125	7.4
Fine sand	125 - 250	7.9
Medium sand	250 - 500	3.6
Coarse sand	500 – 1000	3.3
Very coarse sand	1000 – 2000	0.7
Granule	2000 – 3600	0

2.1.1 Turbidity and suspended sediment concentrations

For this set of experiments we wanted to use similar concentrations to those observed naturally in the Auckland Region and we also wanted to be able compare our results with the laboratory results of Hewitt et al. (2001). Hence we used a range of sediment concentrations of between 0 and 950 mg L⁻¹.

Hewitt et al. 2001 used six levels of suspended sediment concentration for their laboratory experiments (0, 25, 75, 200, 400, 800 mg L⁻¹). Most estuaries have suspended sediment concentrations that range between 20 – 100 mg L⁻¹, although, in periods of high sediment runoff this may increase to as much as 1000 mg L⁻¹ (Fahey & Coker 1992).

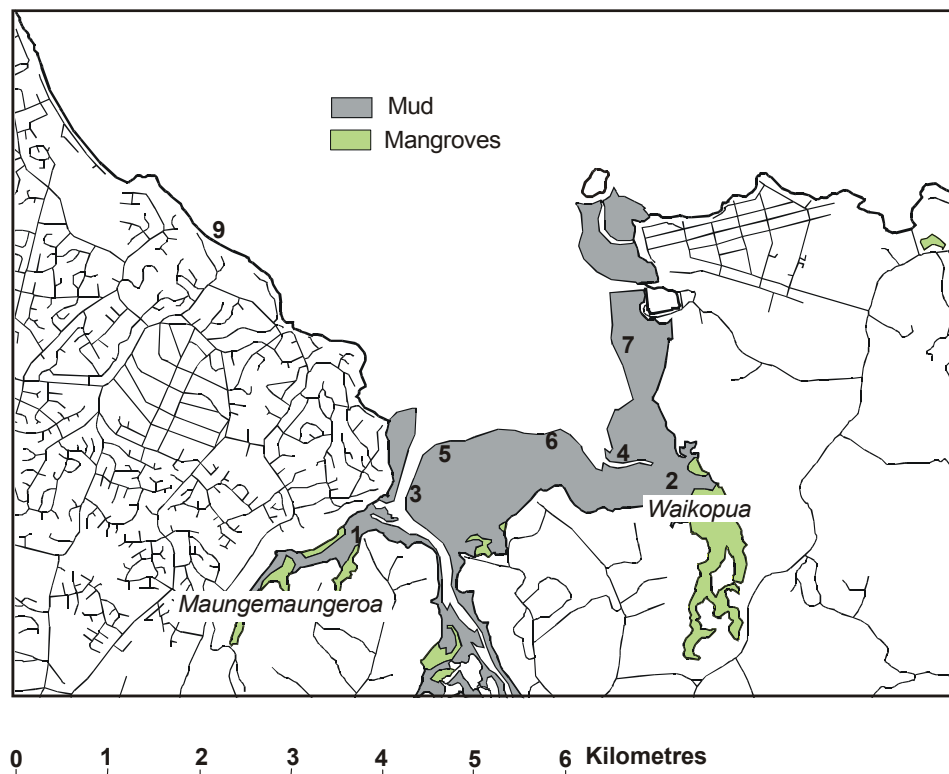


Figure 1: Map of the Whitford embayment showing the positions of optical backscatter sensors, May 2001 (Hewitt et al. 2001).

Table 2: Maximum and mean suspended sediment concentrations at 7 sites within the Whitford embayment in May 2001 (*unpub. OBS data; Hewitt et al. 2001*).

mg L ⁻¹	Site 1	2	3	4	5	6	7
mean	7.74	12.09	34.44	20.54	17.39	18.64	52.34
max	554.75	318.175	640.34	633.31	396.31	677.57	319.10

Figure 1 and Table 2 show the Whitford embayment with the positions of DOBIE wave gauges with optical back-scatter sensors (OBS). Sensors were installed at 7 locations for a period of 3 weeks in May 2001. The table presents results for the mean and maximum suspended sediment concentrations observed during May 2001. This month did not include any unusually intense storm events; nor was it unusually calm or rain-free. Suspended sediment concentrations here ranged between 0 and 700 mg L⁻¹ (*unpub. OBS data; Hewitt et al. 2001*).

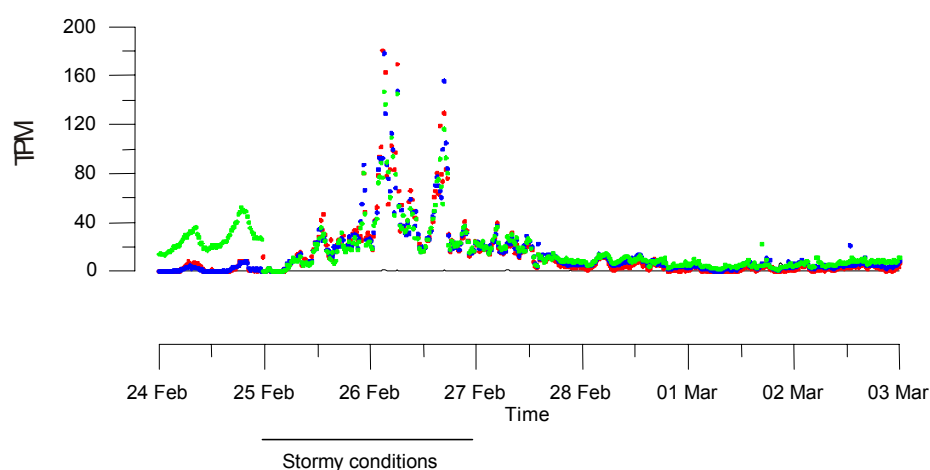


Figure 2: OBS data from on the week of the 25-February-2003 in the Mahurangi Harbour, adjacent to Te Kapa (Lohrer et al. 2003).

Figure 2 shows values for suspended sediment concentrations (TPM) in the Mahurangi Harbour in February 2003, again derived from OBS data. Values increased markedly during the storm activity on the 26th and 27th of February and peak values were an order of magnitude higher during the storm, than they were the previous week. Suspended sediment concentrations here ranged between 0 and approximately 180 mg L⁻¹.

2.1.2 Irradiance (PAR)

The slurry was added in varying amounts to aquaria to give a range of turbidity (5-230), which equates to suspended sediment concentrations of 50-750 mg L⁻¹. While there is generally little information available on turbidity and suspended sediment concentrations just above the seafloor, the information presented here suggests this range is common in Auckland harbours.

The photosynthetically available irradiance (PAR) throughout the water column and reaching the surface of the sediment was measured in aquaria with different suspended sediment concentrations ($\mu\text{mol photons m}^{-2} \text{ s}^{-1}$). The K_d or attenuation coefficient was calculated and used to give the PAR at (a) 30 mm off the surface sediment, and (b) the surface of the sediment. We made these measurements in sediment treated aquaria and in control aquaria to understand the effect of suspended sediment on light attenuation.

2.1.3 Benthic chlorophyll *a*

For all experiments, except those involving *Pecten*, sediment samples were taken for benthic chlorophyll *a* analysis. All sediment was freeze-dried, and a sample (<5 gm) was boiled with 90 % Ethanol. Samples were read on a spectrophotometer at 750 and 665 μm . An acidification step was also included (Sartory 1982).

2.1.4 Organic content and total sugars

Potential food quality of the sediment slurry was assessed as organic content and total sugars concentration.

2.1.5 Water sampling

For all experiments, water samples were taken at the beginning and end of the experiment to allow us to relate water turbidity to total particulate concentrations and food concentrations. The water samples were analysed for the following:

2.1.6 Suspended sediment concentrations (TPM)

To determine suspended sediment concentrations, 25 – 100 ml of water from each aquarium was filtered onto a pre-ashed and pre-weighed GF/F 25 mm filter, which was then dried to a constant weight at 60 °C before reweighing.

2.1.7 Organic matter content

After determining suspended sediment concentrations, the filters used for TPM were ashed at 400 °C for 5.5 hours and the percentage lost on ignition was calculated to determine the organic matter content of the suspended particulates.

2.1.8 Chlorophyll a

Water samples were taken immediately after adding the terrigenous sediment. The water samples (a sub-sample of 5 ml) from each aquarium were extracted in 97% acetone for 12 hours then centrifuged at 3000 rpm for 10 minutes. These were read on a fluorometer with an acidification step (Sartory 1982).

2.2 Experimental set-up

Separate experiments were conducted for each species.

All animals collected were transported in aerated seawater directly back to the NIWA Hamilton site, where they were transferred to fresh filtered seawater (1 µm mesh size) and left to acclimatise for 24 hours in a temperature controlled room (18 °C) with a 16:8 light: dark cycle. The next day, animals were randomly selected for placement in one of six 60 L aquaria. Each aquarium was designated for a different suspended sediment treatment level and fitted with bubblers and a re-circulation pump to keep the particles in suspension. All aquaria, except those involving *Pecten*, had 10 cm of clean sieved sediment placed on the bottom. The sediment was sieved (4 mm mesh) to remove any large macrofauna that may have interfered with the experiment. Food particles (the flagellate *Isochrysis galbana*) were added daily to all aquaria, including controls.¹ We added food to all aquarium for consistency and also because, even for *Zeacumantus*, we did not know the proportion of their diet coming from microphytobenthos living in the sediment and from algae and organics settling out of the water column.

Large aquaria without physical barriers were used for two reasons. Firstly, the presence of physical barriers was likely to enhance rates of sedimentation from the water column. Secondly, the *Zeacumantus* were highly mobile. We did not know enough about their behaviour to predict whether limiting their mobility, or confining them at densities they were not used to, would stress them. We took a conservative

¹ Total particulate matter concentration = food particles + sediment particles. All treatments had 50 mg L⁻¹ of food, so even the controls had a TPM of around 50 mg L⁻¹.

approach and gave them as much space as practical so that they could form their own aggregations. Animals were randomly selected from different sectors of each aquarium during sampling, as part of a stratified random sampling technique.

Treatment levels were maintained at designated total particulate concentrations by measuring turbidity and adding sediment as needed (up to twice a day). Water was changed daily, with the new water brought up to temperature before the change. Before changing the water, the dissolved oxygen concentration was measured to assess oxygen depletion.

Table 3: Summary of experimental set up.

Species	Indicator	Turbidity (NTU)	Suspended sediment concentrations or TPM (mg L⁻¹)	Time (days)
<i>Zeacumantus</i>	Turn over times	5 - 180	50, 100, 150, 300, 650	0, 3, 6, 8, 14
<i>Echinocardium</i>	Burial times	3 - 270	30, 100, 300, 550, 850	0, 1, 3, 4, 5, 6, 7, 8, 11, 14
<i>Boccardia</i>	Proportion feeding	5 - 220	50, 80, 310, 750	0, 1, 3, 6, 8, 14
<i>Macomona</i>	Burial times	5 - 220	50, 80, 300, 550, 750	0, 3, 6, 8, 14
<i>Pecten</i>	Feeding rates	5 - 220	25, 100, 500, 750	0, 1, 3, 8, 14

2.2.1 *Zeacumantus*

Zeacumantus were collected from mid-tide level from the intertidal sandflats in Whitford. Individuals ranged in size from 18 to 25 mm (maximum shell dimension). Twenty-five animals were randomly allocated to each treatment and placed with their dorsal sides upwards in aquaria containing 10 cm of sieved sediment. Animals that did reorient onto their ventral sides after one hour were replaced. On Days 1, 3, 6, 8 and 14, five animals were randomly removed from each aquarium and placed on their dorsal sides on fresh, sieved sediment. The time taken for each individual to reorient or right itself was recorded. Animals were not returned to the aquaria after they were removed.

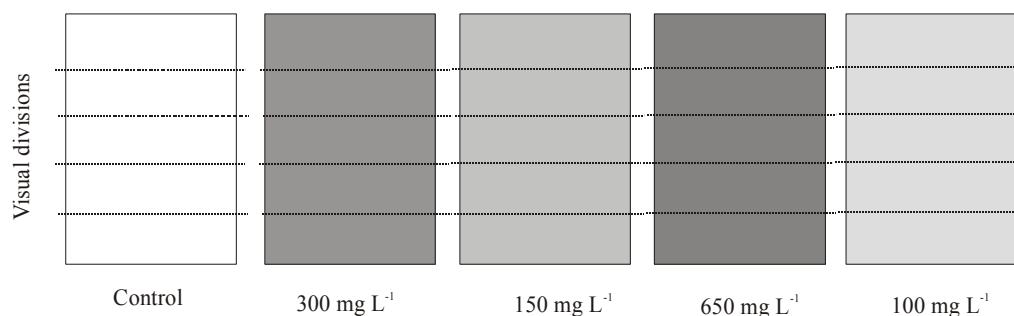


Figure 3: Experimental set up for *Zeacumantus*. Aquaria were randomly allocated to treatment levels.

2.2.2 Echinocardium

Echinocardium, ranging from 31 to 48 mm maximum test diameter, were collected using SCUBA near the entrance to the Mahurangi Harbour. Twelve animals were randomly allocated to each treatment and placed in aquaria containing sieved sediment. Animals that did not bury after 1 hour were replaced. On days 4, 6, 8, and 14 three animals were randomly selected from each aquarium and placed on fresh, sieved sediment. Time taken to rebury was recorded for each individual.

2.2.3 Boccardia

Sediment cores (13 cm diameter x 8 cm deep) containing between 21 – 100 *Boccardia* were collected using SCUBA in Jameson Bay, Mahurangi Harbour, where high densities of *Boccardia* tubes occur. The sediment cores were transferred into 13 cm diameter plastic containers, with a minimum of disturbance to the tubes and the sediment they were in. In the laboratory, one container was randomly allocated to each of 5 treatments. *Boccardia* in each container were observed feeding under a stereo microscope on days 0, 1, 3, 6, 8 and 14. On each occasion, the number of tubes were counted and the proportion of feeding worms was noted.

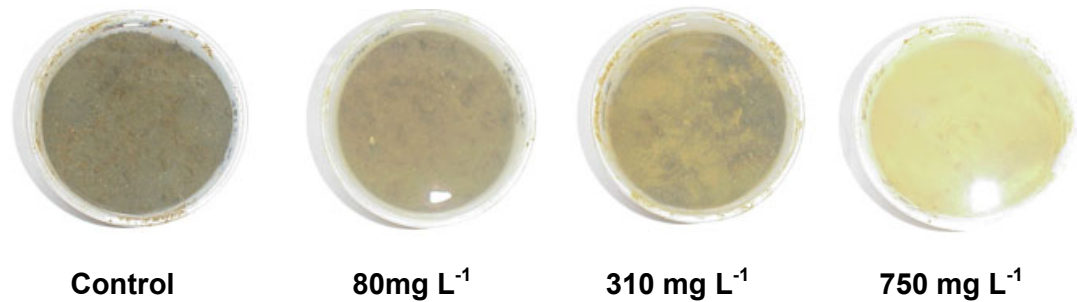


Figure 4: Plastic containers with sediment and *Boccardia*. Each container was 13 cm wide by 8 cm deep. Note the change in water clarity with increasing suspended sediment concentrations, from left to right.

2.2.4 Macomona

Macomona, ranging from 22 to 33 mm (longest shell dimension), were collected from mid-tide level in the Whitford. Twelve animals were randomly allocated to each of 5 treatments and placed in aquaria containing sieved sediment. Animals that did not bury after 1 hour were replaced. On Days 3, 6, 8 and 14, three animals were randomly selected from each aquaria, removed and placed on fresh, sieved sediment. The time required for reburial was recorded for each individual. Animals were sampled without replacement.

2.2.5 Pecten

Pecten, ranging from 94 to 64 mm (longest shell dimension), were collected using SCUBA near the entrance to the Mahurangi Harbour. Five animals were randomly allocated to each treatment and placed in aquaria without sediment. On days 0, 1, 3, 6, 8 and 14, two water samples were taken from each aquarium, one hour apart, after the terrestrial sediment had been added. From these samples, TPM concentrations were calculated. The difference in TPM concentration at the beginning and end of one hour yielded feeding rates, specifically the amount of particles removed and the volume of water filtered.

$$\begin{aligned}
 \text{Amount of particles removed (mg min}^{-1}\text{)} &= \frac{(\text{TPM}_{\text{beginning}} - \text{TPM}_{\text{end}}) \times \text{Vol}}{\text{Time}} \\
 \text{Volume of water filtered (ml min}^{-1}\text{)} &= \frac{\text{Amount of particles removed} \times 1000}{\text{TPM}_{\text{beginning}}}
 \end{aligned}$$

Where Vol = volume of water in ml, and Time = time in minutes.

The dry flesh weight of animals was measured by drying to a constant weight in a 60°C oven and then ashed at 400 for 5.5 hr. The ash flesh weight was calculated as the difference between the dry weight and the ashed weight. Condition was then calculated as ash dry flesh weight corrected for animal size by dividing by dry shell weight. However, the random allocation of animals to treatments resulted in more large animals in the higher TPM treatments. Unfortunately, the correction for animal size was unable to fully remove this effect, and a significant relationship between condition and length was obtained (condition = 1.11 + 0.45 length, $p = 0.0456$). The predicted effect of length was thus removed from the condition value. The residuals were put into the original range by adding the original mean to each value.

2.3 Statistical Analyses

For each experiment, a mean of the response variable(s) was calculated for each treatment level on each day. For *Zeacumantus* the variable was reorientation time; for *Macomona*, reburial time and number of non-burying individuals; for *Boccardia*, proportion of worms feeding; and for *Pecten* the variable was feeding rate, calculated using the amount of water filtered and particles removed.

The relationship between the response variables and the suspended sediment levels, and any changes over time to this relationship, was assessed using analysis of covariance (ANCOVA). This analysis determines whether there is a linear relationship between the dependent and independent variable and whether the slopes and intercepts of this relationship are consistent over time. In some cases, assumptions of normality and homogeneity of variance were not satisfied, and a log-transformation was required. For the amount of particles removed by *Pecten*, response varied from uni-modal to a log decrease, so comparisons were made visually only.

For *Pecten*, the relationship between the condition of the animals at the end of the experiment and treatment level was tested using linear regression with a log transformation on TPM.

3. RESULTS

3.1 Turbidity, Suspended Sediment Concentrations and Photosynthetically Active Radiation

Experimental concentrations of suspended sediments varied over time, as it was difficult to maintain exact concentrations over the duration of the experiments. Table 3 contains the range of turbidity and mean suspended sediment concentrations (TPM) for each treatment. Figure 5 shows the direct relationship between turbidity and suspended sediment concentrations. An ANCOVA showed no difference between experiments in terms of slope ($P = 0.8016$) or intercepts ($P = 0.0753$).

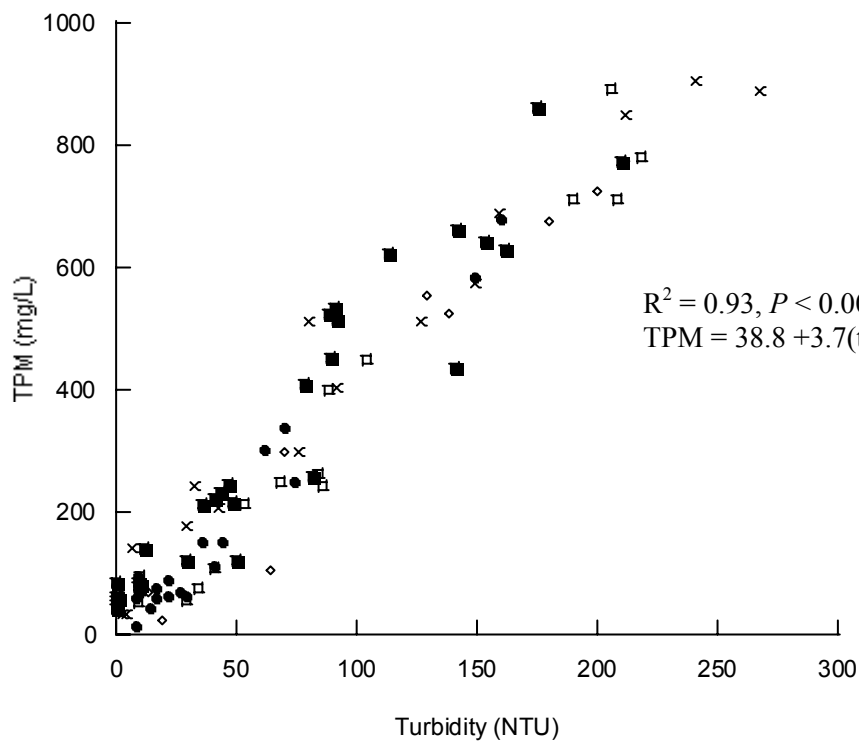


Figure 5: Relationship between turbidity (NTU) and suspended sediment concentrations (TPM). Data from the different experiments are shown as different symbols.

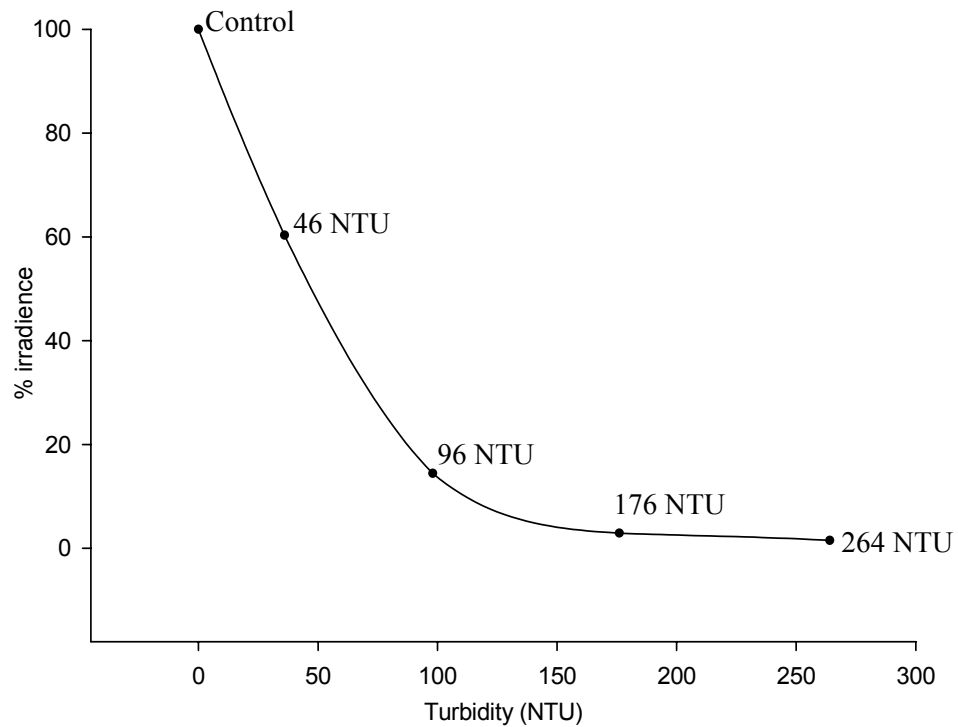


Figure 6: The irradiance of photosynthetically active light (PAR) at the surface of the sediment plotted against turbidity in different suspended sediment concentrations, relative to that in the control treatment.

The PAR declines asymptotically to nearly zero with increasing turbidity (Figure 6). Note, there was almost no light at the sediment surface in the two highest treatment levels. In the treatments with 176 and 264 NTU, the PAR just below the surface of the water was 60% that of the control, which demonstrates that even the top few centimetres of turbid water can attenuate a relatively large amount of light.

3.2 Water sampling and settling fluxes

Dissolved oxygen concentrations in all aquaria were relatively high throughout the experiment (above 80 %). The average amount of chlorophyll *a* in the control treatments was 4.01 mg/ g sediment.

Organic matter content and water chlorophyll *a* content were not correlated to increasing suspended sediment concentrations, however there was some food quality in the sediment we added (see Table 4). Organic content was slightly higher in the treatments with added sediment than in the controls, but total sugars were much higher (8.82 mg/L vs 0.33 in controls), suggesting the presence of bacteria.

Table 4: Potential food quality of sediment slurry compared to seawater with algae added. *NB* the sediment slurry is a concentrate so the amount of total sugars in the treatments is considerably less than this value.

	Organic content (mg l ⁻¹)	Total sugars (mg l ⁻¹)
Sediment slurry	0.079 ± 0.034	8.82 ± 0.43
Seawater	0.065 ± 0.025	0.33 ± 0.04

The proportion of material settling out of suspension in the aquaria was similar for all treatments, including the control (~15% over a 24 hr period). The actual values vary with treatment level from ~ 1.6 mg in the control to ~ 13.6 mg in the highest treatments. These amounts are similar to amounts collected in sediment traps set out over 2 tidal cycles at 8 sites in the Whitford embayment (0.5 - 20 mg, Hewitt et al. 2001). The percent organic content of the material settling out was lower than the percent organic content of the sediment found in the sediment traps quoted by Hewitt et al. (2001). However this was an average of 3 occasions. During rain, Hewitt et al. (2001) found similar percent organic content of the material found in the sediment traps, as we did of the material settling out of the experiments (3.6 ± 0.91 vs 2.7 ± 0.7 respectively).

3.3 Zeacumantus

Turbidity values in the five treatments were 5, 15, 40, 70, 180 which equates to TPMs of 50 (control), 100, 150, 300, 650 mg L⁻¹.

Benthic chlorophyll *a* levels in all treatments were relatively similar prior to the addition of the terrigenous sediment (2.3 - 3.7mg g⁻¹; Table 5). There was a consistent pattern in variation for the highest turbidity treatment alone. For this treatment, sediment chlorophyll *a* decreased progressively over time until Day 14 when levels were 25 % lower than the start.

Table 5: Benthic chlorophyll *a* content (mg/ g sediment) in treatments with *Zeacumantus*.

Treatment	Day 0	Day 3	Day 6	Day 8	Day 14
Control	3.4	3.0	2.3	3.0	3.4
100	3.7	3.0	9.4	4.3	2.7
150	4.1	3.4	2.0	3.7	4.1
300	3.4	3.0	2.7	3.2	3.4
650	3.2	3.2	3.0	2.9	2.7

Regardless of this there was no consistent response in *Zeacumantus* behaviour, either between treatments or over time and no significant interaction between TPM concentration and time ($P > 0.1$) (Figure 7). There was no difference between re-orientation times on Day 14 among all the treatments.

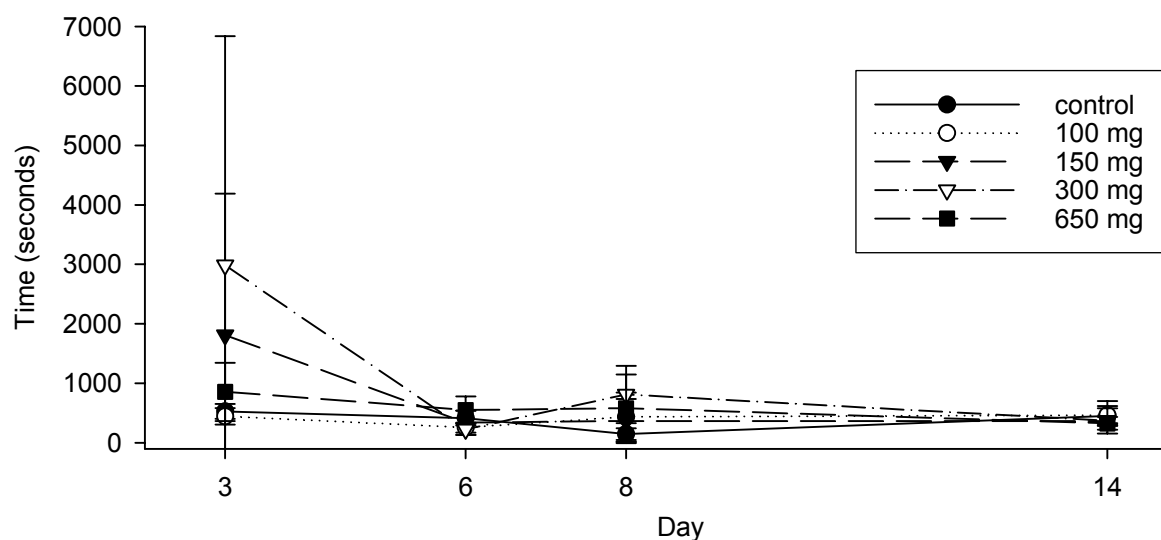


Figure 7: Time taken for *Zeacumantus* to re-orientate onto their dorsal sides (mean +/- 1 sd).

3.2 Echinocardium

Turbidities in the five treatments for *Echinocardium* were 3 (control), 30, 80, 150 and 250, which equates to TPM concentrations of 30, 100, 300, 500 and 850 mg L⁻¹. Sediment chlorophyll *a* concentrations were variable, with no significant differences between treatments or over time (figure 8). Evidence of sediment mixing was apparent, presumably due to bioturbation, as significant amounts of chlorophyll *a* was found deeper than 2 cm.

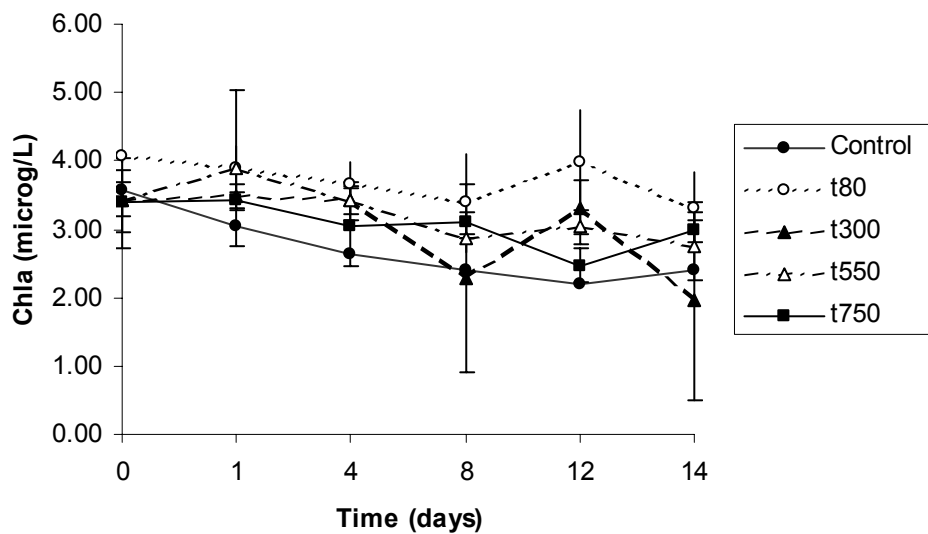


Figure 8: Chlorophyll *a* content of sediment (microg/L) in *Echinocardium* experimental aquaria (mean +/- 1 sd).

Increased TPM concentrations resulted in increased burial times of *Echinocardium* ($p < 0.0001$, Fig. 9), with an indication that this relationship changed over time ($p = 0.0551$). However, the slope and direction of the effect of enhanced TPM did not change significantly with time ($p = 0.7747$). The changes to the relationship observed over time are likely to be due to the increasing numbers of dead animals in the higher sediment treatments. Over the 14 days of the experiment considerably more animals died in the 3 highest TPM treatments (Table 6). In fact, no animals died from the controls.

Table 6: The number of deaths over the 14 day experiment

Treatment	Deaths
Control	0
80	3
300	7
550	5
750	10

In all treatments, *Echinocardium* burial times decreased over the length of the experiment (figure 9). Burial times were longest in the higher sediment treatments. Many of the animals in the 750 mg L⁻¹ treatment would not totally bury themselves within 3 hours, those animals that did, took significantly longer to do so than in the control animals.

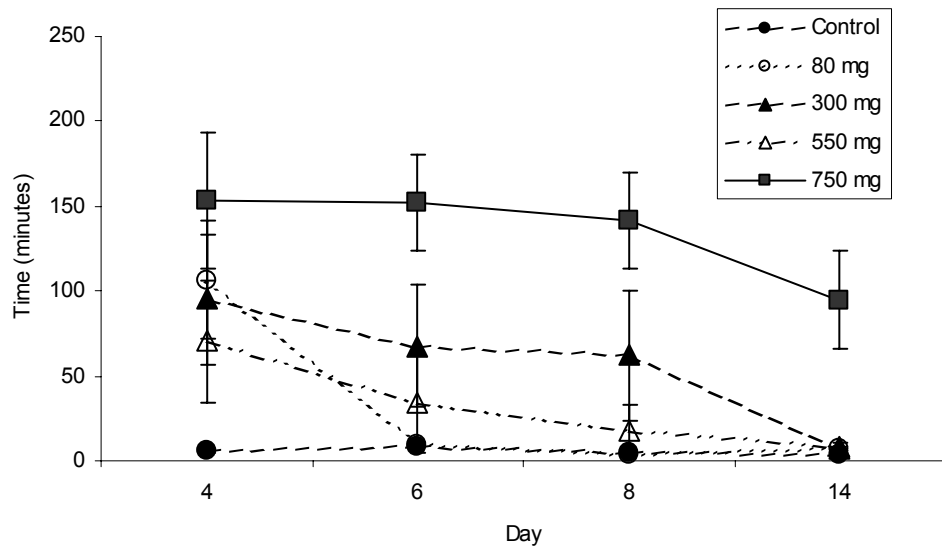


Figure 9: Time (minutes) taken for *Echinocardium* to re-bury (mean +/- 1 sd). Individuals who did not bury in 3 hours, were given a value of 180 minutes.

3.5 *Boccardia*

Turbidity values in the four treatments were 5 (control), 30, 70 and 220, which equated to TPM concentrations of 50, 80, 310, 750 mg L⁻¹ water. There were no obvious trends over time for benthic chlorophyll *a* levels for *Boccardia* that would be consistent with a decrease in microphytobenthos in either the controls or the high TPM treatments. Chlorophyll *a* levels for all the treatments ranged between 3.5 and 6.3 mg/ g sediment on Day 0.

Table 7 shows that on Day 0, 85-95 % of *Boccardia* were observed feeding when the sediment was added. The relationship with TPM concentrations strengthened over time (ANCOVA interaction term, $p = 0.0153$), with TPM concentrations affecting feeding rate the most on Day 14. On Day 14, only 40% of *Boccardia* in the 750 mg L⁻¹ treatment and only 50% in the 310 mg L⁻¹ treatment were observed feeding.

Table 7: Percentage (%) of *Boccardia* feeding over time.

Treatment	Day 0	Day 1	Day 3	Day 6	Day 8	Day 14
Control	95	90	90	90	85	85
80	90	70	65	65	60	70
310	95	90	90	75	75	50
750	95	80	70	50	50	40

3.6 *Macomona*

Turbidity values in the five treatments were 5 (control), 30, 70, 140 and 220, which equated to TPM concentrations of 50, 80, 300, 550, and 750 mg L⁻¹. For *Macomona*, benthic chlorophyll *a* levels on Day 1 ranged between 1.9 mg chlorophyll *a* per g sediment in the 750 mg treatment and 4.5 mg chlorophyll *a* per g sediment in the 550 mg treatment. Again there were no significant changes in sediment chlorophyll *a* over time (Table 8).

Table 8: Benthic chlorophyll *a* (mg/g sediment) in treatments with *Macomona*.

Treatment	Day 1	Day 14
Control	3.2	3.2
80	4.0	3.5
300	4.3	4.5
550	4.5	2.3
750	1.9	3.2

Burial rates for *Macomona* were variable and exhibited no pattern between treatments or days ($P > 0.1$; Figure 10). This was mainly due to the fact that most of the animals in the sediment-treated aquaria never buried themselves. By the end of the experiment, the number of non-burying and dead *Macomona* was greatest in the high turbidity treatments (Table 9). The ANCOVA results for *Macomona* show that the rate of mortality differs over time ($P = 0.0003$). At the beginning of the experiment there is no difference between treatments (Day 3 and 6); however by Day 8 and Day 14, there were more dead animals in the treatments with more terrigenous sediment ($P = 0.002$ and $P = 0.0055$ respectively). For dead and non-burying *Macomona*, there was no significant difference in slope over time ($P = 0.2007$), but an overall significant of increased TPM concentrations ($P = 0.0011$).

Table 9: The number of *Macomona* that did not bury during the experiment.

Treatment	Total not buried
Control	0
80	1
300	3 (2 dead)
550	4 (2 dead)
750	4 (3 dead)

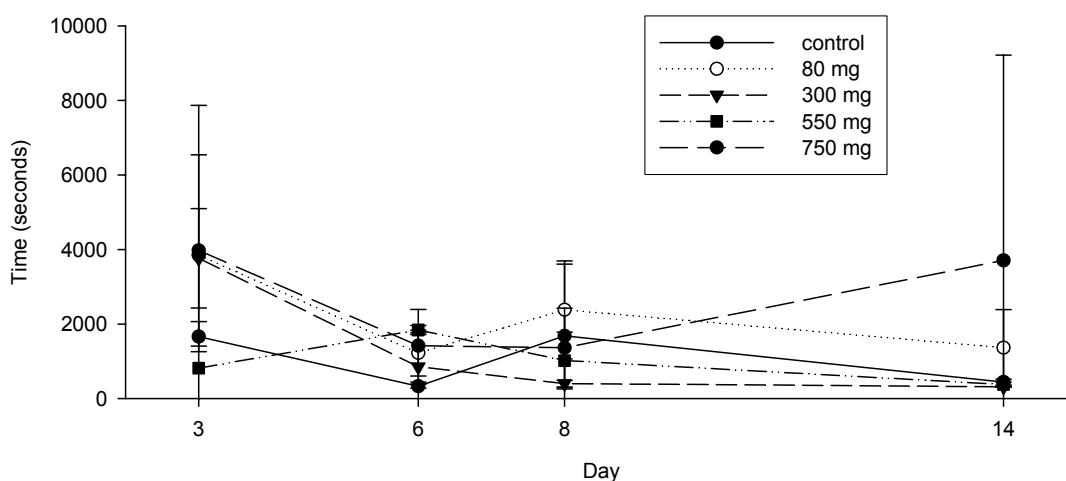


Figure 10: Time (seconds) taken for *Macomona* to bury (mean \pm 1 sd).

3.7 Pecten

The concentration of chlorophyll *a* in the water did not vary between the five experimental treatments, though there were slight variations over time. Organic matter content of the suspended particles was highly variable within the treatments over time.

The volume of water filtered by *Pecten* in the controls was relatively stable over the duration of the experiment (2-2.8 ml hr⁻¹; Figure 11). As expected, there was a negative relationship between the volume of water filtered and the TPM concentration. Over the 14 days of the experiment, this negative relationship changed ($p = 0.0143$), with the response strengthening over time (Figure 11).

Initially, the mass of particles removed from the water per unit time ranged between 135 - 225 mg hr⁻¹ (Figure 12). Removal rates in the controls were relatively stable over the course of the experiment (150 – 200 mg hr⁻¹). Removal rates in the treatments with enhanced TPM concentrations were more variable, which can be indicative of stress, but values overall were very low.

On Day 0 more particles were removed from the 100mg and 500mg L⁻¹ treatment levels than from the controls (Figure 12). But over time, this higher feeding rate with moderate suspended sediment levels decreased. By Day 14, while *Pecten* in the clean seawater are still removing a similar level to particles as on Day 1, all other treatments have decreased levels of particle removal.

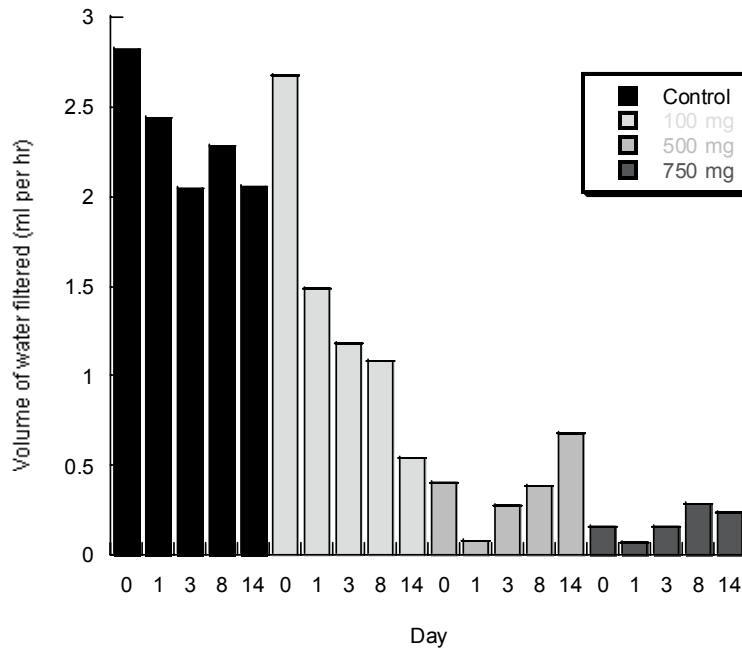


Figure 11: The volume of water filtered by *Pecten* over time (ml hr⁻¹).

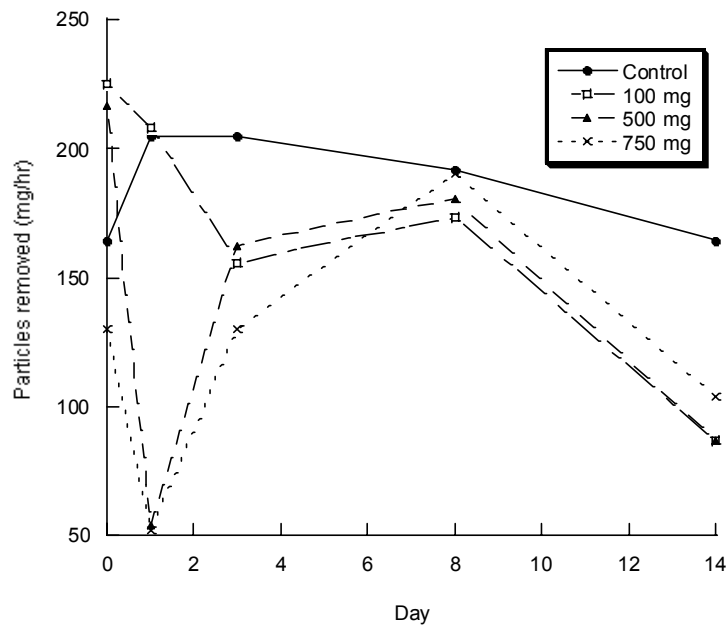


Figure 12: The mass of particles removed by *Pecten* over time (mg/hr).

On Day 14, a decrease in *Pecten* condition with increasing TPM concentrations was observed (Figure 14).

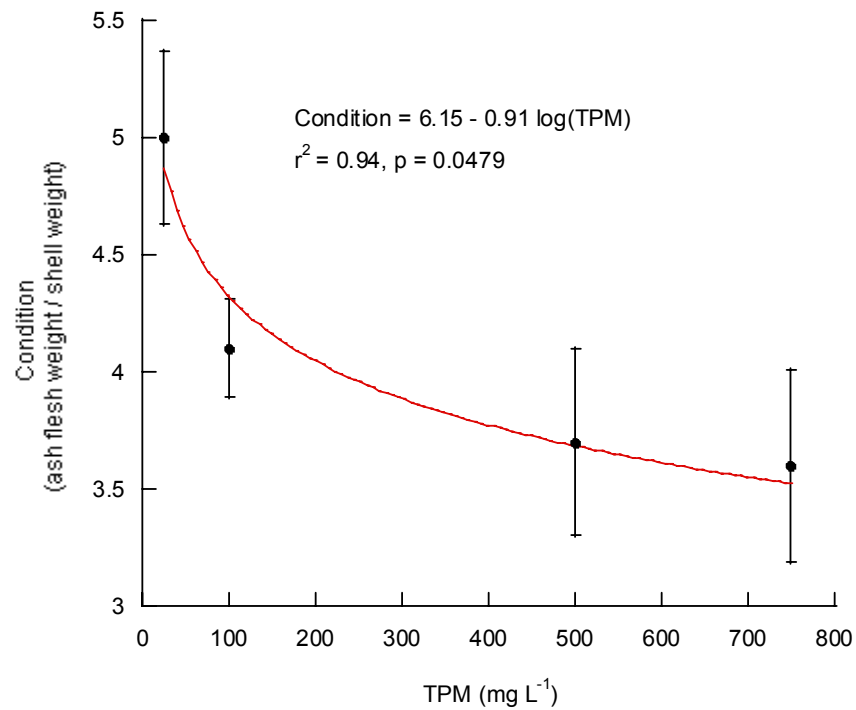


Figure 13: The effect of TPM concentration on the condition of *Pecten* after 14 days.

4. CONCLUSIONS

Sediment chlorophyll *a* concentrations in control treatments were relatively constant throughout the duration of the experiment. Thus, microphyte populations were maintained successfully in aquaria with no sediment added. This suggests that any decline in chlorophyll *a* levels observed over time, in aquaria with suspended sediment added, was a direct result of the higher suspended sediment concentrations attenuating light, preventing photosynthetic production by microphytes at the surface sediments, rather than grazing by macrofauna. PAR results indicate that almost all the light that entered the water is attenuated before it reaches the surface sediments.

The only other decreases in sediment chlorophyll *a* levels over time were observed for the highest treatment level in the *Zeacumantus* experiments. Despite the decreases in chlorophyll *a*, *Zeacumantus*, the only grazer used in our trials, appeared unaffected by suspended sediment concentrations up to 650 mg L⁻¹. We conclude that this species is robust to variations in suspended sediment concentrations in the short term. If the sediment concentrations had been maintained for periods of longer than 14 days, the ability of microphyte communities to photosynthesise, in the low light levels, would have been greatly reduced and *Zeacumantus* may have eventually exhausted their food supply.

It might have been anticipated that in intertidal areas, microphytobenthos productivity would not be much affected by light levels and consequently that lower productivity would not affect animal feeding. However microphyte production is greatly reduced during surface sediment exposure to the air. *Macomona* and *Boccardia* distribution reflect this to some extent with distributions restricted to mid – low on the shore and areas with high concentrations of surface detritus.

Even though there was no detectable decrease in sediment chlorophyll *a* for experiments involving *Boccardia* and *Macomona*, these species showed behavioural changes or increased mortality in treatments with higher suspended sediment concentrations. The sensitivity of these species relative to *Zeacumantus* was unexpected. If anything, we anticipated that we would find stronger results in the species most reliant on the microphytobenthos.

Boccardia feeding activity was not rapidly affected by high suspended sediment concentrations. *Boccardia* are commonly found in fine muds, which are frequently resuspended by wave activity. However, this experiment indicated that, over extended periods (longer than 9 days), suspended sediment concentrations as low as

80 mg L⁻¹ had a negative effect on the feeding rate of *Boccardia*. During the last half of the experiment, in the aquaria with the highest suspended sediment concentrations, *Boccardia* were observed using the terrigenous material we added to extend the length of their tubes. *Boccardia* may do this to escape anoxic conditions nearer the sediment surface by extending their tubes out of the sediment-column and into the water column, or as a way of trying to move out of the more turbid zone, near to the bed.

The ability of *Echinocardium* to bury itself was significantly affected by high suspended sediment concentrations. This result was apparent after only 4 days, suggesting that these animals are very sensitive to increases in water turbidity. The mechanism for this may be deposition, causing a reduction in food quality or a reduction in sediment porosity. A reduction in sediment porosity causes a thinner oxygenated layer at the surface and around the burrow. This conclusion was backed up by observations that the animals in the control chamber were more deeply buried than those in the higher turbidity chambers. The numbers of deaths were also higher in the higher turbidity treatments. Lohrer et al. (2003) documented *Echinocardium* mortalities following terrestrial sediment deposition at subtidal sites in the Auckland Region. Further emphasising sediment effects on these important members of many subtidal communities.

Macomona did not show any obvious behavioural trends with increasing suspended sediment concentrations, however there was increased mortality at concentrations >300 mg L⁻¹ (4 not buried in 750 mg L⁻¹ compared with 0 in the control). One characteristic of benthic bivalves is to stop feeding completely in unfavourable conditions. They close their valves to isolate themselves from environmental stressors. In our experiment, conditions did not improve over time so the mortality rate increased as the animals succumbed. These findings are supported by results from a transplant experiment in Whitford, similar to those described in Hewitt et al. (2001). Over a 3-month period, *Macomona* transplanted to areas which higher turbidity had lower growth rates than those in areas of lower turbidity (Hewitt, *unpubl. data*). Long-term trends of abundance of *Macomona* in Mahurangi Harbour suggest that this species is responding to changes in sedimentation patterns in the harbour (Cummings et al. 2003).

Pecten filtered less water in the higher TPM treatments than it did in the controls. The data on amount of particles removed from the water by *Pecten* also suggests that *Pecten* had difficulty processing the higher TPM concentrations. The condition of *Pecten* tended to be lower in sediment treated aquaria, although those results were not significant. Nevertheless, this suggests that, for short periods of time (<1 week), *Pecten* can deal with increased total particulate concentrations <250 mg L⁻¹. For

periods over a week, total particulate concentrations over 50 mg L⁻¹ will lead to decreased growth.

Three out of five of the species used in these trials are monitored in the ARC intertidal monitoring programmes, thus the results of this study can be used to extend interpretation of patterns in abundances observed by the programmes. To extend our understanding of sediment effects it would be advantageous to compare these results with longer-term field transplants, but this needs to be balanced against the need for more information on a number of other species.

Our laboratory experiments indicate that all animals tested except for *Zeacumantus*, are at risk from increased suspended sediment concentrations in estuaries. These are common and widespread species throughout the Auckland Region. These trials have shown that *Boccardia*, *Echinocardium*, *Macomona* and *Pecten* react negatively to increased suspended sediment concentrations in the short term. These results highlight the potential for indirect and subtle effects of elevated suspended terrestrial sediment concentrations on common soft sediment species in the Auckland region.

5. REFERENCES

- Berkenbusch, K.; Thrush, S.; Hewitt, J.; Ahrens, M.; Gibbs, M.; Cummings, V. (2001) Impact of thin deposits of terrigenous clay on benthic communities. Prepared for Auckland Regional Council. NIWA Client Report ARC01269.
- Cummings, V.J.; Nicholls, P.; Thrush, S.F. (2003) Mahurangi Estuary ecological monitoring programme - report on data collected from July 1994 to January 2003. Prepared for Auckland Regional Council. NIWA Consultancy Report No. ARC03207.
- Cummings, V.J.; Pridmore, R.D.; Thrush, S.F.; Hewitt, J.E. (1995) Post-settlement movement by intertidal benthic macrofauna: Do common New Zealand species drift in the water column? *New Zealand Journal of Marine and Freshwater Research* 29: 59-67.
- Decho, A.W. (2000). Microbial biofilms in intertidal systems: an over view. *Continental Shelf Research* 20: 1257-1273.
- 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. *Journal of Aquatic Ecosystem Stress and Recovery* 7(1): 57-74.
- Fahey, B.D.; Coker, R.J. (1992) Sediment production from forest roads in Queen Charlotte forest and potential impact on marine water quality, Marlborough Sounds, New Zealand. *New Zealand Journal of Marine and Freshwater Research* 26: 187-195.
- Gibbs, M.; Thrush, S.; Sukias, J.; Berkenbusch, K.; Thompson, D.; Bury, S. (2001) Evaluation of terrestrial sediment spatial patterns throughout the Whitford embayment and its benthic food web using stable isotope techniques. Prepared for Auckland Regional Council. NIWA Client Report ARC01270.
- Gray, J.S. (1997). Marine biodiversity: patterns, threats and conservation needs. *Biodiversity and Conservation* 6(1): 153-175.

- Guarini, J.M.; Blanchard, G.F.; Gros, Ph.; Gouleau, D.; Bacher, C. (2000) Dynamic model of the short-term variability of microphytobenthic biomass on temperate intertidal mudflats. *Marine Ecology Progress Series 195*: 291-303.
- Hewitt, J.; Hatton, S.; Safi, K.; Craggs, R. (2001). Effects of suspended sediment levels on suspension feeding shellfish in the Whitford embayment. Prepared for Auckland Regional Council. NIWA Client Report ARC00205.
- Hewitt, J.E.; Legendre, P.; McArdle, B.H.; Thrush, S.F.; Bellehumeur, C.; Lawrie, S.M. (1997) Identifying relationships between adult and juvenile bivalves at different spatial scales. *Journal of Experimental Marine Biology and Ecology 216*: 77-98.
- Hewitt, J.E.; Thrush, S.F.; Cummings, V.J.; Pridmore, R.D. (1996) Matching patterns with processes: predicting the effect of size and mobility on the spatial distributions of the bivalves *Macomona liliana* and *Austrovenus stutchburyi*. *Marine Ecology Progress Series 135*: 57-67.
- Kromkamp, J.; Peene, J.; van Rijswijk, P.; Sandee, A.; Goosen, N. (1995) Nutrients, light and primary production by phytoplankton and microphytobenthos in eutrophic, turbid Westerschelde estuary (The Netherlands). *Hydrobiologia 311*: 9-19.
- Lohrer, A.M.; Hewitt, J.; Thrush, S.F.; Lundquist, C.J.; Nicholls, P.E.; Leifting, R. (2003) Impacts of terrigenous material deposition on subtidal benthic communities. Prepared for Auckland Regional Council. NIWA Client Report HAM2003-055.
- Nicholls, P.E.; Norkko, A.; Ellis, J.; Hewitt, J.; Bull, D. (2000) Short term behavioural responses of selected benthic invertebrates inhabiting muddy habitats to burial by terrestrial clay. Prepared for Auckland Regional Council. NIWA Client Report ARC00258.
- Norkko, A.; Bonsdorff, E. (1996). Population responses of coastal zoobenthos to stress induced by drifting algal mats. *Marine Ecology Progress Series 140*: 141-151.
- Norkko, A.; Cummings, V.J.; Thrush, S.F.; Hewitt, J.E.; Hume, T. (2001a) Local dispersal of juvenile bivalves: implications for sandflat biology. *Marine Ecology Progress Series 212*: 131-144.

- Norkko, A.; Talman, S.; Ellis, J.; Nicholls, P.; Thrush, S. (2001b) Macrofaunal sensitivity to fine sediments in the Whitford embayment. Prepared for Auckland Regional Council. NIWA Client Report ARC01266/2.
- Norkko, A.; Thrush, S.F.; Hewitt, J.E.; Norkko, J.T.; Cummings, V.J.; Ellis, J.I.; Funnell G.; Schultz, D. (1999). Ecological effects of sediment deposition in Okura estuary. Report for Auckland Regional Council, North Shore City Council and Rodney District Council, ARC90243.
- Satory, D.P. (1982) Spectrophotometric analysis of chlorophyll *a* in freshwater phytoplankton. Technical Report 115, Hydrological Research Institute, Department of Environmental Affairs, Pretoria, South Africa.
- Thrush, S.F.; Pridmore, R.D.; Hewitt, J.E.; Cummings, V.J. (1992) Adult infauna as facilitators of colonisation on intertidal sandflats. *Journal of Experimental Marine Biology and Ecology* 159: 253-265.
- Thrush, S.F.; Pridmore, R.D.; Hewitt, J.E.; Cummings, V.J. (1994). The importance of predators on a sandflat: interplay between seasonal changes in prey densities and predator effects. *Marine Ecology Progress Series* 107: 211-222.
- Thrush, S.F.; Hewitt, J.E.; Pridmore, R.D.; Cummings, V.J. (1996) Adult/juvenile interactions of infaunal bivalves: contrasting outcomes in different habitats. *Marine Ecology Progress Series* 132: 83-92.
- 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) The generality of field experiments: interactions between local and broad scale processes. *Ecology* 81: 399-415.