

# Survival of sand-burial by seaweeds with crustose bases or life-history stages structures the biotic community on an intertidal rocky shore

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## Abstract

Responses of a rocky intertidal community to seasonal sand-inundation were investigated on the cool-temperate west coast of South Africa by experimentally testing the hypothesis that the crustose components in certain macroalgae survive burial, enabling them to dominate the community when the shore is sand-free. Twelve 0.25×0.25 m plots served as controls in the mid-eulittoral and 12 in the upper eulittoral zone. Treatment 1 (T1) comprised a further 12 plots in each zone that were cleared of all biota (scraping, wire-brushing and burning) soon after the sand moved off in year 2. Treatment 2 (T2) comprised clearing a further 12 plots in each zone at the end of Year 2, just before sand returned, in case T1 had inadvertently removed early-settling microscopic stages. Mid-eulittoral zone controls developed similar communities each year dominated by *Mazzaella capensis*, *Gymnogongrus complicatus*, barnacles, mussels and small limpets, with smaller covers of several other macroalgae. Both treatments significantly reduced *M. capensis*, *G. complicatus* and *G. glomeratus*, but did not affect covers of other species. These three species persisted as crustose holdfasts, and the latter two also as crustose tetrasporophytes; the crusts probably comprise coalescent sporelings. All other species recruited annually as the sand moved off. In the upper eulittoral zone, T2 had no effect on the biota that developed, indicating that none of the species (including the dominants *Porphyra capensis* and *Chthamalus dentatus*) relied on persistent elements to survive burial. These results confirm that sand-disturbed communities comprise a mixture of opportunistic and disturbance-tolerant species, but experimentally show the importance of crustose elements for survival of these red algae.

**Keywords:** crusts; disturbance; *Gymnogongrus*; *Mazzaella*; sand-burial.

## Introduction

Sand affects significant proportions of the intertidal zones of most shores around the world. For example, about 31% of South Africa's 3000 km coastline comprises "mixed sand and rock" (Bally et al. 1984) and this percentage is probably similar on many coasts. Parts of most rocky coasts are subject to sand inundation (see review by Airoldi 2003), leading Airoldi (op. cit.) to question "the traditional separation between rocky and sandy shores" in many studies. The present study examined the effects of seasonal sand-burial on the biota of a South African intertidal shore in order to test which species survive burial and which species colonize the rock annually.

Sand-inundation of a rocky shore is effectively a disturbance: a change in the physical environment changes the process of succession by removing organisms, resulting in a different community (see Pickett and White 1985). Sand-induced disturbance has been examined with regard to effects on single species (e.g., D'Antonio 1986, Marshall and McQuaid 1989, Pineda and Escofet 1989), effects on total species diversity on the shore (Bally et al. 1984, McQuaid and Dower 1990, Brown et al. 1991) and effects on the abundance and composition of communities (e.g., Daly and Mathieson 1977, Littler et al. 1983). In a recent review, Airoldi (2003) pointed out that the effects of sedimentation on marine organisms may be extremely complex, and that the degrees of sediment effect may vary from slight to extreme, with very different outcomes for species assemblages.

Most of these studies have shown that sand-inundation (usually seasonal) prevents particular organisms from dominating, and leads to the development of a specialized community that often comprises a mixture of species physiologically adapted to tolerate sand and those that would dominate in the absence of sand-inundation (Taylor and Littler 1982, Littler et al. 1983, D'Antonio 1986).

A number of autecological studies of sand-affected communities on the Pacific coast of North America led to the recognition of "psammophytic" or sand-tolerant seaweeds (e.g., Mathieson 1967, Markham and Newroth 1972, Markham 1973, Daly and Mathieson 1977). Lobban and Harrison (1994) summarize the characteristics of psammophytic seaweeds, which include good regenerative ability and physiological adaptations to survive low light (or darkness), anaerobic conditions, nutrient deprivation, and sometimes H<sub>2</sub>S. In a review of the effects of sedimentation on rocky shore organisms, Airoldi (2003) listed similar qualities that are common to many sand-tolerant marine species.

Almost all of the autecological studies of sand effects are concerned with seasonal distribution and growth of organisms, and are essentially descriptive. Exceptions

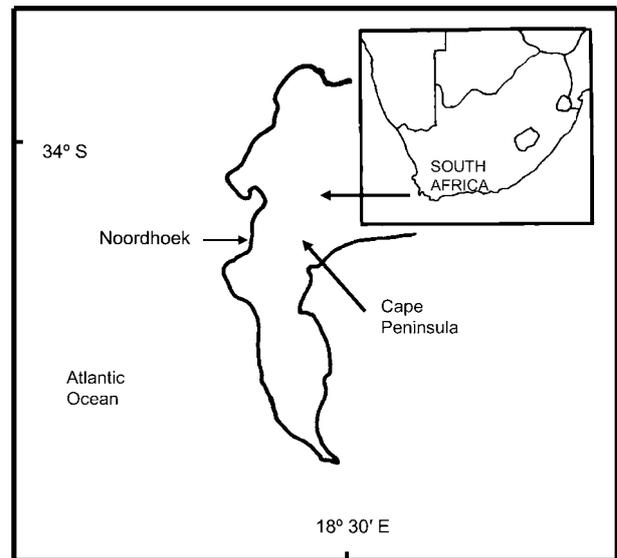
include the studies of Taylor and Littler (1982) and D'Antonio (1986). The former study used experimental removals to demonstrate the strong structuring effect of the sand-tolerant anemone *Anthopleura elegantissima* in a sandy intertidal community. D'Antonio (1986) used laboratory tests and descriptive shore studies to demonstrate that the red alga *Neorhodomela larix* (Turner) Masuda [as *Rhodomela larix* (Turner) C. Agardh] dominates sand-inundated shores on the northwestern coast of the USA because it survives sand-burial for much longer periods than its competitors.

On the South African west coast, certain seaweeds are characteristic of, but not always restricted to, sand-affected shores. These include *Gymnogongrus complicatus* (Kützing) Papenfuss, *G. glomeratus* J. Agardh, and *Mazzaella capensis* (J. Agardh) Fredericq in the mid-eulittoral zone, and *Grateloupia longifolia* Kylin in the lower eulittoral zone [Stegenga et al. 1997, cited as *Ahnfeltiopsis complicata* (Kuetzing) Silva et De Cew], *A. glomerata* (J. Agardh) Silva et De Cew and *Grateloupia doryphora* (Montagne) Howe. Recent studies (e.g., Santelices et al. 2003) have shown the importance of coalescence among sporelings of certain red algae in creating "genetically polymorphic" organisms with improved survival abilities. Notably, *Mazzaella* and *Gymnogongrus* are among the genera with coalescing sporelings. Besides typically psammophytic species, a number of other seaweed species may occur on sand-affected west coast shores of South Africa, together with various animals such as barnacles and limpets. However, the processes controlling the development of these communities have not been investigated.

The present study of a South African west coast shore that is subject to complete seasonal burial by sand aimed to determine which species survived burial and which species colonized annually. Specifically, we experimentally tested the hypothesis that on a seasonally sand-inundated shore, the crustose component in the life-history of certain seaweeds gives them an ability to survive burial and thus an advantage (over the other algae) that allows them to dominate the community.

## Materials and methods

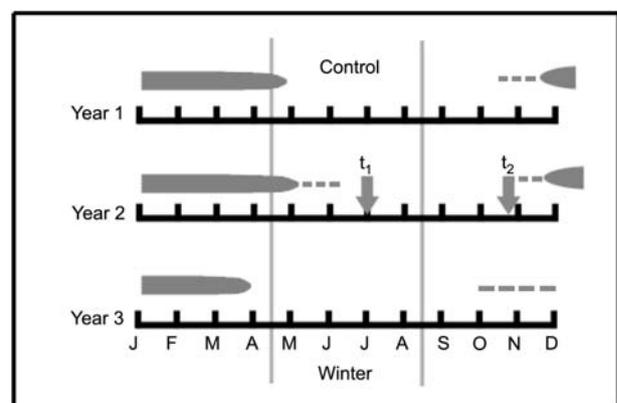
The study site was at Noordhoek on the west coast of the Cape Peninsula, about 30 km south of Cape Town, South Africa (Figure 1). Biogeographically, this area falls within the cool temperate west coast designation of Bolton (1986) and Bolton and Anderson (1997), with an average sea temperature of about 13°C, a minimum of about 9°C during summer upwelling, and a maximum of about 17°C, usually in autumn or winter. The substratum is granite that slopes gently (between 10 and 20°) to face west. The site is open to, and very exposed to the prevailing SW swell. During winter, large SW swells remove sand offshore (usually within one week) and expose the rocks, while during mid-summer the smaller swells result in onshore movement of sand (usually 3–4 weeks) that buries the rocks of the study site to depths of 0.3–1.0 m (see Figure 2 and Results section). The shore was checked during each spring-tide period and the presence



**Figure 1** Location of study site at Noordhoek, west coast of the Cape Peninsula, South Africa.

or absence of sand noted. Once the shore was buried, the depth of the sand was determined by driving a rod vertically down to rock at 3–4 places over the study site (this position was established by reference to two marking bolts on nearby unburied rocks). The effect of the sand is therefore extreme: essentially, the rock is either completely buried, or free of sand, except for the period of 3–4 weeks as sand moves back.

The study was started in June 1988 (Year 1), after the site had been covered with sand for at least 5 months (the sequence of sand-burial events and treatments is shown in Figure 2). Within 2 weeks of the removal of the sand by a large swell, 24 permanent plots (each 0.25×0.25 m) were marked at each corner by drilling into the granite and inserting plastic plugs and stainless-steel screws bearing numbered, plastic cable ties. Twelve plots were placed in the upper eulittoral zone (between 1.2 and 1.5 m above MLWS) and 12 in the mid-eulittoral zone (between 0.6 and 1.0 m above MLWS). In each of



**Figure 2** Sequence of sand immersion (burial) and emersion of rocky shore and of treatments at study site. Horizontal gray bars show periods of sand burial and vertical arrows show timing of T1 and T2 treatments (clearing of substratum).

these zones, the plots were placed haphazardly (scattered within the zone, but positioned to avoid irregular features such as fissures or cracks in the rock). Wave-splash prevented work (drilling and treatments) in the lower eulittoral zone.

The biota that developed in the plots was then recorded approximately monthly during spring low tides, until the sand re-buried the plots in December 1988. Sampling was done non-destructively by estimating percentage cover of all biota except limpets, which were counted. Percentage cover estimates were aided by marking the sides of the 0.25×0.25 m quadrat to indicate the areas occupied by the classes 1, 5, 10, 25 and 50% cover. The data for Year 1 are not presented here, and these plots became the controls for the rest of the study when we decided to carry out clearing (removal) experiments.

In 1989 (Year 2) the sand moved off the site in late June. A second set of 24 plots (among the control plots that were set up in Year 1) was marked out for treatment (clearing the rock of all biota). Again, 12 plots were in the upper eulittoral and 12 in the mid-eulittoral. The clearing treatment (carried out early in July and denoted as T1 in Figure 2) consisted of wire brushing to remove the organic material that had survived sand burial (mainly byssus threads and some algal crusts and remnants of upright shoots) from within each plot and a few centimetres around the edge, then painting carefully with 95% alcohol, and burning with a gas blow-torch. Inspection through a 10× magnification hand-lens showed no signs of any biota. The biota that developed in Year 2 in the control and experimental plots was sampled approximately monthly from mid-winter through to mid-summer during spring low tides, until sand re-covered the site in December. The data from T1 are not presented for the mid-eulittoral zone, because the results were essentially the same as for T2 in this zone.

Just before the site was re-covered by sand in December of Year 2, a second treatment (T2 in Figure 2) was executed in order to test the possibility that the first treatment may have destroyed propagules that arrived immediately after the sand had moved off (in other words to test whether the first few weeks of exposure of the substratum may be crucial for colonization by plants and animals). The second treatment involved clearing a new set of 24 plots (12 upper eulittoral, 12 mid-eulittoral) in November 1989, when the sand was beginning to move back to cover the rocks. Clearing was again done by scraping, wire-brushing, painting with 95% alcohol and burning. The control and T1 plots were not treated in any way in November of Year 2. Within 2 weeks of completing the treatment, the plots were re-buried by sand (by the end of December of Year 2).

When the site was uncovered as the sand moved off in April 1990 (Year 3), inspection with a hand-lens showed no signs of biota in the T2 plots, indicating that the treatment had been effective. The biota that subsequently developed in these plots, as well as in those that had been cleared at the beginning of the previous growing season (T1) and in the control plots was then recorded (as % cover or density, as described above) at four- or six-week intervals during spring low tides until December 1990, when returning sand prevented further

sampling. Since then the site has been examined every few months for almost 15 years, but no further quantitative data were collected.

Results for the mid-eulittoral are presented for Year 3 only because the pattern of recovery was the same in the controls in all 3 years, and the effects of T1 in Year 2 were essentially the same as those of T2 in Year 3. Complete results (percentage cover or density of all species) are presented only for the mid-eulittoral zone because here both control and treated plots developed a fairly uniform cover of species typical of this shore. For the upper eulittoral, only the data for the two dominant species [*Porphyra capensis* Kützting and the limpet *Scutellastra granularis* (Linnaeus)] are presented: other species were too rare or occasional to contribute to the analysis. However, results for the upper eulittoral are shown for both Year 2 and Year 3, because there were important differences that resulted from the different timing of treatments.

For each sampling, comparisons between controls, T1, and T2 for each species were made using a non-parametric Kruskal-Wallis ANOVA by ranks, followed by 2-tailed multiple comparisons in cases where significant differences ( $p \leq 0.05$ ) were indicated (Zar 1984). We did not test for significant differences between sampling times (between sampling periods) because we knew that populations would build up from zero once the sand moved off: we were interested in differences between treatments. In the upper eulittoral zone, data from 1989 as well as 1990 are presented for *Porphyra* and limpets. In 1989 (Year 2) only control and T1 plots existed, so statistical comparisons were made by Mann-Whitney U-test (Zar 1984). All statistics were calculated using Statistica 6 software.

The algal crusts and crustose holdfasts (*Gymnogongrus complicatus*, *G. glomeratus* and *Mazzaella capensis*) were identified by removing small slices with a razor, sectioning them, and examining them under a microscope. When crusts of the former two species could not be distinguished from one another, their positions were noted and they were identified when upright shoots appeared: these were visible within a few weeks of sand emersion when microscopic examination was no longer necessary. Because tetrasporophytic *Gymnogongrus* crusts could not be identified to species, but almost always grew near to recognizable gametophytes of either *G. complicatus* or *G. glomeratus*, they were assumed to represent whichever of these two species they were nearest to. Furthermore, because these tetrasporophytic crusts were rare (contributing <1% cover at most), any error in this assumption is considered unlikely to affect the results significantly.

## Results

### Sand-burial cycles

This shore is subject to a similar seasonal cycle of sand-immersion and emersion each year (Figure 2). The granite rocks up to and including the upper eulittoral were buried progressively over a period of a few weeks in early-mid summer (November–December) of Year 1. The final

depth of sand varied from 0.3 m to more than 1.0 m in places. The rocks remained buried until autumn/early winter of the following year (May), when the first prolonged, large swells of the season removed the sand offshore within a period of a few days leaving them exposed. Observations since 1988 show that the above cycle is typical, but the timing of immersion and emersion may vary by up to a month, depending on weather and swells. However, during some anomalous years burial may be incomplete. For example, in 1990/91 and 2001/02, large summer swells exposed the shore regularly and burial was limited to periods of a few weeks at a time. However, this is fairly unusual and will not be dealt with further.

In Year 1 of this study (1988), the sand had moved off by May, and began being re-deposited at the end of October (Figure 2). By the beginning of December, the study site was completely buried. In Year 2 (1989), the site was only completely free of sand after mid-June, then buried again by mid-December. In Year 3 (1990) the site was free of sand by mid-April, but then was not completely buried at the end of that year.

### Biotic communities

In all quadrats, the abundance (as percentage cover or density) of organisms increased steadily once the sand had moved off, until sand began returning in December, when abundances of most organisms began decreasing. Two distinct groups of organisms became apparent; those that were affected by substratum-clearing treatments of T2 (*Gymnogongrus glomeratus*, *G. complicatus*, *Mazzaella capensis*) and those that were not.

### Mid-eulittoral zone

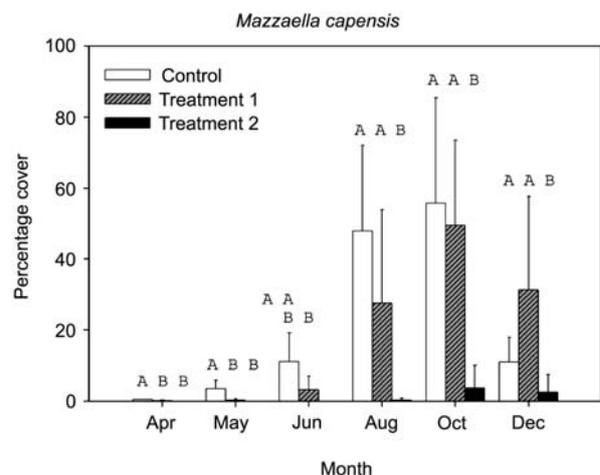
In control plots, after the sand moved off, the only macroscopic signs of organisms in the mid-eulittoral were occasional byssus threads, dead barnacles, and scattered, small (up to 10 mm diameter) spots of red, firm, fleshy crusts. Sections of these crusts revealed that they were either basal (holdfast) crusts of *Mazzaella capensis* or *Gymnogongrus*, or, rarely, fertile (tetrasporophytic) *Gymnogongrus* crusts (as described by Anderson and Bolton 1990). Most crusts were smooth, but a few bore bleached stumps of upright *Gymnogongrus* thalli. The holdfast crusts of both *Mazzaella* and *Gymnogongrus* rapidly produced upright shoots, which reached up to 5 mm within 3 weeks of sand emersion. All the *Gymnogongrus* material was either *G. complicatus* or *G. glomeratus*.

Subsequently (observed each year), the mid-eulittoral community in control plots developed over the winter until it was dominated by *Mazzaella capensis*, *Gymnogongrus complicatus*, mussels [*Mytilus galloprovincialis* (Lamarck)], and small limpets (*Scutellastra granularis*) that were often hidden among the mussels. Usually, the other common but less abundant algae were *Gymnogongrus glomeratus*, *Porphyra capensis*, *Ceramium arenarium* Simons, *Cladophora capensis* (C. Agardh) De Toni, *Aristolamnia collabens* (Rudolphi) Papenfuss and *Centroceras clavulatum* (C. Agardh) Montagne in Durieu de Maisonneuve.

Treatments (T1 and T2) caused a significant reduction in the cover of only three species: *Mazzaella capensis*, *Gymnogongrus complicatus*, and *G. glomeratus*. *Mazzaella capensis* was present in control and T1 plots as soon as the sand moved off, although upright shoots took about 2 weeks to become visible (Figure 3). In the control plots, *M. capensis* then increased its cover steadily up to October. Cover was significantly lower in T1 plots than in controls in May [H (2, n=36)=27.31,  $p<0.001$ ] and June [H (2, n=36)=28.87, d.f.=35,  $p<0.001$ ], but thereafter similar to that in control plots. *M. capensis* was absent from T2 plots until August, and cover reached a maximum of only 4% (in October) compared to 50% and over in T1 and controls. Cover in all plots decreased in December, as sand began returning to the shore.

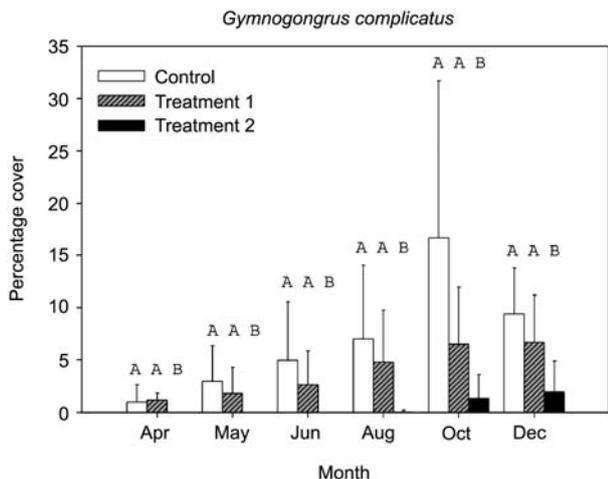
*Gymnogongrus complicatus* (Figure 4) was present as crustose holdfasts and crustose tetrasporophytes and upright shoots were produced from the former in control and T1 plots within 4 weeks when the sand moved off. Cover increased steadily until October, after which it stabilized in T1 plots and decreased in the control plots, and some of the upright shoots died off. However, percentage cover of this species remained statistically similar in controls and T1 plots throughout. In contrast, in T2 plots, *G. complicatus* did not appear until August, and increased to a mean maximum cover of only 2.3% (in December), a significantly lower cover than in controls and T1 [H (2, n=36)=16.01,  $p<0.01$ ].

*Gymnogongrus glomeratus* was found at a very low percentage cover in control and T1 plots when the sand moved off (Figure 5). Upright shoots appeared rapidly, and *G. glomeratus* plants were clearly recognizable within a month of sand emersion. Percentage cover in the control and T1 plots increased steadily until October, then decreased in the controls (as upright shoots died off) and stabilized in T1. Meanwhile in T2, *G. glomeratus* only appeared in August (it was identified in only 2 of the 12 plots), and by December had reached only 0.7%

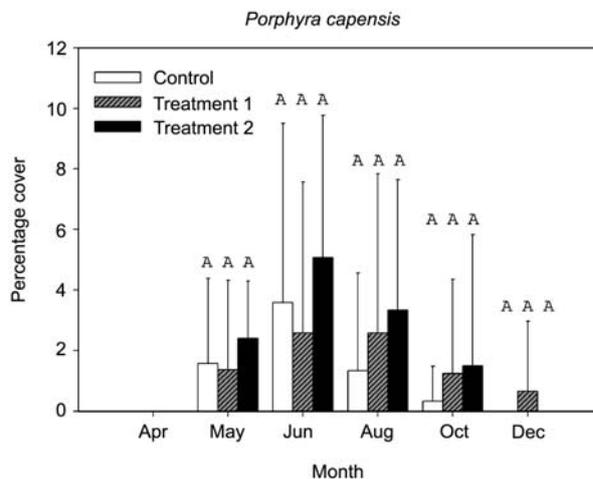


**Figure 3** Mean percentage cover of *Mazzaella capensis* in Year 3 in control, T1 and T2 plots.

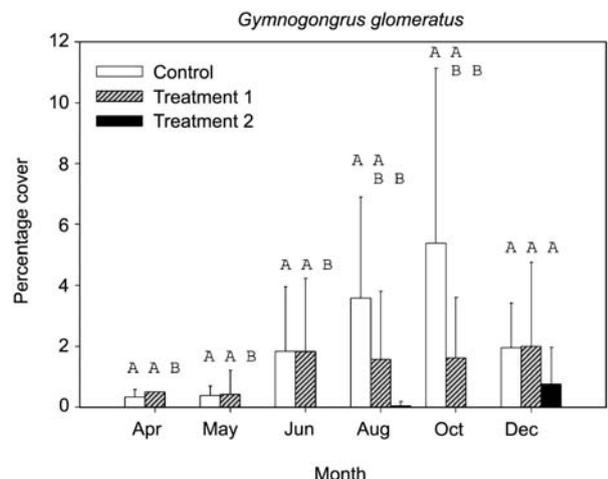
Vertical bars show means+SD and letters above bars show significant differences ( $p<0.05$ ) as determined by 2-tailed multiple comparisons in cases where significant differences ( $p\leq 0.05$ ) were found by non-parametric Kruskal-Wallis ANOVA by ranks.



**Figure 4** Mean percentage cover of *Gymnogongrus complicatus* in Year 3 in control, T1 and T2 plots. Vertical bars show means+SD and letters above bars show significant differences ( $p \leq 0.05$ ) as determined by 2-tailed multiple comparisons in cases where significant differences ( $p \leq 0.05$ ) were found by non-parametric Kruskal-Wallis ANOVA by ranks.



**Figure 6** Mean percentage cover of *Porphyra capensis* in Year 3 in control, T1 and T2 plots. Vertical bars show means+SD and letters above bars show significant differences ( $p < 0.05$ ) as determined by 2-tailed multiple comparisons in cases where significant differences ( $p = 0.05$ ) were found by non-parametric Kruskal-Wallis ANOVA by ranks.



**Figure 5** Mean percentage cover of *Gymnogongrus glomeratus* in Year 3 in control, T1 and T2 plots. Vertical bars show means+SD and letters above bars show significant differences ( $p < 0.05$ ) as determined by 2-tailed multiple comparisons in cases where significant differences ( $p = 0.05$ ) were found by non-parametric Kruskal-Wallis ANOVA by ranks.

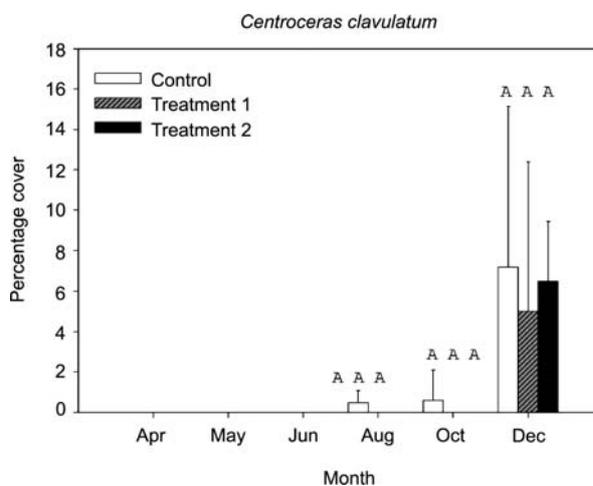
cover, compared to means of about 2% in control and T1 plots. The remaining species in the mid-eulittoral zone were unaffected by the treatments.

*Porphyra capensis* was not visible in any plots in April, but thalli appeared in all plots in May (Figure 6). Cover was uniformly low (averaging 2–3%) and patchy, with high variances as a result of the number of quadrats with zero cover of this species. Percentage cover rose to a maximum in June–August, then decreased through to December. There were no statistical differences between mean percentage cover values in controls, T1 and T2 plots within any of the months. Because we did not find a significant effect, we think it unlikely that one exists. If a difference were detected using a more powerful analysis, the means would indicate a slightly higher cover of *Porphyra* in T2 plots, i.e., a positive effect of T2.

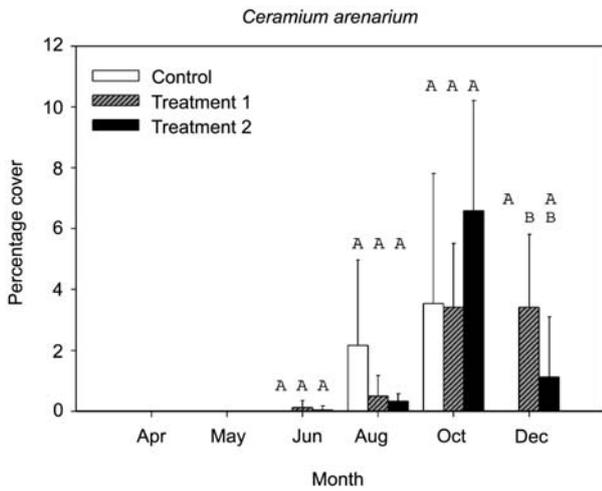
Scattered clumps of *Centroceras clavulatum* (Figure 7) appeared in some of the control plots in August, and remained present in October. By December, thalli of this species were scattered sparsely but more uniformly throughout the mid-eulittoral and in all treatments, covering about 5–6% of the substratum (no statistical differences between treatments).

*Ceramium arenarium* (Figure 8) first appeared in June, and by October had reached statistically similar cover values of about 4–6% in controls and both treatments. As sand began returning in December, *C. arenarium* disappeared from control plots and almost disappeared from T2 plots.

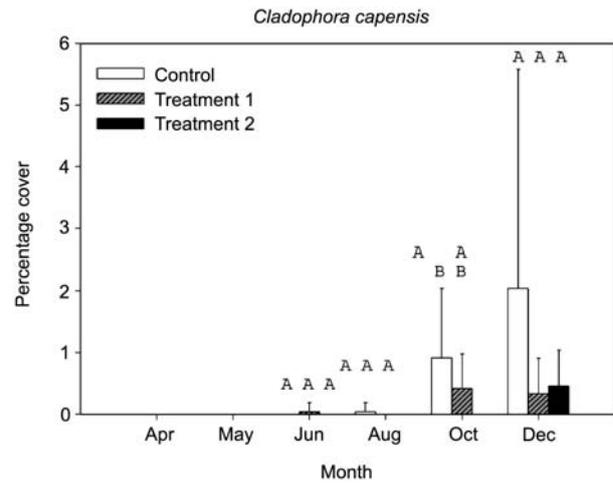
*Aristothamnion collabens* (Figure 9) and *Cladophora capensis* (Figure 10) appeared only in June, as sparse, scattered individuals contributing only a very low per-



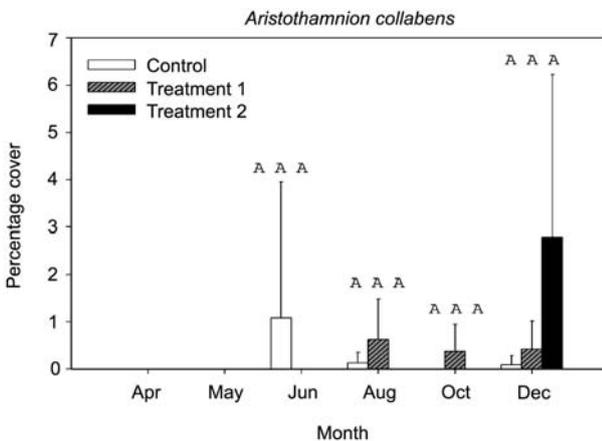
**Figure 7** Mean percentage cover of *Centroceras clavulatum* in Year 3 in control, T1 and T2 plots. Vertical bars show means+SD and letters above bars show significant differences ( $p < 0.05$ ) as determined by 2-tailed multiple comparisons in cases where significant differences ( $p = 0.05$ ) were found by non-parametric Kruskal-Wallis ANOVA by ranks.



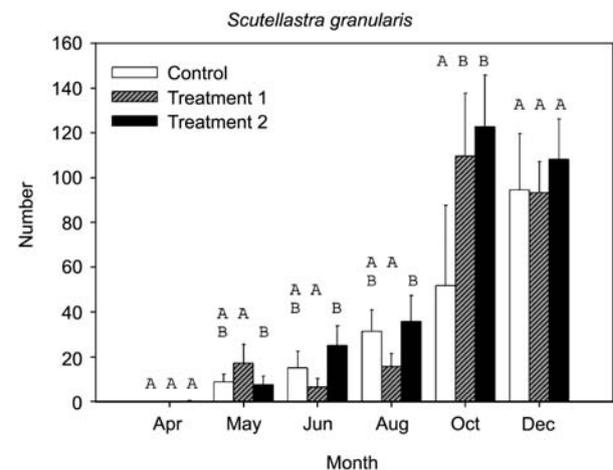
**Figure 8** Mean percentage cover of *Ceramium arenarium* in Year 3 in control, T1 and T2 plots. Vertical bars show means+SD and letters above bars show significant differences ( $p < 0.05$ ) as determined by 2-tailed multiple comparisons in cases where significant differences ( $p = 0.05$ ) were found by non-parametric Kruskal-Wallis ANOVA by ranks.



**Figure 10** Mean percentage cover of *Cladophora capensis* in Year 3 in control, T1 and T2 plots. Vertical bars show means+SD and letters above bars show significant differences ( $p < 0.05$ ) as determined by 2-tailed multiple comparisons in cases where significant differences ( $p = 0.05$ ) were found by non-parametric Kruskal-Wallis ANOVA by ranks.



**Figure 9** Mean percentage cover of *Aristothamnion collabens* in Year 3 in control, T1 and T2 plots. Vertical bars show means+SD and letters above bars show significant differences ( $p < 0.05$ ) as determined by 2-tailed multiple comparisons in cases where significant differences ( $p = 0.05$ ) were found by non-parametric Kruskal-Wallis ANOVA by ranks.



**Figure 11** Mean number per  $0.25 \times 0.25$  m quadrat of limpets (*Scutellastra granularis*) in Year 3 in control, T1 and T2 plots. Vertical bars show means+SD and letters above bars show significant differences ( $p < 0.05$ ) as determined by 2-tailed multiple comparisons in cases where significant differences ( $p = 0.05$ ) were found by non-parametric Kruskal-Wallis ANOVA by ranks.

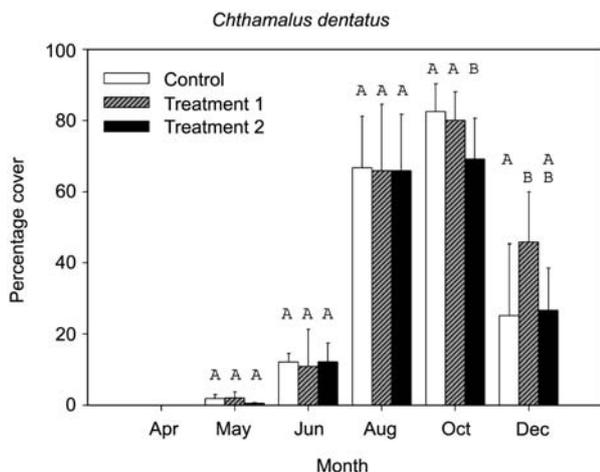
centage cover to the algal canopy. As a result, variances in cover were high, and in neither species could statistical differences be detected between treatments.

A few scattered juvenile individuals of the limpet *Scutellastra granularis* were present in April in T1 and T2, and densities subsequently rose steadily in all plots (Figure 11) until in October and December there were more than 90 individuals per  $25 \times 25$  cm quadrat: the equivalent of more than  $1440 \text{ m}^{-2}$ . The limpets were almost all small; even in December, few had reached 10 mm in length, and most were about 5–6 mm long. Between May and August there were statistical differences in limpet densities between the various treatments, but no consistent pattern emerged, and by December densities were statistically similar in all treatments.

Some dead barnacles (*Chthamalus dentatus* Krauss) were present in control and T1 plots as soon as the sub-

stratum was visible in April. However, these were shells of barnacles that had been present when sand buried the shore the previous December (1989), and there were no live barnacles present in the plots in April 1990. Small, live barnacles appeared in May and were very uniformly distributed all over the mid-eulittoral zone and in all treatments (Figure 12). The percentage cover of live barnacles increased rapidly up until August (a few to more than 60% cover), with no statistical differences between treatments. Statistical differences emerged in October and December, as barnacles began dying in increasing numbers, but there was no apparent pattern in these differences.

Occasional, scattered clumps of juvenile (1–2 mm long) mussels (*Mytilus galloprovincialis*) appeared first in



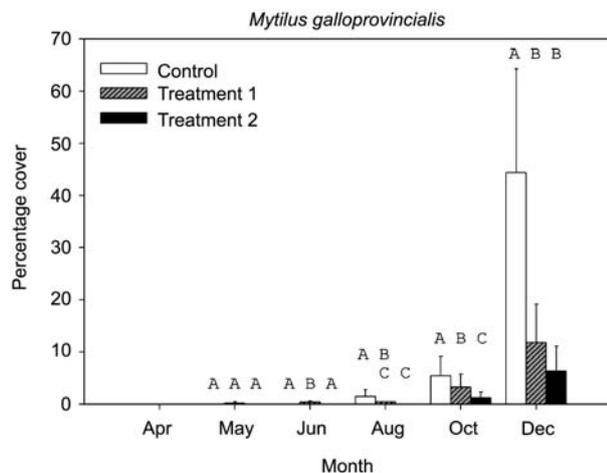
**Figure 12** Mean percentage cover of barnacles (*Chthamalus dentatus*) in Year 3 in control, T1 and T2 plots.

Vertical bars show means+SD and letters above bars show significant differences ( $p < 0.05$ ) as determined by 2-tailed multiple comparisons in cases where significant differences ( $p = 0.05$ ) were found by non-parametric Kruskal-Wallis ANOVA by ranks.

T1 in May, in the control in August, and in T2 in October, by which time there were small but statistically significant differences between the % cover values in the control and treatment plots, although all were low, with <7% cover (Figure 13). By December, mean cover of mussels in control plots was more than 45%, but only 12 and 7%, respectively, in T1 and T2.

### Upper eu littoral zone

By October 1989 (Year 2) the upper eu littoral zone in the control plots (and other untreated areas of shore in this zone) was dominated by *Porphyra capensis* which had appeared after July (Figure 14). *Porphyra* cover in control plots from October to December remained between 50 and 70%. By contrast, in the plots that were cleared in



**Figure 13** Mean percentage cover of mussels (*Mytilus galloprovincialis*) in Year 3 in control, T1 and T2 plots.

Vertical bars show means+SD and letters above bars show significant differences ( $p < 0.05$ ) as determined by 2-tailed multiple comparisons in cases where significant differences ( $p = 0.05$ ) were found by non-parametric Kruskal-Wallis ANOVA by ranks.

July of the same year (T1), *Porphyra* reached significantly lower maximum levels of only 3–6% cover.

In Year 3, when the clearing treatment was carried out before the sand moved back at the end of 1989, the timing of appearance and the cover of *Porphyra* were similar in treatments and controls. *Porphyra* was absent in April, but started appearing patchily in all plots by May and reached 40–50% cover in June–August (no statistical differences between treatments). Cover levels had started declining by October, and by December there were only a few *P. capensis* plants left in some of the control plots.

Besides *Porphyra*, the only organisms present in the upper eu littoral zone in any numbers were limpets (*Scutellastra granularis*). As in the mid-eu littoral zone, most limpets in the upper eu littoral zone were very small when they first appeared, and few individuals grew larger than about 10 mm during any season. In October 1989 (Y2), limpets were present in similar but low numbers in both controls and T1 quadrats (Figure 15). By December, limpets were significantly more abundant in the controls (200 limpets per quadrat) than in T1 (22 per quadrat), which had been cleared in July of that year. In Year 3 (1990), limpet densities rose gradually to between 50 and 100 individuals per quadrat (October and December), but there were no significant differences between controls and treatments.

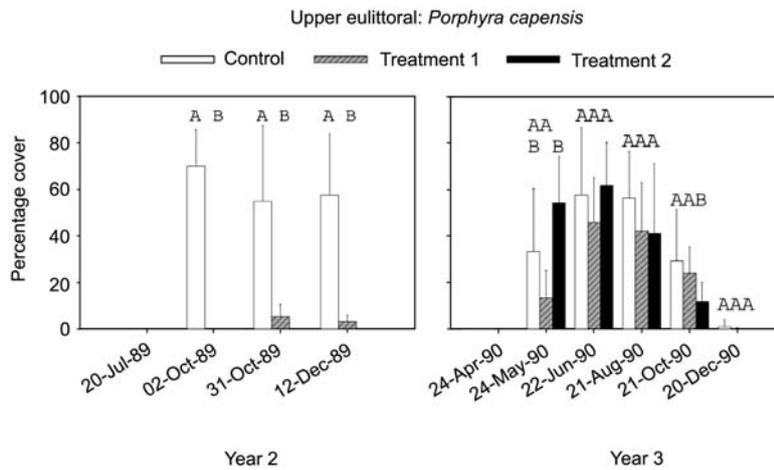
## Discussion

### Mid-eu littoral zone

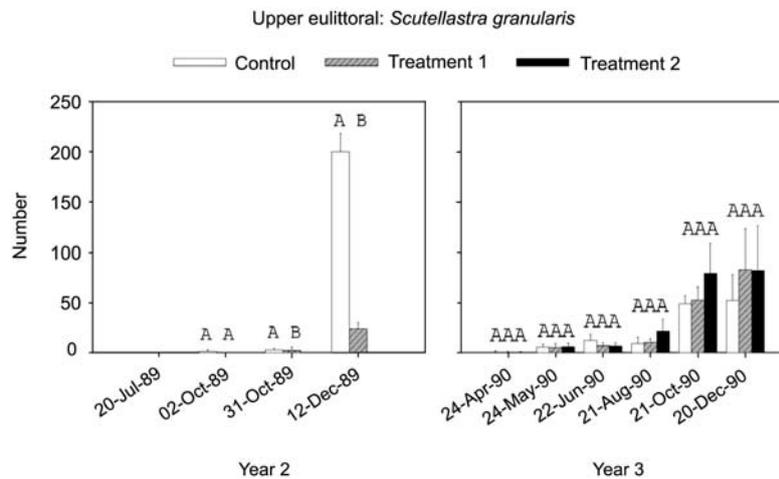
Comparisons between the controls and T2 (clearing just prior to sand-burial in summer) showed that *Mazzaella capensis*, *Gymnogongrus complicatus* and *G. glomeratus* relied on persistent, crustose tissue to survive and re-establish themselves once sand moved off. These three species are typical of sand-affected shores on the South African west coast (Stegenga et al. 1996). By contrast, the recovery of the other seaweed species that were present, as well as the limpets, barnacles, and mussels, was essentially unaffected by T2, indicating that their populations did not rely on persistent tissue that could survive sand-burial, but recruited when the sand moved off the rock.

*Mazzaella capensis* has an isomorphic life-history (Stegenga et al. 1997), with large (up to 25 cm) foliose gametophytes and sporophytes, both with a tough, flat, almost crustose holdfast. This holdfast tissue was observed to survive sand-burial for up to 6 months and to rapidly produce new upright shoots.

*Gymnogongrus complicatus* and *G. glomeratus* have heteromorphic life-histories, with erect gametophytes arising from crustose holdfasts and crustose tetrasporophytes (Anderson and Bolton 1990, Anderson 1994). From our results, both the holdfasts and the tetrasporophytes appear capable of surviving periods of sand-burial for up to 6 months, often under sand at least 0.5 m deep. The new population is then re-established mainly by growth of upright shoots from the holdfast material (as observed), but also presumably from the release of and subsequent germination of spores from the tetra-



**Figure 14** Mean percentage cover of *Porphyra capensis* in Year 2 (T1 and control plots) and Year 3 (control, T1 and T2 plots). Vertical bars show means+SD. Letters above bars show significant differences ( $p < 0.05$ ): for Year 2 according to Mann-Whitney U-test; for Year 3 according to 2-tailed multiple comparisons in cases where significant differences ( $p = 0.05$ ) were found by non-parametric Kruskal-Wallis ANOVA by ranks.



**Figure 15** Mean number (per  $0.25 \times 0.25$  m quadrat) of *Scutellastra granularis* in Year 2 (T1 and control plots) and Year 3 (control, T1 and T2 plots).

Vertical bars show means+SD. Letters above bars show significant differences ( $p < 0.05$ ): for Year 2 according to Mann-Whitney U-test; for Year 3 according to 2-tailed multiple comparisons in cases where significant differences ( $p = 0.05$ ) were found by non-parametric Kruskal-Wallis ANOVA by ranks.

sporic crusts. The recovery of these species to control levels within 2 years (2 growing seasons) in T1 plots does not contradict the prediction of Airoldi (2003) that vegetative propagation rather than reproduction from spores is typical of sediment-resistant organisms. As mentioned, during the “growing season” at this site, there is effectively no sand influence, so that reproduction from spores would remain important in maintaining populations of *Mazzaella* and both *Gymnogongrus* species. Such a seasonal cycle of sand-burial and then complete emersion is quite different from, and cannot be compared to, a chronic, sub-lethal sand effect, as noted by Airoldi (1998).

After clearing, both *Mazzaella* and *Gymnogongrus* took 2 years to regain cover values (in the T1 plots) that were similar to controls. Because none of this recovery could have been from persistent material within the plots, there must be substantial spore-settlement of these species.

It is worth noting that the lower eulittoral zone, where wave-wash prevented experimentation, is dominated by crustose corallines and *Grateloupia longifolia*, with scattered individuals of *Corallina officinalis* Linnaeus, and that the last two species have crustose bases, providing further, though untested, evidence of the importance of the crustose morphology in this sand-disturbed habitat.

Many descriptive studies have noted that seaweeds that are characteristic of sand-dominated shores usually have crustose bases or crustose life-history phases: these species have been called psammophytes (e.g., Mathieson 1967, Markham and Newroth 1972, Markham 1973, Daly and Mathieson 1977). D’Antonio (1986) showed that *Neorhodomela larix*, which dominates many sand-affected shores in the northwestern USA, can survive long periods (up to 3 months in the laboratory) of sand-burial, producing new upright shoots from a perennating holdfast. Littler et al. (1983) cautioned against call-

ing such species psammophilic (sand-loving) since they probably do not grow better under sandy conditions, but simply survive burial better than competitors.

The three seaweeds in this study that survived burial did so by means of their crustose bases. It is almost certain that all of them have coalescent sporelings (see below), that is, individual spores germinate into discs that are capable of coalescing to produce crusts. These crusts may therefore comprise a “chimaera” or “genetically polymorphic” organism, with several advantages for surviving disturbance (Santelices et al. 1996).

*Gymnogongrus complicatus* (as *Ahnfeltiopsis complicata*) and *G. glomeratus* (as *A. glomerata*) were cultured by Anderson and Bolton (1990), and although we did not then appreciate that coalescence was occurring, we observed individual crusts grown on glass slides to eventually fuse into a single thick crust covering most of the slide. These species are closely related to the two species of this genus that Santelices et al. (1999) showed to produce coalescent crusts, namely *Ahnfeltiopsis furcellata* (C. Agardh) Silva et De Cew (formerly *Gymnogongrus furcellatus*) and *A. durvillaei* (Bory) Silva et De Cew (formerly *G. durvillaei*). Similarly, *Mazzaella capensis* is closely related to *M. laminarioides* (Bory) Fredericq, which has been shown to coalesce both in culture (Santelices et al. 1999) and in the field (Santelices et al. 2003). Santelices et al. (1999) found that 33 out of 35 species in the Order Gigartinales (which includes *Mazzaella* and *Gymnogongrus*) that have been tested produce coalescent sporelings (one of the exceptions is a taxonomically uncertain genus and the other is an unusual parasite). We consider it extremely likely that *M. capensis* and our two *Gymnogongrus* species have coalescent crusts.

Why may coalescence be important for these species? Coalescent sporelings produce upright shoots earlier, grow faster, and produce more upright shoots than non-coalescent sporelings (Jones 1956, Tvetter and Mathieson 1976, Maggs and Cheney 1990). Sporeling coalescence increased survival rates among a wide range of species tested in the laboratory by Santelices et al. (1999), and these authors consider coalescent species in the field to be more resistant to grazers, dislodgement, and overgrowth by competitors, and probably to emerge faster from under sand or mud. Furthermore, holdfasts of even well-developed *Mazzaella laminarioides* individuals can coalesce in the field (Santelices et al. 2003). If, as seems very likely, *Mazzaella capensis*, *Gymnogongrus complicatus* and *G. glomeratus* do have coalescent sporelings, the above characteristics would help to explain their survival and persistence on this severely sand-disturbed, cool-temperate, southern African shore.

In Year 3, almost all the organisms in the mid-eulittoral zone reached their highest cover values in October and then began to decline in December. This may have been caused by increasing desiccation during spring low tides as the weather warmed with the onset of summer, or gradual encroachment of shallow sandy patches, or both factors.

The algae that were unaffected by any clearing treatment apparently had no element in their life-histories that was present on these shores and that survived sand burial for the periods experienced in this study. This group

comprised *Centroceras clavulatum*, *Aristothamnion collabens*, *Ceramium arenarium*, *Cladophora capensis* and *Porphyra capensis*. The first three of this group belong to the Ceramiaceae and have isomorphic life histories (no crusts or cryptic phase) and furthermore exhibit bipolar germination, with spores that do not coalesce (Santelices et al. 1999). Similarly, *Cladophora capensis* has isomorphic generations and no cryptic or crustose phase (Stegenga et al. 1977). *Porphyra capensis* has a microscopic conchocelis phase (Stegenga et al. 1997), which may or may not survive sand burial. Even if it did, subsequent colonization by the gametophyte phase (which we were measuring) might not be affected by our treatment, because these gametophytes arise from settlement and germination of conchospores and the conchospores could come from untreated substrata. Populations of all of these species, except for *Porphyra* (see below), built up over several months, indicating a small but steady rate of recruitment from spores. All showed a similar pattern of relatively low percentage cover and, almost invariably, no between-treatment (within-month) statistical differences. Where differences did occur (e.g., *Cladophora capensis* in October only) they may indicate either real, but unimportant changes in the population or the difficulties of sampling small cover values accurately. In either case they do not obscure the general pattern of these species that colonize the shore annually and have no persistent element. *Porphyra* was somewhat different in that propagules appeared to arrive relatively early so that the population reached a maximum by June, when most of the “annual colonizers” had only just appeared. This will be discussed later in relation to the dominance of this species in the upper eulittoral zone.

A striking feature of this shore was the very high densities of small limpets (*Scutellastra granularis*) that recruited and built up as the growing season progressed. By December, individuals reached only about 5–8 mm in length, indicating that there were unlikely to be adults present (this species can grow to over 30 mm: see Branch 1976), and that annual recruitment occurs from larvae. Growth and therefore mean size of *Scutellastra granularis* is reduced as cover of *Chthamalus dentatus* increases (Branch 1976). In our study, cover values of *C. dentatus* were more than 60% in August and 80% in October, and were high enough, according to Branch (1976), to have reduced the mean size of *S. granularis* in our plots, but he notes that limpet densities remain unaffected by high barnacle cover.

It is not surprising that *Scutellastra granularis* is eradicated by the complete sand-burial of this shore, and that new recruitment occurs each year, because this species is not physiologically capable of surviving sand-burial (Marshall and McQuaid 1989), and there is no adjacent, unburied rock from which adults could migrate.

The presence of numerous (albeit small) limpets on this shore raises the question of the effects of grazers on this community. *Scutellastra granularis* feeds on a wide range of algae and algal sporelings, as well as on newly-settled animal larvae (Branch 1971, Branch 1976: as *Patella granularis* Linn.), and once the number of juveniles of this limpet builds up, they might be expected to strongly affect the settlement and survival of other organisms.

Among the algae, species with crustose phases would be at an advantage, since crusts are considered to be more resistant to grazing, to the extent that in some systems the crustose phase is considered to be “grazer-dependent” (Slocum 1980). Cohen (1966) was aware of this in proposing the term “bet-hedging” as a partial explanation for the evolution of the crustose phase in the life histories of some heteromorphic algae. While the crustose holdfasts of *Mazzaella capensis*, *Gymnogongrus complicatus* and *G. glomeratus* and the crustose tetrasporophytes of the last two species distinguish them as psammophytes, these algae may also persist on this shore because they can survive grazing better than other species.

The mussel *Mytilus galloprovincialis* is common in the mid- and lower eulittoral zones of this shore. However, it only forms continuous sheets in places where sand-burial does not occur. Observations of this shore between 1988 and 2003 showed that during anomalous years (e.g., 1990/91) the mid-eulittoral zone can be almost completely dominated by mussels, which cover 80–100% of the rock. Then *Mazzaella* almost disappears, and *Gymnogongrus complicatus* is reduced to a few patches, with upright shoots squeezed between mussel shells. During “normal”, annual cycles between sand-burial, the mussel population builds up, but is then killed by the sand in summer. No mussels survived burial in our plots, only byssus threads remained when the sand moved off, and re-colonization appeared slow and patchy up until October, by which stage other organisms had generally reached their maximum cover. Mussels showed two unusual trends. First, their percentage cover continued to increase in December (Figure 13), when that of all the other major space-occupiers (including barnacles) was decreasing. This may result from decreased competition for space, or a greater tolerance to sand, which by December, was beginning to return to the shore. Second, cover in control quadrats was higher than in treatments in August, October and particularly December, suggesting possible facilitation by the higher cover of algae in the controls. It is also possible that byssus threads, which were removed during the clearing of T1 and T2 quadrats, but remained in the controls, may facilitate recruitment or survival of new mussels.

The statistical similarity between barnacle (*Chthamalus dentatus*) cover in all plots up until August indicates that they were unaffected by clearing, and that populations rely on annual re-colonization by larvae after the sand moves off. According to Bokenham (1938) and various authors cited by Branch (1976), dense larval settlements of this species occur during autumn and spring; the former would coincide with exposure of our study site as the sand moves off. While we have no provable explanation for the statistically lower barnacle cover in October in T2, it may be related to the onset of dry summer spring tides or encroaching sand because by December the population of live barnacles had fallen considerably.

### Upper eulittoral zone

In the upper eulittoral zone in Year 3, the fact that the T2 clearing had no effect on recruitment showed that neither of the two dominant species (*Porphyra capensis* and the

limpet *Scutellastra granularis*) nor any other organisms survived sand-burial in any form. The question arises – why did *Porphyra* settle in control plots but not T1 plots in Year 2? We think that propagules of *P. capensis* had already arrived on the newly-exposed rock and were destroyed when the T1 clearing was done in early July 1989. These results indicate that in the mid-eulittoral zone, this species must settle very soon after sand-emersion (compared to other non-persistent species) in order to establish before the limpets become numerous and large enough to prevent *Porphyra* recruitment. Although limpet densities remained very low in T1 plots in 1989 (Y2), limpets are mobile and were numerous outside T1 plots and in control plots. Furthermore, we have observed that on nearby rocks that are never buried by sand there is usually a 10–20 cm-wide bare zone between large *Porphyra* patches and the extensive, neighboring mussel beds, and we ascribe this to herbivory by the very numerous limpets that find refuge among the mussels. The suggestion that sediments deter herbivores, or that sediments weaken competition or predation (see Airoldi 2003) cannot be tested in our study, because during winter, when a biotic community develops, there is effectively no sand present. For the same reason, we cannot confirm or deny the findings of Engledow and Bolton (1994) (from the coast of Namibia) of negative correlations between limpet densities and sediments.

In Year 2 in the upper eulittoral zone, limpet densities mirrored the pattern shown by *Porphyra* cover; both were low in T1 plots and high in controls. The most obvious explanation for this is that these small limpets seek refuge (at least during low spring tides) under *Porphyra* thalli, and were avoiding areas from which *Porphyra* was almost absent. We observed this in our plots and adjacent areas of the upper eulittoral zone, where there is almost no algal cover except for *Porphyra*. Even if the T1 clearing had removed limpet larvae along with *Porphyra* propagules, there seems no reason why limpets should not have moved in from outside the plots, unless the seaweed-free substratum was made unattractive by the lack of sheltering *Porphyra* fronds.

The exceptionally high densities of limpets in December 1989 (Y2) in control plots (double those found in 1990 Y3) were apparently a result of their upward migration as sand moved steadily up the shore. At that stage the lower eulittoral zone was completely covered by sand and patches of sand extended into the mid-eulittoral zone. At the same time we found isolated rocks with only their tops unburied, and most of these were covered by limpets, sometimes several individuals deep, that were retreating from advancing sand.

### Conclusion

Our study shows that this highly sand-disturbed habitat is characterized by organisms that are either disturbance-tolerant (*Mazzaella* and the two *Gymnogongrus* species) or those that are opportunistic (the remainder), confirming the findings of Littler et al. (1983) on a sand-affected California rocky shore. Furthermore, we clearly

show that the mechanism by which members of the two genera above survive severe sedimentation is via crustose holdfasts (both genera) or crustose tetrasporophytes (in *Gymnogongrus*) that are physiologically capable of surviving burial. The biotic community on this sand-disturbed, cool-temperate shore appears to be highly “self-stabilizing”, because a similar community develops every year after complete sand-burial (results here, and observations up until 2006), and even when the persistent species are removed, they return to “normal” levels within two seasons. Such communities are clearly maintained in an early successional stage, and competitive interactions within them are probably poorly developed compared to mature communities. Considering the prevalence of sand-disturbed rocky intertidal communities worldwide, they are worthy of more attention than they have received so far.

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