

Effects of Periodic Disturbances from Trampling on Rocky Intertidal Algal Beds Author(s): Michael J. Keough and G. P. Quinn Source: *Ecological Applications*, Vol. 8, No. 1 (Feb., 1998), pp. 141-161 Published by: Ecological Society of America Stable URL: <u>http://www.jstor.org/stable/2641317</u> Accessed: 25/01/2010 14:06

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EFFECTS OF PERIODIC DISTURBANCES FROM TRAMPLING ON ROCKY INTERTIDAL ALGAL BEDS

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Abstract. We investigated the ability of an assemblage of animals and plants on rocky shores in southeastern Australia to resist and/or recover from repeated pulse disturbances in the form of trampling. Disturbances of four different intensities were applied experimentally over six summers, with no human access at other times of the year. The dominant intertidal plant, the brown alga *Hormosira banksii*, was affected by trampling, but the effects were heterogeneous between sites. At two sites, a series of pulse disturbances produced a series of pulse responses, although the effect of a given pulse varied among years, possibly related to the severity of summer desiccating conditions each year. At the third site, pulse disturbances produced a press response; at high levels of trampling, *Hormosira* was almost eliminated within 2 yr, and at two intermediate levels of trampling showed little small-scale spatial variation. Untrampled areas did fluctuate through time, often as a result of summer burnoff of algae. Natural disturbances occurred irregularly through the study, and their effects varied on very small spatial scales (among plots <30 m apart).

Trampling enhanced the densities of a range of herbivorous mollusks, especially limpets, and reduced the abundance of articulated coralline algae, which were abundant in the understory of *Hormosira* mats. These effects varied among sites but showed much less variation on smaller spatial scales. The reductions in coralline algae may be a direct effect of trampling, but increases in mollusk abundance occurred some time after changes to *Hormosira* cover, and those changes may be an indirect effect of trampling.

We compared the effects of trampling on areas of the shore that had been trampled for two and four summers, to test whether a past history of disturbance influenced the effect of a new disturbance. No significant effects were found on algae or mobile animals, although a mild summer may have made our test of history relatively weak.

Hormosira banksii fits the definition of a keystone species or engineer and, as such, is an appropriate focus for management and as an indicator. Spatially heterogeneous effects of a constant physical perturbation, however, mean that management of these rocky shores requires more complex models and indicate that caution should be used in adopting this species as a uniform indicator of environmental change.

Key words: disturbance, pulse and press; Hormosira; human impact; intertidal algae; press disturbance; pulse disturbance; rocky shores, management of; trampling.

INTRODUCTION

Human activities often constitute a disturbance to natural environments, and in attempting to assess the impacts of those activities or to develop models that lead to their management, it is important to determine how they compare to natural disturbances that may be present.

In nearshore coastal environments, anthropogenic disturbances vary in nature. Some, such as industrial discharges, are more or less continuous stresses, and there is an extensive literature on their effects and the methodology for detecting these impacts (e.g., Schmitt

Manuscript received 27 August 1996; revised 20 May 1997; accepted 16 June 1997; final version received 24 July 1997.

and Osenberg 1996). In the terminology of disturbance (Bender et al. 1984), these events are press disturbances. Other human activities are more variable in time, and have been termed pulse disturbances. Spills of toxicants often are short pulses through a system; other inputs of nutrients and toxicants often vary greatly in association with high rainfall events and associated storm water runoff. Many commercial fisheries are seasonal, and any impacts of human recreational activities are likely also to show annual cycles, reflecting seasonal changes in visitation to coastal areas. These latter activities may be a series of pulses of disturbances, followed by potential recovery periods.

Many natural disturbances also have spatially variable effects and/or patterns of recovery (e.g., Connell 1979, Paine and Levin 1981, Dayton et al. 1984, 1992, and see reviews by Sousa 1984, 1985, Connell and Keough 1985, Lake 1990), although there are relatively few natural disturbances showing periodicity (but see, e.g., Bertness and Ellison 1987).

Periodic activities can be viewed as a series of pulse disturbances, and a population or assemblage could respond in a number of ways. If the disturbance is not too intense or the system has high resilience, it may be able to recover in the intervals between disturbances (Petraitis et al. 1989). Recovery may also occur if the interval between disturbances is long. In the terminology of recent disturbance theory, repeated pulse disturbances may produce a series of pulse-like recoveries, or act as a press disturbance. Whether a particular disturbance regime produces pulse or press responses is also likely to depend on the intensity of the disturbance: low intensity disturbances, i.e., those that cause little damage during a given pulse, may allow rapid recovery, but there may be a critical intensity beyond which persistent changes occur.

On rocky shorelines of southern Australia, one of the most prominent species is the perennial fucoid alga *Hormosira banksii*, which forms extensive monotypic stands at midtidal levels of rock platforms (Fig. 1). *Hormosira* beds are habitat for a range of mobile animals, and their presence is negatively associated with other species. *H. banksii* is sensitive to short-term trampling (Povey and Keough 1991) and is deleteriously affected by other anthropogenic activities, including discharge of sewage (Brown et al. 1990, Fairweather 1990). We used this alga to test the effects of recurrent disturbances at a range of intensities, with the disturbances recurring annually over six summers.

In particular, do seasonally recurrent disturbances caused by humans produce pulse or press responses? Are the responses spatially consistent? Does the kind of response to disturbance vary with intensity of disturbance? We also compared the (controlled) human disturbances to changes produced by natural events.

We also considered the possibility that organisms' sensitivity to new disturbances might be related to their history. For example, a history of competition may make an organism more sensitive to physical disturbance (Peterson and Black 1988) or change some life history parameters later in its life (Scott 1994). Tanner et al. (1996) provide an overview of historical effects, although their own data did not show a strong effect of history on community dynamics and structure. A natural or anthropogenic disturbance may stress an organism, inhibiting its ability to respond to new challenges, repeated occurrences of the same disturbance or novel stresses. Intertidal algae could become stressed by desiccation and become more vulnerable to trampling, or vice versa. We took advantage of our long-term experiment to contrast the responses of plants with a long history of disturbance to those of plants with little or no history of trampling.

METHODS

Our main study areas were extensive rocky limestone platforms within Mornington Peninsula National Park, in southeastern Australia. The national park extends over ~ 30 km of moderately exposed ocean coastline, and is accessible to the general public. A section of 8 km was formerly under the control of the Department of Defence, and was incorporated into the national park in 1989. This section of the park has remained closed to public access, so shores in that area have been protected from direct human influence for >75 yr. The dominant intertidal habitat is provided by the fucoid alga Hormosira banksii, which forms large monotypic beds (Fig. 1). The individual plants have a basal holdfast, from which are produced fronds. Fronds are composed of chains of vesicles (Fig. 1). The general description of the major habitat types in this area is provided by Povey and Keough (1991). Hormosira beds provide habitat for a range of smaller gastropod mollusks and crustaceans. Other mollusks feed primarily in open (i.e., lacking macroalgal cover) areas, and their abundances are negatively correlated with the presence of large algae (G. P. Quinn and M. J. Keough, personal observations).

Experimental designs

The main trampling experiment ran for 6 yr, and consisted of areas of the shore being trampled over summer, followed by a recovery period from midautumn to early summer. On these shores, there are relatively low levels of visitation by humans until late December, when levels become high through January during a major holiday period, taper off in February, and remain at that level until approximately Easter (March) when another brief holiday period occurs (King 1992). Our experiment followed those broad patterns of use.

We established three trampling sites at hapazardly chosen areas within the protected area of the national park. Two sites were on different parts of the intertidal platforms at Cheviot Beach; Harry's Pool was adjacent to a large rock pool and Cheviot Mid was $\sim 200 \text{ m}$ along the shore, but set back from the edge of the platform. The third site, Grenade Range, was at a platform ~ 1 km away, separated from Cheviot Beach by two headlands. At each site, we initially established two plots, $\sim 10 \times 3$ m, separated by 30–50 m, where the percentage cover of Hormosira exceeded 90. We marked eight trampling strips within each plot, each strip being 50 cm wide, and 2-3 m long, with the exact length varying among plots, depending on the size of the Hormosira patch in which the plot was placed. Strips were separated by at least 1 m and parallel to each other. Each plot included two replicates of each trampling treatment.

The main trampling experiment used four intensities of trampling. Our focus here is on changes occurring



FIG. 1. Hormosira banksii plants. The top panel shows a false-color infrared image of a small rock platform at Cheviot Beach. The red area in the center of the platform is dense Hormosira, with small patches elsewhere on the platform. The photograph covers an area ~ 50 m wide. The lower panel shows individual plants that have been subject to moderate trampling, with some reduction in cover. Note the morphology of the plants, with fronds of spherical vesicles in long chains, and a combination of intact and damaged chains. The picture covers an area ~ 10 cm wide.

each summer, so the intensity of disturbance is the number of passages per summer (which is equivalent to the number/day), as the number of trampling days was consistent across treatments. One passage consisted of a person of average size walking at normal pace along a strip, and strips received either 0, 5, 10, or 25 passages on a given low tide. For repeated passages, tramplers moved beyond the end of the strip before turning, to prevent more severe forces associated with pivoting of the feet. All trampling was done by average-sized adults, wearing rubber-soled athletic shoes or sandals, footwear of a similar type to that used by recreational visitors (Povey 1989). Each summer, we used 6-8 d of such trampling on every strip, spread haphazardly over the suitably low tides during summer. We began the trampling in the summer of 1990-1991 and continued through the summer of 1995–1996. The experiment has continued, and in this paper we present analyses of five years of data, plus descriptions of events occurring during the sixth summer (1995-1996).

We sampled the experiment twice annually, at the beginning of summer, and again after Easter, after the last trampling period. Easter holidays represent the last major recreational influx to coastal areas before winter. The measurement after Easter was intended to assess the effects of trampling, while the measurement in early summer provided a measure of recovery over the preceding seasons. Each strip was sampled using a 70×35 cm quadrat placed in the center of each strip, with its long axis running parallel to the strip. We photographed the quadrat with color slide film (first 3 yr) or Hi-8 video (second 3 yr), and back in the laboratory, we projected the images and calculated the cover of *Hormosira* using 100 randomly placed dots superimposed on the image.

On two occasions, after three and five summers (i.e., in autumn of 1993 and 1995) we counted understory algae and mobile animals. We did this using two quadrats, placed end-to-end in the center of each strip. Algae were estimated using a grid of 100 points, and we counted all algae beneath each point. Animals were identified and counted, after a thorough search of each quadrat. We used two quadrats because some animals were uncommon, and we required a larger sample, but numbers were averaged to provide a single value for each strip. We did not do complete censuses often, because we considered the sampling procedure to be potentially disruptive to understory algae or associated invertebrates.

Historical effects.—After 2 yr, we tested whether plants with a history of disturbance and recovery might be more resilient or more sensitive to a new disturbance, by adding a new plot to the Harry's Pool and Cheviot Mid sites. At both sites, *Hormosira* had recovered by the beginning of summer. At Grenade Range, *Hormosira* had declined in treatment plots (see *Results*), so we could not compare the response of these plants to that of previously untrampled areas. The new plots were identical to the existing two at each site, and were within the same large algal mat. We repeated this procedure at the beginning of the summer of 1994– 1995, so at Harry's Pool and Cheviot Mid, we had two plots that had been trampled for 4 yr, one that had been trampled for 2 yr, and one with no history of trampling. All of the new strips were trampled and sampled in the manner described above, including a census of the complete fauna in autumn of 1995.

Analyses

All data were analyzed by analysis of variance. Our design for the main experiment involved six factors, and corresponded to a split-plot or repeated-measures design. We use the latter terminology, for clarity. The spatial component of the design was partly nested, with Sites, and Plots within Sites. Both factors were crossed with Trampling, with two strips within each Plot-Trampling combination. Each strip was then sampled 10 times, with those 10 samples falling into 5 yr, and before/after each summer. In repeated-measures terminology, the "subjects" were strips, the between-subjects factors were Site, Plot, and Trampling, and the within-subjects factors were Years and Before-After Summer. Trampling, Before-After Summer, and Years were fixed factors, the latter because we had sampled for all five years in the period. Strips, Plots, and Sites were random factors, the latter to allow us to generalize about spatial variation in responses to disturbance.

The detailed censuses at the end of 3 and 5 yr were each analyzed by partly nested analysis of variance, i.e., the above design with no within-subjects factors (Plots within Sites, crossed with Trampling, and two replicates). We analyzed the abundance of all common taxa. Coralline algae can not be identified to species in the field, although they are numerically dominated by species of Corallina, and we separated them into articulate and encrusting forms because of the different ecological properties of those growth forms (Steneck and Dethier 1994). Uncalcified turfing or encrusting algae were also abundant enough to analyze, even though individual species, such as Cladophora and Ralfsia, could not be analyzed. We pooled all algae other than Hormosira to create a further plant variable. The animals were dominated by mollusks, and herbivores in particular. The predatory whelk Thais orbita and the scavenging Cominella lineolata were present, but not sufficiently abundant for analysis. We analyzed abundance of the two true limpets Cellana tramoserica and Patelloida alticostata, the two pulmonate limpets Siphonaria diemenensis and S. zelandica, plus the littorinid Bembicium nanum. We created two additional pooled herbivore groups, (true) limpets (Cellana + Patelloida alticostata + P. latistrigata) and nonlimpet grazers (Siphonaria spp., Bembicium, plus Austrocochlea constricta, Turbo undulata). We also assessed the performance of various "community" statistics; we calculated the taxonomic richness (number of recogTABLE 1. Analysis of changes in cover of Hormosira banksii through time, as a function of level of trampling.

		Denom.	·····			Andreas and a second
Source of variation	df	no.†	MS	F	Р	P (Chev)
Between-strips (i.e., pooled across time)	effects					
1. Sites (S)	2	2	2255.4	4.26	0.133	0.815
2. Plots within Sites (P{S})	3	6	529.2	0.44	0.725	
3. Trampling (T)	3	6	15778.5	13.19	0.000	
4. Trampling \times Site	6	5	4186.9	15.67	0.000	0.087
5. T \times P{S}	9	6	267.1	0.22	0.988	
6. Strips within Plots (Residual)	24		1196.5			
Within-strips (i.e., temporal) effects						
7. Years (Y)	4	13	17 053.7	84.67	0.000	
8. Year \times Site	8	9	1804.9	3.91	0.017	0.302
9. Years \times P{S}	12	13	462.1	2.29	0.013	
10. Year \times Trampling	12	13	284.4	1.41	0.201	
11. $\mathbf{Y} \times \mathbf{T} \times \mathbf{S}$	24	11	450.3	2.25	0.013	0.458
12. $\mathbf{Y} \times \mathbf{T} \times \mathbf{P}{\mathbf{S}}$	36	13	200.0	0.99	0.493	
13. Strips \times Years (Residual)	96		201.4			
14. Before–After Summer (BA)	1	20	32 472.3	394.82	0.000	
15. BA \times Sites	2	16	124.8	0.13	0.880	0.897
16. BA \times P{S}	3	20	936.6	11.39	0.000	
17. BA \times Trampling	3	20	826.2	10.05	0.000	
18. BA \times S \times T	6	19	107.8	2.35	0.120	0.279
19. BA \times T \times P{S}	9	20	45.9	0.56	0.817	
20. Strips \times BA Residual	24		82.2			
21. Years \times Before–After Summer	4	27	2919.5	38.17	0.000	
22. Y \times BA \times S	8	23	534.5	0.90	0.546	0.383
23. T \times BA \times P{S}	12	27	594.4	7.77	0.000	
24. Y \times BA \times Trampling	12	27	516.4	6.75	0.000	
25. Y \times BA \times T \times S	24	26	68.3	0.79	0.728	0.336
26. $\mathbf{Y} \times \mathbf{BA} \times \mathbf{T} \times \mathbf{P}\{\mathbf{S}\}$	36	27	86.8	1.14	0.308	
27. Y \times BA \times Strips Residual	96		76.5			

Notes: Significant effects (at $\alpha = 0.05$) are shown in **boldface**. The right-most column shows the *P* values associated with tests for heterogeneous effects of trampling at the two sites on the Cheviot Beach Platform.

[†] Terms are numbered, and the denominators used to test each effect are indicated using those numbers.

nizable taxa), species richness of gastropods, total number of individuals, and the Shannon-Wiener diversity index (H').

The experiment to examine history of disturbance was analyzed using data collected at the end of the 1994-1995 summer. In the analysis, we found no significant variation between the two Cheviot sites (at α = 0.25), so we omitted them from the analysis, to give four levels of trampling, and three levels of history (0, 2, or 4 yr) with either four, two, or two plots within each level of history, respectively. The data were analyzed as a partly nested analysis, with History, Plots{History}, Trampling, $H \times T$, and $T \times Plots$ as the terms in the analysis, and History and Trampling as fixed factors and Plots as a random factor. Our conclusions would not be altered by the more conservative step of retaining sites within the analysis. We analyzed Hormosira cover and abundances of all common taxa. To be more confident of detecting an effect on Hormosira, we analyzed the percentage covers from the postsummer 1994-1995 survey, and data from pre- and postsummer of 1995-1996, so we could examine the profile through time of plots with different histories. The three values were treated as repeated measures, using the statistical model described above.

All data analysis was done using SYSTAT for Windows, version 5.03 (SYSTAT Incorporated, Evanston, Illinois). For all analyses, we examined primarily the assumption of normality, by examining residuals by probability plots. There were generally too few replicates at a given level of the design for a meaningful comparison of variances. When we used repeated-measures or partly hierarchical analyses, we also examined the more conservative Greenhouse-Geiser and Huynh-Feldt corrected F tests, which provide some protection against violations of assumptions of compound symmetry. Those tests did not produce results markedly different from the uncorrected ones, and we saw no evidence of strong violation of these assumptions, so only the standard F tests are presented here.

Note, in all analysis tables, probabilities are rounded to three decimal places for brevity; values <0.0005 are shown as 0.000.

RESULTS

Effects on Hormosira banksii

We found striking temporal and spatial variation in the percentage cover of *H. banksii*, and find it helpful to separate effects involving trampling from those that presumably represent natural variation.

Effects of trampling.—Trampling affected *Hormosira* beds dramatically, with the effects varying through time and through space (Table 1). Individual plants



FIG. 2. Changes in cover of *Hormosira banksii* on two platforms, under different levels of trampling. Data were pooled from the two sites at Cheviot Beach, as they showed no significant heterogeneity. The bar at the top of the figure indicates periods during which trampling occurred (as dark blocks) and times when there was no disturbance (clear blocks). The error bars at the base of each figure indicate three standard errors, calculated using the variance components for error terms used to test Trampling × time effects, using data from Table 1. The left error bar is the geometric mean of the time × Strips residuals from Table 1, the middle error represents the Trampling × time × Plots term (based on three components: Year × T × P, BA × T × P and Y × BA × T × P). The right error bar indicates variance for assessing variation that is independent of trampling, i.e., time × Plots terms.

were initially damaged by the loss of chains of vesicles, and ultimately by whole fronds, as described by Povey and Keough (1991). Under severe damage, they were reduced to holdfasts (Fig. 1). The effects of trampling were quite different at the three sites (see Trampling \times Site, Year \times Site \times Trampling interactions on Table 1). At Grenade Range, there was a decline in percentage cover after the first summer's trampling, and the rate of decline was proportional to the intensity of trampling (Fig. 2). The plants recovered by the beginning of the following summer, but then declined even more under the second year's trampling. There was little subsequent recovery, and in the third and fourth years plants in the two intermediate treatments remained at 60–70% cover through to late 1994. Plants in control strips covered 80–100% of space until late 1994, while the major changes occurred in the most heavily disturbed areas, where cover declined after each period of trampling, with little or no recovery in the intervening seasons, so that by late 1994, cover had fallen to <10%. In the austral summer of 1994–1995, there was a major decline across all treatments, with cover falling by $\sim30\%$ in controls and the two intermediate levels of disturbance, and falling to a few percent in the most heavily disturbed areas (Fig. 2). After this decline, there was some recovery in the control and intermediate treatments, although cover did not return to its levels of the spring of 1995, and there was little recovery in the heavily disturbed areas. Trampling in the summer of 1995–1996 had little apparent effect (Fig. 2).

The situation was very different at the two Cheviot Beach sites. The effects of trampling did not differ significantly between the two sites (Table 1). We therefore discuss the two sites together. For the first two years, the Cheviot sites followed a trajectory similar to that shown by Grenade Range, with an initial decline, a complete recovery, then a more severe decline during the disturbances of the second year (Fig. 2). From that stage, however, all plots recovered completely, and for the next 3 yr, we saw little effect of trampling. There was a marked decline in cover in the summer of 1994-1995, as at Grenade Range, but this decline was consistent across all trampling treatments. There had been complete recovery by midspring of 1995, and trampling had little effect in that summer, with an increase in cover in three treatments, and a decline only under heavy trampling.

The variation that we observed in the effects of trampling was almost all at larger spatial scales; we were able to test whether replicate plots at each site showed the same effect of trampling, and all four tests incorporating a Trampling \times Plot interaction were nonsignificant (Table 1). Similarly, the variation among replicate strips within plots was quite small; the four terms incorporating Strips on Table 1 together accounted for only 18% of the total sum of squares in the analysis (compared to ~35% for trampling effects).

Temporal variation independent of trampling.—The pattern of variation was different when we examined the effects that were unrelated to trampling. There was strong variation in percentage cover of Hormosira among Years and Before-After Summer (Table 1), as well as small-scale variation in cover. Changes over summer reflect burning-off of the algae, with a consequent loss of biomass and/or cover, and these effects varied among years (Years \times BA interaction; Table 1). This pattern was not significantly heterogeneous among the three sites. Cover declined over the summers of 1990-1991 and 1994-1995, and showed either weak changes (1991-1992) or no discernible change (1992-1993, 1993-1994, 1995-1996) in the other summers (Fig. 2). The variation among years was not consistent among the three sites, but this effect was small, and not clear from the graphs (Fig. 2).

In contrast to the trampling effects, there was smallscale variation in the effects of Year and Before–After Summer, with significant interactions between Plots and these two factors.

Effects on other organisms

Trampling affected other organisms, but they were generally heterogeneous among the three sites. After 5 yr, the effects of trampling varied significantly among sites, rather than among plots (Table 2), with the sites effect generated by the difference between Grenade Range and the two Cheviot Sites. There were significant Site \times Trampling interactions for articulate coralline algae, total algae, Cellana tramoserica, Siphonaria diemenensis, and the pooled categories of limpets and nonlimpet grazers. When the data for the two Cheviot platforms were analyzed, the only significant effect of trampling was a Plots \times Trampling interaction for Patelloida alticostata (Table 2). For Cellana and S. diemenensis, there was no consistent relationship between intensity of trampling and abundance at the Cheviot sites, but at Grenade Range, a 2-4-fold increase in abundance at the highest intensity of trampling (Fig. 3). There were similar patterns for Patelloida and S. zelandica, although they were more variable, and the analyses did not show significant effects after 5 yr. When the data were pooled, the nonlimpet grazers and limpets showed strong relationships with trampling at Grenade Range, but again, no apparent pattern at the two Cheviot Beach sites.

Articulate corallines varied dramatically in abundance between sites, and responded variably to trampling. They formed a major part of the understory at Cheviot Mid, with a mean cover of ~50%, yet covered no more than 10% at the other two sites (Fig. 3). At the two Cheviot sites, there was no relationship with trampling, but at Grenade Range, their cover declined with trampling from ~8% in control areas to 0 in the most heavily trampled treatments (Fig. 3). There was no pattern for encrusting corallines or for turfing algae, and the patterns for total algae reflected the heterogeneous results of individual taxa.

At the time of the first census, after three summers of trampling, the only species to show consistent effects of trampling was the limpet Cellana tramoserica (Table 3). There were isolated small-scale effects of trampling on another limpet, Patelloida alticostata, and the cover of articulated coralline algae, both of which showed significant Trampling \times Plot variation (Table 3). There was also a significant effect of trampling on all limpets pooled. Almost all common taxa varied significantly among plots, but not among sites (Table 3). When the two Cheviot sites only were compared, the results were similar except that there was no effect of trampling on the abundance of *Patelloida*, and significant Plot \times Trampling effects on the abundance of the pulmonate limpet Siphonaria diemenensis, Cellana tramoserica, and the pooled categories of nonlimpet grazers and limpets (Table 3).

The derived variables showed relatively weak effects. There was no significant effect of trampling on taxonomic richness, gastropod species richness, or H', regardless of whether all sites or just the Cheviot platforms were compared (Table 3). The number of individuals was affected by trampling, with the effect varying between sites (Table 3). For this variable, residual plots did not completely support the assumptions of the analysis for raw or log-transformed data, but were intermediate. However, the effect of trampling was consistent for raw and log-transformed data, and disap-

TABLE 2.	Analyses of	the abundance	of major	animals a	and plants	after 5 yr	of trampling	highlighting	effects of	trampling
at all thr	ee sites and	at only the two	sites on	Cheviot I	Beach plat	form.				

Trampling	df (num.)	df (denom.)	Articulate corallines	Encrust. corallines	All corallines	Turf	All algae
Overall (all sites)						···-	
Sites (S)	2	3	0.343	0.786	0.359	0.584	0.382
Trampling (T)	3	6	0.388	0.499	0.624	0.130	0.615
$S \times T$	6	9	0.018	0.916	0.283	0.565	0.013
Plots within Sites	3	24	0.000	0.244	0.000	0.000	0.000
$T \times Plots$	9	24	0.997	0.105	0.397	0.272	0.870
мs Residual	24		38.8	0.02	66.9	0.01	72.8
R^2			0.98	0.53	0.96	0.82	0.96
Cheviot only							
Sites	1	2	0.362	0.821	0.354	0.745	0.359
Trampling	3	2	0.343	0.807	0.436	0.647	0.532
S׍	3	6	0.143	0.190	0.169	0.138	0.113
Plots within Sites	2	16	0.000	0.266	0.000	0.000	0.000
$T \times Plots$	6	16	0.983	0.765	0.912	0.749	0.893
мs Residual	16		52.0	5.2	49.8	45.1	43.4
R^2			0.98	0.41	0.98	0.75	0.98
Historical effects							
History	2	5	0.665	0.388	0.464	0.689	0.645
Trampling	3	15	0.690	0.882	0.195	0.914	0.852
History \times Trampling	6	15	0.185	0.031	0.379	0.312	0.468
Plots within Histories	5	32	0.000	0.289	0.015	0.000	0.000
Trampling \times Plots	15	32	0.781	0.930	0.976	0.752	0.535
MS Residual	32		56.4	13.5	144.9	70.6	58.7
R^2			0.97	0.45	0.51	0.96	0.97

Notes: The table also shows the results of analyses to assess the effects of a history of trampling for Cheviot platform. For each taxon, the table shows the probabilities from the ANOVA associated with tests of hypotheses, plus the residual MS and the variance explained by the model and the degrees of freedom associated with numerator and denominator for each F ratio. Combining the degrees of freedom, P values, and MS Residual allows reconstruction of the complete analysis table. All tests of significance were done at $\alpha = 0.05$. Significant effects are shown in bold.

peared when only the Cheviot sites were compared, indicating that the primary difference was, again, between Grenade Range and the two Cheviot sites, with the number of individuals rising strongly at Grenade Range as the intensity of trampling increased. All variables also showed strong variation among plots that was unrelated to the levels of trampling.

Because a particular level of trampling produced a different cover of *Hormosira* at different sites, it is probably not surprising that most of the effects on other

TABLE 3. Analyses of the abundance of major animals and plants after three summers of trampling, highlighting effects of trampling at all three sites and at only the two sites on Cheviot Beach platform.

Trampling	df (num.)	df (denom.)	Articulate corallines	Encrust. corallines	All corallines	Turf	All algae
Overall (all sites)					· · · · · · · · · · · · · · · · · · ·		
Sites (S)	2	3	0.415	0.092	0.427	0.184	0.464
Trampling (T)	3	6	0.980	0.243	0.990	0.236	0.668
S׍	6	9	0.510	0.456	0.402	0.539	0.464
Plots within Sites	3	24	0.000	0.516	0.000	0.012	0.000
$T \times Plots$	9	24	0.030	0.931	0.061	0.694	0.355
мs Residual	24		15.4	0.005	17.1	0.007	37.6
R^2			0.99	0.45	0.99	0.70	0.98
Cheviot only							
Sites	1	2	0.412	0.292	0.415	0.869	0.432
Trampling	3	$\overline{2}$	0.975	0.720	0.981	0.470	0.899
$S \times T$	3	6	0.387	0.700	0.329	0.298	0.387
Plots within Sites	2	16	0.000	0.068	0.000	0.017	0.000
$T \times Plots$	6	16	0.057	0.399	0.065	0.716	0.423
MS Residual	16		22.8	0.0	22.1	0.0	37.1
R^2			0.99	0.58	0.99	0.56	0.99

Notes: For each taxon, the table shows the probabilities from the ANOVA associated with tests of hypotheses, plus the residual Ms and the variance explained by the model and the degrees of freedom associated with numerator and denominator for each F ratio. Combining the degrees of freedom, P values, and Ms Residual allows reconstruction of the complete analysis table. All tests of significance were done at $\alpha = 0.05$. Significant effects are shown in bold.

TABLE 2. Extended.

Cellana tramoserica	Patelloida alticostata	Siphonaria diemenensis	Siphonaria zelandica	Bembicium nanum	Nonlimpet grazers	Limpets
0.705	0.839	0.692	0.153	0.604	0.494	0.747
0.532	0.519	0.606	0.469	0.543	0.562	0.508
0.005	0.191	0.001	0.086	0.092	0.001	0.006
0.000	0.041	0.000	0.098	0.000	0.000	0.000
0.579	0.471	0.913	0.889	0.343	0.950	0.645
3.07	2.15	1355	489	0.30		6.95
0.82	0.60	0.80	0.62	0.88	0.76	0.80
0 766	0.942	0.721	0 542	0.929	0.693	0.814
0.987	0.265	0.966	0.274	0.528	0.055	0.788
0.166	0.203	0.198	0.736	0.128	0.151	0.350
0.000	0.001	0.000	0.000	0.000	0.000	0.000
0.538	0.048	0.465	0.957	0.150	0.497	0.332
2.5	0.85	718	29.0	0.24	742	3.6
0.80	0.75	0.87	0.69	0.90	0.89	0.84
0.581	0.304	0.072	0.030	0.572	0.074	0.507
0.301	0.304	0.972	0.930	0.372	0.974	0.307
0.743	0.000	0.922	0.499	0.855	0.952	0.732
0.000	0.000	0.000	0.157	0.403	0.702	0.000
0.384	0.000	0.574	0.000	0.345	0.546	0.359
2 23	0.57	1535	29.0	0.45	1674	3 29
0.79	0.76	0.71	0.67	0.84	0.74	0.82

organisms were manifest as a Site \times Trampling or Plot \times Trampling interaction. Our conceptual model for these shores is that *Hormosira* is the habitat-forming species, and that the abundances of other organisms may track changes in *Hormosira*. To take account of variation in cover of *Hormosira*, we reanalyzed the data in the upper part of Table 2 (i.e., all three sites) as a nested analysis of covariance (Sites, Plots within Sites, and cover of *Hormosira* as the covariate, with Sites

and Plots as random effects). We found only one significant interaction between *Hormosira* cover and Site, for *Cellana tramoserica*, and no significant Plot \times *Hormosira* interaction, suggesting that the trampling effects may have been indirect responses to changes in *Hormosira*.

There were significant effects of *Hormosira* for articulated corallines, all coralline and all algae, *Patelloida, Siphonaria diemenensis,* and the nonlimpet graz-

TABLE 3. Extended.

Cellana tramoserica	Patelloida alticostata	Siphonaria diemenensis	Siphonaria zelandica	Bembicium nanum	Nonlimpet grazers	Limpets
0.735	0.527	0.670	0.638	0.102	0.775	0.639
0.027	0.313	0.181	0.182	0.253	0.152	0.044
0.894	0.430	0.355	0.684	0.396	0.388	0.805
0.062	0.004	0.000	0.000	0.119	0.000	0.006
0.570	0.017	0.094	0.913	0.099	0.124	0.187
0.932	0.276	64.0	0.781	0.100	70.7	1.604
0.52	0.78	0.78	0.64	0.75	0.77	0.68
0.720	0.669	0.750	0.530	0.147	0.820	0.696
0.029	0.562	0.377	0.547	0.509	0.197	0.047
0.917	0.249	0.236	0.467	0.272	0.520	0.862
0.003	0.008	0.000	0.002	0.095	0.000	0.000
0.035	0 744	0.007	0.921	0.116	0.027	0.029
0 188	0.172	5 37	1.00	0.119	11.0	0.266
0.79	0.60	0.93	0.63	0.77	0.90	0.85

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Level of Trampling

FIG. 3. Abundance of algae and herbivorous snails after 5 yr of trampling. The organisms are articulate coralline algae, encrusting coralline algae, the limpets *Cellana tramoserica* and *Patelloida alticostata*, the pulmonate limpets *Siphonaria diemenensis* and *S. zelandica*, the littorinid snail *Bembicium nanum*, and a group of foliose algae (Turf). Each panel on the graph shows the mean abundance, as percentage cover or number per square meter (N). Three standard error bars are shown at the lower left corner of each panel. The left bar indicates the variation among replicate strips within plots, the middle bar indicates the Plots {Site} × Trampling variation, while the third indicates the Plots {Site} variation. The middle bar is the most important for interpreting the figures, as it represents the error term used to assess the Sites × Trampling interaction. Note that encrusting coralline algae and turf algae are plotted as arcsine transformed values, and *Bembicium* data are shown as square-root transformed values. These scales represent the data used in the analyses.

	Direction	Al	l sites	Grenad	le Range	Chev	viot sites
Taxon	+/-	r^2	P	r^2	P	r^2	Р
Articulated coralline algae	+	16	0.000	73	0.000	18	0.001
Encrusting corallines	+	4	0.068	4	0.461	6	0.052
All corallines	+	20	0.000	25	0.047	21	0.000
Turf algae	-	6	0.031	11	0.202	13	0.003
All algae	+	22	0.000	41	0.007	22	0.000
Cellana tramoserica	-	35	0.000	56	0.001	23	0.000
Patelloida alticostata	_	21	0.000	31	0.024	12	0.006
Siphonaria diemenensis	_	50	0.000	61	0.000	43	0.000
Siphonaria zelandica	-	18	0.000	30	0.029	10	0.010
Bembicium nanum	_	14	0.001	9	0.269	27	0.000
Nonlimpet grazers	-	50	0.000	60	0.000	43	0.000
Limpets	_	35	0.000	52	0.002	24	0.000
Austrocochlea constricta	+	2	0.266	14	0.150	1	0.584
Derived variables							
Taxonomic richness	-0++	2	0.343	<1	0.865	13	0.040
Gastropod richness	_	3	0.237	12	0.189	2	0.418
Total individuals	_	57	0.000	60	0.000	52	0.000
Log (individuals)	_	64	0.000	73	0.000	65	0.000
H'	+-+‡	2	0.381	20	0.082	15	0.026

Note: Significant effects are shown in bold.

† Overall negative effect, weak positive at Grenade Range, negative at Cheviot sites.

‡ Overall positive, negative at GR, positive at Cheviot.

ers and limpets. Simple regressions of the abundance of each of these taxa against Hormosira cover at the time of the census were used to indicate the direction of the effects. These regressions were significant for most taxa, although the strong relationships were with cover of articulate coralline algae, Cellana, Patelloida, Siphonaria diemenensis, and the composite grazing categories (Table 4). We also analyzed Grenade Range and the two Cheviot sites separately, and relationships were generally stronger at Grenade Range than Cheviot (Table 4; paired t test using r^2 values for each taxon, t = 3.12, df = 12, P = 0.009). At Grenade Range, there were particularly strong effects of Hormosira cover for articulate coralline algae, Cellana and Siphonaria diemenensis. Cover of both kinds of coralline algae (and the pooled variables total coralline and total algae) varied positively with Hormosira cover, as did the abundance of the herbivorous snail Austrocochlea constricta, whereas the slopes of the regressions were negative for turfing algae and all other herbivorous snails (Table 4).

Trends in the derived variables also became clearer with the analysis of covariance. The Site \times Trampling effects on the number of individuals disappeared, and there was a very strong overall effect of *Hormosira* cover (Fig. 4). There was no effect of algal cover on either taxonomic or gastropod richness, and, interestingly, a positive effect of *Hormosira* on H' at the Cheviot sites and a (nonsignificant) negative trend at Grenade Range (Table 4).

Historical effects of trampling

We found few strong effects of history. We analyzed the cover of *Hormosira* at three times (pre- and postsummer of 1995–1996, and postsummer 1994–1995), and considered the temporal profiles using a repeatedmeasures analysis. Over that time period, we did not find even a significant effect of trampling (see Table 5), with only a marginally nonsignificant main effect of trampling after summer of 1995–1996 even hinting at a change. There was significant variation through time and among plots, but all effects involving history (i.e., the main effect, plus the interactions with time and trampling) were far from significant (Table 5). The lack of a significant effect did not appear to be a result of low power; rather, plots with the three different histories of trampling showed very similar patterns (Fig. 5).

The censuses of other plants and animals after 5 yr also showed little effect of history. There were no significant simple effects of history, and only a single interaction with trampling, for encrusting coralline algae (Table 2). Main effects of history would be difficult to identify, as we found substantial variation among replicate plots, the level of variation used for assessing this main effect. The test of the History \times Trampling interaction, however, had 6 and 15 degrees of freedom, and there was little variation among plots in the effect of trampling. The Plots \times Trampling interaction was used to test the History \times Trampling term. The mean abundances of the major taxa showed no hint of an effect, with the plots with no history having the highest means for some taxa, while plots with the longest history of trampling were greatest for other taxa (Fig. 6). Even the one taxon showing a significant effect, the encrusting coralline algae, did not have a pattern of means that could be easily interpreted with respect to the effects of history or trampling (Fig. 6).



FIG. 4. Variation in derived variables listed on Table 6, plotted as a function of *Hormosira* cover. On each panel, the three symbols indicate main sites (squares are Grenade Range, and triangles and stars represent the two Cheviot Platform sites). Filled and unfilled symbols identify the two plots at each site, and each point is a replicate strip.

Source of variation	df (num.)	df (denom.)	Postsummer 1994–1995	Presummer 1995–1996	Postsummer 1995–1996	All data (repeated measures)
History	2	5	0.791	0.848	0.871	0.849
Trampling	3	15	0.583	0.659	0.062	0.273
History \times Trampling	6	15	0.795	0.589	0.758	0.565
Plots within Histories	5	32	0.000	0.325	0.094	0.015
Trampling \times Plots	15	32	0.771	0.930	0.763	0.912
MS Residual	32		405.2	337.2	243.3	774.3
r^2			0.61	0.34	0.48	
Repeated measures analysis: within-s	trips effec	ts				
Time	2	10				0.016
Time \times History	4	10				0.917
Time \times Trampling	6	30				0.536
Time \times History \times Trampling	12	30				1.000
Time \times Plots within Histories	10					0.000
Time \times Trampling \times Plots	30					0.459
Time \times мs Residual	64					105.6
r^2						0.70

TABLE 5. Effects of history of trampling on *Hormosira banksii*. The table shows the results of analysis of variance of the percentage cover of *H. banksii* at each of three times (upper panel), together with a repeated measures analysis examining all time simultaneously (lower panel).

Notes: Probabilities are shown, with significant effects (at $\alpha = 0.05$) shown in bold. The multiple r^2 is shown for each analysis, and for the repeated measures, the r^2 was calculated by treating the two residual (MS Residual and Strips MS Residual) terms as unexplained variation.



FIG. 5. Effects of history of trampling on the percentage cover of *Hormosira banksii*. Each panel shows the mean cover of *H. banksii*, pooled over plots at the two Cheviot platform sites, against the level of trampling, and data are shown for three censuses. Error bars are shown in the corner of each panel, calculated as described in Fig. 3.

The community variables also showed no effect of history, whether we examined taxonomic or gastropod species richness, total numbers of animals, or diversity of the animals (Table 6).

DISCUSSION

Anthropogenic disturbances and Hormosira

For this intertidal system, a series of repeated pulse disturbances did not consistently produce either a pulse or press response. At our two Cheviot sites, each disturbance pulse produced a response, but recovery generally occurred over the following 8–9 mo, so we saw essentially a series of pulse responses. After six summers of trampling, we found no strong effect of repeated disturbances, and certainly no cumulative effect. In contrast, the series of pulses at Grenade Range resulted in a rapid decline in the dominant alga and little recovery, a press response. At all sites, there was a relationship between change in algal cover and intensity of disturbance, but nowhere did increasing intensity of disturbance cause a shift from a pulse to a press response. There was no hint of any "intermediate" effect of disturbance (Connell 1978, Lubchenco 1978); trampling at intermediate levels produced results that were intermediate, and there was no hint of a peak in measures of diversity at intermediate levels.

Why were the effects different at the three sites? We found strong variation among sites in the effect of trampling, but little variation in the effects of trampling at the level of plots, suggesting that variation in responses to disturbance is determined by habitat variation at larger spatial scales. All three sites and all plots were on horizontal sections of rock platform, and were at approximately the same height on the shore. Our impression was that the Grenade Range site was slightly more exposed to wave action, but we expected any difference to reduce the levels of desiccation, and make the algae more, rather than less resilient. It is difficult to identify a cause of this variation; at the largest spatial scale, we had only three replicate sites, and to correlate the sensitivity of a site with environmental variables (e.g., coastal geomorphology, height, orientation, and other factors) would require data from many more sites. Our study was designed to assess variation among sites in general, rather than focusing on these three precise locations (hence sites as a random factor in the analyses).

Another primary aim of our study was to identify "thresholds" of disturbance, levels of trampling that could be sustained, but beyond which recovery was incomplete. Again, we did not reach a simple conclusion, but instead have shown increased complexity in the relationship with intensity of disturbance (level of trampling). At the two Cheviot sites, there was a relationship between the intensity of disturbance during those summers when trampling had a strong effect. In other years, we found little effect of trampling, and hence no relationship between intensity and change in algal abundances. In contrast, there was clear evidence of a nonlinear relationship between intensity of disturbance and algal cover at Grenade Range: intense disturbances produced a very large change, but the two intermediate levels (5 and 10 passages/day) produced very similar patterns of algal abundance, and resulted in Hormosira cover being intermediate between undisturbed and heavily disturbed areas.

Were the effects of trampling on other species direct or indirect?

The changes in the abundances of other organisms seemed not to happen at the same time as changes in *Hormosira*. After three summers, few species showed strong effects, even though there had been considerable changes in *Hormosira* cover by that time. These species

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FIG. 6. Effects of history of trampling on the abundance of algae and herbivorous snails. The species are described in the caption to Fig. 3. Each panel shows the mean abundance of the taxon for four levels of trampling and three histories. The error bars are the first two bars described in Fig. 3.

may have been directly affected by trampling, but just responded more slowly (and positively in some cases!), but our results for herbivorous snails are consistent with short-term trampling experiments on the platforms at Cheviot Beach. Povey and Keough (1991) found that increases in the densities of herbivorous snails occurred some time after the cessation of trampling in *Hormosira* mats, suggesting a response to the removal of macroalgae, rather than a direct effect of feet. They repeated their experiments in areas lacking macroalgae, and found little direct effect on gastropod abundances, although their test may not have been sensitive because of the likelihood of movement of individuals between experimental and surrounding areas. Supporting evidence is provided by our analyses of the 1995 census in which we replaced the level of trampling with the cover of *Hormosira*, and found that the interactions between trampling and space (sites, plots) disappeared. TABLE 6. Analyses of derived variables after five years of trampling, highlighting effects of trampling at all three sites and at only the two sites on Cheviot Beach platform. The variables were taxonomic richness (S), species richness of gastropods (S_{east}) , numbers of animals (raw and log-transformed), and Shannon-Wiener diversity (H').

Trampling	df	df (denom)	5	<u> </u>	N	Log N	H'
maniphing	(IIuIII.)			D gast			
Overall (all sites)							
Sites (S)	2	3	0.719	0.492	0.508	0.678	0.883
Trampling (T)	3	6	0.730	0.872	0.555	0.785	0.814
$S \times T$	6	9	0.071	0.331	0.001	0.019	0.507
Plots within Sites	3	24	0.003	0.027	0.000	0.000	0.000
$T \times Plots$	9	24	0.873	0.826	0.946	0.913	0.688
мs Residual	24		2.063	1.438	2956	0.112	0.262
R^2			0.6	0.5	0.8	0.7	0.7
Cheviot only							
Sites	1	2	0.698	0.450	0.703	0.839	0.721
Trampling	3	2	0.387	0.175	0.948	0.545	0.990
S×T	3	6	0.078	0.746	0.162	0.367	0.498
Plots within Sites	2	16	0.000	0.008	0.000	0.000	0.000
$T \times Plots$	6	16	0.934	0.555	0.486	0.719	0.460
мs Residual	16		1.406	1.063	800.1	0.104	0.246
R^2			0.71	0.64	0.89	0.76	0.75
Historical effects							
History	2	5	0.564	0.318	0.978	0.964	0.309
Trampling	3	15	0.190	0.039	0.939	0.977	0.574
History \times Trampling	6	15	0.089	0.116	0.688	0.518	0.682
Plots within Histories	5	32	0.000	0.002	0.000	0.000	0.000
Trampling \times Plots	15	32	0.913	0.909	0.545	0.827	0.572
MS Residual	32		1.797	1.5	1750	0.114	0.214
R^2			0.69	0.65	0.75	0.68	0.78

Notes: The table also shows the results of analyses to assess the effects of a history of trampling for Cheviot platform. For each variable, the table shows the probabilities from the ANOVA associated with tests of hypotheses, plus the residual Ms and the variance explained by the model and the degrees of freedom associated with numerator and denominator for each F ratio. Combining the degrees of freedom, P values, and Ms Residual allows reconstruction of the complete analysis table. All tests of significance were done at $\alpha = 0.05$, and significant effects are shown in bold.

Our interpretation is that, for the other animals, we were not seeing spatially variable direct effects of trampling, but *spatially consistent* indirect responses to the loss of *Hormosira* canopies. The abundances of a range of common herbivores were correlated negatively with the cover of *Hormosira*. The weakest relationship was with the pulmonate limpet *Siphonaria zelandica*, which occurs in small, wet depressions on the rock surface. These depressions occur independently of the presence of *Hormosira*. In general, the animals in trampled areas were established individuals, so increased abundances were the result of migration, rather than settlement.

Algal responses varied; we found positive correlations between *Hormosira* and the two groups of coralline algae, and negative correlations with the abundance of fleshy turfing and encrusting algae. We can not determine whether the effect on articulated coralline algae was direct or indirect. It was seen only at Grenade Range, where losses of *Hormosira* were most severe. These algae form dense mats on the seaward, more exposed edges of the platforms, where *Hormosira* is absent (Povey and Keough 1991), so they are not associated obligately with *Hormosira*. Povey and Keough ran short-term trampling experiments in areas at Cheviot Beach dominated by coralline algae, and a decline in coralline algae only under very intense trampling. However, we have frequently observed bleaching events, in which coralline algae lose pigment and fragment, usually after midday low tides on very hot summer days. It is possible that *Hormosira* canopies ameliorate these effects. Algal turfs were weakly, but negatively, correlated with the presence of *Hormosira*, but again, we can not determine whether this result reflects direct or indirect effects. *Hormosira* may compete with some species in this category, either by direct shading or by preempting recruitment, and its removal could allow some of these algae to establish before the immigration of herbivores. We have no direct experimental evidence to address these possibilities.

Our results from the two Cheviot sites emphasize the value of long-term studies. After two years, which is a long time for ecological experiments, the change in *Hormosira* cover was consistent with a long-term decline, with incomplete recovery of the trampled plants and increasing levels of damage in the second year. Had we terminated the experiments at that stage, we would have concluded that repeated pulse disturbances produce a press response at higher intensities of disturbance. Continuing the experiments over the next few years saw any such trend vanish. The relatively few other long-term studies on marine hard substrata have also found that results from one or two years are not necessarily representative of patterns over longer time

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periods (Dayton et al. 1992, Connell et al. 1997), a finding consistent with other habitats.

We found no significant effect of a prior history of trampling on the sensitivity of Hormosira to a new season's trampling, nor was there any effect on associated organisms. We do not regard the two attempts at this experiment, in the third and fifth summers, as conclusive, however. In the first attempt, the summer was very mild, and plants may not have been stressed (see Discussion: Natural disturbances), and trampling had only a weak effect on any plot at Cheviot Beach. In our second attempt, with three levels of history, a major natural disturbance overrode any effects of trampling. When there is only a weak effect of trampling in any plot, our ability to detect differences in responses among plots with different histories will be restricted severely. It is possible that some strong historical effects would have been apparent, had they occurred, so we regard our nonsignificant result with caution. We view these results with some additional caution because, despite the relatively long-term nature of this study compared to most experiments, it is possible that historical effects develop over very long time scales (10s to 100s of years), especially if they involve genetic adaptation in a long-lived perennial plant such as Hormosira. In this case, historical effects will be very difficult to detect. Perhaps more interestingly, a history of trampling did not affect the plants' responses to the natural disturbance in 1994-1995, suggesting that the plants' resistance had not been altered by trampling. The history treatments do show that the increased effects of trampling shown in the first 2 yr at Cheviot Beach represent year-to-year variation in effects of trampling, and we can refute the hypothesis that plants are initially affected strongly, but then become more resistant.

Natural disturbances

The cover of Hormosira also changed naturally, as seen in the trajectories of control plots. The most obvious source of natural disturbances that we have observed is burnoff, in which large sections of plants turn brown, shrivel, and break off. In most summers, there is some reduction in cover from this cause, but occasionally there are severe events that result in large changes. King (1992), for example, reported a burnoff in the Bunurong Marine Reserve, ~80 km east of our sites, in which some plots fell by $\sim 70\%$ as the result of a single hot day. In southeastern Australia, there are mixed semidiurnal tides, and the lower of the pair of low tides occurs in the daytime in summer and at night in winter, in contrast to many areas of North America. As a result, summer low tides are likely to be physiologically stressful. The dominant weather systems in southern Australia are fronts that travel rapidly eastwards, and can have significant effects on tidal exposure. As a high pressure system moves across, the winds become northerly, and the combination of off-



FIG. 7. Changes in *Hormosira* cover in untrampled areas over each of six summers. The graph shows three panels, one for each site, and on each panel, bars show the mean change in cover for two replicate control areas on each plot, with differently shaded bars representing replicate plots. Note that the two rightmost bars in each cluster are plots from the history of disturbance treatment. They were recorded for a limited number of summers.

shore winds, high temperatures, and locally high atmospheric pressure results in lower than predicted tides, and consequently greater duration of exposure of animals and plants at low tide. When these weather events coincide with new or full moons and midday low tides, exposure increases further. Disturbances may also come from wave action, which occasionally tears up plants, or from deposition of sand, but our subjective impression is that these two sources are much less common than burnoff.

To examine these natural changes, we replotted all data from untrampled areas to show the change in cover that occurred each summer. Over the six summers at Pt Nepean, the change in algal cover varied greatly, and the pattern of changes over that period varied on large (among sites) and small (among plots) spatial scales (Fig. 7). We have so far observed one major burnoff (1994–1995), two years in which little change occurred over summer (1992–1993 and 1995–1996), and three years with overall declines over the summer (1990–1991, 1991–1992, and 1993–1994).

What causes variation among years? The biggest changes occurred in 1994-1995, and were associated with a burnoff that occurred in early October. They resulted from a single day of unusually hot spring weather, and plants immediately began to turn brown. Our estimates of that change were underestimates because some loss of tissue had occurred before our first sample that year. To understand some of the variation among years, we obtained climate records over the time period of our experiment, including daily maxima from a weather station on Phillip Island, 50 km to the east, and hourly tidal records from Pt. Lonsdale, 5 km west of Pt. Nepean. We designated 28°C as a hot day, corresponding approximately to the 90th percentile of summer maxima. For each hot day, we identified the time of daytime low tide. We could also calculate the number of hourly recordings for which our sites were exposed, using 0.5 m above MLLW as the tidal height at which the platform was first exposed. The duration of exposure ranged from 0 to 7 h, with the most frequent durations being 3, 4, 5, and 6 h (19, 16, 34, and 17% of days, respectively). The number of such hot days varied dramatically between summers, as did the number of days on which high temperatures and midday low tides coincided (Fig. 8). The hottest summer was 1994-1995, with 11 such days. Interestingly, there were only three spring days over the whole period when the maximum temperature exceeded 28°C; on one day, the platform was barely exposed, but the other occasions were consecutive days in October 1994 (see Fig. 8). The predicted low tide was not low enough to expose the platform, but the actual low tide was 20 cm lower than predicted on those days. In contrast, in 1995-1996 most plots showed an overall increase over the summer (Fig. 7), and the summer of 1995-1996 was unusually mild, with relatively humid weather and high rainfall, a mean daily maximum temperature close to the long-term average, but no hot days with midday low tides. The other years varied; there were only three hot midday tides in 1991-1992, and on those days, the temperature did not exceed 30°C. However, the platform was exposed for six or more hours on each event. In 1992–1993 there was only one occasion when very hot days were accompanied by midday low tides. The other hot period did not coincide with a low tide. In 1993-1994, there were four exposure periods, but only one coincided with temperatures $>30^{\circ}$ C. These observations of weather events are broadly consistent with changes occurring in control plots in those years.

The three sites showed different patterns through time, but not in any consistent manner (Fig. 7). We have already dealt with our inability to explain the different responses of the sites to trampling, and the same limitation applies here. A research priority is, therefore, to describe mesoscale changes in algal beds, most likely through remote sensing, and to correlate the changes with properties (e.g., aspect, slope of shore) of individual platforms. The small-scale patchiness in the effects of natural disturbances was striking; a given event, such as the 1994–1995 burnoff, did not have effects that were uniform over whole platforms. Rather, a group of apparently similar plots might show very different responses (e.g., Cheviot Mid, 1995, Fig. 7). Variation among plots was common to all years; even when conditions were favorable or slightly unfavorable (e.g., 1996 and 1991, Fig. 7), individual plots varied widely. We have no clear explanation for this variation; plots were established on apparently uniform sections of *Hormosira*, with little vertical relief and consistent plant cover.

Natural vs. anthropogenic disturbances

A central question about anthropogenic activities, whether they act as physical disturbances or predation, is the extent to which they represent selective pressures at novel spatial and/or temporal scales, rather than just changes in the frequency of existing comparable natural events. On these rocky shores, natural disturbances happen in some years, but not others. Over the 5-6 yr of our study, they did not happen at a predictable time of year, although they were concentrated between late spring and early autumn. A particular combination of weather conditions, i.e., a disturbance of a particular apparent intensity, has effects that are variable on at least two spatial scales.

In contrast, disturbances from trampling occur regularly; on these shores, there are low levels of visitation during autumn, winter, and parts of spring, when weather conditions are less pleasant, and suitable low tides occur more often at night. There is a predictable rise in visitation in summer, and different rock platforms may have consistent rank orders of their levels of visitation (King 1992; M. J. Keough and G. P. Quinn, *personal observations*). The effects of an experimentally controlled level of trampling were very patchy at the level of whole rock platforms. A constant level of disturbance applied to plots separated by 50–100 m produced similar results, and there was little variation between replicate strips up to 8 m apart.

Anthropogenic disturbances, then, show quite different patterns of temporal and spatial predictability from natural ones. Perhaps more importantly, the effects of these disturbances on the dominant algae show quite different scales of spatial variation.

Our conceptual model of these platforms, from our work and that on eastern Australian shores by Underwood and colleagues (Underwood 1980, Underwood and Jernakoff 1981, 1984, Underwood and Kennelly 1990), is that established *Hormosira* mats are true habitat formers; they offer damp, shaded refuges to some plants and animals (G. P. Quinn, M. J. Keough, and N. Gust, *personal observations*), at the same time reducing microalgal abundances on rock surfaces (Underwood and Jernakoff 1981, 1984). Reductions in microalgal abundance result in mobile herbivores emigrating. As the cover of *Hormosira* is reduced, there are higher



FIG. 8. Physical conditions during the period of the experiment. The figure shows, for each spring-summer period, daily maximum temperatures from 1 September through 31 March. The horizontal line on each panel indicates 28°C, and symbols above a particular temperature value indicate that a low tide of a height sufficient to expose the rock platform occurred between 1100 and 1500 on that day. Numbers adjacent to the symbols indicate the number of daylight hours that the sites were exposed.

standing crops of microalgae, the primary molluscan food source (Underwood 1979, 1980, 1984, Creese and Underwood 1982), leading to increased densities of herbivores. Underwood and Jernakoff (1984) suggested that newly recruited macroalgae are vulnerable to herbivores, and at Cheviot Beach, a range of snails can reduce microalgal standing crops (Keough et al. 1997; B. Burton, *personal communication*). Established *Hormosira* plants appear to have few or no predators, are not colonized extensively by other sessile organisms, and probably can only be removed by disturbance or senescence. Their ability to regenerate from the holdfasts suggests that they may be very long-lived, and we have marked plants that have survived for 5 yr and were mature when tagged. Underwood and Jernakoff's hypothesis was that areas free of macroalgae and dominated by molluscs and areas dominated by macroalgae are alternative community states. *Hormosira* can take over bare areas, but herbivores can not cause the reverse change. Any process that removes *Hormosira* February 1998

mats or, in the case of anthropogenic effects, that increases the rate of disturbance, can have persistent effects. *Hormosira* may be viewed as a keystone (sensu Paine 1995) in this intertidal system, or even an autogenic engineer (Jones et al. 1994).

Management implications

Our results have implications for marine conservation, but also for environmental impact monitoring. The most important implication for monitoring is the difference in sensitivity of these algal mats. These plants are sensitive to trampling, but there is not a critical level of trampling that is sustainable. Rather, individual shores separated by only a few kilometers may be very different. Natural disturbances show similar mesoscale variation in their effects. King (1992) examined the ability of Hormosira plants in the Bunurong Marine Reserve to recover from an intense disturbance (a reduction in percentage cover to 5%). She found that the rate of recovery also varied between sites separated by a few kilometers, but, as with our study, was unable with only three sites to correlate resilience with environmental variables.

These combined results suggest a few options for management of marine reserves that receive many visitors (Keough 1996). At the moment, there is the potential for severe damage, but no way of predicting the sensitivity of an individual rock platform. One might acknowledge this limitation, and zone marine reserves into high and low access areas, and be prepared to tolerate some damage to high access areas, while maintaining low access areas in a more natural state. If they could be identified, it would be desirable to designate resistant areas, such as Cheviot Beach, as high access. Such an option would require little ongoing management. Alternatively, one could rotate areas, opening some to visitors and closing others. The "open" and "resting" times for an area would need to be designated conservatively, choosing the times for sensitive areas that had low resistance and low resilience. Such a management scheme would require ongoing management action, to open and close access tracks, but would not require ongoing monitoring. The third alternative would be to open most areas to access, but close them if any signs of damage became apparent. This method would recognize the variation among shores, but would require continuous monitoring to detect declines in algal beds and respond to them. Such an option also requires monitoring of low-access areas as controls, to distinguish changes caused by visitor access from those that reflect natural disturbances. It may be possible to monitor large areas of coastline using remote sensing, and to detect changes at a range of areas.

Hormosira is sensitive to other human activities, such as sewage discharge (Brown et al. 1990, Fairweather 1990), and has been developed as a bioassay species for toxicants from pulp mills and the petroleum industry (Gunthorpe et al. 1995). It has also been recommended as a suitable indicator for routine coastal monitoring (Quinn and Keough 1993). Our present results suggest some caution, however. With variation in sensitivity of beds on different rock platforms, a monitoring program could be influenced by the chance designation of an unusually sensitive or resistant site as a control or impact location. Such a problem would be reduced by the use of multiple control or impact areas, but at the very least, the variation documented here would increase the background variation in the system, and most likely would result in a given "impact" having a variable effect. Glasby and Underwood (1996) have suggested that detection of pulse and press disturbances requires more sophisticated sampling designs than are often used. Our results suggest that both may be plausible responses for a single species, so monitoring designs may require additional complexity.

On shores of southeastern Australia, other recreational activities affect intertidal biota. Harvesting of molluscs in the intertidal and shallow subtidal has strong direct (Keough et al. 1993) and some indirect (Marshall and Keough 1994, Sharpe and Keough 1997) effects near Melbourne, the major urban center. On those shores, there are no extensive algal canopies, so trampling is of little concern. In contrast, we have found only very weak effects of harvesting along the coastline used in the present study (G. P. Quinn, M. J. Keough, and N. Gust, *personal observations*) or in areas to the east (King 1992). Trampling seems potentially more important than harvesting along these coastlines.

Elsewhere in the world, harvesting has severe effects on the biota of rocky shores of South Africa and South America (reviewed extensively in Siegfried 1994). Trampling has received much less attention, with only a handful of studies, which vary in their design (Beauchamp and Gowing 1982, Brosnan and Crumrine 1994). In particular, it has received little attention in those areas where harvesting has such striking effects, such as Chile and the Transkei region of South Africa (Siegfried 1994), and it is difficult to imagine that any effects of trampling could rival these impacts.

For rocky shores of southeastern Australia, we cannot classify disturbances from pedestrian traffic simply as pulse or press. Some physical processes take the form of repeated pulses, not only on rocky shores, but in other habitats (Lake 1990, Riffell et al. 1996). Such pulses do not necessarily produce simply a press or a pulse response, but the response may vary between apparently similar habitat patches, and a press-pulse split is too simple for many situations. Further complications could occur if pulses occur at random, rather than regular intervals, or if there is a lag between a pulse of disturbance and the response of the organisms. An appropriate theory of disturbance for this system, then, must deal with the spatially heterogeneous effects of natural pulse disturbances, which do not occur predictably in time, but also must describe the highly variable responses to a constant level of periodic anthropogenic disturbances.

Acknowledgments

This work was supported by grants from the Australian Research Council. The National Parks Service gave us permission to work at Pt Nepean, without realizing how much damage we'd do. Various people helped with the field work, including Nick Gust, Michael Holloway, Laura Stuart, Michael Shirley, Jim Radford. We greatly appreciate all their efforts, particularly those of Nick Gust. Air temperature data were provided by the Australian Bureau of Meteorology and tide information was provided by the National Tidal Facility. The manuscript benefited from comments by Sam Lake and Barbara Downes, and we appreciate discussions with them and Joe Connell. Peter Petraitis and an anonymous reviewer provided helpful suggestions.

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