

Sediment disturbance associated with trampling by humans alters species assemblages on a rocky intertidal seashore

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ABSTRACT: Our observations reveal that species living on rocky intertidal reefs can be positively and negatively associated with increasing sediment load. We therefore tested the hypothesis that sediment disturbance, including increased sediment loads associated with trampling by humans, alters the abundance of macroinvertebrates on a sheltered rocky intertidal platform in southern Australia. First we trampled the reef in shallow water at several disturbance intensities, simulating different numbers of people walking on the platform on a rising tide, and determined that sediment load was directly related to trampling intensity. Trampling displaced sediment, and up to an order of magnitude more sediment accumulated on the reef near intensively trampled areas compared to those with natural sedimentation. We then manipulated sediment load on the reef to mimic increased sedimentation due to trampling and other potential human (e.g. terrestrial runoff) and natural (e.g. storms) disturbances, and monitored changes to dominant species. Sediment addition increased the cover and depth of sediment on the reef. Increased sediment load negatively impacted barnacles, but not mussels, which occur naturally bound in a sediment matrix in small depressions on the platform. The dominant grazing gastropods *Nerita atramentosa* and *Bembicium nanum* were negatively influenced by increased sediments, although not at levels associated with trampling, whereas other gastropods were not affected or responded positively to increased sediment load. Changing sediment loads, including the cumulative effects of small-scale disturbances such as trampling, can alter macroinvertebrate species assemblages on rocky reefs and favour species that tolerate a range of environmental conditions and habitat types.

KEY WORDS: Australia · Grazing gastropod · *Hormosira* · Human impacts · Intertidal macroalgae · Marine invertebrate · Mussel bed · Resilience

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INTRODUCTION

Increased sedimentation on coastal reefs due to human activity is an emerging environmental problem (see review by Airoidi 2003). Changing sediment loads resulting from natural disturbances, such as storm waves and flooding, have been observed to dramatically alter species assemblages on rocky

intertidal shores (e.g. Daly & Mathieson 1977, Robles 1982, Littler et al. 1983, Branch et al. 1990). Indeed, studies manipulating sediment loads have demonstrated changes to ecological processes and species assemblages on intertidal and subtidal rocky reefs (e.g. Airoidi 1998, Irving & Connell 2002, Connell 2005, Airoidi & Hawkins 2007, Balata et al. 2007, Huff & Jarett 2007, Vaselli et al. 2008, Atalah &

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Crowe 2010). A significant source of increased sediment deposition on coastal reefs is run-off from terrestrial habitats, particularly in urban and agricultural landscapes (Rogers 1990, Airoidi 2003, Thompson et al. 2002). Less recognised but perhaps equally important are the cumulative impacts of numerous small-scale disturbances from human recreational activities on intertidal and shallow subtidal reefs (e.g. Zedler 1978, Kingsford et al. 1991, Addessi 1994, Fletcher & Frid 1996, Keough & Quinn 1998, Thompson et al. 2002, Hardiman & Burgin 2010, Luna-Pérez et al. 2011).

Trampling by humans during the collection of food and bait and recreational activities is an important small-scale agent of disturbance that has been shown to alter species assemblages in a diversity of marine habitats (rocky intertidal reefs: Beauchamp & Gowing 1982, Ghazanshahi et al. 1983, Bally & Griffiths 1989, Povey & Keough 1991, Brosnan & Crumrine 1994, Keough & Quinn 1998, Araújo et al. 2009; coral reefs: Liddle & Kay 1987, Neil 1990, Liddle 1991; seagrass: Eckrich & Holmquist 2000; mud and sand flats: Wynberg & Branch 1997, Rossi et al. 2007; mangroves: Ross 2006; salt marshes: Headley & Sale 1999). Studies of trampling on intertidal reefs have largely focused on direct impacts, particularly the crushing and dislodgement of intertidal organisms when the reef is exposed at low tide (e.g. Povey & Keough 1991, Keough & Quinn 1998). Trampling in coastal habitats occurs not only when intertidal and shallow subtidal reefs are exposed at low tide, but also when people wade or swim through shallow water over the reef (e.g. walkers, anglers, swimmers, snorkelers and SCUBA divers) (e.g. Thompson et al. 2002, Addison et al. 2008). Walking when the reef is submerged and swimming can indirectly impact reef organisms through increased sedimentation stress as sediment is resuspended with movement through shallow water.

Studies examining how human movement affects sedimentation are uncommon. Neil (1990) showed that walking by humans on coral reefs mobilised sediment in the water column and increased sediment deposition on the reef at loads that had the potential to cause moderate stress in corals. Zedler (1978) showed that trampling by humans reduced the abundance of coralline algal turf, resulting in a loss of sand associated with these mats of algae and in turn the organisms that rely on these sediments for habitat (see also Brown & Taylor 1999). On rocky intertidal reefs, increased sedimentation is predicted to have dramatic impacts on filter feeders and grazers because sediments can also smother

and obstruct the feeding apparatus of sessile barnacles and mussels, and impede movement and reduce the amount of emergent rock substratum necessary for feeding by snails and limpets (e.g. Airoidi & Virgilio 1998, Pulfrich et al. 2003, Schiel et al. 2006). For example, Airoidi & Hawkins (2007) demonstrated that a 1 mm thick layer of sediment could substantially reduce the grazing rates of intertidal limpets. In contrast, other intertidal species may respond positively to the presence of sediments (see Thompson et al. 2002). For example, Huff & Jarett (2007) found that psammophilic snails increased in abundance following the addition of sand to intertidal coralline turf.

In many coastal landscapes, rocky intertidal seashores are adjacent to sandy beaches and soft-sediment subtidal habitats, resulting in the influx and deposition of sediment on these rock platforms, which can be naturally dynamic in space and time (e.g. Littler et al. 1983, Airoidi 2003). In sheltered regions, these rock platforms often accumulate sand, particularly in shallow depressions and pools common in the rock surface and within and around turfing and foliose macroalgae and invertebrates that bind sediment (Airoidi 2003), and the platform can shift from exposed rock to being covered by sand. Human activity in these regions, and particularly trampling, can potentially influence the distribution and load of sediment on the rock platform. Importantly, sediment is often integrally associated with species, such as in mussel–sediment or algal turf–sediment matrixes; these matrixes form an integral part of the reef habitat, which may in turn influence the abundance and composition of infauna as well as mobile and sessile species present (Airoidi 2003). The present study investigated how sediment deposition affects species assemblages on a sheltered, rocky intertidal platform in southern Australia dominated by mats of mussels, barnacles and a suite of gastropods. We tested the hypothesis that trampling by humans indirectly influences the abundance of macroinvertebrates on the platform through increased sediment load. We did this by simulating various intensities of trampling on a reef when it was covered by shallow water and then measuring sedimentation on the reef. Based on these estimates and a range of potential sediment loads that might occur on the reef due to human (e.g. terrestrial run-off from land clearing) and natural disturbance (e.g. storms), we then manipulated sediment load on the reef and monitored the response of the dominant macroinvertebrate species.

MATERIALS AND METHODS

Study location and intertidal communities

The study was carried out over the austral summer on a rocky intertidal platform at Coobowie on the Yorke Peninsula, which is a rural area approximately 70 km southwest of Adelaide, South Australia (35° 03' 16" S, 137° 43' 45" E). The platform is on the southern side of a sheltered inlet (Salt Creek Bay) and experiences minimal wave action. Typical coastal vegetation borders the landward edge of the rock platform and the seaward edge gradually leads into soft-bottom, subtidal habitat, which is the likely source of sediments (Airoidi 2003). The rock platform is almost flat and extends 2 km alongshore and 0.8 km from landward to seaward. Maximal tidal range during the study was 2.41 m.

Sediments (primarily sand) transported onto the platform are typically associated with 2 types of intertidal communities that are prevalent in the region: one dominated by the habitat-forming macroalga *Hormosira banksii* (hereafter referred to as macroalgal habitat), and one dominated by patches of the mussel *Xenostrobus inconstans* with byssus threads bound in a sediment matrix (hereafter referred to as mussel habitat), which lacks canopy-forming macroalgae, has less sediment and occurs at slightly higher tidal elevations. The entire rock platform is pitted with small shallow depressions, allowing patches of sediment to accumulate on the platform at low tide. These habitats are home to species that are common and abundant in sheltered to moderately exposed bays throughout the region and more generally in southern Australia, including mussels, barnacles, macroalgae and a suite of grazing, predatory and scavenging gastropods (e.g. Keough & Quinn 1998, Underwood 1998).

Relationships between sediment cover and macroinvertebrate abundance

The relationship between the cover of sediment and abundance of dominant macroinvertebrate species was quantified in the mussel habitat by sampling quadrats (1 × 1 m) with varying levels of sediment cover (0, 20, 40, 60 and 80%; n = 3 per cover level). The primary substratum of the mussel habitat is dominated by the mussel *Xenostrobus inconstans* and the barnacle *Elminius modestus*, and there are small patches of sediment in a thin layer covering the bare rock. Common species of gastropods include the

grazers *Nerita atramentosa*, *Bembicium nanum*, *Austrocochlea porcata* and *A. constricta*, the predator *Haustrum vinosum* (formerly *Lepsiella vinosum*), and *Cacozeliana granarium* (formerly *Bittium granarium*), which feeds on microalgae and particulate matter.

Abundances of bare rock, sediment overlying the rock, and the mussel *Xenostrobus inconstans* were estimated by their percent covers using the point-intercept method, with 100 uniformly spaced points over the 1 × 1 m quadrat. The depth of sediment was also estimated at 3 randomly selected places in each quadrat. Densities for the majority of gastropods were also quantified in the 1 × 1 m quadrat. Due to their great abundances and patchy distribution, however, densities of *Bembicium nanum* and *Elminius modestus* were randomly sampled in 16 smaller (9 × 9 cm) quadrats (an area of 1296 cm²) within the larger 1 m² quadrat. Linear regression with untransformed data (n = 15 observations: n = 3 replicates for each of 5 sediment cover levels) was used to examine the relationship between percent cover of sediment and dependent variables (sediment depth, cover of bare rock and macroinvertebrate abundance).

Sediment load due to trampling

Changes to the loading (i.e. net effect of removal and deposition) of sediment on the rock platform due to trampling by humans were determined in both the macroalgal and mussel habitats. A 50 × 100 m area was selected in each of the macroalgal and mussel habitats. Twenty quadrats (0.3 × 1.0 m), separated by a least 2 m, were located in each of these habitats and permanently marked. To minimise initial variation in the abundances of organisms and sediment dynamics, quadrats in each habitat were randomly selected where there was a relatively similar cover of the dominant, habitat-forming species: 53 ± 2.1% (mean ± SE; n = 20) cover of *Hormosira banksii* in the macroalgal habitat; and 41 ± 1.7% (mean ± SE; n = 20) cover of *Xenostrobus inconstans* in the mussel habitat. Four intensities of trampling were randomly allocated to the 20 quadrats (n = 5 quadrats per trampling intensity): 0, 15, 30 or 60 trampling passes. A trampling pass consisted of one person (weight 75 kg, height 175 cm) wearing rubber-soled shoes (the most commonly worn footwear in intertidal areas; Bally & Griffiths 1989) walking at a normal pace across the length of the quadrat (i.e. 1 or 2 steps in the 1 m long quadrat per trampling pass). Trampling was performed when water covered the plat-

form to a depth of 15 to 30 cm (ankle to calf depth) and within 2 h of the platform being covered by water during a rising tide. Trampling at this time was most likely to alter sediment deposition and to simulate accurately visitation to the reef for recreational activities (e.g. walking, fishing and swimming).

There were 6 trampling days from mid-November to mid-December, with trampling on each of 2 consecutive days over 3 successive low tide periods (i.e. each 2-d trampling event was separated by approximately 14 d). Intensities, frequency and timing of trampling were chosen to represent weekend visitation to metropolitan rocky intertidal reefs with the onset of summer (e.g. Kingsford et al. 1991). The effect of trampling on loading of sediment onto the rock platform in each habitat was quantified at 2 times: immediately after the third and fifth days of trampling. Therefore, sediment loads reflected the effects of trampling of a single trampling day. Sedimentation was quantified by placing 2 circular trays (diameter = 18 cm, area = 254.5 cm², depth = 2.5 cm) 0.5 m away from and at opposite ends of each of the 20 quadrats, trampling on a rising tide, and then collecting the sediment in the trays. Trays were collected in the same order as they were trampled, allowing each tray to collect sediment for approximately 45 min. Due to logistical constraints associated with having the same person trample each quadrat while ensuring constant water depth while trampling, trays in the mussel habitat had to be left overnight (ca. 16 h) and were collected the following morning. Trays were collected by placing them in plastic bags, and then sediment was rinsed and filtered to remove large pieces of organic matter, dried to a constant mass in an oven at 60°C, and weighed. The total value from the 2 sediment trays was used to estimate sediment load per quadrat (i.e. g sediment per 509 cm² area of sediment tray). Differences in sediment load among trampling intensities and habitats for each of the 2 trampling times were analysed with 2-factor ANOVA using untransformed data.

The cover of sediment in all quadrats in the macroalgal habitat was also measured before and after the 6 d of trampling to determine whether trampling intensity influenced the removal or accumulation of sediment on the rock platform. Differences in sediment cover in the macroalgal habitat before and after 6 d of trampling was analysed with one-factor ANOVA using untransformed data. For both the cover and loading of sediment, Student-Newman-Keuls (SNK) multiple comparisons tests were used to determine the location of differences among means after significant ANOVA.

Effect of sediment load on macroinvertebrate abundance

To determine the effect of sediment load on species living in the mussel habitat, various amounts of sediment were added to the rock platform from early January to mid-February and the response of dominant macrofaunal species was assessed before the first addition of sediment until early March. A total of 42 quadrats (1 × 1 m), each separated by at least 2 m, were randomly located in areas where there was 20 to 30% cover of the mussel *Xenostrobus inconstans*. Six intensities of sediment disturbance were randomly allocated to the 42 quadrats: 0, 125, 250, 500, 1000 and 2000 g of dry sediment (n = 7 replicates per intensity). These sediment loads were chosen to mimic disturbances, ranging from those recorded here due to trampling by humans (up to 313 g m⁻² after a trampling day; see 'Results; Sediment load due to trampling') to natural and anthropogenic processes such as those resulting from storms and urban run-off (see Branch et al. 1990, Airoidi et al. 1996, Airoidi 2003, Connell 2005, Airoidi & Hawkins 2007). Natural sediment loading into the habitat (quantified as described in the previous subsection) for 2 periods spanning the duration of the experiment ranged from 13.2 to 17.6 g m⁻² d⁻¹. Sediment was added 3 times at approximately fortnightly intervals, which simulated 3 pulse disturbances resulting from trampling by humans during weekend visits to the rock platform during summer (or other larger sediment disturbances). Sediment was collected from the intertidal platform, dried and applied at low tide. Sediments were distributed evenly throughout the quadrat using a coarse grade sieve (i.e. the sieve did not retain any of the sediment) held approximately 0.5 m above the rock platform.

The response of the dominant macroinvertebrate species was quantified at 3 times: (1) before the first addition of sediment (and there were no significant differences among sediment addition treatments for any of the dependent variables; authors' unpubl. data); (2) approximately 2 wk after the first sediment addition (and before the second sediment addition); and (3) approximately 2 wk after the third and final sediment addition (ca. 6 wk after the first sediment addition). The effects of sediment addition were quantified in each quadrat by sampling the percent cover of sessile species occupying the substratum (except for *Elminius modestus*, where density was measured) and the densities of all dominant macroinvertebrate species. Abundances of bare rock, sedi-

ment overlying the rock, and the mussel *Xenostrobus inconstans* were estimated by their percent covers using the point-intercept method, with 100 uniformly spaced points over the 1 × 1 m quadrat. The depth of sediment was also estimated at 3 randomly selected places within each quadrat. Densities for the majority of gastropods were also quantified in the 1 × 1 m quadrat. Due to their small numbers, densities of *Austrocochlea porcata*, *A. constricta*, *Haustrum vinosum* and *Cacozeliana granarium* (all of which showed positive associations with sediment cover; see 'Results') were combined and collectively referred to as 'other gastropods'. Again, densities of *Bembicium nanum* and *E. modestus* were randomly sampled in 16 smaller (9 × 9 cm) quadrats (an area of 1296 cm²) within the larger 1 m² quadrat. Differences in percent cover (sediment, bare rock and the mussel *X. inconstans*; all arcsine-transformed), sediment depth (log-transformed) and macroinvertebrate densities (*E. modestus*, *Nerita atramentosa*, *B. nanum* and other gastropods; all log-transformed) among sediment disturbance intensities were analysed 6 wk after the first addition of sediment (i.e. 2 wk after the third addition of sediment) with one-factor ANOVA, and SNK multiple comparison tests were used to determine location of differences among means after significant ANOVA.

RESULTS

Relationships between sediment cover and macroinvertebrate abundance

The cover and depth of sediments on the rock platform were strongly correlated (Fig. 1), with some areas with 80% cover having sediments 1 cm deep. Not surprisingly, areas of the platform with increasing sediment cover had declining availability of bare rock (Fig. 1). There were both positive and negative relationships between the cover of sediment on the rock platform and the abundance of macroinvertebrates, and these were dependent on functional group and species. The abundance of filter feeders was negatively associated with sediment cover (Fig. 1), including cover of the mussel *Xenostrobus inconstans*, and the barnacle *Elminius modestus* was not present in areas with greater than approximately 20% sediment cover. The direction and strength of associations of gastropods with sediment cover were highly variable. The grazers *Nerita atramentosa* and *Bembicium nanum* were negatively related to

increasing sediment cover, whereas the grazers *Austrocochlea porcata* and *A. constricta*, the predator *Haustrum vinosum*, and *Cacozeliana granarium* were positively related to sediment cover (Fig. 1).

Sediment load due to trampling

In both the macroalgal and mussel habitats, all intensities of trampling increased the deposition of sediment onto the rock platform above natural levels of sedimentation, with the most intensive trampling resulting in more than an order of magnitude more sediment deposited on the platform (Fig. 2). After the third trampling day, sediment load was directly related to trampling intensity in both habitats, and was consistently higher in the macroalgal than mussel habitat (Time 1 in Fig. 2; trampling intensity: $F_{3,16} = 136.7$, $p < 0.001$; SNK: 60 > 30 > 15 > 0 trampling passes; habitat: $F_{1,16} = 7.35$, $p = 0.015$). Indeed, maximum sediment loads were 313 and 283 g m⁻² in the macroalgal and mussel habitats, respectively.

In contrast, after 5 trampling days, substantial components of the species assemblage were removed due to direct trampling impacts, and sediment load in trampled areas was reduced (and more variable) than after 3 trampling days (compare Time 1 with Time 2 in Fig. 2). Nevertheless, in both habitats, sediment load in trampled areas remained greater than in areas with natural levels of sedimentation (Time 2 in Fig. 2; trampling intensity: $F_{3,16} = 5.8$, $p = 0.007$; SNK: 60 = 30 = 15 > 0 trampling passes). In the macroalgal habitat, there was a trend for increased sediment load with trampling intensity, but sediment load in the mussel habitat was extremely variable and reduced at the highest compared with the more moderate levels of trampling intensity. Regardless, there was no difference in sediment load between habitats (Time 2 in Fig. 2; habitat: $F_{1,16} \ll 0.1$, $p = 0.993$).

Trampling in the macroalgal habitat dramatically reduced sediment cover, with close to a 90% reduction in the most intensively trampled areas (0 passes = 21.4 ± 5.5%; 15 passes = 5.9 ± 1.9%; 30 passes = 7.7 ± 3.8%; 60 passes = 2.3 ± 2.3%; mean ± SE, $n = 5$). There was no significant difference in sediment cover among trampling intensities before sampling ($F_{3,16} = 1.7$, $p = 0.213$), and sediment cover in control quadrats without trampling remained remarkably consistent before (20.0 ± 3.1%; $n = 5$) and after trampling, whereas 6 trampling days significantly reduced sediment cover in trampled areas ($F_{3,16} = 5.2$, $p = 0.011$; SNK: 0 > 15 = 30 = 60 trampling passes).

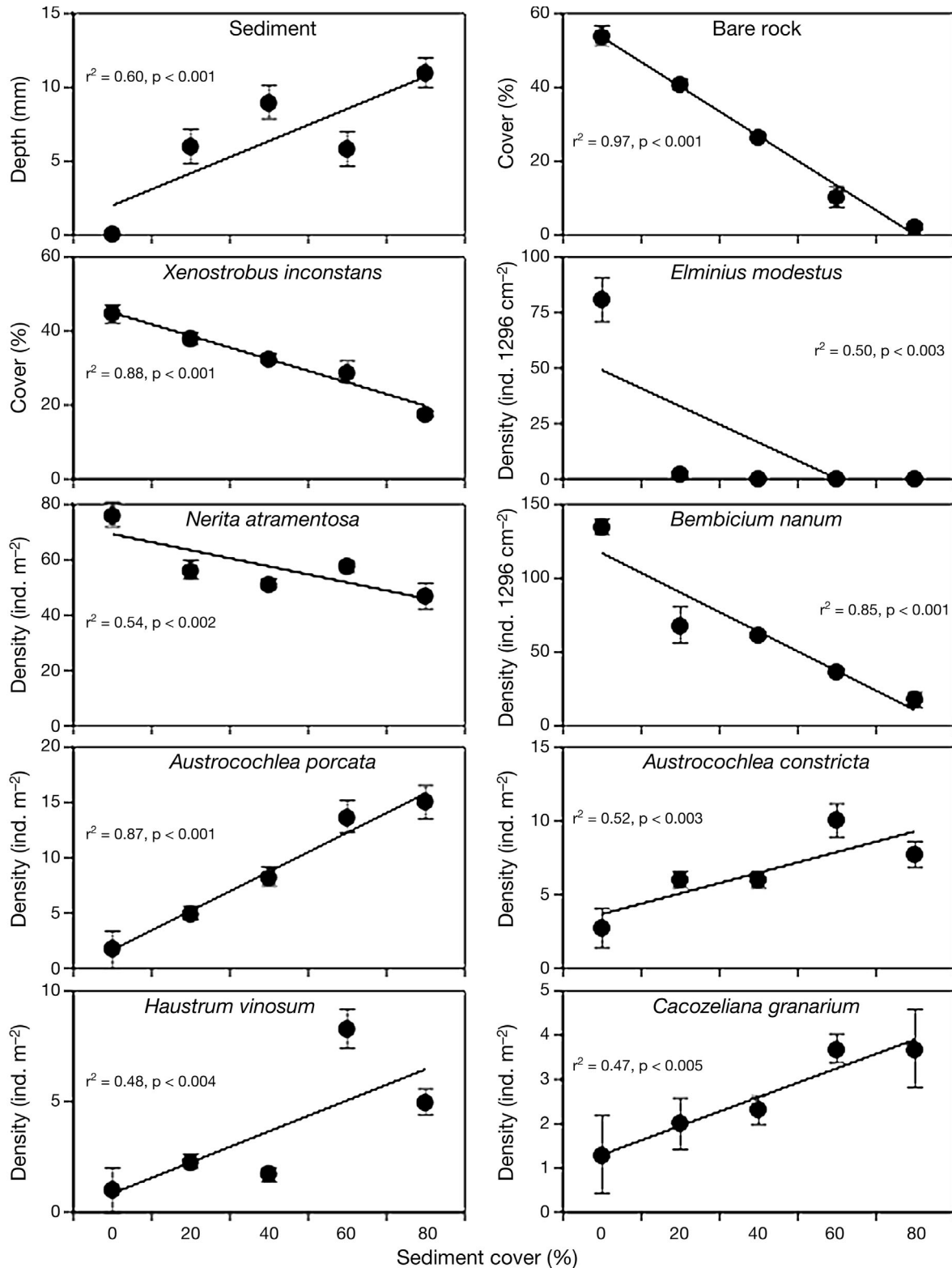


Fig. 1. Relationships between sediment cover on the rock platform and sediment depth, bare rock cover, *Xenostrobus inconstans* cover, and density of *Elminius modestus*, *Nerita atramentosa*, *Bembicium nanum*, *Austrocochlea porcata*, *Austrocochlea constricta*, *Hastrum vinosum*, *Cacozeliana granarium* in the mussel habitat. Points represent means (± 1 SE) of 3 replicate quadrats for each level of sediment cover. Lines depict significant linear relationships (r^2 and p values are given in panels, $n = 15$ quadrats for each)

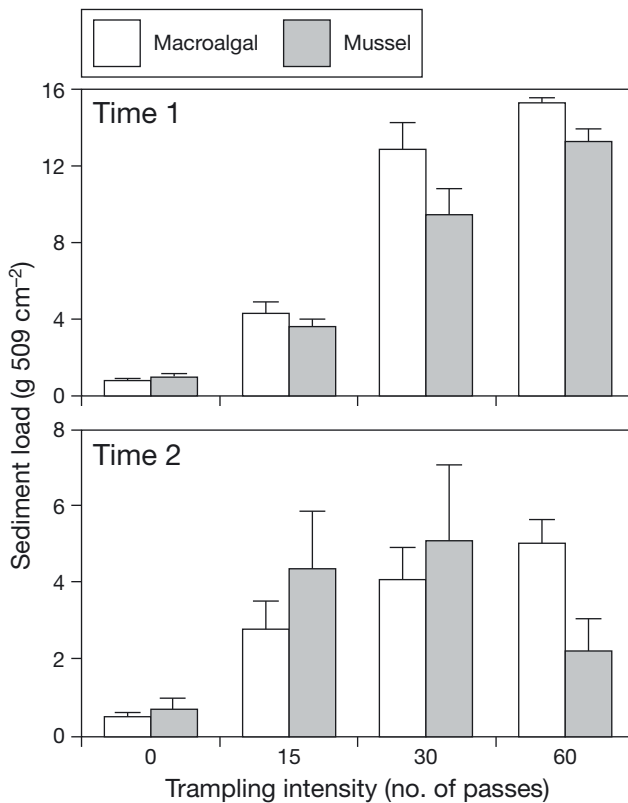


Fig. 2. Mean (± 1 SE) sediment load ($1 \text{ g } 509 \text{ cm}^{-2} \approx 19.6 \text{ g m}^{-2}$) in macroalgal and mussel habitats following various trampling intensities (0, 15, 30 or 60 passes) for each of 2 trampling times: immediately after the third trampling day (Time 1) and immediately after the fifth trampling day (Time 2). Note differences in scale on y-axes

Effect of sediment load on macroinvertebrate abundance

There was a natural influx of sediment onto the rock platform due to a storm in the first 2 wk of the experiment: sediment cover (but not depth) tripled in control areas where sediment was not added, but after 6 wk it had gradually returned to levels similar to those at the start of the experiment, demonstrating the dynamic nature of sediment disturbance on this reef (Fig. 3). Interestingly, trends in abundance in relation to sediment addition, if not their magnitudes, were generally the same after 2 and 6 wk (Fig. 3). After 6 wk, there was a strong, positive relationship between the cover and depth of sediment on the rock platform with the addition of sediments to the mussel habitat (sediment cover: $F_{5,36} = 32.8$, $p < 0.001$; sediment depth: $F_{5,36} = 85.9$, $p < 0.001$; Fig. 3), indicating that sediment accumulated on the platform over time as more sediment was added. Further, although the cover of sediment on the platform declined from 2 to

6 wk after application, the depth of sediment increased, indicating that sediments initially formed a relatively thin layer but then were swept into and accumulated in particular areas on the platform over time. Not surprisingly, as sediment accumulated on the platform with each application, the cover of bare space decreased, with approximately 50% less available space at the greatest level of sediment load compared with areas where no sediment was added ($F_{5,36} = 22.0$, $p < 0.001$; Fig. 3).

Cover of the rock by patches of the mussel *Xenostrobus inconstans* was remarkably consistent over the entire study period and, despite the addition of sediment, even increased marginally from that at the start of the experiment ($F_{5,36} = 2.4$, $p = 0.053$; Fig. 3). There was also no influence of sediment addition on the abundance of the only other dominant sessile species in the mussel habitat, the barnacle *Elminius modestus* ($F_{5,36} = 1.3$, $p = 0.274$; Fig. 3). Nevertheless, there was a trend for decreased barnacle abundance with sediment addition, but abundances were highly variable and the patterns were strongly influenced by densities in quadrats where 125 g of sediment was added (Fig. 3).

The mobile gastropods responded to sediment addition in generally the same manner as observed when examining their patterns of abundance in association with sediment cover (see Fig. 1). There was an influx in the abundance of the grazing gastropods *Nerita atramentosa* and *Bembicium nanum* to all quadrats after the start of the experiment, except those receiving the largest loads of sediment (Fig. 3). After 6 wk, densities of these grazers generally declined with increasing sediment load, but this reduction was most pronounced only at the highest level of sediment addition (*N. atramentosa*: $F_{5,36} = 8.1$, $p < 0.001$; SNK: 0 = 125 = 250 > 1000 = 2000 g sediment added; *B. nanum*: $F_{5,36} = 11.1$, $p < 0.001$; SNK: 0 = 125 = 250 = 500 = 1000 > 2000 g sediment added; Fig. 3). In contrast to *N. atramentosa* and *B. nanum*, the small densities of other gastropods (*Austrocochlea porcata*, *A. constricta*, *Haustrum vinosum* and *Cacozeliana granarium*) were positively influenced by sediment load, with numbers increasing at the 2 highest levels of sediment addition ($F_{5,36} = 3.0$, $p = 0.219$; SNK: cannot be resolved; Fig. 3).

DISCUSSION

The present study has shown that sediment disturbance impacts the abundance of species living on this sheltered rocky reef, and while increasing sedi-

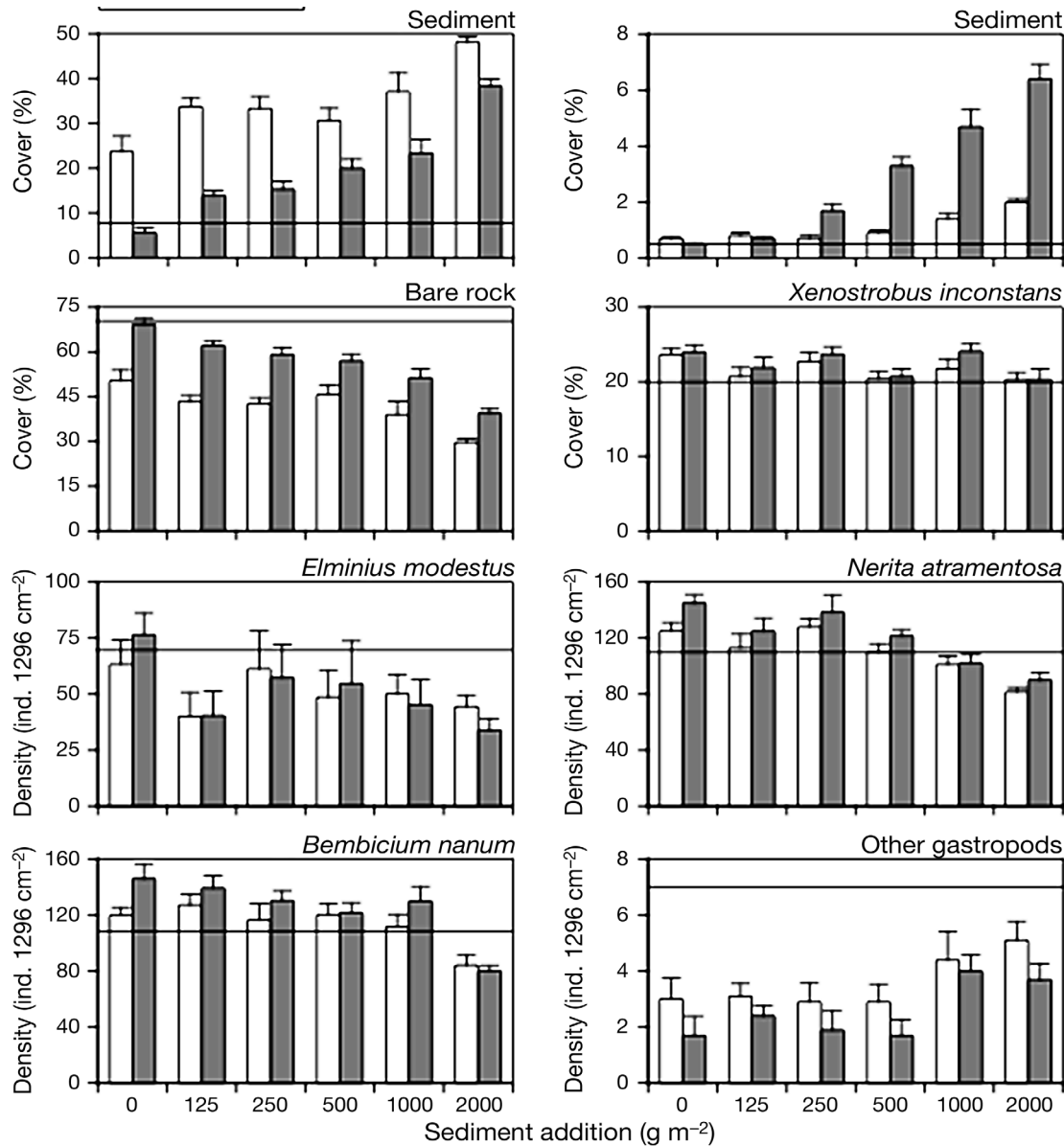


Fig. 3. Mean (± 1 SE) sediment cover, sediment depth, bare rock cover, *Xenostrobus inconstans* cover, and density of *Elminius modestus*, *Nerita atramentosa*, *Bembicium nanum* and other gastropods (*Austrocochlea porcata*, *A. constricta*, *Haustrum vinosum* and *Cacozeliana granarium*) in the mussel habitat after approximately 2 wk (i.e. 2 wk after the first sediment addition) and 6 wk (i.e. 2 wk after the third sediment addition) for various sediment loads (0, 125, 250, 500, 1000 or 2000 g m⁻²). Horizontal line in each graph is the mean value for all 42 quadrats at the beginning of the experiment

ment load negatively influenced most species, some displayed positive responses. Trampling by humans resulted in the redistribution of sediment on the rock platform, but loading of sediment at levels associated with trampling had only minor effects on species' abundances. In contrast, at higher levels of sediment addition there were dramatic effects on the abundance of the majority of species, suggesting potential shifts in species composition on the rock platform from species sensitive to higher sediment environ-

ments to those that tolerate or favour increased sediment loads (Thompson et al. 2002, Airoidi 2003).

Trampling when shallow water covered the rock platform increased sedimentation by up to an order of magnitude beyond natural levels. It was clear that trampling disturbed sediment on the rock platform, suspended it in the water column, and then it was deposited back onto the rock platform (Neil 1990). Sediment load increased outside of trampled areas and sediment cover was reduced and the availability

of bare rock increased within trampled areas, indicating that trampling redistributes (and possibly results in a net loss of) sediment on the reef. Brown & Taylor (1999) also found that trampling by humans on a rock platform in New Zealand reduced the amount of sand on the platform, and this was primarily due to losses of coralline algal turfs with which sand is associated. In our study we also noticed losses of sediment associated with reductions in cover of the macroalga *Hormosira banksii* and the mussel *Xenostrobus inconstans*, species that trap and bind sediment (Povey & Keough 1991, Airoidi 2003).

The effect of trampling on sedimentation is complex because trampling not only resuspends sediment directly but also alters sediment dynamics by removing species that bind sediment. For example, after the first trampling event, sedimentation (i.e. suspension of sediment due to trampling and deposition) on the rock platform in both habitats was directly related to trampling intensity. Loading of sediment onto the rock platform following the second trampling event was, however, less than that following the first trampling event, and the trend for increased sedimentation with trampling intensity had changed, with the most severely trampled areas having reduced loading of sediment compared with areas that had been less intensively trampled. These differences in the relationship between trampling intensity and sediment load occurred because the absolute amount of sediment on the platform that could be resuspended was reduced with increasing trampling and the loss of sediment-binding species. Therefore, the influence of trampling intensity on the redistribution of sediment load across the rock platform is likely non-linear, with sedimentation in the local area increasing with increasing trampling intensity, and then declining when trampling is so intense that unbound sediment and sediment bound within the biotic community are removed from the platform. Heavily trampled platforms would therefore be expected to be largely free of both sediment and species that depend on it, such as epifauna and infauna associated with sediment-bound biological communities (e.g. Brown & Taylor 1999).

Abundances of sessile species, particularly the mussel *Xenostrobus inconstans* and the barnacle *Elminius modestus*, were not influenced by sediment addition. We initially predicted that sessile species would be most affected by sediment addition because they are not able to move away from impacted areas. Indeed, previous studies have shown that burial by sediment on rocky reefs can cause mortality of mussels and barnacles (Seapy & Littler 1982, Branch

et al. 1990), although burial was not common in our study. The amount of sediment added in our study was less than that associated with extreme storm events that bury and kill sessile intertidal invertebrates (Daly & Mathieson 1977, Littler et al. 1983), and this might account for differences here (although the trend for reduced barnacle abundances with sediment addition should be noted). It is possible that, at the highest sediment loads applied in our experiment, sessile species experienced minimal and only transient burial given the dynamic sediment environment on this rocky reef. Indeed, over time, the cover of sediment diminished, but sediment became deeper and accumulated in particular areas on the platform, such as depressions in the rock, or was bound in the byssus of mussels. Consequently, although cover of sediment increased with sediment addition, much of the rock platform was free of substantial amounts of sediment or was merely covered by a thin sediment layer, even at the highest levels of sediment addition. We would nevertheless predict that the barnacle *E. modestus*, which was killed by burial in some places at highest sediment loads, would be more greatly affected by increased sedimentation than the mussel *X. inconstans*. This mussel not only inhabits rocky intertidal shores, but also lives in sheltered sedimentary habitats (Buschbaum et al. 2009), such as salt marshes, where it is fed upon by *Haustrum vinosum* (Morton 2004). Moreover, *X. inconstans* binds sediment and lives within or at the surface of the sediment–mussel matrix, providing habitat for infauna such as polychaete worms (Buschbaum et al. 2009, authors' pers. obs.), and thus may come to dominate the rock platform should increased sediment loading shift the rocky shore to a soft-sediment habitat.

Changes to the load of sediment and availability of bare rock on the platform strongly contributed to changes in the abundance of gastropods. In both mensurative and experimental studies, the grazing gastropods *Nerita atramentosa* and *Bembicium nanum* were negatively influenced by increasing sediment load (Daly & Mathieson 1977, Seapy & Littler 1982, Littler et al. 1983). Both of these species graze on microalgae that are typically refreshed on the rock substratum with each successive tide (Underwood 1975, 1984), and individuals were thus likely to reduce feeding activity or move out of areas that received sediment and reduced food resources (Airoidi & Hawkins 2007, Huff & Jarett 2007, Atalah & Crowe 2010). Similarly, Airoidi & Hawkins (2007) experimentally manipulated sediment load in the laboratory and found that 1 mm thick layers of sedi-

ment equivalent to 500 g m^{-2} were sufficient to substantially reduce the grazing activity of the limpet *Patella vulgata*. Effects on *N. atramentosa* and *B. nanum* in our study were most pronounced at the highest levels of sediment addition, indicating that smaller magnitudes of sediment deposition and thin layers of sediment on the rock, such as those recorded due to trampling here, are likely tolerated by these species. Indeed, *N. atramentosa* appeared to bulldoze the thin layers of sediment (Bertness 1984). Importantly, sediment mostly comprised sand, although precise grain size structure was not determined, and fine fractions have been found to have greater impacts on grazers than coarse sediments (Airoldi & Hawkins 2007). Higher sediment loads change the physical characteristics of the substratum and create microhabitats well known to influence the movement of such gastropods.

Some gastropods displayed positive associations and responses to increasing cover and addition of sediment on the rock platform, including the grazers *Austrocochlea porcata* and *A. constricta*, the predator *Haustrum vinosum*, and *Cacozeliana granarium* (Huff & Jarett 2007). These associations were confirmed by experimental addition of sediment, particularly for *H. vinosum* and *C. granarium*, but numbers were small. Some of these rocky-shore gastropods, such as *H. vinosum*, also inhabit soft-sediment habitats with hard substrata, such as mangrove forests and salt marshes, where they prey on barnacles and the mussel *Xenostrobus inconstans*, respectively (e.g. Bayliss 1982, Morton 2004), and thus may be able to cope or respond opportunistically to the presence of sediment and perhaps the paucity of other gastropods. Our results therefore suggest that on this sheltered rock platform increased sediment loads may lead to changes in the composition of gastropods and other species, favouring those that tolerate or are facilitated by sediment (Daly & Mathieson 1977, Brown & Taylor 1999, Thompson et al. 2002, Huff & Jarett 2007). More generally, species that are flexible in their use of habitat (e.g. mussels such as *X. inconstans* and the predator *H. vinosum*) are more likely to be represented across habitats that are exposed to environmental change, such as rocky coasts subjected to increased sedimentation or variable sediment regimes.

A key element of the present study was that we applied the trampling disturbance when shallow water covered the rock platform. The vast majority of studies examining the impacts of trampling by humans on reefs have been performed on emergent rock at low tide when there is no water covering the

platform; however, it is common for people to walk, fish and swim on the rock platform when it is covered by water, particularly in sheltered areas where sediment loads might be expected to be greatest (e.g. Thompson et al. 2002, Addison et al. 2008). Neil (1990), for example, showed that sediment resuspension and deposition is an important component of the overall impact of trampling on coral reefs, with people trampling in 30 cm of water substantially increasing sedimentation on the reef. Our findings across 2 different habitat types confirm the influence of trampling on sediment dynamics, but reveal that, at least for levels of trampling used in this study, sediment deposition associated with trampling has only small impacts on the benthic species assemblage in the mussel habitat (and less than those of the direct impacts of trampling). Nevertheless, we have demonstrated that trampling has the potential to impact rocky-reef species at higher sediment loads, and trampling could create such impacts if sediment load was in naturally greater abundances on the rock platform, trampling intensities were increased or trampling occurred under different conditions (water depth, wave exposure, etc.). Therefore, the importance of tidal state, which produced these indirect effects on the species assemblage through changes in sediment load, needs to be incorporated into the suite of human visitation and trampling impacts, particularly across rocky shores of varying wave exposure (sheltered versus exposed platforms have different sediment dynamics) and habitats with varying sediment environments (e.g. rocky reefs, coral reefs and mangrove forests). For example, the loss of species that trap and bind sediment might be particularly important to maintaining species composition on the rock platform.

The present study shows the dramatic effects that sediment disturbance can have on species assemblages living on rocky shores. Patterns of sedimentation in response to trampling were generally similar across both the macroalgal and mussel habitats, suggesting that such disturbances might be generally important across a range of habitats (Neil 1990). Although experiments were only performed at one site in the mussel habitat, thus limiting our ability to generalize the results to other locations, results of experimental manipulations were consistent with patterns of species abundance in the habitat in relation to sediment cover, providing support for the impacts of sedimentation on species assemblages.

The cumulative effect of small-scale disturbances such as trampling may have impacts similar to those of larger-scale disturbances due to sediment run-off

from the terrestrial environment or storm events. The persistence of the current species assemblage in our study is likely due to the dynamic nature of sedimentation across the shore and features of the platform—such as depressions in the rock and the presence of species that retain sediment—that influence sediment accumulation. With increasing sediment loading of coastal waterways from urban and agricultural development, however, species assemblages on rocky reefs may shift to be dominated by species that can resist or thrive in multiple habitats, particularly those with fluctuating sediment regimes (e.g. Taylor & Littler 1982, Branch et al. 1990, Irving & Connell 2002). To predict the influence on sedimentation on coastal habitats, ecologists will need to quantify the magnitude and characteristics of sediment loaded into coastal communities in space and time so that mensurative and manipulative experiments can be carried out to assess impacts on and understand mechanisms driving changes in species assemblages (Airoidi 2003).

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