

Sediment on rocky intertidal reefs: Effects on early post-settlement stages of habitat-forming seaweeds

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Abstract

Modification of the coastal environment by human activities often leads to an increase in sedimentation of nearshore waters, with potential impacts on benthic marine assemblages. Here we assess the relationships between the levels of sedimentation, wave exposure and benthic organisms on rocky intertidal platforms around the Kaikoura Peninsula in southern New Zealand. We designed and tested five sediment traps to provide a tool for measuring the relative abundance of sediment across sites. Using field- and laboratory-based experiments, we tested hypotheses concerning whether different levels of sedimentation affected algal germling survival and algal zygote attachment, and whether the interactions of grazers and sediments affected germling survival. Levels of sediment and exposure were inversely related across seven sites. The furoid alga *Hormosira banksii* characterized the more sedimented wave-sheltered and intermediately wave-exposed sites, with up to 80% cover in the lower mid-tidal zone, while the bull kelp *Durvillaea antarctica* characterized the three most wave-exposed sites. Grazing molluscs were found across all sites but species abundances varied by sediment and exposure levels. We did two 11-day trials testing the effects of different levels of sediment and different species of molluscan grazers on the survival of 1-week-old *Hormosira* germlings. Generally, there was no significant treatment effect of grazers, but mortality varied considerably among sites. In particular, one site had very high levels of sediment, which resulted in 100% mortality of germlings across all grazer treatments. Removing sediment at 1-week, 2-week and 4-week intervals made no difference to the survival of *Hormosira* germlings. In laboratory-based experiments, a light dusting of sediment reduced the percentage of zygotes of *Hormosira* by 34% and *Durvillaea* by 71% that attached to primary substratum, and a complete cover of sediment prevented attachment altogether. Overall, the effects of sediments and its interaction with molluscan grazing were highly variable but often large, particularly on the attachment of zygotes to primary substratum.

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1. Introduction

Sediments can affect rocky reef assemblages in numerous ways but assessing their role in intertidal community structure is difficult. In any one place, the amount of sediment can be highly variable through

time, with considerable movement during periods of storms and heavy wave action (Littler et al., 1983; Stewart, 1983). Sediments can have several adverse effects on benthic organisms (Abelson and Denny, 1997). Coarse sediments such as sand and gravel may scour surfaces and abrade tissue from organisms or remove them completely from a reef. Suspended particles may interfere with filter feeding of benthic invertebrates and the deposition of fine sediments can interfere with settlement and growth and photosynthetic activity

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of organisms (Airoldi, 2003). Each of these types of processes can affect assemblage structure. For example, some species of red algae are resistant to sand abrasion and thrive in areas where few other species survive (D'Antonio, 1986). Sediments can also interfere with settlement and other processes in the early life histories of many algae (Vadas et al., 1992), affect the light environment of early stages already settled (Devinsky and Volsø, 1978; Chapman and Fletcher 2002) or create anoxic conditions and smother benthic organisms (D'Antonio, 1986; Airoldi 2003). Early post-settlement stages of algae are particularly vulnerable to these processes (Vadas et al., 1992; Airoldi 2003).

“Sediment” is a broad term that includes a wide range of material including silt, sand and gravel from both terrigenous and marine sources. The effects of sedimentation on reef assemblages depend not only on the types of organisms present and their life history stages, but also on the flow and turbulence of water and the grain size of particles in the sediment (Abelson and Denny, 1997; Gorostiaga et al., 1998), which affect both the suspension and the movement of particles and their deposition on the substratum. Cover, depth and flux of sediment, therefore, often covary with hydrodynamics, turbidity, salinity and organic pollutants (Airoldi, 2003).

Much of the early ecological work on temperate rocky reefs mentioned the potential role of sand on algal assemblages, noting the absence or diminished number of kelp in sandy portions of habitats. Several studies on kelp communities observed or tested the effects of sand or sediment on recruitment or assemblage structure (Kitching et al., 1934; North, 1971; Foster, 1975a,b; Airoldi 2003). In the intertidal zone, Littler et al. (1983) found that the lower limits of habitat-dominating mussels and grazing molluscs were set by sand inundation but that opportunistic algae and highly reproductive invertebrates such as barnacles quickly colonized during periods when sand was absent. Other species, such as the surfgrass *Phyllospadix*, accumulate sediment and thrive in these impacted areas. In heavily sedimented habitats, the local distribution and accretion of sediments can be controlled by the biota present (Airoldi, 2003). In the Mediterranean Sea, turfing algae bind and stabilize sediment, keeping a constant accumulation of sediment (Airoldi et al., 1996; Airoldi, 1998; Airoldi and Virgilio, 1998; Airoldi, 2003). Grazing gastropods can also regulate the distribution of sediments through bulldozing it from hard substrata or by grazing microalgae, which trap sediment thereby shifting community structure from a soft-bottomed to a hard-bottomed assemblage (Bert-

ness, 1984). Grazers may therefore counter the negative effect of sediment burial on algae by moving around reefs.

More recent studies have examined the role of finer sediments in the formation and maintenance of turfing algal assemblages. For example, Kendrick (1991) found in a shallow subtidal lagoon at the Galapagos Islands that crustose coralline algae colonized new surfaces early in succession and when sediments were experimentally removed from rocks. When left in natural conditions, however, turfs of filamentous algae and sediments soon overlaid rocks.

There have been relatively few studies on the effects of sediments on larger intertidal algae (Taylor and Littler, 1982; Littler et al., 1983; D'Antonio, 1986). Furoid and laminarian algae can be particularly vulnerable in their microscopic stages during settlement and early development (Amsler et al., 1992; Airoldi, 2003). In most species, these tend to be highly seasonal, so even the ephemeral presence of sediments could have an influence on recruitment. Deleterious effects could occur through prevention of settlement of propagules, smothering of those already settled, abrasion of small settlers or through the interaction of sediments with other factors such as light availability and grazing (Hawkins and Hartnoll, 1983; Vadas et al., 1992; Reed, 2000). Although the effects may be comparable between the intertidal and subtidal zones, there are potentially important differences, particularly due to the increased turbulence and flow in breaking waves of intertidal areas (Gaylord, 1999) and to the tidal movement of water. Across sites with different levels of wave exposure, sediment sizes and effects could differ. There is likely to be more settlement and accretion of fine sediments in sheltered areas and more re-suspension and abrasion by coarse sediments in wave-exposed places.

Measuring the settlement and accretion of these sediments across wave-exposure gradients, however, is problematic. Many designs and variations of traps have been used and tested in a wide variety of freshwater and marine habitats. Some marine studies have simply measured the depth or weighed accumulated sediments to give a relative indication of the levels or differing rates of accumulation among sites or treatments (Norton, 1978; Littler et al., 1983; Bertness, 1984). These types of measurements are probably best applied in more sheltered places where sediments accumulate. In subtidal environments that are not directly impacted by waves and swell, sediment traps can be deployed to provide a relative measure of the amount and size fractions of sediment being deposited in par-

ticular habitats (Hakanson, 1994). As water flow increases, the efficiency of traps in catching the various size fractions of sediment changes, both because of material being washed out of traps or because traps are better at catching some size fractions than others (Butman et al., 1986). Under full immersion in flowing water, traps with a height-to-mouth diameter (H/D) ratio >3:1 are generally most efficient (Butman, 1986). Mouth diameters less than about 45 mm may miss some of the organic material (Blomqvist and Kofoed, 1981). In recent subtidal marine studies, traps with H/D ratios of 3.9 have been used to give a measurement of sediment amount and of the differing size fractions (Kendrick, 1991; Airoidi and Virgilio, 1998). Airoidi et al. (1996) also found that traps set within 50 cm of the sea bed caught more sediment than those 200 cm above the sea bed, presumably because the lower traps caught more re-suspended material.

In New Zealand, as elsewhere, there is concern that increased sedimentation from changes in land use, urbanization, forestry, farming and coastal dredging is affecting nearshore marine communities (cf. Lotze et al., 2000; Madsen et al., 2001; see Airoidi, 2003 for review). Sediments are brought into coastal waters through rivers and streams or direct run-off. Any prediction about the potential effects of increased sedimentation must be based on knowledge about how present biotic assemblages are related to and affected by different levels of sedimentation. This study is an initial determination of such effects on coastal rocky reefs on the central east coast of the South Island of New Zealand. It was done at sites with different degrees of wave exposure, different levels of accumulated sediments and different intertidal communities, all of them dominated to some degree by macroalgae. The major species of macroalgae on these shores are the fucoid *Hormosira banksii* (Turner) Descaisne and the southern bull kelp *Durvillaea antarctica* (Chamisso). Both of these species have a wide austral distribution, with *Hormosira* being the common intertidal fucoid alga of New Zealand (Schiel, unpublished data) and eastern Australia (Underwood, 1998), and *Durvillaea* occurring extensively in New Zealand, the subantarctic islands and Chile (Santelices, 1990; Hay, 1994). This study aimed to: (i) design a sediment trap that would be useful across wave exposures in the intertidal zone and use these to characterize the levels of sedimentation across sites and wave-exposure; (ii) quantitatively describe the relationships between wave exposure, levels of sedimentation and dominant biota; (iii) test hypotheses in the field about sediment accretion and algal germling survival; (iv) test the effects of different levels

of sediment on algal germling attachment; (v) test the interactions of grazers, sediments and algae. Relevant hypotheses are explicitly stated in Section 2.

2. Methods

2.1. Sediment traps

Collecting sediments in the intertidal zone poses special problems because of the turbulent flow in breaking waves. Our early designs using H/D ratios <10 simply had the sediments washed from them in semi-protected shores. We therefore tested traps with ratios >10 and also developed new designs. Subtidally, traps with H/D ratios this large can have the greatest variability among replicate traps (Blomqvist and Kofoed, 1981), but intertidally they had the advantage of retaining a wide size fraction of the sediments. Vertical tube traps are problematic in the intertidal zone, however, because they protrude well above a reef into turbulent water or else must be embedded into the reef, which is usually impractical.

Here, we test and compare five trap designs, all made from PVC pipe. These were the only designs of the many configurations we tested that retained sediments in moderate to exposed sites (Fig. 1): (1) a “honeycomb” design. This was constructed from 19 tubes of 1.2 cm internal diameter (ID) and 18 cm long (H/D=15) that were squeezed within a larger tube (10.3 cm ID, 53 cm long). These smaller tubes effectively acted as baffles in the larger tube. This was capped at the bottom and mounted on a welded support base in the low intertidal zone. (2) A “small” j-shaped tube, 2.8 cm ID, 42 cm long (H/D=15). This was mounted level on the shore with the long axis perpendicular to the sea and the mouth on the seaward end. (3) A “medium” j-shaped tube, 5.5 cm ID, 82 cm long (H/D=15). This was treated as (2) above. (4) A “large” j-shaped tube, 9.0 cm ID, 135 cm long (H/D=15). This was treated as (2) and (3) above. (5) An “embedded” tube. This was a 7.5 cm ID, 112 cm long tube (H/D=15) embedded in a hole drilled into a reef. These traps were tested simultaneously from 20 to 25 August 2001 at a moderately wave-exposed site (Wairepo Flats; maximum significant wave height ca. 0.6 m). Traps 1 to 4 were also tested at a more exposed site (Seal Reef; maximum significant wave height ca. 1.8 m).

Traps were emptied daily by pouring the contents into a bucket, which was then sealed and taken back to the laboratory. The contents were poured through sieves of graduated hole sizes to separate the size fractions, then held on filter paper. These were dried for 72 h at 50 °C and then weighed.

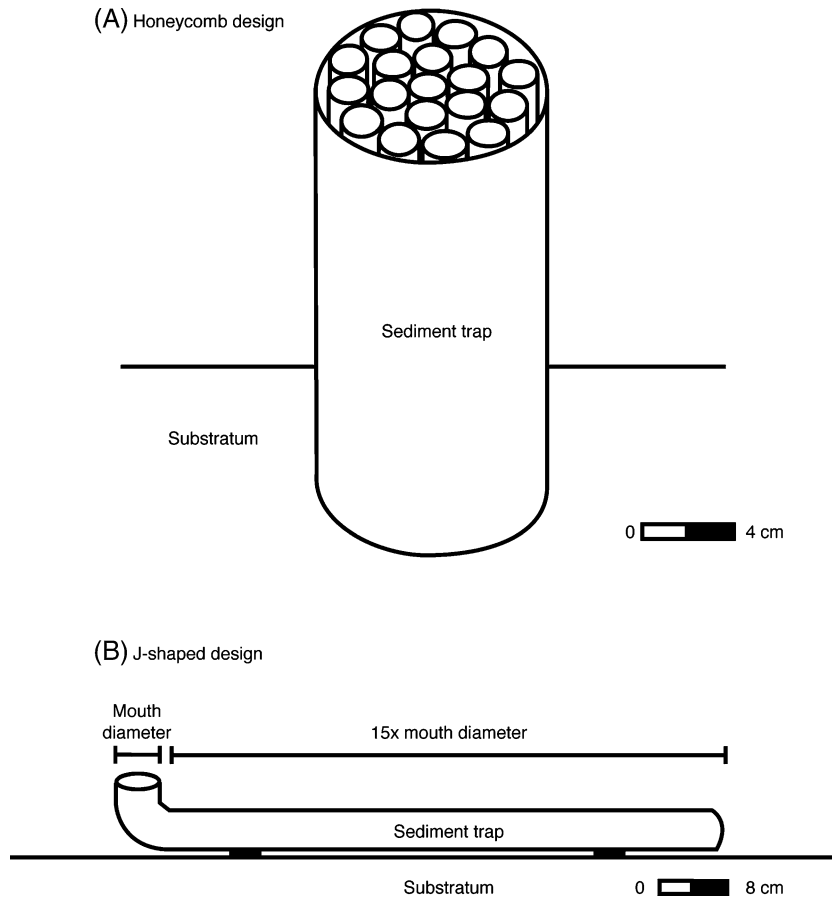


Fig. 1. Schematic drawings of sediment traps. (A) “Honeycomb” trap; (B) horizontal j-trap design, constructed in small (28 mm internal mouth diameter), medium (55 mm internal mouth diameter) and large (90 mm internal mouth diameter) sizes, each with a height (length)-to-mouth diameter ratio of 15.

The trap that we eventually chose for use (see Section 3) was tested for its ability to retain sediments of various size fractions across different flow velocities. This was done in a laboratory flume in which sediments collected from a reef were put into a series of flows from .04 to 0.25 m/s and left for 6 h. Size fractions of sediment were separated, dried and weighed (as above). Data were plotted as the percentage of recovered sediment vs. flow.

2.2. Study sites and assemblage sampling

We examined sites around the Kaikoura Peninsula to test the relationships between sediment, wave exposure and assemblage structure within localised sites. Seven accessible sites were haphazardly chosen around the peninsula to represent a range of exposure conditions (Fig. 2). All sites were sampled quantitatively during November–December 2001 for algae and invertebrates. A 50 m long transect tape was laid out haphazardly at

the 0.5 m level (i.e., in the lower mid-tide zone at the same elevation as the sediment traps). Ten random 0.25 m² quadrats were sampled for all visible organisms. Mobile gastropods were counted and the percentage cover of attached organisms was recorded. Sediment traps were put out for a period of 1 week to gauge the short-term relative differences and to rank sites in their sediment load for this period. Dynamometers (Bell and Denny, 1994) were used to characterize and rank sites for wave exposure. An exposure index was derived from dynamometer data to obtain a standard measure of relative wave force for all sites. Data from the most exposed site was rated 100 on an arbitrary scale and then all other sites were scaled as a proportion of this.

2.3. Field-based experiments

Several experimental manipulations were done to test the effects of sediments on algal germlings. Three sites with similar wave exposure (Kean Point, South

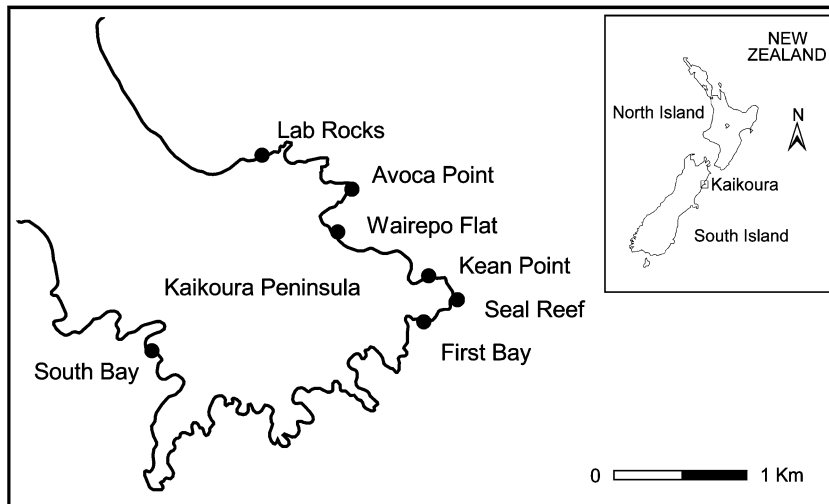


Fig. 2. Map of Kaikoura peninsula showing locations of the seven study sites.

Bay and Wairepo Flats, see Section 3) were used. The degree of sedimentation of these sites was measured by the quantity of accumulated sediments and sediment trap data. All sites are heavily sedimented at times and have populations of the seagrass *Zostera novae-landica* (Setchell) and the fucoid alga *H. banksii* (Turner) Descaisne. “Sites” were treated as a random effect.

Six treatments were set up within each site and there were two runs of the experiment, each lasting 11 days in December 2001 and January 2002. The variable measured was the survival of 1-week-old *Hormosira* germlings. These were settled in the laboratory at around 100/cm² on experimental plates measuring 10 × 10 cm, which have been shown as good surfaces for fucoid algal attachment (Taylor and Schiel, 2003). We hypothesised that grazers would move sediments and keep them from consolidating, thereby reducing potential negative effects of sediment on germling survival. This experiment, therefore, tested the hypothesis that the survival of algal germlings would decrease with increased levels of sedimentation, but survival would increase when sediments and molluscan grazers co-occurred through the grazers bulldozing the sediments away from the germlings. It was anticipated that the degree of sediment removal would vary across different species of molluscan grazers. The major mobile gastropods on non-bare areas of reef in the area were the trochid *Melagraphia aethiops* (Gmelin), the turbinid *Turbo smaragdus* (Gmelin) and the potamidid *Zeacumantus subcarinatus* (Sowerby). The treatments were: *Melagraphia* present, *Turbo* present, *Zeacumantus* present, No gastropods present, Cage control (access holes in sides) and Open control (no cages). A similar

biomass of grazers was placed into the grazer treatments (3 *Melagraphia* and 3 *Turbo* of 20 mm total length, or 100 *Zeacumantus* of ca. 8 mm). It was necessary to constrain gastropods around the experimental plates. This was done with “cages”, which were stainless steel fences (hole width: 5 mm) measuring 20 × 20 cm that were bolted to the reef surface. A thin plastic netting (strawberry mesh) was stretched over the tops to prevent gastropods from leaving or entering. Plates seeded with 1-week-old *Hormosira* germlings were put into all treatments at all sites during the same tide. They were removed and re-counted after 11 days. There were three replicates of each treatment. Each 11-day run of the experiment was analysed with a two-way ANOVA, with factors “site” (=3), “grazing treatment” (=6) and their interaction.

A sediment manipulation experiment was done to test the hypothesis that algal germling survival is positively affected by the increased frequency of sediment removal. *Hormosira* plates were settled as above. These were allocated to two treatments: gently rinsed with a wash bottle to remove sediments either weekly or every 2 weeks. A control treatment was left unmanipulated for the duration of the 4-week experiment. To test the hypothesis that grazers move sediment and affect germling survival, we used another treatment in which the grazer *T. smaragdus* was added at the beginning of the experiment. The density was 1 grazer per 10 × 10 cm treatment. All plates were put into cages, as in the previous experiment. Four replicates of each treatment were put into two sites (Kean Point and Laboratory Rocks), both of which are sheltered. Two-way ANOVA was used to test the effect of sites (=2,

treated as a random factor), treatments (=4, fixed factor) and their interaction on percent germling survival after 4 weeks.

2.4. Laboratory-based experiments

We tested the hypothesis that different levels of sediment had no effect on the attachment of *Hormosira* and *Durvillaea* zygotes to primary substratum. Plates of 10 × 10 cm (as above, with three replicates for each species) were randomly placed within a large seawater tank (approx. 3 m × 1 m × 30 cm high). Plates were covered with either coarse sediment (approx. 2 mm deep), lightly dusted with sediment or left uncovered. The light cover was a thin dusting that covered 75% of plates with an average dry weight of 1.3 g/100 cm² plate, equivalent to 131 g/m². The dense cover was over 100% of the plate surfaces, with an average dry weight of 7.3 g, equivalent to 731 g/m². A slurry of algal zygotes was poured over the plates and allowed to settle. Plates were sufficiently far apart that there was no movement of sediment across them. After 3 days, plates were gently lifted from the tanks and all attached algae were counted. Separate experiments were done for *Hormosira* and *Durvillaea*.

To test the abilities of different gastropods to move sediment, unsettled plates were put within a larger tank (as above) and covered to a depth of about 3 mm with sediment taken from a nearby sheltered shore (Lab Rocks). Plates were placed within cages with either *Melagraphia*, *Turbo*, *Zeacumantus* or no gastropods (as in the field experiments). The amount of sediment remaining on plates after 8 days was measured and tested across gastropod treatments using one-way ANOVA.

3. Results

3.1. Sediment traps

The five different sediment traps had variable success in capturing the different size fractions of sediment (Fig. 3). The honeycomb and large traps caught similar amounts of most size fractions, except for the larger sand in the 80–1100 μm fractions. All traps caught about the same amount of the two smallest and the largest size fractions. The traps had different mouth areas, but their proportional differences did not translate overall to the sediment caught. Therefore, the different traps had unequal abilities to catch or retain sediments. For example, the honeycomb trap had a mouth area of 83.3 cm² compared to the 65 cm² of large traps and 23.7 cm² of the medium trap. However, the honeycomb and large traps caught only about 1.5 times the amount of the medium trap in the 60–80 μm size fraction.

All traps except the embedded tubes were trialed at a more wave-exposed site (Seal Reef) with generally similar results (not presented). However, the honeycomb traps, which protruded above the reef, were quickly demolished by waves, so we considered this type of trap to be impractical for intertidal work. The embedded tube traps offered no advantages over any of the others. We considered it to be impractical to drill holes into reefs for these traps, and they were difficult to anchor securely, remove and replace. Overall, we considered the medium traps to be most useful. These could be readily mounted on reefs in a level position and were easy to employ, remove, empty and replace, while collecting a greater proportion of the sediment than the smaller traps. We therefore used these traps in the remainder of the study.

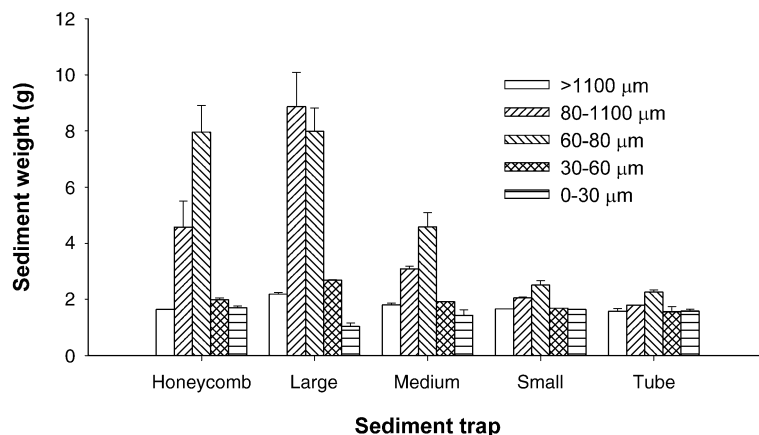


Fig. 3. Comparisons of the average daily weight (± 1 S.E.) of sediment in different size fractions caught by the five different traps over 9 days.

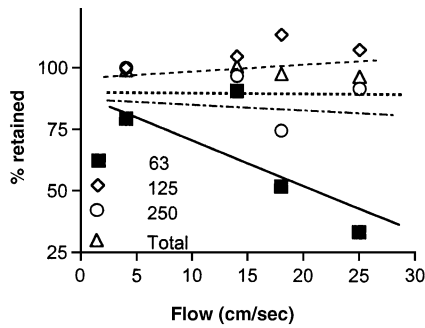


Fig. 4. Results of flume experiments with “medium” sediment traps showing the percentage loss of different size fractions of sediment under different flow velocities.

We tested the medium traps for their ability to retain sediments of different size fractions in different water flows in a laboratory flume (Fig. 4). Size fractions above 125 µm were retained across all flows up to 25 cm/s. However, up to 60% of the smallest size fractions (the fine silts in the 63–125 µm category) were lost from flows around 15 cm/s. These represented a small

proportion of the total weight of sediment and their loss made almost no difference to the weight of all sediments across flows.

3.2. Sampling across sites

From the dynamometer data, sites were ranked by exposure and then sediment levels were plotted against these (Fig. 5A). There were significant differences in sediment loads between sites ($F_{1,6}=2.577, p=0.026$); SNK tests indicated that the four most sheltered sites (KP, LR, SB, WF) and the three most exposed sites (AP, SR, FB) formed separate groups.

The different size fractions of sediment also varied across sites of different exposures (Fig. 5B). Sites were generally similar in the very fine silt fraction (0–30 µm) but they varied considerably in the 125–1100 µm fractions, which included sand. The more exposed sites (AP, SR, FB) had little sand. Because there was sand in the subtidal regions near these sites, this may have been a reflection either that the traps did not catch these

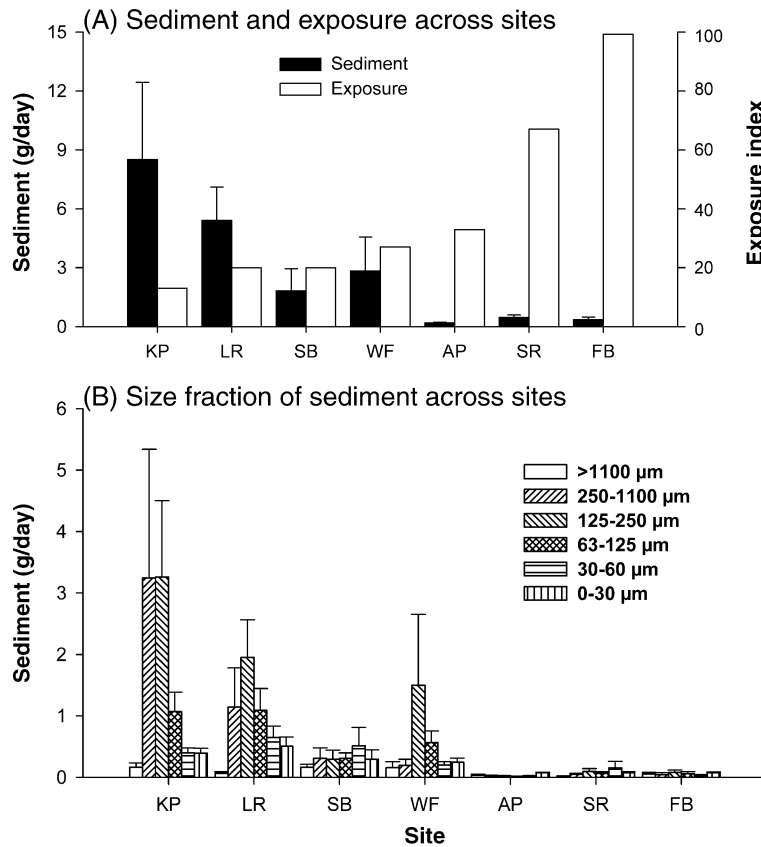


Fig. 5. (A) The sediment caught per day (± 1 S.E.) vs. the relative exposure across the study sites: Kean Point (KP), Lab Rocks (LR), South Bay (SB), Wairepo Flats (WF), Avoca Point (AP), Seal Reef (SR) and First Bay (FB). (B) Histograms of the average size fractions (mean ± 1 S.E.) of sediments caught daily by medium traps in the seven study sites.

middle size fractions or that the dense algal beds nearby (see below) reduced the movement of sand to the intertidal zone. Overall, there was a negative correlation between the amount of sediment and wave exposure ($r = -0.82$, $p < 0.001$, $n = 70$, log-transformed data).

The abundance of most organisms varied across exposures (Fig. 6). The major habitat-forming algae, *Hormosira* and *Durvillaea*, generally occupied different sites along an exposure gradient around the peninsula (Fig. 6A). *Hormosira* was the dominant algae at the four most sheltered sites, but did occur in small patches at the more exposed sites. It reached its greatest average cover of 80% at the intermediate site Wairepo Flats. *Durvillaea* occurred only at the three most exposed sites, reaching an average of around 80% cover at the two most exposed places. The seagrass *Zostera* was very abundant at the most sheltered site but occurred at the four least exposed sites. On a scale of quadrats across all sites ($n = 70$), *Durvillaea* was negatively correlated with *Hormosira* ($r = -0.56$, $p < 0.001$) and sediment ($r = -0.56$, $p < 0.001$), while both *Hormosira* ($r = 0.46$, $p < 0.001$) and *Zostera* ($r = 0.49$, $p < 0.001$) were positively correlated with sediment.

Some species of grazing invertebrates also varied among exposures. The small (up to 15 mm length) grazer *Z. subcarinatus*, reached average densities of 200 per 0.25 m² at the most sheltered site and was

not seen at the three most exposed sites (Fig. 6B). Over all quadrats, it was positively correlated with sediment ($r = 0.45$, $p < 0.001$). The trochid *M. aethiops* and the turbinid *T. smaragdus* were found at combined average densities of around 1–3 per 0.25 m² at the sheltered and intermediate sites (Fig. 6B). They were associated more with sandy substrata ($r = 0.36$, $p = 0.002$) than with fine sediments ($r = -0.16$, $p = 0.20$, ns). The major limpets (*Cellana* spp.), however, were found mostly at the more exposed sites (Fig. 6B) and were negatively correlated with sediment ($r = -0.35$, $p = 0.003$).

Encrusting corallines generally increased with exposure, reaching up to 80% cover at the most exposed site, but they were also abundant at one of the sheltered sites (Fig. 6C). On a quadrat scale, they were negatively correlated with sediment ($r = -0.49$, $p < 0.001$). Turfing corallines, however, had no relationship with exposure (Fig. 6C) or with sediment ($r = -0.09$, $p = 0.44$, ns).

We examined the relationship between the sediment cover on quadrats within sites (measured as percent of primary substrata covered by sediment) and the total weight of sediment measured in sediment traps over 9 days at each site. There was a strong positive correlation between them ($r = 0.98$, $p < 0.005$, $n = 7$), indicating that the sites with the highest load of suspended sediments also had the greatest amount of deposited sediment.

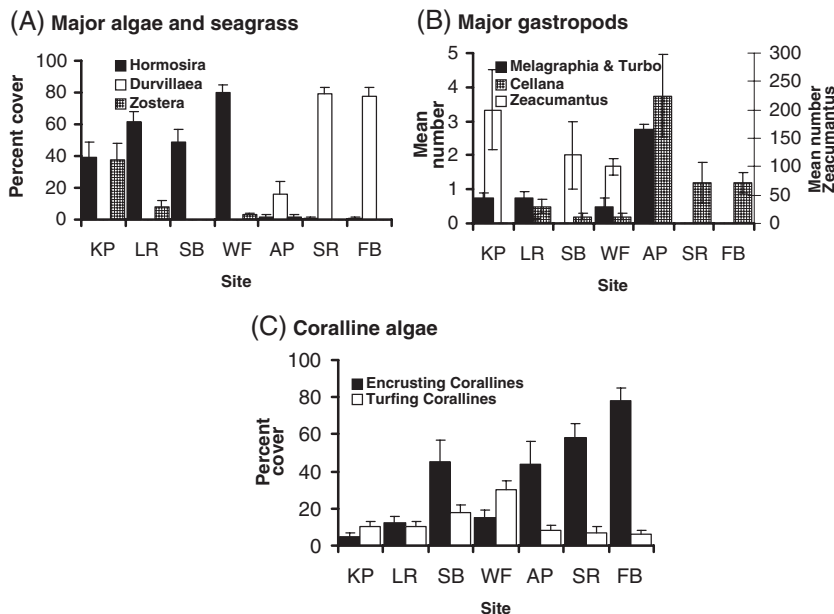


Fig. 6. The abundances of organisms across the study sites, ranked from least to most exposed. (A) Percent cover (mean \pm 1 S.E.) of *Hormosira banksii*, *Durvillaea antarctica* and *Zostera novazelandica*; (B) the number per 0.25 m² (mean \pm 1 S.E.) of *Melagraphia aethiops* and *Turbo smaragdus* (combined), *Cellana denticulata*, *C. ornata* and *C. radians* (combined), and *Zeacumantus subcarinata*; (C) the percent cover (mean \pm 1 S.E.) of encrusting coralline algae and turfing coralline algae.

3.3. Experiments

We used the natural sediment loads between sites of similar exposures to test for the effects of sediment on *Hormosira* germlings. It was not possible to achieve different sediment loads naturally within single sites, but using multiple sites has the disadvantage of potentially introducing other site artefacts.

In the first trial of this experiment, there were clear differences among the three sites (Fig. 7A). At the site with most sediment (KP), there was no survival of *Hormosira* germlings after 11 days. This site had significantly more sediment than the other two sites during the experiment ($F_{2,3}=49.1$, $p=0.005$), with an average of five times the sediment load.

South Bay (SB) had close to 100% survival while Wairepo Flats (WF) had only 75% although these were not significantly different ($F_{1,24}=1.82$, $p=0.19$; site KP was omitted from analysis because all values were 0). Within these latter two sites, there were no significant treatment effects (Fig. 7B; $F_{5,5}=2.29$, $p=0.19$) or interactions ($F_{5,24}=0.46$, $p=0.80$). Treatment means ranged from a low of around 15% survival, in the control fences that were open to external grazers, to a high of around 95% in the treatments with *Zeacumantus*. However, variation within all treatments was high and there was no evident effect of grazing gastropods. The sec-

ond run of this experiment had different results from the first trial with respect to sites (Fig. 7C). All sites were similar in the survival of *Hormosira* germlings, including the most sedimented site (KP) ($F_{2,36}=0.41$, $p=0.67$). Again, there were no differences in the overall effects of grazers ($F_{5,10}=0.75$, $p=0.60$) and no significant interaction ($F_{10,36}=1.15$, $p=0.35$). All treatments had >50% survival (Fig. 7D) but the order of treatment means was different from the first trial. In particular, the mean of the control cages was 75% and the *Zeacumantus* plates had only 56% survival. Trial 2 treatments had similar sediment loads ($F_{2,3}=1.1$, $p=0.439$), which were relatively light and similar to sites SB and WF in the first trial. Overall, plates at all sites were occasionally covered completely with sediment, but only site KP in the first trial became completely bound in sediment.

The experimental tests of different rates of sediment removal showed little effect on the survival of *Hormosira* germlings (Fig. 8A–H). There were similar rates of survival after 4 weeks at both sites ($F_{1,24}=0.05$, $p=0.82$), with 3.6% (± 1.55 S.E.) at Lab Rocks and 4.1% (± 1.63) at Kean Point. There were differences in the treatment means and in their levels between sites, but the variation within treatments was high (Fig. 8A,B). The grazer *T. smaragdus* generally had a suppressive effect on germling survival, but there was no

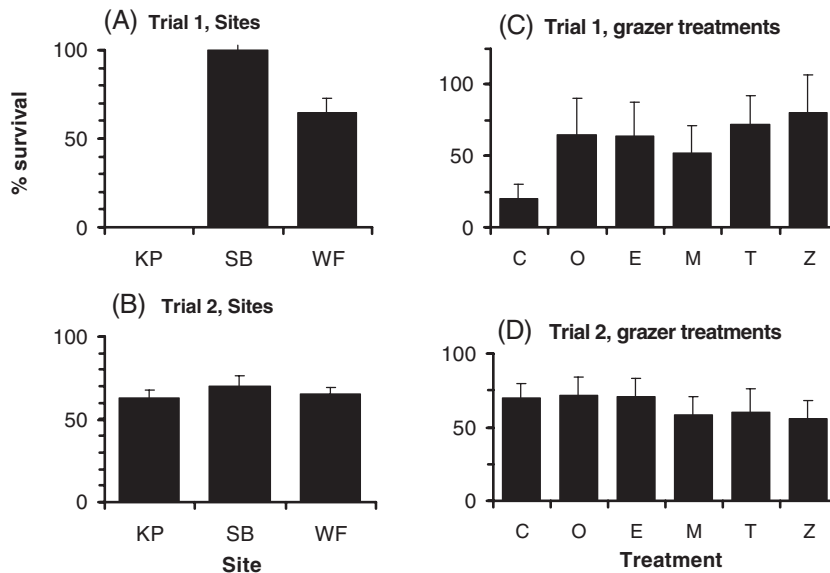


Fig. 7. Results of two trials of the sediment experiment with grazers at Kean Point (KP), South Bay (SB) and Wairepo Flats (WF). (A) Percent survival (mean \pm 1 S.E.) of *Hormosira banksii* germlings (initially 1 week old) over 4 weeks in first experimental run at the three sites; (B) percent survival (mean \pm 1 S.E.) in treatments across sites; (C) percent survival (mean \pm 1 S.E.) of *Hormosira banksii* germlings (initially 1 week old) over 4 weeks in second experimental run at the three sites; (D) percent survival (mean \pm 1 S.E.) in treatments across sites. Treatments on x-axis: C=control (cage with holes), O=open (no cage), E=exclusion (closed cage with no gastropods), M=*Melagraphia* inclusion, T=*Turbo* inclusion, Z=*Zeacumantus* inclusion.

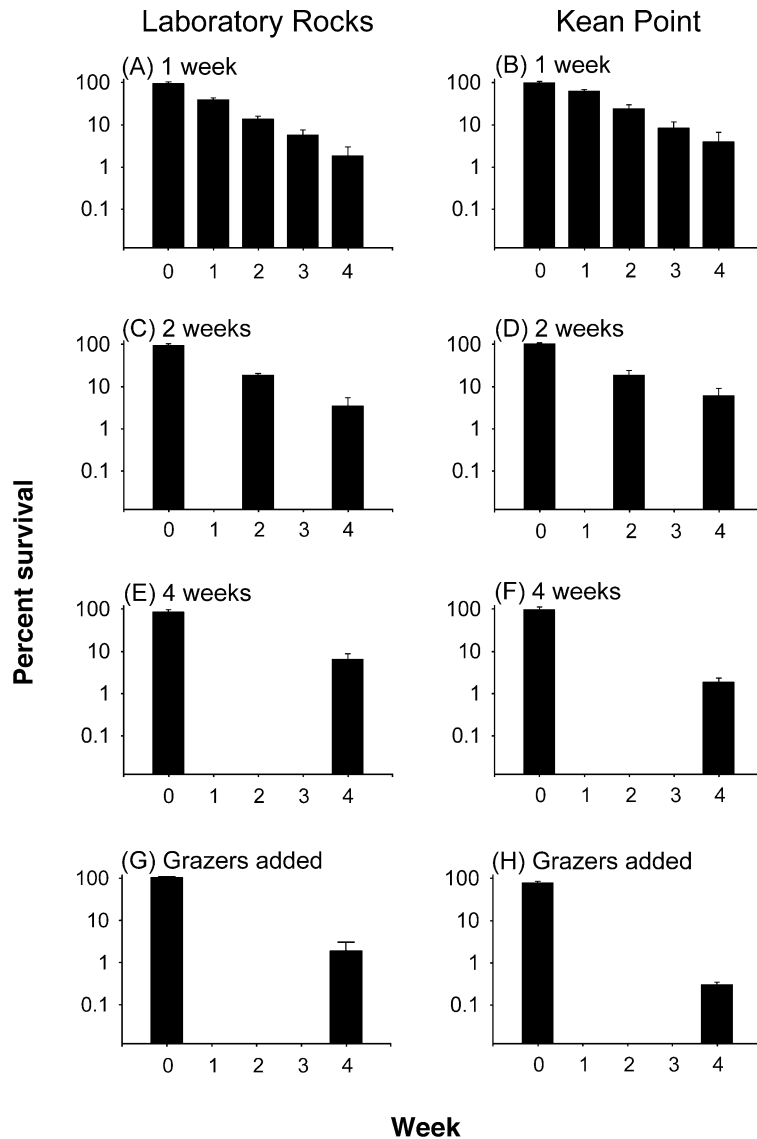


Fig. 8. Results of sediment removal and grazer addition experiment done at Laboratory Rocks (LR) and Kean Point (KP). Bars (log₁₀ scale) show percent survival (mean \pm S.E.) of germlings over 4 weeks (shown on x-axis). Sediment removed and monitored at weekly intervals at site LR (A) and KP (B); sediment removed and monitored at 2-week intervals at LR (C) and KP (D); sediment removed and monitored after 4 weeks at LR (E) and KP (F); grazers added after 2 weeks, then monitored after 4 weeks at LR (G) and KP (H).

effect of removing sediment at different time intervals. Overall, neither the treatments ($F_{3,3}=0.95$, $p=0.515$) nor the site \times treatment interaction ($F_{3,24}=0.85$, $p=0.478$) were significant. While it was clearly evident that *Turbo* was moving sediments, either this made no difference to survival or else their grazing effects on germlings equalled that of the sediment effects so that no treatment effects were obvious.

We had parallel treatments in which a 5 mm deep cover of sediment was added to treatments, in an attempt to manipulate sediment levels. These made no

difference to germling survival in any of the treatments or sites (i.e., all F -values were ns). We also tested the hypothesis that the presence of algal germlings affected the accumulation of sediment. Plates with 4-week-old germlings (around 0.5 mm long) accumulated an average of 50.2% cover (± 4.81 S.E.), while plates without germlings had a 32.8% (± 4.58 S.E.) cover of sediment ($F_{1,142}=6.9$, $p=0.009$).

The field-based experiments above showed that, once germlings were settled and attached to substrata, there were varying effects of sediments on their survival. In the

laboratory, we addressed the question: what are the effects of sediment on the settlement and attachment of algae? To test this, we used two levels of sediment, either a light cover or a dense cover around 2 mm deep, and determined whether *H. banksii* and *D. antarctica* could successfully attach. There were significant effects on germling attachment among treatments for both species (*Hormosira*: $F_{2,6}=635.1$, $p<0.001$; *Durvillaea*: $F_{2,6}=596.2$, $p<0.001$). Even a thin layer of sediment reduced attachment in both species but the effect was more pronounced in *Durvillaea* (Fig. 9A,B). *Hormosira* had 66% attachment but *Durvillaea* had only 29%. Very few individuals of either species attached to plates with a 100% cover of sediment. In both species, germlings began to develop and attach by rhizoids after around 48 h. On the substrata covered with a thin layer of sediment, many individuals managed to attach to the primary substratum and many could be seen attached to small grains of sand, which were then washed from the plates. On the denser sediments, most individuals were merely lying on the surface and were either unattached or else attached to sand grains.

We tested the ability of gastropods to move sediment in controlled conditions in the laboratory. There were significant differences among the four treatments ($F_{3,8}=4.2$, $p=0.048$). *Turbo* bulldozed 88% and *Melagraphia* 70% of sediment cover from plates. The *Zeacumantus* plates and controls were similar. Although *Zeacumantus* clearly moved through the sediment, they actually removed very little of it.

4. Discussion

There were clear and unequivocal effects of sediment on the early life stages of major habitat-forming algae on the rocky intertidal shores of southern New Zealand. Even a light dusting of sediment reduced attachment of newly settled germlings by up to 70%, while a complete cover of sediment prevented attachment altogether. Once settled, burial of germlings by

sediment for even a few days could result in 100% mortality, although this effect was highly patchy in occurrence. These results suggest that much of the variability in algal recruitment, at least in protected and semi-protected sites, may be due to sedimentation and that the differences in assemblage structure across exposures may be at least partially due to sedimentation or its interactions with waves. Measuring sediments, however, remains a problem in intertidal habitats.

4.1. Sediment traps

Many studies have assessed or reviewed the performance of sediment traps, generally concluding that their performance varies in different hydrodynamic conditions (Butman et al., 1986; White, 1990). A wide range of trap sizes and shapes, including funnels, cylinders, boxes, jars and flasks have been tested in the laboratory (Gardner, 1980a; Butman, 1986) and in the field (Gardner, 1980b; Blomqvist and Kofoed, 1981). Sediment traps are meant to obtain a representative sample of the material moving or settling through the water column, but have frequently been deployed in hydrodynamic conditions that exceed the conditions for which they were tested (White, 1990). Cylindrical traps with a height-to-mouth diameter ratio (H/D) ≥ 3 are generally considered to work best. They trap sediments that either fall directly into traps or else are carried into traps by the turbulence induced by them, which effectively influences fluid only about 1 cm above the trap mouths (Butman, 1986). In testing a range of H/D ratios from 0.5 to 8, Blomqvist and Kofoed (1981) found that H/D ratios ≥ 3 collected similar amounts of particulate matter and beyond 8 that sediment trapping was more variable than at lower ratios. Traps deployed in flow velocities greater than about 0.1 m/s may catch less sediment (White, 1990) and those deployed in surf zones present particular challenges (Kraus, 1987).

None of the cylindrical or baffled traps that we used in the intertidal zone worked across all exposures. Those

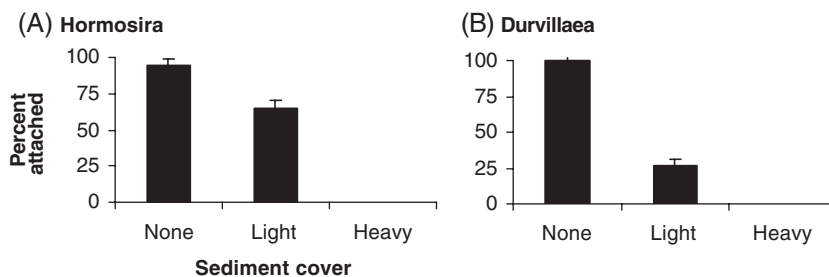


Fig. 9. Percent (mean \pm S.E.) of germlings attached after 2 days in laboratory-based settlement experiment with *Hormosira banksii* (A) and *Durvillaea antarctica* (B) on open plates, plates with a light layer of sediment and plates with a heavy (2 mm) layer of sediment.

that protruded above the reef could not be secured in anything beyond mild sea conditions, and those embedded into the reef were labour-intensive, harmful to the reef and produced no better results than other types we tested. Our best compromise across all conditions was the j-shaped, medium trap, with a mouth diameter of 55 mm and a length of 820 mm (i.e., H/D ratio = 15). This was easy to attach, remove and empty, and it caught a full size range of sediment when compared to the other traps. Our flume experiments showed that the finest size fractions of silt were washed from these traps beyond a flow rate of around 0.2 m/s. However, this comprised very little weight so did not affect the overall weight of the sediment. It was not our intention to test, and we have no way of knowing, how well these traps measured the actual sediments in all its size fractions in the waters above the intertidal zone of our sites. However, all reviews of traps have highlighted how difficult it is to be reasonably sure how well a trap performs in different conditions. We conclude that our traps gave a good relative measure of sediment among sites, and there was an almost perfect correlation between sediment cover on the reef and measurements from traps. However, they may have under-performed at exposed sites. The mouth of our traps was only about 25 cm above the substratum, so they may have contained a high proportion of resuspended material (cf. Airoidi et al., 1996). For benthic organisms, this may be the most relevant measure because they will be affected most by the sediments immediately above them.

Clearly, using traps to assay sediments in the intertidal zone will require more testing, particularly in how the sediments they capture relate to the total flux at a site. However, if finer sediments are increasing from changes in coastal usage (cf. Kautsky et al., 1986), some form of measurement other than accumulation (e.g., suspension or abrasion) will also be useful.

4.2. Sediment effects on macroalgae

The strong correlation between the abundances and types of organisms inhabiting temperate shores and the degree of exposure to waves has been noted from the early days of marine ecological studies (Stephenson and Stephenson, 1949). Although the interactions of processes such as predation, competition and grazing across exposure gradients has been explored considerably (e.g., Dayton, 1975; Menge and Sutherland, 1976, 1987; Hawkins and Hartnoll, 1983), it is far more difficult to test directly in the field the effects of broad-scale physical processes. Sedimentation is a wider process that undoubtedly varies over different

exposures. Fine sediments including silt and fine organic matter can accumulate in sheltered conditions (Airoidi et al., 1996), while more wave-exposed areas are likely to be affected by sand scour and higher levels of erosion (Van de Koppel et al., 2001).

Our study showed an inverse relationship between the degree of wave exposure and the amount of sediment around the fairly localized sites of the Kaikoura Peninsula. These sites also showed differences in the dominant biota. The most exposed sites were characterized by the southern bull kelp *D. antarctica*, which never occurs in sheltered conditions, and associated molluscs such as limpets and chitons. Although geniculate and non-geniculate corallines are abundant in exposed conditions, they are also common across reefs in most exposures. Despite the presence of patchy sand habitats that occur just below the *Durvillaea* zone, neither sand nor other sediments accumulated on the high-energy sites in the intertidal zone. The most sheltered sites were characterized by an accumulation of fine sediments and an extensive cover of *Z. novaezelandica*. This seagrass is really an estuarine species in New Zealand but also occurs on sheltered to intermediate rock platforms (Morton and Miller, 1973). It seeds into sand patches in tide pools, then spreads and accumulates sediments as it grows, often to a depth up to 50 cm (Ramage and Schiel, 1999). The intermediate sites were characterized by *H. banksii*, a fucoid species that dominates platforms of intermediate exposure but which extends into both sheltered and exposed conditions.

We aimed to decouple the influences of exposure and sediments on the habitat-forming algae and thereby clarify the interactions of these species with important physical factors, through a series of tests. Previous field and laboratory experiments showed that *Hormosira* zygotes have a limited ability to attach to substrata in even slightly wavy conditions, which makes it difficult for this species to colonize exposed shores (Taylor and Schiel, 2003). *Durvillaea* zygotes can attach quickly and securely in all exposures but plants rarely survive more than a few months except in exposed places (Taylor and Schiel, 2003). In this study, the presence of sediments across sites of similar wave exposure produced variable results on the early life stages of *Hormosira*. In most cases, there were no significant effects of sediment on survival of 11-day-old germlings. However, one of the replicate runs at one site resulted in 100% mortality. This was due to smothering by a thick layer of sediment that remained on the reef for the duration of the experiment.

Most studies of sediments on rocky shores have noted the variable arrival and departure of sediments

and consequently the variable effects on algal assemblages (Littler et al., 1983; Stewart, 1983; Airoidi et al., 1996). For example, Taylor and Littler (1982) found that sand cover went from 0% to 55% during the winter months at a southern California site, affecting the relative abundances of an anemone, a sand tube worm and macroalgae. They concluded that the reduction in algae was due to the interaction of sand, desiccation and thermal effects on spores. D'Antonio (1986) found that the red alga *Rhodomela larix* could withstand sand scour and the anoxic conditions of lengthy burial to survive where few other species could on low intertidal shores. On the platforms of central New Zealand, macroalgae both benefit and suffer from the accumulation of sediments. We found a greater cover of sediment on plates with algal germlings compared to bare plates. As young germlings grow, they often trap sediment so that only their tips are exposed at low tide. These sediments appear to retain water during most low tide periods and are likely to reduce the desiccation stress on young plants. *Hormosira* is composed of fluid-filled beads and is one of the most desiccation-resistant fucoids on New Zealand shores (Dromgoole, 1980; Brown, 1987). However, newly settled juveniles are undoubtedly more prone to drying out than are larger plants.

In this study, burial by sediments did cause mortality of *Hormosira* germlings, an effect that was highly variable and which seemed to depend not only on the amount of sediment but also on the period of retention and how cohesive it became. Several studies have shown that sediments can quickly become colonized by diatoms and small filamentous algae. For example, Airoidi (1998) found that the patchiness in space and time of sediments contributed to the patchiness in assemblage structure of turfing algae, even though the overall assemblage composition was similar across different study areas. We have seen a high degree of patchiness in sediment composition across single reefs. The major effect on small algae is through prolonged burial, combined with the sedimented patches forming a gel-like structure bound by a matrix of diatoms.

In addition to the effects of burial, a light coating of sediment severely reduces propagule attachment. Fucoid algae are notoriously patchy in their recruitment into intertidal areas (Gunnill, 1980; Sousa, 1984; Chapman, 1985) and even the ephemeral presence of fine sediments may contribute to this variability. For example, up to 90% of kelp spores fail to attach to primary substratum when a thin layer of sediment is present (Devlinny and Volse, 1978; Norton, 1978; Vadas et al., 1992). In our study, even a fine layer of sediment

greatly reduced the attachment of both *Hormosira* and *Durvillaea*, and a slightly thicker layer entirely prevented attachment. The differences between these species in the percentage of zygotes that attached in light sediments may be due to their differing abilities to stick quickly. Zygotes attach initially by mucilage and *Hormosira* zygotes do not do this as quickly or as firmly as *Durvillaea* zygotes (Taylor and Schiel, 2003). It appeared that *Hormosira* zygotes rolled and settled between sediment grains, while *Durvillaea* zygotes stuck immediately to the surface sediment. Some of the unexplained variation in recruitment of *Durvillaea*, *Hormosira* and other fucoids may therefore be accounted for by the patchy deposition of sediments that is common on reef platforms. Furthermore, these very young life stages may be particularly prone to removal by sand scour (Bellgrove et al., 1997), suggesting an interaction between sedimentation and water motion in recruitment. Recent work has shown that water motion alone, both within and between shores of different exposures, accounts for some of the patchiness of fucoid recruitment (Taylor and Schiel, 2003). It seems unlikely, therefore, that across sites of different exposures the effects of sediment will be independent of water motion (Gorostiaga et al., 1998).

4.3. Interactions with grazers

Sediment, grazers and algae can interact in various ways. For example, Bertness (1984) showed that an introduced European periwinkle, *Littorina littorea*, modified intertidal habitats in New England, greatly affecting assemblages. Where snails were removed, several species of algae recruited and sediments accumulated and remained, leading to the recruitment of invertebrates characteristic of soft-sediments. Where snails remained, however, sediment was bulldozed and the grazing by snails prevented the establishment of macroalgae. Situations where there is silt accumulation and diatom growth can be relatively stable (Van de Koppel et al., 2001). In our study, there were no obvious effects of grazers on the sediments in the field, although there were in the laboratory, and no significant grazing effect on algal germlings. We hypothesized that the grazers would move the sediments and keep them from binding, thereby diminishing the chances of smothering. The absence of a grazing effect in most of the experiments suggests sediments may reduce the effectiveness of grazers. At the one site where sediments became cohesive, grazers simply moved over the top of the sediment. The movement of sediment by mobile grazers was clearly variable in

occurrence over the short term of these experiments and grazer effects on sediments could be more pronounced in the longer term. Of all the reef gastropods, limpets may be the most effective in pushing sediments around, but on most reef platforms dominated by seaweeds along eastern New Zealand, large limpets (i.e., *Cellana* spp.) tend to occur in large bare patches that are long-term features of reefs, rather than in smaller patches among the algae (Dunmore, 1996). In these habitats, no fucoid algae recruit, even with the removal of limpets.

Overall, we conclude from this study that sedimentation plays an important role in the attachment of the early life stages of perennial algae on southern New Zealand rocky shores. Effects of sediment on the survival of fucoid germlings were variable, but can cause high levels of mortality if burial is deep and prolonged. If sedimentation increases in the coastal zone, it is likely to have its greatest effects along the sheltered harbours and sites of intermediate exposure (cf. Hawkins and Hartnoll, 1983), around which are most of the large population centres of New Zealand.

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