

Effects of fine sediments on settlement and survival of the sea urchin *Evechinus chloroticus* in northeastern New Zealand

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ABSTRACT: Populations of the sea urchin *Evechinus chloroticus* were monitored at wave-exposed low-sediment reefs and wave-sheltered high-sediment reefs in the Hauraki Gulf, northeastern New Zealand. Urchin populations on both wave-exposed and sheltered reefs were dominated by adults. Wave-exposed reefs supported higher densities (2.7 to 9.6 ind. m⁻²) than did wave-sheltered reefs (0.1 to 6.6 ind. m⁻²). Juvenile urchins (<30 mm test diameter [TD]) were 25 times more abundant on wave-exposed reefs. Urchin settlement of 0.2 to 0.6 ind. 100 cm⁻² was recorded at wave-exposed reefs but was undetectable at wave-sheltered reefs. Laboratory experiments were conducted to assess whether the volumes of sediment loads observed on sheltered reefs could affect the survivorship of early life stages of urchins in the absence of other environmental factors. Results indicated that fine sediments at one-third and two-thirds of concentrations found on wave-sheltered reefs inhibited the settlement of larvae and reduced the survival of urchin recruits (2 to 5 mm TD) and juveniles (10 to 30 mm TD). Survival rates of juveniles were higher than for more recent recruits, suggesting size-dependent mortality. A lack of significant differences between high and low treatments in all experiments suggests that urchin settlement and survival can be affected negatively at low levels of sediment that are common in natural environments.

KEY WORDS: Urchin populations · *Evechinus chloroticus* · Sedimentation · Recruitment · Subtidal rocky reefs

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INTRODUCTION

Sea urchins play an important role in determining the composition and persistence of subtidal macroalgal communities (Bernstein et al. 1981, Dayton 1985, Andrew 1988, Andrew & Underwood 1993, Benedetti-Cecchi et al. 1998). The most dramatic and well known effect of sea urchins is their ability to transform macroalgal habitat to barrens habitat (Breen & Mann 1976, Watanabe & Harrold 1991, Hagen 1995, Scheibling et al. 1999).

Since urchins are of ecological importance, a greater understanding of how biological and physical factors influence fundamental demographic processes (e.g. growth, survivorship and reproduction) is necessary in

understanding temporal and spatial variations in population abundance and distributions. Deterministic factors such as pre- and post-settlement processes are highly spatially and temporally variable (Harrold et al. 1991, Balch & Scheibling 2001, Lamare & Barker 2001). Physical factors such as upwelling, water temperature (Wing et al. 2003) and periods of offshore winds (Ebert et al. 1994) influence larval supply and are also important processes in the settlement and recruitment of sea urchins.

Sediments are harmful to a variety of subtidal species (Airoldi 2003) and can smother or scour adult or juvenile stages or even prevent settlement of propagules (Airoldi 2003). On coral reefs, sediments decrease coral fertilisation, larval survival and the settlement of

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some species of coral leading to significant reductions in recruitment (Hodgson 1990, Babcock & Davies 1991, Gilmour 1999).

On temperate rocky reefs, sedimentation can play an important role in the structuring of subtidal algal communities (Dayton 1985, Shaffer & Parks 1994, Airoidi & Cinelli 1997, Airoidi & Virgilio 1998, Irving & Connell 2002a,b, Airoidi 2003). However, no published accounts exist on the effect that fine sediment has on the settlement and post-settlement survival of the many invertebrate herbivorous species commonly found in association with macroalgal communities.

In New Zealand, grazing effects of the sea urchin *Evechinus chloroticus* are similar to those reported for echinoid species from other temperate regions (Shears & Babcock 2002). J. W. Walker & R. C. Babcock (unpubl. data) found that wave-sheltered subtidal reef communities of the inner Hauraki Gulf, northeastern New Zealand, supported low densities of *E. chloroticus* (0.1 to 2.7 ind. m⁻²), with juvenile urchins (<30 mm test diameter [TD]) very rare and 12 to 25% of the substratum covered by fine sediments. In another study, J. W. Walker & R. C. Babcock (unpubl. data) found that sediment was the single most important physical variable in explaining variations in community structure in this same area. In addition, Andrew & Choat (1985) hypothesised that fine sediments were responsible for juvenile urchin mortality in *E. chloroticus*. In South

America, Dayton (1985) similarly found that the urchin *Loxechinus albus* was rare at wave-sheltered sites and juveniles were not found. Dayton (1985) attributed this pattern to reduced salinity or unsuccessful settlement due to high sediment load. The present study examines the role sedimentation may play in influencing the observed low adult and lower juvenile urchin abundances on sheltered subtidal reefs in the Hauraki Gulf.

In this study sea urchin populations and recruitment from a wave-exposed, low sediment location were compared with a wave-sheltered, high sediment location. Laboratory experiments examined the effect of terrestrially derived sediments on the settlement of urchin larvae and the continued survival of newly recruited and juvenile urchins. These experiments investigated one of many possible mechanisms that could be driving the observed patterns in sea urchin populations on wave-sheltered reefs. Such a mechanism is logistically impractical to observe and isolate in the field. Furthermore, these experiments determined what effect increases in sediment runoff from land development may have on urchin population dynamics on these reefs.

MATERIALS AND METHODS

Study sites. Monitoring of sea urchin populations was undertaken at 2 localities within the Hauraki Gulf in northeastern New Zealand (Fig. 1). These locations were selected to compare urchin settlement and recruitment on high-sediment reefs with low-sediment reefs. The first location was Leigh, a wave-exposed site with few deposited sediments (J. W. Walker & R. C. Babcock unpubl. data). Sampling of urchin populations at Leigh was undertaken at a 4 to 5 m depth in the urchin barren habitat (Ayling 1978, Choat & Schiel 1982, Andrew 1988). The second location, Little Manly, was sheltered from the dominant wave direction and 15 to 25% of the reef was dominated by fine sediments (J. W. Walker & R. C. Babcock unpubl. data). The urchin barren habitat was not present at the Little Manly sites, as it was dominated by a shallow mixed algal assemblage (Shears et al. 2004). Physical gradients, such as wave-exposure and sedimentation, covary within the Hauraki Gulf (Grace 1983, J. W. Walker & R. C. Babcock unpubl. data). This aspect of the natural environment inhibited an appropriate interspersed of sites with high and low sedimentation at the 2 locations. Therefore, sediment levels were manipulated in an attempt to understand the physical processes influencing urchin population on wave-sheltered reefs with high sediment loads.

Urchin size structures. Twenty haphazardly placed 1 m² quadrats were used to sample the size structure of

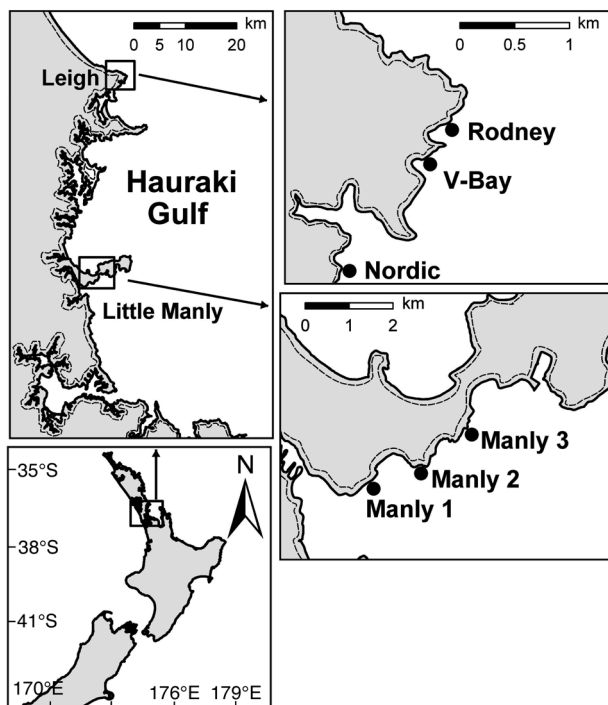


Fig. 1. Location of sampling sites at Leigh and Little Manly in the Hauraki Gulf, northeastern New Zealand

sea urchins from 3 replicate sites at each location (Leigh and Little Manly). This was done on 9 occasions at Leigh and 8 occasions at Little Manly between April 2002 and April 2004 (sampling took place every third month, see Fig. 2) at depths between 2 and 5 m. Subtidal reefs at Little Manly were flat to gently sloping with small crevices and small cobbles. To minimise variations in micro-habitats among the sites, areas of reef were sampled at Leigh that had similar topographic features to those at Little Manly sites. The TDs of urchins were measured to the nearest 5 mm using plastic scale bars and particular attention was paid to searching under rocks and in crevices for juvenile urchins.

Urchin settlement. Settlement of *Evechinus chloroticus* was examined between November 2003 and March 2004 using an underwater suction sampling technique (Taylor et al. 1994). Suction sampling of the substratum for newly settled *E. chloroticus* was undertaken in 5 replicate 100 cm² quadrats at 2 to 5 m depths every month. Each sample was taken in the same area (~20 m² of reef) and sampling the same area of substratum in consecutive months was avoided. Each quadrat was scraped and suctioned simultaneously to ensure turfing algae, which may harbour newly settled urchins, were sampled. Samples were sieved through 200 µm mesh bags underwater. The contents of each sieve bag were rinsed into containers, stored in 5% formalin and sorted under a dissecting microscope.

Sampling of sediments. Estimates of the quantities of sediments covering the substratum at each site were made using a large bore syringe (135 ml). Sediments were suctioned from 3 replicate 100 cm² quadrats at each site and placed into plastic Ziplock bags underwater. The contents of each plastic bag were filtered through 2 µm filter paper to remove excess water and dried at 65°C for 24 h. Samples were then soaked in Calgon (2.5 µg l⁻¹ for 24 h) to disperse particles <63 µm and wet sieved to determine the amount of fine sediments (<63 µm) covering the substratum (mg cm⁻²).

Sedimentation experiments. Larval settlement experiment: *Evechinus chloroticus* larvae were reared at 19°C in 10 replicate 1 l glass jars (2 to 3 larvae ml⁻¹) with moving plastic paddles to keep larvae and food in suspension. Seawater was changed (filtered to 1 µm and sterilised with UV light) every 2 to 4 d and larvae fed a 50:50 mixture of *Chaetocerus calcitrans* and *Isochrysis galbana* (6000 cells ml⁻¹). Three natural substrata were tested for larval settlement preference: crustose coralline algae (CCA), bare rock and *Coralina officinalis* (hereafter referred to as C. turf).

Each substratum was placed into separate petri dishes (24 cm²) and arranged so that the bottom of each dish was covered. Three replicate dishes of each substratum were used to assess the effects of silt on the

settlement of urchin larvae. Treatments were: (1) a high sediment treatment, ca. two-thirds ambient levels of sediments (see 'Results') found on wave-sheltered reefs (20 mg cm⁻² = 0.48 g added to treatments); (2) low sediment treatment, one-third natural levels (10 mg cm⁻² = 0.24 g added to treatments) and (3) control (no sediment). These concentrations of sediments were used in all experiments described in the present article. Sediments were terrestrial in origin and obtained from an area considered to be free of toxins. Sediments were dried (at 65°C for 24 h) and sieved to <63 µm. For each sediment treatment, individual slurries were made from the prescribed amount of sediment and 20 ml of seawater (filtered to 1 µm and sterilised with UV light). Slurries were added to each replicate dish of each of the 3 substrates. The slurry was left to settle before adding 10 competent larvae to each replicate (n = 3) of each treatment (n = 3) for each substratum (n = 3). All replicates were sampled at 0.5, 1 and 18 h after adding larvae. Larvae were counted at 2 stages: (1) swimming in the water column and (2) crawling or motionless on the bottom attached to the substratum (as in Lamare & Barker 2001).

Survivorship of new recruits: The survivorship of sea urchin recruits (2 to 5 mm TD) subjected to fine sediment was tested. This was undertaken by using 15 plastic containers (18 cm × 12 cm; surface area, 215 cm²) with 10 urchin recruits in each container. Plastic containers had a constant flow of seawater filtered to 1 µm. One of 3 treatments was randomly assigned to each container to test the effects of sediments on urchin survival: (1) high sediment treatment (20 mg cm⁻² = 4.3 g of sediment added), (2) low treatment (10 mg cm⁻² = 2.2 g of sediment added) and (3) control (no sediment). Sediments were dried for 24 h at 65°C and sieved to <63 µm. Urchins were left for 7 d before starting the experiment. Sediments were sprinkled into each container to evenly distribute sediments within containers. The number of surviving urchins were counted 3 d later, 4 d after the first count (1 wk) and then every 7 d thereafter for a total of 28 d. Urchins were fed a diet of *Ulva* sp. weekly.

Survivorship of juvenile urchins: An additional experiment was undertaken to assess the effect of sediment deposition on the survival of juvenile urchins (10 to 30 mm TD). Juvenile urchins were collected from subtidal reefs (5 to 7 m depth) at Leigh. Juvenile urchins were placed into 15 plastic containers (20 cm × 20 cm; surface area = 400 cm²) with each container housing 10 juveniles. Containers had a constant flow of seawater and were randomly assigned one of 3 treatments: (1) high sediment treatment (20 mg cm⁻² = 8.0 g of sediment added), (2) low treatment (10 mg cm⁻² = 4.0 g of sediment added) and (3) control (no sediment). Sediments were dried for 24 h at 65°C and sieved to

<63 μm . Sediment treatments were sprinkled into each container to evenly distribute sediments within containers. Urchins were left for 7 d before starting the experiment. Urchins were fed *Ulva* sp. and counted weekly. This experiment ran for 49 d.

Statistical analysis. Variations in the abundance of adult and juvenile sea urchins were tested separately. For both adult and juvenile urchins comparisons between wave-exposed and wave-sheltered locations and sites nested within locations were made using a generalised linear mixed model (Millar & Willis 1999) fitted to a Poisson distribution using residual (restricted) maximum likelihood employing the GLIMMIX macro in SAS (Littell et al. 1996). The most complicated model was fitted first then simplified by back-fitting (i.e. removing non-significant interactions). Back-fitting releases degrees of freedom, thereby increasing power for testing main effects (McCullagh & Searle 2001). The GLIMMIX macro uses the containment method to calculate denominator degrees of freedom (DDF) unlike traditional analysis of variance techniques. The containment method searches the random effects that syntactically contain fixed effects. Among the random effects that contain the fixed effects, GLIMMIX computes their rank contribution to the (XZ) matrix. The DDF assigned to fixed effects is the smallest of these rank contributions. If no effects are found, the DDF for fixed effects is set equal to the residual degrees of freedom (for further details on this method see Littell et al. 1996, Schaalje et al. 2001). Fixed factors included in the analysis were Location (Leigh and Little Manly), Month and the interaction term (Location \times Month). Covariance parameter estimates were calculated for Sites (random) nested within Location and crossed with Month (Month \times Site (Location)) and the auto-regressive error structure, AR(1), to model temporal autocorrelation among sites. The AR(1) models a covariance structure for observations made at equal distances over time and denotes that correlations between observations will be larger for adjacent times than observations that are made farther apart (Littell et al. 1996). Modelling a suitable covariance structure is essential so valid inferences about the analysis can be made (Littell et al. 1996). The effect of time and treatment on the proportion of urchin larvae settling were analysed using GLIMMIX with fixed factors Time (0.5, 1, 18 h), Substratum (bare rock, C. turf and CCA), Treatment (high, low and control) and interaction terms for all combinations of main effects. Covariance parameter estimates were calculated for Replicates (random) nested within Treatments along with the AR(1) to account for the repeated factor (Replicate). The proportion data were tested using a binomial distribution and back-fitted as described. The effects of sediment on the survivorship

of both urchin recruits and juveniles were also analysed using a generalised linear mixed model with fixed factors Day, Treatment and the interaction term (Day \times Treatment). Covariate parameter estimates for Replicates (random) nested within Treatment and the AR(1) for the repeated factor (Replicate) were also calculated. Count data were modelled using a Poisson distribution and back-fitted. Pair-wise comparisons of significant fixed effects and interaction terms were investigated using LSMEANS ($\alpha = 0.05$).

RESULTS

Sea urchin densities

Univariate analysis found significant differences in the densities of adult urchins at Leigh and Little Manly ($F_{1,41} = 22.28$, $p = 0.0001$) and among sites within locations ($Z = 2.66$, $p = 0.0039$). At Little Manly, Sites 2 and 3 supported urchin densities ranging between 0.8 and 4.9 and 1.7 and 6.6 ind. m^{-2} , respectively, while Site 1 had consistently low adult densities (0.1 to 0.8 ind. m^{-2} , Fig. 2A). At Leigh, adult densities varied spatially (Fig. 2B). Densities at Nordic and V-Bay ranged from

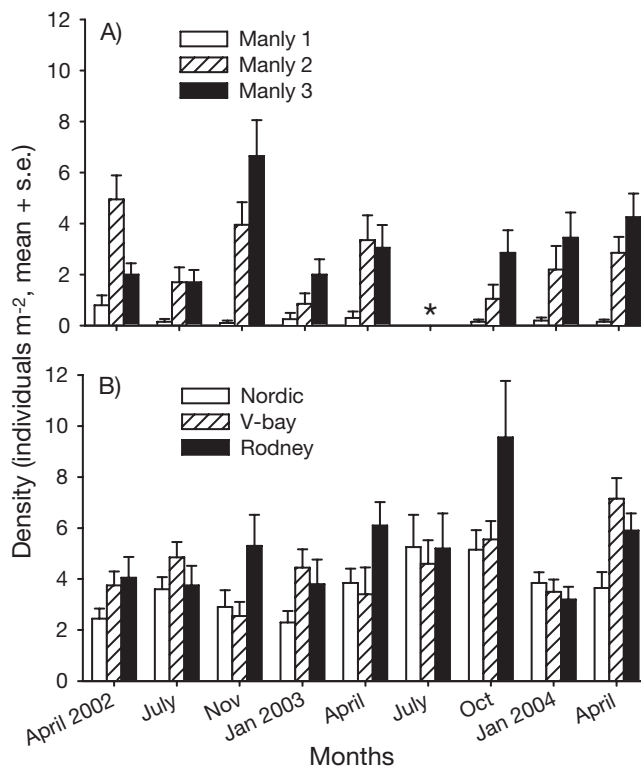


Fig. 2. *Evechinus chloroticus*. Adult densities counted in 20 replicate 1 m^2 quadrats at 3 sites from (A) a wave-sheltered location, Little Manly, and (B) a wave-exposed location, Leigh. Sampling was carried out every 3 mo from April 2002 to April 2004. *: no data

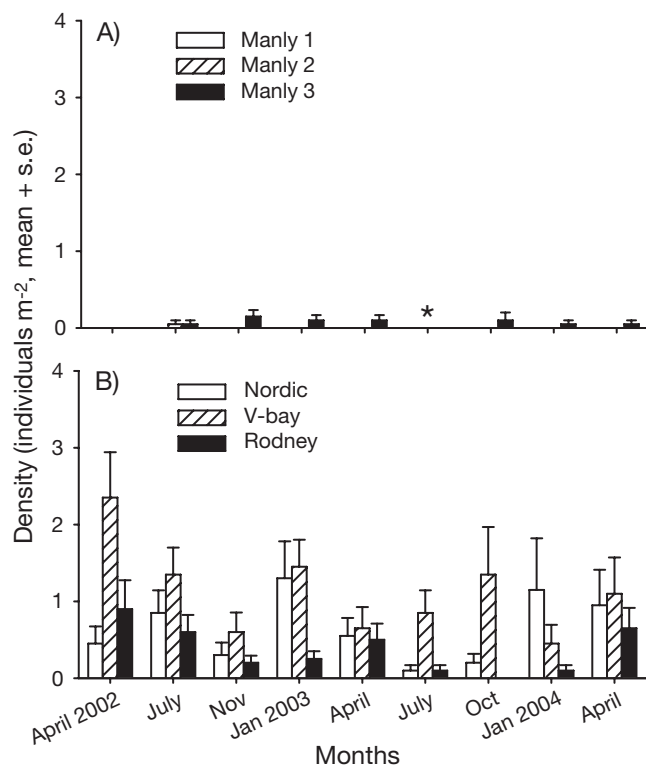


Fig. 3. *Evechinus chloroticus*. Densities of juveniles (<30 mm test diameter) counted in 20 replicate 1 m² quadrats at 3 sites from (A) a wave-sheltered location, Little Manly, and (B) a wave-exposed location, Leigh. Sampling was carried out every 3 mo from April 2002 to April 2004. *: no data

2.7 to 5.3 and 2.9 to 7.9 ind. m⁻², respectively. Highest adult densities were recorded at Rodney and ranged from 3.9 to 9.8 ind. m⁻² (Fig. 2B). Univariate analysis also detected no significant difference in the abundance of adult urchins over time (Months, $F_{8,41} = 0.43$, $p = 0.897$) and for the interaction of Location \times Month ($F_{7,34} = 0.75$, $p = 0.631$).

The abundance of juvenile urchins was significantly lower at Little Manly compared with sites at Leigh ($F_{1,41} = 49.91$, $p = 0.0001$, Fig. 3). Juveniles recorded at Leigh (total number = 332) were 25 times more abundant than the number of juveniles found at Little Manly (total number = 13). Highest densities of juveniles were consistently recorded at Nordic and V-Bay (0.1 to 1.3 and 0.5 to 2.4 ind. m⁻², respectively, Fig. 3B) while Rodney supported the lowest densities (0.1 to 0.9 ind. m⁻²). At Little Manly, juvenile densities were lower still and were only recorded at Manly 3 (0.05 to 0.1 ind. m⁻², Fig. 3A). The GLIMMIX analysis detected significant differences in the abundance of juvenile urchins over time (Months, $F_{8,41} = 0.82$, $p = 0.042$), while the interaction of Location \times Month was not significant ($F_{6,34} = 0.33$, $p = 0.922$). Significant differences among sites within locations were also detected ($Z = 2.35$, $p = 0.0094$).

Variability in urchin settlement

Newly settled urchins were only found at Leigh and none were found at Little Manly. The numbers of newly settled urchins at Leigh ranged between 0.2 and 0.6 ind. 100 cm⁻². Both temporal and spatial variability were evident in patterns of settlement at Leigh with no newly settled urchins found during November 2003. During December 2003 and January 2004, settlers were found at Nordic and Rodney. During February 2004 newly settled urchins were only found at V-Bay (0.4 ind. 100 cm⁻²). During March 2004 the highest numbers of settlers were recorded at Rodney (0.6 ind. 100 cm⁻²) with the same level of settlement at V-Bay as found for the previous month (0.4 ind. 100 cm⁻²).

Sediment sampling

Greater quantities of fine sediments (<63 μ m) were found covering the substratum at the Little Manly sites. The mean weights of sediment obtained from the 3 Little Manly sites ranged from 30 to 40 mg cm⁻². Quantities of sediments were considerably lower at Leigh and ranged from 1 to 7 mg cm⁻². Averaged across sites, sediments were 9 \times higher at Little Manly (35 ± 5 [SE] mg cm⁻²) than at Leigh (3.8 ± 0.9 mg cm⁻²).

Sedimentation experiments

Larval settlement

The percentage of larvae settling to controls was higher compared with the 2 sediment treatments across all substrata (Fig. 4). After 0.5 h, larval settlement on the CCA control was highest ($40 \pm 5.7\%$, mean \pm SE) compared with all treatments and substrata. After 1 h, larval settlement on controls for all 3 substrata increased (bare rock = 56%, C. turf = 53% and CCA = 50%). At this time, larval settlement increased on low sediment treatment for C. turf (10%) and CCA (10%). Conversely for bare rock, more larvae had settled to the high sediment treatment (13%) compared with the low treatment (7%). After 18 h, settlement on controls was higher compared with sediment treatments for all substrata. Analysis by GLIMMIX identified significant differences among time and treatment, and found no effect of substratum on larval settlement. All interaction terms were non-significant (Table 1). Pair-wise comparisons (LSMEANS, $\alpha = 0.05$) among times revealed larval settlement at time 1 (0.5 h) differed significantly from both times 2 and 3 (1 and 18 h), and time 2 (1 h) differed significantly from time 3 (18 h). Pair-wise comparisons among treatments

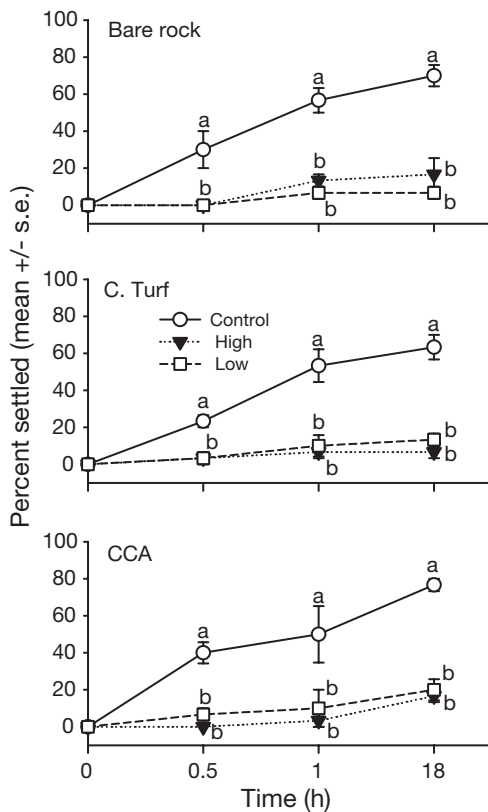


Fig. 4. *Evechinus chloroticus*. Percentage settlement of urchin larvae to 3 substrata (bare rock, *Corallina officinalis* [C. turf] and crustose coralline algae [CCA]) with 3 sediment treatments (control, no sediment; high sediment, 20 mg cm⁻²; and low sediment, 10 mg cm⁻²). For each data point of each treatment, n = 3. Sampling was undertaken at 0.5, 1 and 18 h after the start of the experiment. Data points labelled with the same lower-case letter indicate contrasts among treatments do not differ significantly (LSMEANS, α = 0.05)

found settlement of controls to be significantly different to settlement in both high and low treatments, while no significant differences were detected between the 2 sediment treatments (Fig. 4).

Survivorship of new recruits

The survivorship of new recruits varied significantly among sediment treatments (Table 2) and declines in survivorship over time resulted in a significant Day effect, while the interaction of Day × Treatment was also significant (Table 2). A significant Day × Treatment interaction indicated a significant difference in urchin survival among the 3 treatments and

Table 1. Results from GLIMMIX analysis on the proportion of sea urchin larvae settling over time (0.5, 1 and 18 h to different substrata (bare rock, *Corallina officinalis* and crustose coralline algae subjected to varying sediment treatments (high, 20 mg cm⁻²; low, 10 mg cm⁻²; and controls, no sediment). Model back-fitted by removing non-significant interaction terms. Significant p-values are given in **bold**. AR(1): auto-regressive error (see 'Materials and methods')

Source of variation	F-value	p
Fixed effects		
Time (T)	$F_{2,4} = 17.21$	<0.0091
Substrata (S)	$F_{2,4} = 0.45$	0.6664
T × S	$F_{4,8} = 1.89$	0.2057
Treatment (Treat)	$F_{2,4} = 77.91$	<0.0006
T × Treat	$F_{4,8} = 1.09$	0.4225
S × Treat	$F_{4,8} = 1.24$	0.3683
T × S × Treat	$F_{8,16} = 0.68$	0.7011
Covariate estimates		
Replicate (Treat)	1.01	0.1553
AR(1)	0.13	0.8905

these differences varied over time (Fig. 5). To simplify the interpretation of the interaction of Day × Treatment, variations among treatments were analysed separately for each day (LSMEANS, α = 0.05). Within the first 3 d, urchin survival decreased to 70% in the high treatment and 68% in the low treatment and pair-wise comparisons found significant differences among all 3 treatments (Fig. 5). After 7 d, urchin survival in controls (94%) differed significantly from both high (66%) and low treatments (48%) with no significant difference between high and low treatments. On Day 14, urchin survival in controls (90%) did not differ significantly from survivors in high treatments (64%) and there was no significant difference between high and low (44%) treatments (Fig. 5). After 28 d, survival in

Table 2. Results from repeated mixed model analysis on the survival of urchin recruits and juveniles subjected to 3 sediment treatments (high, 20 mg cm⁻²; low, 10 mg cm⁻²; and controls, no sediment). Model back-fitted by removing non-significant interaction terms. Significant p-values are given in **bold**

Source of variation	Recruits		Juveniles	
	F-value	p	F-value	p
Fixed effects				
Day	$F_{5,60} = 38.66$	<0.0001	$F_{7,84} = 15.09$	<0.0001
Treatment (Treat)	$F_{2,12} = 31.47$	<0.0001	$F_{2,12} = 7.64$	0.0072
Day × Treat	$F_{10,60} = 8.00$	<0.0001	$F_{14,84} = 5.22$	<0.0001
Covariate estimates				
Replicate (Treat)	1.44	0.0750	2.08	0.0185
AR(1)	-1.04	0.2966	2.05	0.0399

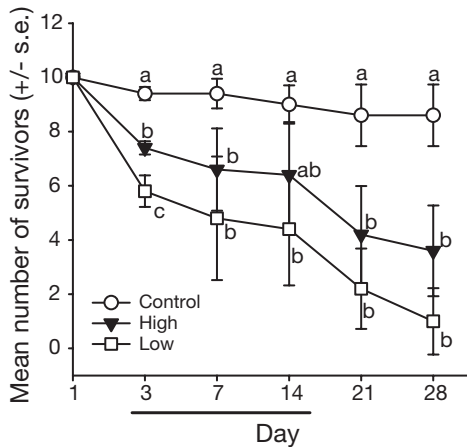


Fig. 5. *Evechinus chloroticus*. Counts of surviving recruits (2 to 5 mm test diameter) made from 3 treatments (control, no sediment; high sediment, 20 mg cm⁻²; and low sediment, 10 mg cm⁻²). For each data point of each treatment, n = 5. Data points labelled with the same lower-case letter indicate contrasts among treatments for each day do not differ significantly. Underlined days do not differ significantly for contrasts for the effect of day (LSMEANS, $\alpha = 0.05$)

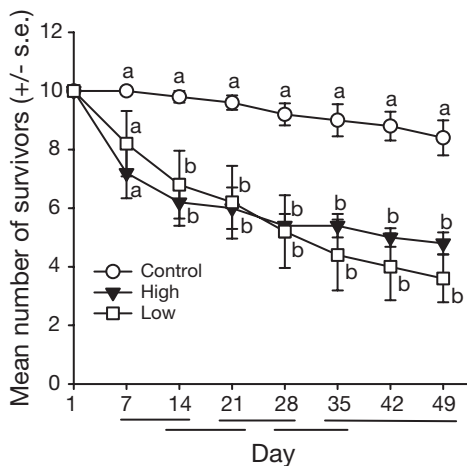


Fig. 6. *Evechinus chloroticus*. Counts of surviving juveniles (10 to 30 mm test diameter) made every 7 d from 3 treatments (control, no sediment; high sediment, 20 mg cm⁻²; and low sediment, 10 mg cm⁻²). For each data point of each treatment, n = 5. Data points labelled with the same lower-case letter indicate contrasts among treatments within each day do not differ significantly. Underlined days do not differ significantly for contrasts for the effect of day (LSMEANS, $\alpha = 0.05$)

controls declined (86%) but was significantly higher than that in both the high (36%) and low (10%) sediment treatments and no significant differences were found between high and low treatments. Contrasts for the effect of day revealed the number of surviving urchins did not differ significantly during Days 3, 7 and 14 and all other comparisons among days were significantly different. Comparisons among treatments iden-

tified significant differences between controls and both high and low treatments and there was no significant difference between high and low treatments.

Survivorship of juvenile urchins

Declines in the survivorship of juvenile urchins were similar to that found for recruits and significant differences among days, treatments and their interaction were also identified (Table 2). The interaction of Day \times Treatment suggested the number of survivors differed among treatments and variations in survivorship among treatments varied from day to day. Variations among treatments were analysed separately for each day (LSMEANS, $\alpha = 0.05$). Differences among treatments were non-significant on Day 7. On Day 14, controls differed significantly from both sediment treatments and there was no significant difference between high and low treatments (Fig. 6). After 28 d, survivorship was significantly higher in controls (92%) than in the 2 sediment treatments (high = 54%, low = 52%). On Day 35, survivorship in the low sediment treatments dropped below that of the high treatments (Fig. 6) and by Day 49 survivorship for both high and low sediment treatments had decreased further (high = 48%, low = 36%). Comparisons of the effect of day determined Day 1 to vary significantly from all other days. Comparisons between consecutive days were not significant, as were comparisons among Days 35, 42 and 49 (Fig. 6). All other day comparisons were significantly different. As was found for the previous experiment using urchin recruits, there was a significant difference between controls and both high and low treatments and no significant difference between the 2 sediment treatments.

DISCUSSION

This study investigated the effect that fine sediments have on the settlement and recruitment of the sea urchin *Evechinus chloroticus*. Laboratory experiments revealed that higher proportions of larvae were observed settling in the control groups than in the sediment treatments for all 3 substrata and there were no apparent preferences for the different types of algal substrata or bare rock. These findings clearly demonstrate fine sediments are an important inhibitor of urchin settlement. Similar results of reduced settlement of larvae and propagules have been found for the coral *Acropora digitifera* (Gilmour 1999), the macroalga *Macrocystis pyrifera* (Devinney & Volse 1978) and the red abalone *Haliotis rufescens* (Raimondi et al. 1997). Furthermore, in the present study urchin larvae

settling to silt covered substrata became trapped by silt and eventually died. This is similar to observations made for 2 other small coral organisms (Fabricius & Wolanski 2000).

The survival of new recruits and juvenile urchins was also reduced by the presence of fine sediments. Survival of new recruits in sediment treatments was significantly lower than in controls. This pattern was also seen in the numbers of juveniles surviving. Survival rates of juvenile urchins were higher than that of new recruits indicating size-dependent mortality. These results further support the hypothesis that sedimentation influences settlement and survival of sea urchins on wave-sheltered reefs.

The lack of newly settled and juvenile urchins at the Little Manly sites indicates these populations to be recruitment limited with no significant recruitment for at least 6 yr based on published growth rates (Walker 1981). Conversely at Leigh, juvenile urchins were consistently recorded through time at 2 of the 3 sites, indicating settlement and recruitment to be spatially variable, but continuous. While recruitment over the study period at Little Manly was so low that it was undetectable, variable recruitment appears to be adequate to maintain urchin populations at Little Manly. An analogous situation was reported for the urchin *Strongylocentrotus purpuratus* in California where only a single recruitment pulse was recorded over a 10 yr period (Pearse & Hines 1987).

Urchin populations at Leigh and Little Manly were dominated by adults. Adult and juvenile densities were highest at Leigh, whereas at Little Manly considerable variations in urchin densities were observed and numbers of juveniles were consistently low. Furthermore, urchin settlement was recorded at Leigh and no appreciable settlement was detected at Little Manly. These observations suggest that recruitment limitation is clearly contributing to the contrasting structure of urchin populations of Little Manly and Leigh. Urchins that were found were all large (55 to 105 mm TD), whereas urchins at Leigh were found in all size classes (J. W. Walker & R. C. Babcock unpubl. data).

Experimental results from this study strongly suggest that fine sediments are contributing to the lack of sea urchin recruitment at Little Manly through a combination of their inhibitory effect on recruitment, and increased mortality of recruits and juveniles under increased levels of sedimentation. The settlement of larvae in laboratory experiments was <20% (Fig. 5) and these results are not consistent with the levels of settlement in the field. Juvenile urchins were recorded at wave-sheltered reefs at very low densities (J. W. Walker and R. C. Babcock unpubl. data). Urchin larvae may be able to settle to these reefs due to the spatially variable nature of sediment coverage along with varia-

tions in reef topography. On the scale of an urchin larva (300 to 500 μm), a high probability exists for areas of reef to be free from sediment coverage due to topographic variations (e.g. high points in the reef protruding from sediment cover). Tidal flushing, wave action and algae sweeping across the substratum will also resuspend sediments (pers. obs.).

Several alternative mechanisms may contribute to differences in the structure of urchin populations of Leigh and Little Manly. Recruitment limitation is an important process in the structuring of a population (Menge & Sutherland 1987), and post-settlement mortality of sea urchins during early developmental stages is often intense (Rowley 1989). Studies on the settlement and recruitment of *Strongylocentrotus franciscanus* have shown that recruitment is strongly influenced by variations in larval supply resulting from the abundance and distribution of adults (Levitan et al. 1992) and hydrodynamic forces (Ebert et al. 1994, Hereu et al. 2004b). These same processes are important in the recruitment of *Evechinus chloroticus* in New Zealand. Wing et al. (2003) found a positive relationship between the settlement of larvae and adult density, while Lamare & Barker (2001) suggested variations in hydrodynamic forces influenced settlement of *E. chloroticus* at their study sites, with lower settlement at an open coast site compared with settlement in a semi-enclosed fjord (Lamare & Barker 2001).

Differing levels of predation of post-settled urchins may also contribute to variations in settlement intensity and juvenile abundance at Leigh and Little Manly. In the Mediterranean Sea, predation of post-settled juvenile urchins was predominantly by small labrid fishes. Micro-predators, such as crustaceans and polychaetes inhabiting algal habitats, were suggested as additional causes of mortality (Hereu et al. 2004a). The effects of micro-predators on *E. chloroticus* populations warrant further investigation.

While disease, predation and physical processes can influence settlement and post-settlement survivorship of urchins, studies of patterns in habitat structure in the Hauraki Gulf ecosystems indicate that sediment cover on reefs is the single most important physical variable associated with variation in reef communities (J. W. Walker & R. C. Babcock unpubl. data). Previous studies have suggest that deposition of fine sediments influences survival of juvenile urchins (Andrew & Choat 1985, Dayton 1985). This early work was confounded by a variety of other factors that may have also influenced urchin survivorship (e.g. depth and wave motion). In this study the effect of sediment was isolated in the laboratory. Due to a lack of differences between high and low sediment treatments for all 3 urchin experiments, this study suggests urchin settlement and survival is affected at lower sediment con-

centrations than those used in these experiments, which are still within the range of concentrations found on wave-sheltered reefs.

Experiments presented here provide evidence for fine sediments to be an important determinant of urchin populations by reducing both larval settlement and the survival of recruits and juveniles. This is the first study to demonstrate that fine sediments are capable of affecting the early life stages of an invertebrate herbivore that has a strong influence on the composition of rocky reef algal communities. Furthermore, increases in sedimentation due to urban development could lead to further suppression of urchin recruitment and other rocky reef organisms on wave-sheltered reefs.

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