

Effects of sediment deposition on the New Zealand cockle, *Austrovenus stutchburyi*

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Prepared by:

Henry Barrett,
Tara J. Anderson,
Don Morrisey (Cawthron Institute)

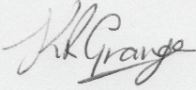


For any information regarding this report please contact:

Tara J. Anderson
NIWA
Nelson
+64-3-545 7746
tara.anderson@niwa.co.nz

National Institute of Water & Atmospheric Research Ltd
217 Akersten Street, Port Nelson
PO Box 893
Nelson 7040
New Zealand

Phone +64-3-548 1715
Fax +64-3-548 1716

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Executive summary

This report provides information on several short-term laboratory experiments, undertaken by NIWA for Marlborough District Council, to examine the effects of sediment deposition on the infaunal New Zealand cockle, *Austrovenus stutchburyi*. The New Zealand cockle is widespread and abundant within the Nelson-Marlborough region and has economic and cultural importance.

All experiments presented in this study were undertaken using native sediments (i.e., sediment grain sizes that cockles naturally occur in) on locally sourced cockles. Three laboratory experiments were undertaken to examine the ability of cockles to resurface after being buried by varying amounts of sediment over time. The importance of cockle-orientation at the time of burial was also examined to determine whether physical disturbance to cockles during a disturbance-event may alter or inhibit their ability to resurface by placing cockles either in a natural (upright) orientation, or in an inverted position in the sediment.

Cockles were found to be highly mobile and capable excavators, able to resurface within days (often hours) from under 2, 5 and 10 cm, and even 25 cm, of native sediment where no physical disturbance to their natural (in situ) orientation had occurred. Cockles repeatedly re-surfaced following daily reburial, indicating they were resilient to at least low levels of repeated deposition.

Cockles were much slower to re-orientate following disturbance to their natural orientation (inverted at the time of burial), and while able to resurface from an inverted position under low levels of deposited sediment they were significantly impeded in their ability to resurface when buried under greater sediment loads (5 and 10 cm), with significantly fewer adults resurfacing than sub-adults.

It is likely that natural or anthropogenic sediment deposition-events that deposit native sediments (with similar grain sizes to those already present) would be expected to have only limited direct impacts on local populations of *A. stutchburyi*. However, if cockles were also physically disturbed with orientations up-ended, then some mortality of larger sized cockles would be predicted, with higher losses predicted with thicker deposits of sediments. In contrast, based on previous studies, finer grained sediments (e.g., silts) or those that contain even small compositions of terrestrial clays are likely to have much more significant effects, with potential changes in community structure and loss of critical species likely to occur.

1 Introduction

Infaunal bivalves are important, and often critical, functional species that can improve water quality, stabilise sediments, oxygenate sediments as active bio-engineers, and can provide critical-habitat, both as living bivalve beds and through the accumulation of biogenic shell debris that can support highly diverse benthic assemblages. Knowledge of how infaunal bivalve species respond to increased sedimentation and event-deposition is a critical gap in our knowledge, and is particularly important as New Zealand faces increased levels of sediment deposition in the coastal environment from land-based activities, along with growing interest in resource-extraction and farming activities within the marine environment. Recent resource consent applications considered by the Environmental Protection Authority (EPA) have highlighted how little we really know about the likely impacts of sediment deposition on marine organisms, either on species already living in naturally-disturbed soft-sediment systems or those in more stable sediment environments. Consequently, knowing how these species respond to varying levels of sediment deposition is critical to understanding and predicting the likely impacts of increased sedimentation and deposition on New Zealand's coastal marine life.

Many estuary and harbours are subjected to increasing sedimentation, deposition and erosion (Anderson et al. 2004), that in turn affects the associated soft-sediment communities that reside there (e.g., bivalve beds, macroalgae, seagrass, and animals that live on and in these sediments). There are a number of potential reasons for sedimentation and depositional events to occur. Natural causes include the re-suspension and deposition of marine sediment during storms, and increased terrigenous sediment inputs due to heavy rainfall, and associated landslips - although these usually only pose short-term issues for the ecosystem (Norkko et al. 2006). However, increased forestry, agriculture and coastal developments that exacerbate land erosion whereby sediment runoff may pose longer-term issues with higher and on-going sedimentation effects (Morrison and Browne 1999; Stewart 1999; Thrush et al. 2003). Marine farming (e.g., shellfish and fish farming), infrastructure (e.g., marinas and piers), waterway engineering (e.g., dredging channels and harbours), benthic fishing activities (e.g., dredging and bottom trawling) and resource extraction (e.g., for oil, gas and minerals), may also alter local rates of sedimentation and deposition or erosion. The magnitude of sediment deposited and the frequency of delivery are likely to be important factors in understanding the likely impacts to the underlying communities and predicting population and community resilience and recovery (Thrush et al. 2003; Gibbs and Hewitt 2004).

The New Zealand cockle, *Austrovenus stutchburyi*, (also known as the little-neck clam, or tuangi) is a common intertidal clam endemic to New Zealand's coastal waters, and is a recreationally, customary and commercially harvested species (Morrison et al. 2009). *A. stutchburyi* is a shallow-burrowing suspension-feeder that is commonly found in sediment flats (mostly soft mud and fine to coarse sand) in sheltered estuaries and harbours around New Zealand (Morton and Miller 1968; Grange et al. 1996), where they can form extensive beds with densities of up to 3000 ind. m⁻² (Stephenson 1979). Individual cockles bury just below the sediment surface to enable their very short siphons to open just above the surface sediments to feed (Stephenson 1981; Hewitt et al. 1996). Cockles are able to move up and down and across and through sediments by digging and crawling using their muscular foot, with distances crawled varying from a few centimetres to 1.5 m per tide, but are rarely found deeper than 5-10 cm below the sediment surface (Larcombe 1971; Stephenson 1981; Mouritsen 2004).

The New Zealand cockle, when in high densities (e.g., beds) has been shown to be a functionally important species that can substantially influence water clarity, nutrient cycles, the productivity of

microphytobenthos on sediment flats, as well as being positively correlated with seagrass cover, organic matter and the efflux of ammonium from sediments (Lohrer et al. 2016). Knowledge of how bivalves respond to disturbances caused by deposition events is particularly relevant to New Zealand given the dramatic increases New Zealand has witnessed in land-based sedimentation effects within our coastal water ways. A decline in coastal conditions has led to losses of cockles or reduced densities in some areas (Marsden 2004). Increasing human population in New Zealand and worldwide have put increasing stress on coastal bivalve beds. Large cities, such as Auckland, are expected to reach a population of 2 million by 2050, while increasing populations nationwide will bring increased development, coastal urbanisation, with associated higher land-based inputs into the adjacent marine ecosystem (Lohrer et al. 2004; Morrison et al. 2009).

Studies examining the sedimentation effects in intertidal soft-sediment infauna have identified negative relationships between the health of bivalve populations and sedimentation, especially for functional species associated with low- or moderate- depositional environments (Norkko et al. 2002; Anderson et al. 2004; Lohrer et al. 2004). For example, terrigenous deposition in excess of 3 cm on sandflats has been shown to cause a decrease in macrofaunal populations by 90% after 10 days (Norkko et al. 2002). Susceptibility or resilience of organisms to depositional-events may be dictated by a combination of physiological tolerances (e.g., depth and sediment range) and behavioural responses (e.g., benthic mobility) (Hinchey 2006). Norkko et al. (2006) found that storm events that increased turbidity and sedimentation over a short time frame (<10 days) did not have significant direct-impacts on the associated bivalve population, but repeated turbidity and sedimentation events over 3–5 months led to increased muddiness in estuaries and a significant negative impact on bivalve physiology. Both anthropogenic and natural sediment deposition-events may also physically disturb *in situ* animals, whereby the process of depositing sediment on to the seafloor in large volumes (e.g., dredge spoil dumping, landslides) has the potential to disorient bivalves living on the seafloor before burying them. Animals whose orientation becomes disturbed (upended or knocked over) during a sedimentation event may incur more intense impact than those left in a natural upright orientation (Glude 1954).

1.1 Aims

The objective of this study was to undertake several short-term laboratory experiments examining the effects of sediment deposition on the infaunal New Zealand cockle, *Austrovenus stutchburyi*. Two forms of sediment deposition (the amount of sediment deposited [0, 2, 5 and 10 cm], the frequency of deposited [2 cm daily for 5 days]) and cockle orientation (natural-orientation [upright] versus disturbed-orientation [inverted]) were examined. *A. stutchburyi* was chosen as it is widespread and abundant in the Nelson-Marlborough region, as well as throughout New Zealand waters; is a good biological indicator of sediment and water quality conditions, and has economic and cultural importance (Cole 2001; Luca-Abbott 2001; Morrison et al. 2009). Marlborough District Council (MDC) is interested in information about the effects of sediment deposition on bivalve beds, such as cockles and green-lipped mussels, within the top of the south. Following experimental set-up issues with green-lipped mussel, the scope of this project was reduced in consultation with MDC to focus on the New Zealand cockle, *Austrovenus stutchburyi*.

2 Methods

2.1 Experimental overview

Three sets of laboratory experiments were performed to determine the ability of cockles to resurface after being inundated by native sediments (Table 1). Experiments 1 and 2, were undertaken to examine the ability of sub-adult (< 15 cm) and adult (\geq 20 cm) cockles to resurface from beneath increasing ‘amounts of sediments’ (2 cm, 5 cm and 10 cm amounts) and from a pulsed disturbance event (2 cm added daily for 5 days). For these experiments, adult and sub-adult cockles were positioned in either a natural (upright) orientation [Experiment 1] or a disturbed (inverted) orientation to simulate a possible maximum dis-orientation during a deposition event [Experiment 2a and 2b]. Experiment 3 examines adult and sub-adult cockles’ ability to resurface following a deep (25 cm) burial (natural-orientation only).

Table 1: Summary of deposition experiments.

Experiment	Orientation	Deposition (cm)	Cockles	Monitored
1	Natural (upright)	0, 2, 5, 10, 2x5	5 sub-adult, 5 adult	Daily for 7 days
2a	Disturbed (inverted)	<i>No deposition</i>	5 sub-adult, 5 adult	Hourly for 6 hours
2b	Disturbed (inverted)	0, 2, 5, 10, 2x5	5 sub-adult, 5 adult	Daily for 7 days
3	Natural (upright)	25	5 sub-adult, 5 adult	Daily for 7 days

2.1.1 Aquaria setup

Experiments 1 and 2 were undertaken in thirty plastic aquaria (20.3 cm high x 18 cm wide) setup within NIWA-Nelson’s small 2000 litre recirculating aquarium system (Figure 1a) that supplies a three-tiered shelf of up to twenty-two larger glass aquaria (60 long x 35 cm wide) (Figure 1b). For experiments 1 and 2, three plastic aquaria were placed in each of ten glass aquaria (e.g., Figure 1c). For experiment 3, six larger plastic aquaria (40.6 cm high x 30.5 cm wide) were placed in each of six glass aquaria. In all experiments, each plastic aquarium had its own direct water supply (hose-fed). Water overran from all three plastic aquaria into the surrounding glass aquarium, with the pooled water then draining from each aquaria via a pipe and gravity down to the recirculating reservoir, where it was filtered and recirculated back to the aquaria¹. Water temperature was kept at 18-20°C by controlling the air temperature of the room.

¹ The recirculating aquarium, which contains a bio-filter with layers of filter foam and gravel to support bacterial colonies, was biological active for ~3 months prior to the onset of these experiments, with water quality (pH, Ammonia, Nitrate and Nitrite) monitored and maintained for the duration of the experimental period.

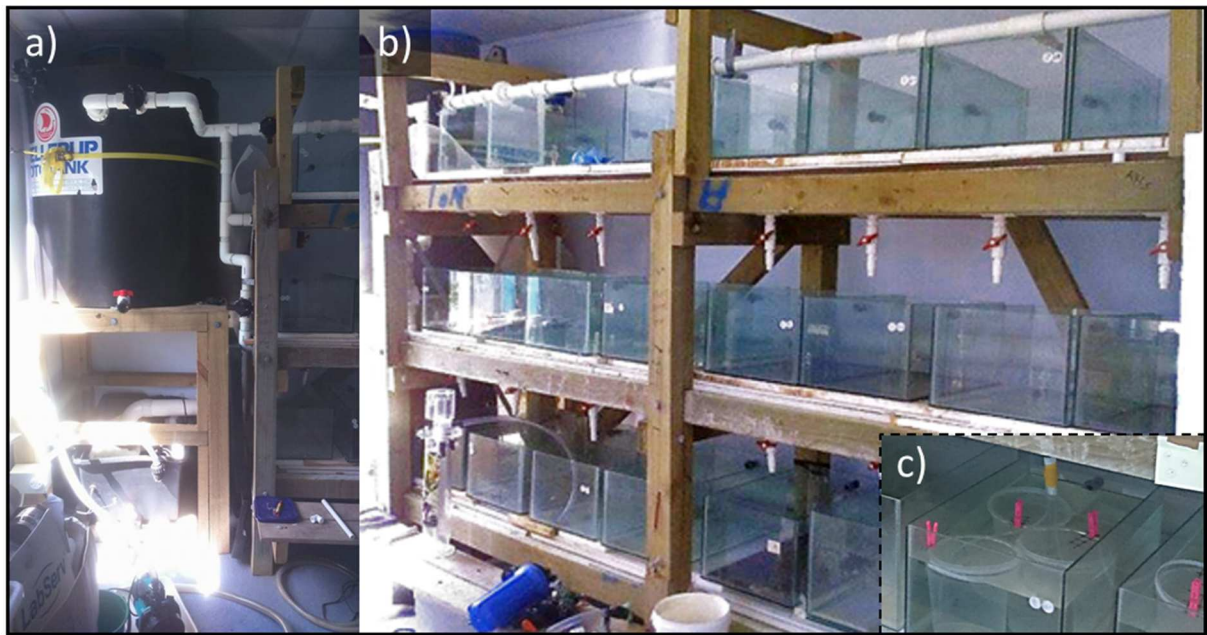


Figure 1: 2000 L recirculating aquarium setup. a) Recirculating tank and pump: Large black water drum above, and bio-filter tank below; b) 3-tiered aquarium rack with individual water-fed glass aquaria; c) Three plastic-aquaria example - each with a direct water hose/source - per glass aquaria.

2.1.2 Native sediment and cockle collections:

All experiments were undertaken using native sediments (i.e., sediment grain sizes that cockles naturally occur in). Native sediments were collected during low tides from the same general location where the cockles were collected - an extensive cockle bed in Delaware Bay ($41^{\circ}10'S$, $173^{\circ}26'E$), 25 km north east of Nelson (Figure 2). Sediment sub-samples were taken at the time of collection (subsequently frozen) and later analysed to determine mud, sand and gravel % composition of these native sediments (see Section 2.6, below). Basal and depositional sediments were collected and transported immediately to the laboratory, where they were coarsely sieved to remove large (> 1 cm) organisms and shell debris and placed in large holding aquaria with a bubbler for oxygenation.

Cockles were collected during low tides from an extensive cockle bed on the intertidal sediment-flats directly offshore of Pa Road boat ramp (Figure 2). To quantify how well cockles of two different life stages excavate through deposited sediment, two size classes of cockles, representing sub-adult (≤ 15 mm max width) and adult (≥ 20 mm), were collected for use in these experiments. Individual cockles (75 individuals of each size class) were carefully gathered from the intertidal sediments, sized using callipers and then placed in one of the two size-class buckets². The buckets were then drained of excess water and transported immediately to the experimental laboratory where they were placed in two large plastic aquaria (one for each size-class) with several bubblers for oxygenation.

² Cockles were collected under NIWA's special permit (597) issued by the Ministry for Primary Industries (MPI).



Figure 2: Location of native sediment and cockle collections from Delaware Bay, 25 km northeast of Nelson, New Zealand. Yellow dotted circle depicts the sediment and cockles collection area.

2.2 Natural (upright) orientation, 0-10 cm depositions (Experiment 1)

In this experiment, we examine the ability of cockles to resurface after being inundated by native sediments, when placed in an upright natural orientation. To do this, a 5 cm basal layer of sediment was placed in each of the thirty experimental buckets and left to settle and the water in recirculation system to clear for 24 h. After this time, 5 x sub-adult or 5 x adult cockles were carefully pushed into the basal sediment of each bucket in an upright natural orientation (i.e., siphons facing up, as they would occur in their natural environment) to a depth of half their body height - giving 150 cockles in total, fifteen buckets per size-class. All cockles (per size group) were haphazardly positioned within the buckets, but interspaced equally between each other and the bucket edges. Cockles were left to bury and acclimatise for 24 h.

Four treatments and a control were then randomly assigned to buckets within aquaria using a fully orthogonal random design³, with three replicate buckets assigned for each treatment/control per size class. Two forms of sediment deposition ('one-off-amount' and 'repeated-deposition') were applied, whereby sediment was experimentally deposited in 0 cm (control, where buckets were not altered), 2 cm, 5 cm and 10 cm amounts (treatments 1-3, respectively), while repeated-deposition was experimentally examined by adding 2 cm of sediment each day for 5 days (treatment 4) (Figure 3). The addition of treatment sediments on top of cockles was carefully but systematically added in a water slurry to allow even settlement of deposited sediments. This gave a design of 150 cockles in total, 2 size classes with three replicate buckets per size class and treatment/control.

³ Using a random number generator to assign each treatment/control/replicate to a pre-numbered bucket, within a block design so that no glass aquaria could have more than one replicate of each treatment.

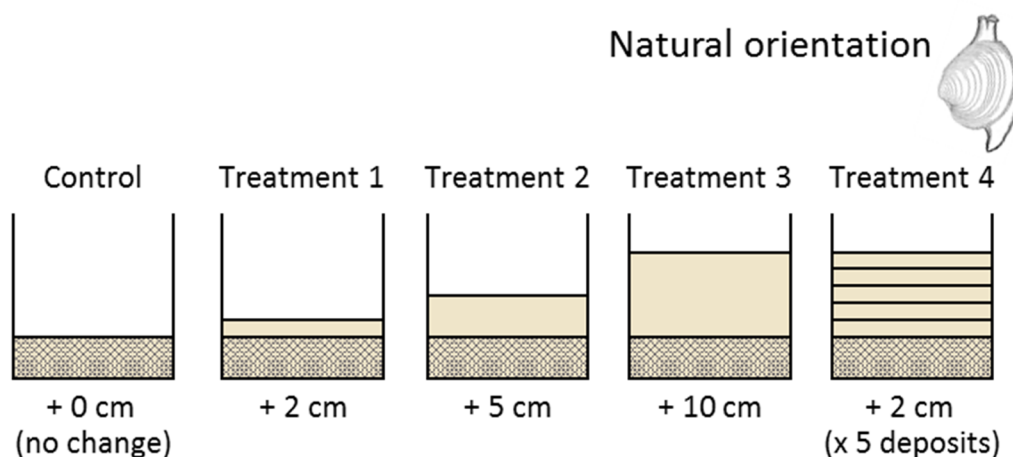


Figure 3: Experimental design for sediment deposition, where cockles were placed in a natural (upright) orientation. Each bucket had a 5 cm basal sediment layer prior to 5x cockles (in 2 size classes) being placed in an upright position within the buckets. Control buckets were not altered; treatments 1-3 varied in the amount of sediment deposited (2 cm, 5 cm and 10 cm respectively); while treatment 4 had 2 cm deposited daily for 5 days (10 cm total).

The experiment was then monitored daily for seven days. Each tank was visually-inspected each day with the number of sub-adult and adult cockles seen at the sediment surface (cockles and/or siphons and siphon holes present at the sediment surface), recorded. At the end of the 7 days, all cockles at the surface were removed and measured with callipers to the nearest mm across the maximum girth of the cockle (max. cockle width). Each bucket was then removed and drained. Any cockles that had not excavated to the surface were exhumed by systematically removing layers of sediment, centimetre at a time, following the method of Krantz (1974), with the depth at which they were found (relative to the surface mark) and size of the cockle measured and recorded.

2.3 Disturbed (inverted) orientation, no deposition (Experiment 2a)

In this experiment, we examine the ability of cockles to re-orientate themselves following a disturbance – simulated by placing adult and sub-adult cockles upside down in an inverted position in the sediment. As with experiment 1, a 5 cm basal layer of sediment was placed in each of the thirty experimental buckets and left to settle and the water in recirculation system to clear for 24 h. After this time, 5 x sub-adult or 5 x adult cockles were carefully pushed into the basal sediment of each bucket to a depth of half their body height in an inverted position (i.e., hinge pointing upwards, simulating cockles that have been up-ended). All cockles per size group were haphazardly positioned within the buckets, but interspaced equally between each other and the bucket edges. No sediment was deposited in this experiment. This gave a design of 150 cockles in total, 2 size classes with fifteen replicate buckets per size class. Cockles in these tanks were then monitored every hour for 6 hours, with the relative orientation of each cockle recorded. At the end of 6 hours, each cockle was removed, sized with callipers, its final orientation recorded, and the time taken ‘if reoriented to an upright position’ recorded to the nearest hour.

2.4 Disturbed (inverted) orientation, 0-10 cm depositions (Experiment 2b)

In this experiment, we examine the ability of cockles to resurface after being inundated by native sediments, when placed in an inverted disturbed orientation. Except for the orientation of adult and sub-adult cockles all other conditions and treatments were identical to experiment 1. Five x sub-adult or 5 x adult cockles were carefully pushed into the sediment in an inverted position (i.e., hinge pointing upwards, simulating cockles that have been re-orientated due to disturbance) to a depth of half their body height (150 cockles in total, fifteen buckets per size-class). All cockles (per size group) were haphazardly positioned within the buckets, but interspaced equally between each other and the bucket edges. Cockles were left to bury and acclimatise for 24 h.

Following the same design as experiment 1, four treatments and a control were then randomly assigned to buckets – this time with inverted cockle positions - using a fully orthogonal random design⁴, again with three replicate buckets assigned for each treatment/control per size class. In an identical manner to experiment-1, sediment was experimentally deposited in 0 cm (control, where buckets were not altered), 2 cm, 5 cm and 10 cm amounts (Treatments 1-3, respectively), while repeated deposition was experimentally examined by adding 2 cm of sediment each day for 5 days (treatment 4) (Figure 4). In this experiment all cockles were inverted at the time of burial, and in the case of repeat treatments the specimens at the surface were also inverted with each new addition. The addition of treatment sediments on top of cockles was again carefully but systematically added in a water slurry to allow even settlement of deposited sediments. As with experiment 1, this gave a design of 150 cockles in total, 2 size classes with three replicate buckets per size class and treatment/control.

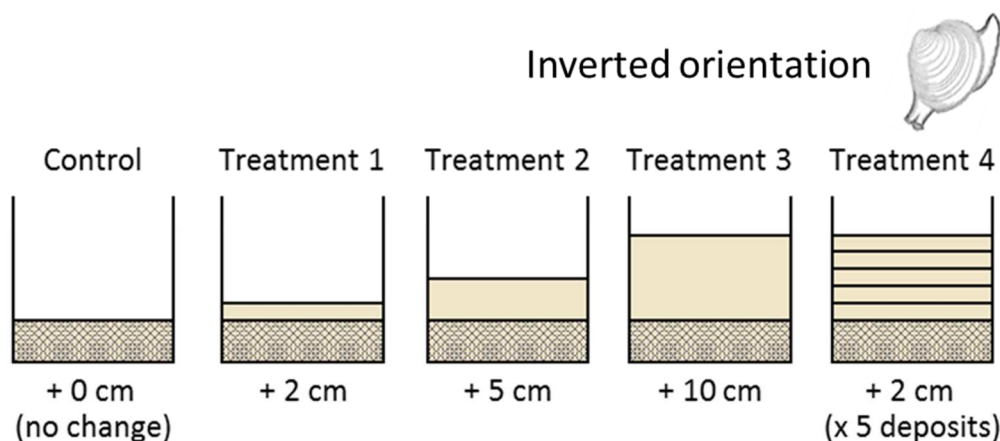


Figure 4: Experimental design for sediment deposition, where cockles were placed in a disturbed (inverted) orientation. Five cockles were paced inverted into the basal sediment (hinge up) within each plastic aquarium (for sub-adult and adult cockles). Experiment 2a No sediment was added (= control buckets); In experiment 2b treatments 1-3, varied in the amount of sediment deposited (2 cm, 5 cm and 10 cm respectively); treatment 4, had 2 cm deposited daily for 5 days (10 cm total), while control buckets were not altered (as per experiment 1).

⁴ Using a random number generator to assign each treatment/control/replicate to a pre-numbered bucket, within a block design so that no glass aquaria could have more than one replicate of each treatment.

The experiment was monitored daily for seven days. Each tank was visually inspected each day with the number of sub-adult and adult cockles seen at the sediment surface (cockles and/or siphons and siphon holes present at the sediment surface), recorded. At the end of the 7 days, all cockles at the surface were removed and measured with callipers to the nearest mm (max. cockle width). Each bucket was removed and drained. Any cockles that had not excavated to the surface were exhumed by systematically removing layers of sediment, centimetre at a time. For each excavated cockle, its orientation (inverted, partially-turned, upright), depth at which it was found, and its size (mm) was recorded.

2.5 Deep (25 cm) burial (Experiment 3)

Cockles are found intertidally within sheltered estuaries with relatively low levels of sediment disturbance in terms of burial frequency. Consequently, prior to these experiments it was expected that 10 cm amounts of deposition would likely be an upper maximum by which cockles could excavate to resurface, and that this amount would likely incur some level of excavation-impedance or mortality in the cockles. However, cockles were found to be very capable excavators. As a consequence, we decided to undertake an additional 'deep burial' experiment by depositing 25 cm of sediment in an attempt to determine their maximum excavation potential.

In this experiment, six larger plastic buckets (40.6 cm high x 30.5 cm wide) were placed in each of six glass aquaria. Each of these tall buckets was given a 5 cm basal layer of sediment and left to settle for 24 h. After this time, 10 x sub-adult or 10 x adult cockles were carefully pushed into the basal sediment of each tall bucket in an upright position to a depth of half their body height. This design gave three buckets of sub-adult cockles and three buckets of adults (i.e., 60 cockles in total, 2 size classes); with three replicate buckets per size-class. As with the previous experiments, all cockles were haphazardly positioned within the buckets; interspaced equally between each other and the bucket edges. Cockles were left to bury and acclimatise for 24 h. After this time, 25 cm of sediment was systematically deposited into each bucket and left to settle.

The experiment was then monitored daily for seven days. Each tank was visually-inspected each day with the number of sub-adult and adult cockles seen at the sediment surface (cockles and/or siphons and siphon holes present at the sediment surface), recorded for each numbered bucket. At the end of the 7 days, any cockles at the surface were removed and measured with callipers to the nearest mm across the maximum girth of the cockle (max. cockle width). Each bucket was then removed and drained. Any cockles that had not excavated to the surface were exhumed by systematically removing layers of sediment, centimetre at a time, with the depth at which they were found (relative to the surface mark) and measured-size of the cockle recorded.

2.6 Sediment grain size

To ensure that the sediment grain sizes used in the experiment were comparable to the native sediments in Delaware Bay, a 50 ml sediment sub-sample was then taken from a random selection of buckets at the end of each experiment. This subsample was a composite of sediment taken from the removed sediments. These grain-size sediment samples, along with those subsamples taken at the time of sediment collection, were then placed in individual labelled metal trays. The proportion of mud, sand and gravel (grain-size distribution) was determined by oven drying each sediment sample at 100 °C overnight and washing each subsample through stacked sieves with meshes of 2 mm and 63 µm sieves, to provide the proportion of gravel (>2 mm), sand (63 µm – 2 mm), and silt (<63 µm).

The fraction retained on each sieve was dried and reweighed. The dry weight of each fraction was then subtracted from the total weight, and expressed as a percentage of the total dry weight.

2.7 Statistical analyses

A Spearman's rank correlation coefficient test was run to find any correlation between cockle size and resurfacing rate for each experiment. To determine if adults and sub-adults differed in their ability to resurface beneath 2, 5, and 10 cm sediment in upright (experiment 1) vs inverted (experiment 2) orientations, and 25 cm deep sediment (experiment 3) repeated measures Analysis of Variance (ANOVA) with Tukey post-hoc tests were run using proc Mixed Procedure in SAS. Resurfacing rates were calculated as percentage of total cockles resurfaced for each experiment. The mean percentage \pm standard errors (SE) were then calculated and graphed for each size-class and treatment.

3 Results

3.1 Orientation and depth of burial

Cockles placed in a natural upright orientation and then buried by 2, 5 or 10 cm of sediment, resurfaced quickly and were observed feeding at the surface within a week (Figure 5a-c). When buried under 2 and 5 cm of sediment, naturally orientated cockles quickly resurfaced with >90% of cockles present at the surface within 2 days and almost all cockles resurfacing after 1 week (Figure 5a). When buried under 10 cm of sediment, most naturally orientated cockles, in both size classes, also quickly resurfaced with >70-80% of cockles present at the surface within 2 days, and >80-90% after 1 week (Figure 5b, c). Although the total number of cockles recorded at the surface over time differed significantly between adults and sub-adults in some treatments ($F_{(1,5)}=24.0$, $p<0.0001$) (e.g., Figure 5b), there was no consistent trend in adult versus sub-adult cockles ability to resurface (Figure 5a-c).

Cockles placed in a disturbed (inverted) orientation, but with no sediment added, were slow to re-orientate to an upright position, with only < 25% of all cockles re-orientating within the first 6 hours (Figure 6). This is likely only indicative of righting potential as tidal-entrained cockle movement may not have been optimal for this 6 hour period. There was no significant difference in the ability of inverted adult and sub-adult cockles to right themselves, partly due to between size class variability (Figure 6).

Cockles placed in a disturbed orientation with sediment then deposited on top of them were much slower to resurface than those placed in an upright position (Figure 5d-f), with resurfacing varying as both a function of cockle size and the amount of sediment deposited. When buried under 2 cm of sediment, most inverted cockles were able to right themselves and resurface within 48 hours (>75%) with almost all cockles observed feeding at the surface within a week (Figure 5d). In contrast, when buried under 5 and 10 cm of sediment, many inverted cockles failed to re-surface, with significantly fewer adults resurface than sub-adults ($F_{(1,5)}=15.38$, $p<0.001$, $F_{(1,5)}=21.81$, $p<0.0001$, 5 and 10 cm treatments respectively) (Figure 5e-f). The number of sub-adults resurfacing from an inverted position decreased as higher amounts of sediment was added, but most sub-adults had re-orientated themselves and re-surfaced in less than 2-3 days (> 70-80%), with most sub-adult cockles found feeding at the surface after 3 days (Figure 5e). In contrast, significantly fewer inverted adults resurfaced over the same time frame, with resurfacing success rates significantly declining with higher amounts of deposited sediment (Figure 5f). Inverted adult cockles fared worst when buried under 10 cm of sediment, with only 40 % of adult cockles able to right themselves and resurface over the course of a week. Excavation found that most of the buried adults were still beneath 8-10 cm of sediment, indicating little to no vertical movement had occurred.

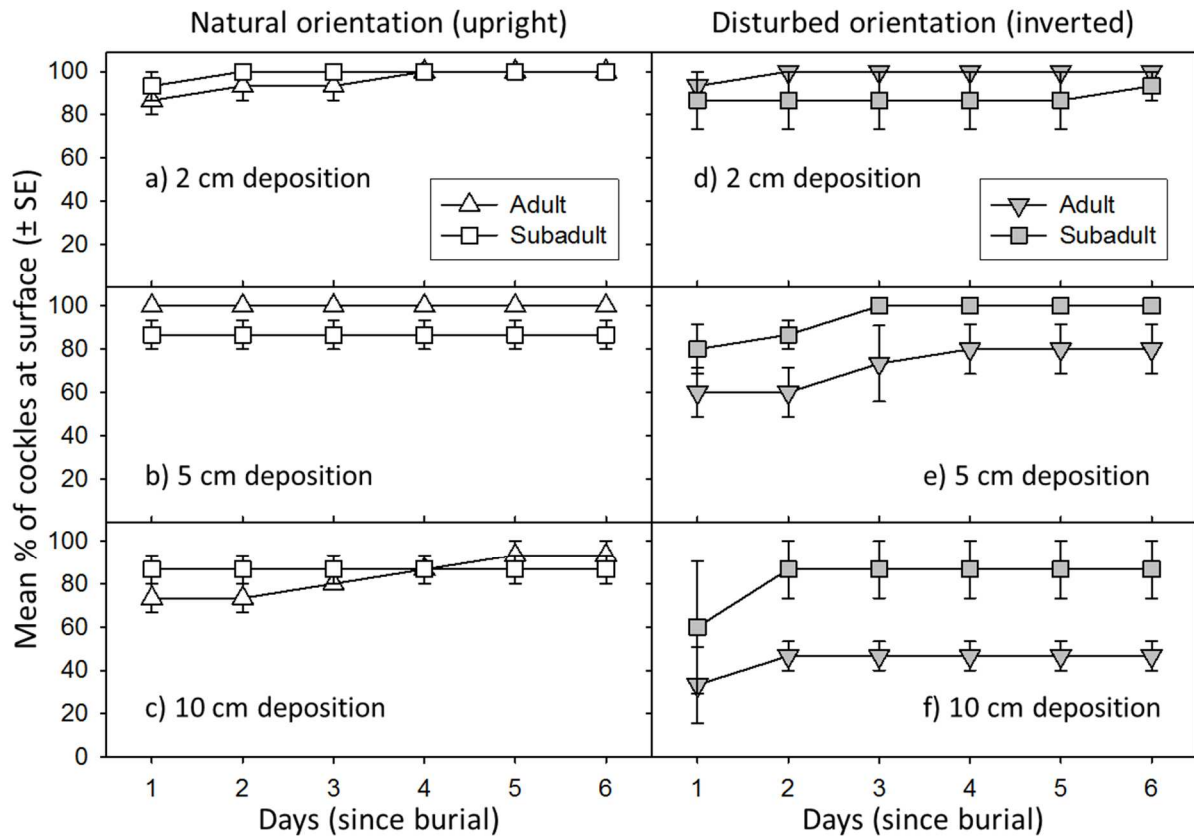


Figure 5: Cockle resurfacing success relative to 0, 2, 5 and 10 cm deposition events. Percentage of adult versus sub-adult sized cockles excavated to the surface in days since burial. a-c) Cockles placed in a natural upright position at the time of deposition, versus d-e) Cockles placed in a simulated disturbed (inverted) orientation.

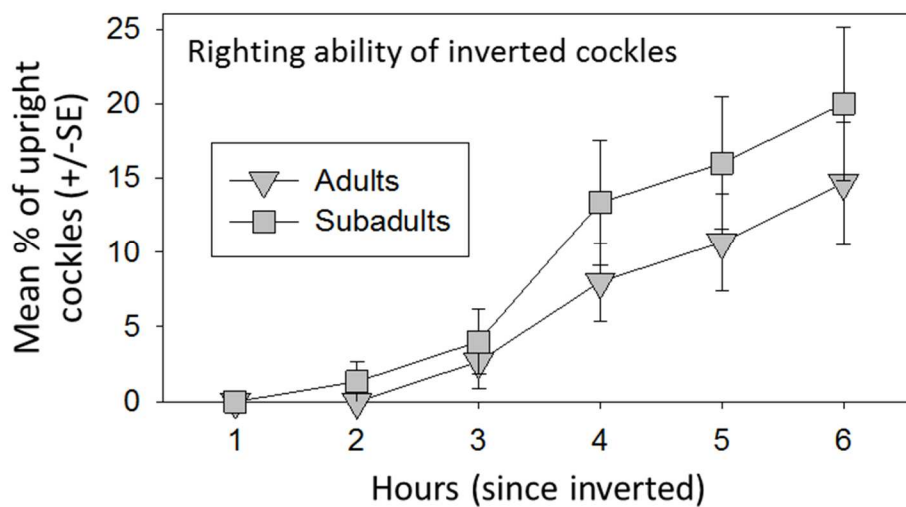


Figure 6: Cockle righting success after being inverted into the sediment (no sediment added). Mean percentage of adult versus sub-adult cockles found upright every hour for six hours following simulated disturbance (i.e., cockles placed inverted into the sediment).

3.2 Deep burial (25 cm)

Naturally orientated (upright) cockles were able to ascend quickly through 25 cm of native sediment. Within 2 days, >50% of all cockles, regardless of size, had reached the surface, with >70% of cockles resurfacing after 1 week (Figure 7). There was no significant difference in resurfacing rate or success between adult and sub-adult cockles ($p > 0.5$) (Figure 7). Excavated cockles were found at a range of depths mostly between 10-18 cm, showing they had made good vertical progress, while three cockles (2 adult and 1 sub-adult) were still in their original position having made no progress at all (one of which had clearly died). While those cockles that had not moved either had or would likely perish, it is unclear whether some of the cockles still buried between 10-18 cm depths could have resurfaced given more time, especially given no horizontal-asymptote had yet been reached with new cockles still surfacing at the end of 1 week (Figure 7).

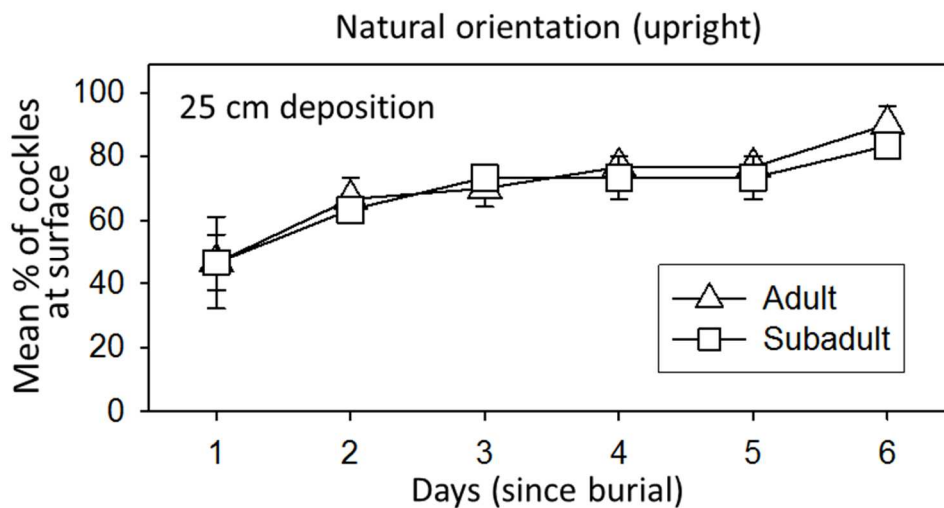


Figure 7: Cockle resurfacing success under deep sediment burial. Percentage of adult versus sub-adult sized cockles found at the surface each day following the burial under 25 cm of sediment after being placed in a natural (upright) orientation.

3.3 Continual reburial (2 cm daily x 5 days)

Cockles quickly resurfaced after being buried under 2 cm of sediment (>70% of all cockles had resurfaced 24 h after the first burial). However repeated daily burial under 2 cm of sediment deposited each day for 5 days, impeded some cockles, with fewer cockles resurfacing on days 2 through 5. Fewer sub-adults re-surfaced on these days than adults ($F_{(1,5)} = 6.53$, $p < 0.05$) (Figure 8a), although this was not significant across the entire week (size class*time $p > 0.5$). Inverted cockles did not differ in their resurfacing rates compared to naturally orientated cockles, although a similar reduction in re-surfacing rates was observed on days 3 and 4 for sub-adult sized cockles, size comparisons were not significant due to within treatment variability ($p > 0.5$) (Figure 8b).

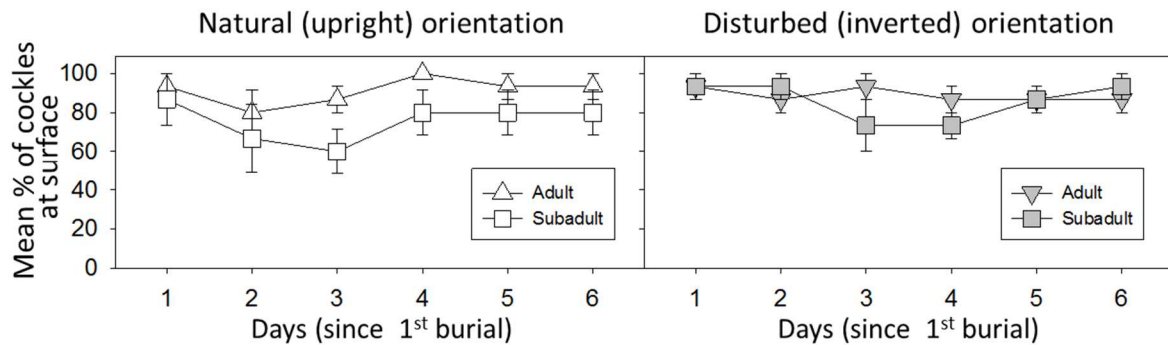


Figure 8: Cockle resurfacing success after repeated depositional events (burial under 2 cm of sediment daily deposition for 5 days). Percentage of adult versus sub-adult sized cockles found at the surface each day following the repeated daily burial under 2 cm of sediment after being placed in either a natural (upright) or disturbed (inverted) orientation.

3.4 Sediment grain size

There was no significant difference in the grain size composition between the native sediments from Delaware Bay and those used in the experiments (Figure 9). The native sediment from the cockle bed in Delaware Bay, Nelson was dominated by sand (>90%), with small quantities of mud (4-8%) and rare amounts of gravel (<1%) (Figure 9). Coarsely sieving sediments, to remove large animals and shell debris, did remove some gravels, but these differences were negligible (<0.02%) and were not significantly different between experimental treatments and/or controls.

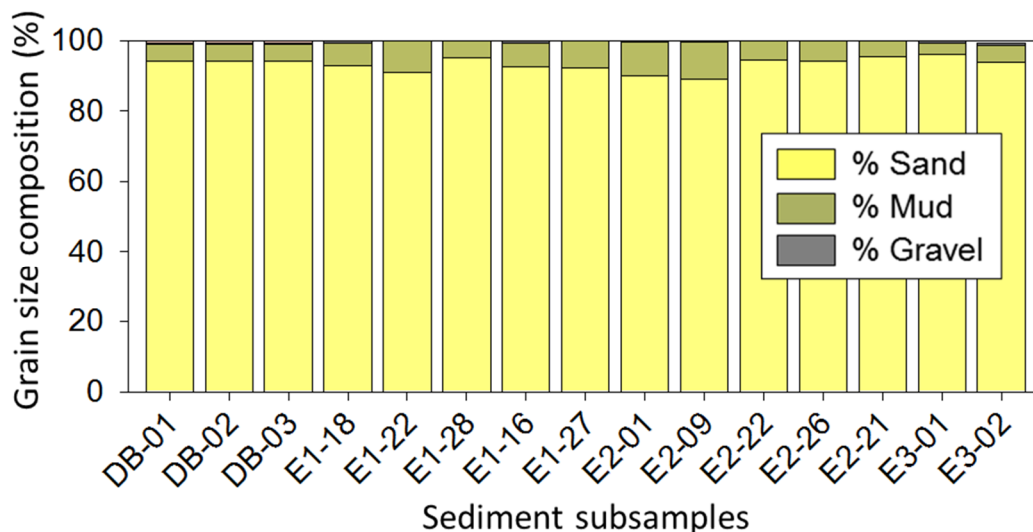


Figure 9: Grain-size sediment composition. Comparisons between native *in situ* sediments from Delaware Bay (DB) and those sieved for experiments 1, 2 and 3 (E1-E3, respectively). Sediment sample number after hyphens, depict replicate sample/bucket numbers.

4 Discussion

4.1 Deposition and orientation

Cockles were found to be highly mobile and capable excavators, able to resurface within days (often hours) from under 2, 5 and 10, and even 25 cm of native sediment where no physical disturbance to their natural (*in situ*) orientation had occurred. However, cockles were much slower to re-orientate following physical disturbance to their natural orientation (simulated by placing cockles in an inverted position in the sediment), and while able to resurface from an inverted position under low amounts of sediment deposition (2 cm), cockles were significantly impeded in their ability to resurface from an inverted position when buried under greater amounts of sediment (5 and 10 cm). Hull et al. (1998) examined reburial and resurfacing capabilities in the New Zealand pipi, *Paphies australis* and found that pipis were equally capable excavators that were able to rapidly resurface following native sediment deposits of 1, 5 and 10 cm. Hull et al. also found that disturbed pipis that were laterally placed in the sediment took longer to resurface than naturally oriented (upright) ones. Similarly, Glude (1954) in a study of the soft-shell clam, *Mya arenaria*, found that the chance of clam survival decreased as both a function of increased burial depth and clam size; where *M. arenaria* buried in upright and horizontal positions were more likely to survive than those placed in an inverted position.

Most soft-sediment infauna live in the upper 5 cm of benthic sediment, as increasing sediment weight and lack of pore space at depth can be a significant barrier to penetration of the sediment by benthos (Hines and Comtois, 1985). Glude (1954) suggested that given animal-size to sediment weight (with increasing amounts of deposition), deposition events would likely be more damaging to animals that have been dis-orientated and inverted, than to those remaining upright or knocked over. In a study carried out on *Clinocardium nuttallii*, cockles buried under ≤ 5 cm of sediment were able to re-establish siphon contact with the sediment surface in less than 24 h (Chang and Levings 1978), but only 50% resurfaced under 10 cm depositions, with none surviving 20 cm depositions. Chang and Levings (1978) found that the broader shell of *C. nuttallii* cockles meant that they met more resistance when burrowing under heavy amounts of sediment, impeding their ability to resurface.

However, in our study, cockle size was not a significant factor in the ability of naturally-orientated cockles to resurface, even from under 25 cm of sediment. Larcombe (1971) and Stephenson (1981) found smaller size-classes of cockles to have moved extensively between tides, but found this degree of movement rare in larger cockles, unless it was in response to a disturbance. In our study, cockle size impeded resurfacing only when cockles had been inverted prior to burial. This pattern suggests that 'righting-ability' relative to the weight of the overlying sediment is likely to be the factor impeding the surfacing success of adult *A. stutchburyi*, rather than the 'excavation-ability' to the surface *per se*. This was also supported by the fact that many to most of the inverted cockles that had failed to resurface were still in their original basal sediment position. Adult sizes used in our experiments ranged from 20 to 27 cm, compared to sub-adult sizes of 9 to 15 cm. *A. stutchburyi* adults can grow to 60 mm in length (Powell, 1979), but these larger sizes were not consistently present at the Delaware Bay collection site. We would predict, however, that based on the lower resurfacing rate of adult cockles in this experiment, that much larger sized cockles would incur even more resistance during righting, and thus would have even lower predicted resurfacing success than those found for the smaller-sized adult examined during this study.

In contrast to native sediments, Lohrer et al. (2004) in a study of the effects of terrigenous sediment on soft-sediment macrobenthos, found that only small amounts of terrestrial sediments over 10 days (3 mm deposits of fine terrestrial mud) was enough to cause significant changes to the macrofaunal community, with declines in diversity and richness. Sediment not native to the habitat, such as that derived from land-based activities, seems to be the most damaging. For example, a study on New Zealand Horse mussel, *Atrina zelandica*, indicated that clay deposition led to a 50% reduction of population size after 3 days and more than 90% after 10 days, regardless of sediment depth (Norkko et al. 2002). Although the clay deposition was gradually broken up by other fauna, recovery was still incomplete after 408 days, showing long-lasting habitat change affecting bivalve populations there. Anderson et al. (2004) found fine terrestrial sediments were damaging to benthic infauna even in small quantities, especially when in the form of repeated additions over time.

In our study, cockles repeatedly re-surfaced following daily reburial (i.e., 2 cm added daily for 5 days), indicating that cockles were resilient to at least low levels of repeated deposition. Hull et al. (1998) in their experimental study on *P. australis* found that the number of pipis at the surface declined through time when reburied daily under 5, 10 and 15 cm of sediment. Equivalent treatments of continual burial were not examined in this study due to a lack of aquarium capacity. However, this level of continual reburial would be valuable to assess in any future studies.

4.2 Deposition-events

Sediment deposition events can smother the sediment surface burying the infaunal animals that live there (Glude 1954). *Austrovenus stutchburyi* (New Zealand cockles), *Perna canaliculus* (green lipped mussels), *Paphies australis* (pipi) and *P. subtriangulata* (tuatua) are all important harvested species that are known to be vulnerable to sedimentation and deposition-events (Morrison et al. 2009; Anderson et al. 2004; Österling et al. 2010). Extreme smothering of bivalve beds as a consequence of sedimentation events has been historically documented for a wide range of species (e.g., Stephenson 1981; Morrison et al. 2009; Grange 1996), whereby increased sedimentation can cover beds to depths too deep for individuals to re-surface from. Species such as cockles that live at the interface between the land and the sea may be particularly vulnerable to both land- and marine- based sedimentation events. Many estuaries that are now dominated by mud/silt, have been found to have layers of dead cockle shell several feet below the surface, highlighting how vulnerable coastal populations can be to sedimentation events (Marsden and Adkins 2010; Morrison et al. 2009). For example, Reeve (1854), cited in Stephenson 1981) described the death of extensive mature cockle beds in south Canterbury following inundation by a thick (50-60 cm) layer of distinctive mud from the Avon and Heathcote Rivers in the early 1950's. Stephenson (1981) noted that 'beds of shells in a natural orientation have been noted' providing further evidence of this event. However, it is clear from more recent studies that the amount and frequency of the sediment-event will influence the response, resilience and recovery of infaunal bivalves and associated infaunal communities (e.g., Hull et al. 1998; Thrush et al. 2004; Lohrer et al. 2004; this study). Both anthropogenic and natural sediment deposition events are likely to physically disturb *in situ* cockles. Maurer et al. (1986) suggested that vertical migration can be a process which, under certain conditions, can be relied upon (along with larval settling and immigration from outside areas) as a mechanism for the recovery of a dredge disposal area. This however, relies upon the level of sediment deposition being sub-lethal to bivalve populations in the area, and would need to take into account on-going physiological-impacts (e.g., Norkko et al. 2006).

Mobility, physiological and behavioural differences are all likely to play important roles in understanding species-specific responses of bivalves to increased sedimentation. Movement in response to unfavourable conditions has been recorded for a range of bivalve species, especially in response to chemical contamination of sediments (e.g., Roper et al. 1994). For example, McConway (2008) while undertaking his dissertation examining the effects of contaminated sediments on *A. stutchburyi*, found that his experimental cockles crawled out of experimental field containers, with escapes higher in treatments dosed with contaminated sediments than in native-sediment controls. Behavioural and morphological responses may also be used by some species. For example, while many bivalve species may respond to lower oxygen levels in the sediment by simply adjusting their depth to move closer to the surface, other species may respond to the same conditions by elongating their siphons up into the water column (Marsden and Bressington 2009; Diaz and Rosenberg 1995). Other species, such as the heart cockle, *Clinocardium nuttallii*, use jets of water when confined or disturbed to help loosen the sediment around it to help it to resurface (Krantz 1974; Chang and Levings 1978). Grain size distribution of deposited sediment is also likely to be an important factor in the resurfacing success and survival of bivalves. Finer sediments, for example, can smother and choke suspension-feeders, while sediments with higher organic matter content, may lead to O₂ reduction, be less permeable to O₂ and result in anoxic conditions.

It is therefore likely that natural or anthropogenic sediment deposition events that deposit native sediments (with similar grain sizes to those already present) would be expected to have only limited direct impacts on local populations of *A. stutchburyi*. However, if bivalves were also physically disturbed with orientations upended, then some mortality of larger sized cockles would be predicted, with higher losses predicted with thicker deposits of sediments. In contrast, where sediments contain finer grains or are comprised of terrestrial muds then changes in community structure and loss of critical species may occur. This information will provide an important review and critical new knowledge to help Marlborough District Council (and also Nelson City Council and Tasman District Council) manage and conserve cockle beds within the Top of the South; will help inform the ongoing coastal zone management of the Marlborough District Council, and will be an input to support the regional coastal planning framework.

Finally, the act of depositing sediment onto the seafloor in large volumes (e.g., dredge spoil dumping, landslides) has the potential to dislodge and up-end bivalves as they are buried. For the cockle, *A. stutchburyi*, the majority of individuals reside just beneath the sediment surface. As such, sediment disturbance during a surface deposition event may provide little if any dislodgement of cockles. To examine this question, field deposition experiments that replicate different forms of deposition events would be required.

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