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Effects of human trampling on marine rocky shore communities

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Abstract

The effects of human trampling on two marine intertidal communities were experimentally tested in the upper-shore algal-barnacle assemblage and mid-shore mussel bed communities. On two shores, we trampled experimental plots 250 times every month for a year, and then allowed plots to recover for a further year. Results from the upper shore community showed that foliose algae were susceptible to trampling, and suffered significant declines shortly after trampling started. Canopy cover remained high in untrampled control plots. Barnacles were crushed and removed by trampling. Algal turf was resistant to trampling, and increased in relative abundance in trampled plots. In general the algal-barnacle community recovered in the year following trampling. In the mussel bed community, mussels from a single layer bed were removed by trampling, By contrast, mussels at a second site were in two layers, and only the top layer was removed during the trampling phase. However, mussel patches continued to enlarge during the recovery phase, so that by the end of the second year, experimental plots at both sites had lost mussels and bare space remained. Mussel beds did not recover in the 2 years following cessation of trampling. Control plots lost no mussels during the trampling and recovery phase. Barnacle and algal epibionts on mussels were significantly reduced by tramping. Overall, trampling can shift community composition to an alternate state dominated by low profile algae, and fewer mussels.

Key words: Alga; Barnacle; Disturbance; Epibiont; Human impact; Mussel; Rocky Shore; Trampling

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1. Introduction

The last decade has seen increased interest in human impact on intertidal areas. Studies have focused on harvesting (e.g. Moreno 1984; Castilla & Duran, 1985; Olivia & Castilla, 1986; Ortega, 1987; Castilla & Bustamente 1989; Duran & Castilla, 1989; Godoy & Moreno, 1989; Underwood & Kennelly, 1990), and more recently on trampling (Zedler, 1976, 1978; Beauchamp & Gowing, 1982; Ghazanshai et al., 1983; Cole et al., 1990; Kingsford et al., 1991; Povey & Keough, 1991; Brosnan & Crumrine, 1992a,b; Brosnan, 1993). Trampling is an important ecological phenomenon on many shores, and its effects are likely to increase as use of shore areas increases.

Effects of trampling have been studied in terrestrial systems since 1917 (Jeffreys, 1917; Shantz, 1917). Bates (1934, 1935) began the systematic study of trampling effects on terrestrial habitats. Since then numerous studies have shown trampling to be detrimental in alpine meadows, forests, and sand dunes (e.g. Burden & Randerson, 1972; Liddle, 1975; Hylgaard & Liddle, 1981; Nickerson & Thibodeau, 1983). In marine systems, repeated surveys of rocky intertidal communities near areas of dense human population indicated that marine communities had changed as population density increased (Widdowson, 1971; Boalche et al., 1974; Thom & Widdowson, 1978). More recent studies have confirmed that human impact can affect marine communities. For example, certain algal and bivalve species normally common on rocky shores have been found to be rare in heavily visited sites (Beauchamp & Gowing, 1982; Povey & Keough, 1991; Brosnan & Crumrine, 1992a,b; Brosnan, 1993).

In this paper we address the effect of human trampling on rocky intertidal areas on the Oregon coast of the Pacific Northwest, USA. We carried out an experimental study of trampling and looked at post-trampling recovery. Our interest in this is twofold. Trampling may change community composition and diversity, and hence is of concern to ecologists, conservation biologists, and managers of shore areas. Secondly, Pacific rocky shores are well studied, and abiotic disturbance is an important structuring force in this community (Harger, 1970; Harger & Landenberger, 1970; Dayton, 1971; Sousa, 1979, 1984a,b, 1985; Suchanek, 1978, 1979, 1981; Paine & Levin, 1981; Farrell, 1989). Trampling, because it removes biomass and alters space utilization, is a disturbance. We compare the effects of trampling with other disturbances such as log damage and wave shear.

Trampling affects marine organisms in a variety of ways:

- Directly, by removing all or part of an individual through crushing and dislodgement, or by weakening attachment strength, which increases the risk of dislodgment during storms.
- (2) Indirectly, by removing other species that interact through competition, predation, or habitat provision. For instance, mussels *Mytilus californianus* Conrad provide a habitat for more that 300 matrix species (Suchanek, 1978). We hypothesized that these effects would cause changes in both community composition and susceptibility to storm damage.

The effects of human trampling were studied in two exposed rocky intertidal

communities: the upper shore barnacle-algal assemblage, and mussel beds in the mid-intertidal zone. In mussel beds we studied the organisms occupying primary space, (mussels and gooseneck barnacles), and also those occupying secondary space (epibionts on mussels).

2. Methods

2.1. Study sites and communities

Trampling experiments were conducted at two sites on the Oregon coast: Fogarty Creek (44.51° N:124.03° W) and Little Whale Cove (44.20° N:124.05° W). Both sites consist of exposed rocky (basalt) platforms. Algal-barnacle and mussel communities were found on slightly sloping surfaces. We chose these sites because human access to them is restricted, and we did not want existing trampling to confound our results. It is necessary to cross private property to reach the shore from land, and heavy surf prevents access by boat. In addition, these sites are similar in exposure and substrata to other shores on the Oregon coast where trampling is more intense (Brosnan & Crumrine, 1992a,b). Apart from other marine biologists, humans were rarely present when we visited these sites. At each site we set up experiments to look at the effect of human trampling on two communities.

2.1.1. Uppershore algal-barnacle assemblage

Rock surface on the upper shore is occupied by a variety of sessile invertebrates and algae. These include acorn barnacles (*Semibalanus glandula* Darwin and *Chthamalus dalli* Pilsbry), small mussels (*Mytilus californianus*, and *Mytilus trussolus* Gould), mussel recruits, and a variety of algal species including fucoids, *Pelvetiopsis limitata* (Setchell) Gardner *Fucus distichus* Linnaeus; and red algae *Iridaea cornucopiae* Setchell and Gardner, *Mastocarpus patillatus* Kutzing, and *Endocladia muricata* (Postels and Ruprecht) J. Agardh). In this part of the shore, no one algal species was dominant. *Endocladia muricata* grew as both a canopy (tall and upright growth form) and a turf-like species. The remaining algae are foliose canopy forming species. Mobile herbivores such as limpets (*Colisella digitalis* Lindberg, *Lottia strigatella* Eschoscholtz, and *Lottia pelta* Eschoscholtz), and snails (*Littorina scutulata* Gould) are common, but were not studied in this experiment.

2.1.2. Mussel bed community

Primary space. Primary space in the mid-intertidal zone is dominated by mussels *Mytilus californianus*. Mussels form dense beds of one to many layers which provide habitat for many invertebrate and algal species (Suchanek, 1978). Logs and winter storms dislodge mussels and create patches of bare space (e.g. Harger, 1968; Dayton, 1971; Harger & Landenberger, 1979; Sousa, 1979, 1984b, 1985; Paine & Levin, 1981). In our study areas, mussels occupied about 95% of the primary space, and gooseneck barnacles (*Pollicipes polymerus* Sowerby) covered the remaining 5% (there was no bare

space). The Fogarty Creek experimental mussel bed was two layers thick; mussels were tightly packed, and it was difficult to move any individual mussel. The mussel bed at Little Whale Cove was a monolayer, and mussels were less tightly packed than at Fogarty Creek.

Epibionts on mussel shells. Mussels outcompete algae and other sessile invertebrates for primary space on rocky shores (Paine, 1966, 1974; Dayton, 1971; Paine & Levin, 1981). Many of these competitively subordinate species subsequently settle on mussel shells and persist as epibionts (Lee & Ambrose, 1989). Because these epibionts protrude from the bed, they may be more vulnerable to the effect of trampling. Barnacles *Semibalanus glandula*, and *Chthamalus dalli* are the main invertebrate epibionts on mussel shells. These were abundant on mussels at both sites. *Endocladia muricata*, a common algal epibiont on mussel shells in Oregon (Brosnan, 1990, 1992), was common on Little Whale Cove mussels but was rare on mussels in Fogarty Creek plots.

2.2. Experimental design

The effects of trampling on intertidal communities were tested using a randomized block design. At each site we set up four blocks in the algal-barnacle assemblage (from about +2 to +2.5 m above mean low water (MLLW)), and four blocks in the mussel bed community (from about +1 to +1.5 m above MLLW). There were two treatments per block, trampled and non-trampled controls. These were randomly assigned to plots within each block. Trampled and non-trampled plots within a block were separated by 0.5 m. Algal-barnacle plots measured 20×20 cm and plots in the mussel bed were 20×30 cm. The corners of each plot were marked with unleaded model paint. Mussels in each plot were individually marked with a spot of non-toxic paint, and counted at the beginning of the experiment. We trampled the experimental "trample" plots 250 steps on one day every month, from March 1990 to March 1991. Trampling consisted of walking across an experimental plot. We selected this intensity from studies of humans visiting nearby shores, where up to 228 steps per h were recorded (Brosnan & Crumrine, 1992a,b). Two hundred and fifty steps per month represents a low disturbance at these two shores.

2.2.1. Recovery

Recovery of experimental plots was monitored in July 1991, September 1991 (6 months after trampling stopped) and again in April 1992 (one year after trampling).

2.3. Data collection and statistical analysis

Data were collected on percent cover of primary space, bare space, secondary space (epibionts) and canopy species. Percent cover of each species was estimated by placing a clear vinyl sheet, marked with 100 randomly placed dots, directly over the plot. The number of dots directly over a species was counted. For algae and barnacles, primary percent cover was defined as the percent of the substratum on which a species is directly attached. Algal canopy was defined as the percent of the rock surface

that a non-encrusting alga covers, although it may not be attached at that particular point. For mussels and goose-neck barnacles, percent cover was defined as the percent of rock surface covered by a species. We did not distinguish between the two species of acorn barnacle (*Chthamalus dalli* and *Semibalanus glandula*) since many individuals were too small to be identified. Data were collected on epibiont abundance by estimating the percent cover of epibionts on 10 randomly chosen mussels in each plot. For each mussel, the number of dots on a mussel-shaped vinyl sheet that were directly above a species was counted. We collected data on epibionts on all plots prior to trampling. Subsequently, we collected data monthly from April to July 1990 only, because mussels were lost due to trampling after July 1990. Initial pre-trampling data were collected from all plots.

Data were arcsine or log transformed to reduce heteroscedasticity (Sokal & Rohlf, 1981) and analyzed by ANOVA using SYSTAT (Systat Inc. Evanston, IL). Transformations did not eliminate heteroscedasticity in primary mussel cover data during the trampling phase of the experiment. Consequently, these data were analyzed using a non-parametric Kruskal-Wallis test. Initial pre-trampling data were analyzed to check for statistically significant differences between treatment and control plots prior to trampling. Data from each sampling period were analyzed separately to detect if and when statistically significant differences began and ended.

3. Results

3.1. Algal-barnacle assemblage

3.1.1. Algae

Algal canopy was high at both sites at the start of the experiment (Fig. 1). For both sites combined, there was no difference between algal cover in trampled versus untrampled plots at the beginning of the experiment (F = 0.014, p = 0.091, df = 1). Total canopy was similar on all trampled plots (mean = 81.7%, sE = 3.6) and on all control plots (mean = 80.2%, sE = 4.7) (Fig. 1). Canopy cover in trampled plots declined rapidly at both sites after the onset of trampling, and remained at a consistently low level of 13-22% for the remainder of the trampling period (Fig. 2). Control plots did not show such a decline; canopy cover remained high but tended to fluctuate more than in the trampled plots, and ranged from 60 to 97%. (Fig. 2).

At each site, trampling significantly reduced algal cover within 1 month of trampling. At Fogarty Creek, algal cover in trampled plots decreased from 83.3% (sE = 2.5) in March 1990 to 22.5% (sE = 5.3) in April 1990, while canopy in control plots was 60% (sE = 6.6) in April (ANOVA for April 1990, F = 17.6, p = 0.006, df = 1). After that, algal cover remained low in trampled plots for the remainder of the experimental trampling period, and ranged from 5 to 9.5%. By contrast, canopy cover in control plots ranged from 58.4 to 87% in the same period. At Little Whale Cove, algal cover in trampled plots fell from 80% (sE = 7.1) in March 1990 to 33% (sE = 5.1) in April 1990. Canopy in control plots was 79.3% (sE = 3.6) in April 1990 (ANOVA for April 1990, F = 45.24, p = 0.001, df = 1). During the remainder of the trampling period, canopy remained low



Fig. 1. Percent cover of algal canopy at (a) Fogarty Creek, and (b) Little Whale Cove, during trampling phase March 1990 to March 1991, and during the recovery phase, April 1991 to April 1992, when trampling had stopped. * and ** indicates significant difference between trampled and control plots at p = 0.05 and p = 0.01 levels, respectively; error bars are standard error.

on trampled plots and ranged from 19 to 35%. Canopy in control plots ranged from 63 to 92% in the same period.

Foliose algae were more susceptible to trampling, and when grouped together, mean cover decreased in trampled plots from 75% (sE = 3.5), to 9.1% (sE = 3.2) by August 1990. By contrast, foliose algal cover in control plots averaged 70% (sE = 8.1) in August 1990 (ANOVA for August 1990, F = 12.45, p = 0.001, df = 1). Fucoids and *Mastocarpus papillatus* showed large declines in trampled plots (from 9 to 1%) (Fig. 2). In control



Fig. 2. Canopy percent cover of individual algal species in trampled and control plots during trampling and the recovery phases. Results from Fogarty Creek and Little Whale Cove are combined.

plots, *Mastocarpus papillatus* increased from 11 to 15% during summer 1990, and subsequently declined over winter.

Fucus distichus cover decreased in both trampled and control plots in spring 1990 (Fig. 2). However, in control plots, it gradually rebounded through summer 1990 and declined again during the following winter. By contrast in trampled plots, *Fucus distichus* remained low throughout the summer and winter (cover ranged from 1 to 3%). *Pelvetiopsis limitata* declined rapidly from 16 to 1.5% in trampled plots. Cover in control plot

ranged from 6 to 12.5% from March 1990 to March 1991. In winter 1991, cover was low in all plots (Fig. 2).

Iridaea cornucopiae showed a large decrease in response to trampling (from an initial 38 to 14% in the first month). *Iridaea cornucopiae* canopy continued to decline in trampled plots until February 1991 when it rose from 4 to 8%. Percent cover in control plots remained high throughout the experiment, ranging from 29 to 52% (Fig. 2)

Endocladia muricata showed the least changes in percent cover as a result of trampling. Initial cover in trampled plots was 5% (SE = 1.5) and cover remained at 3 to 5% for the experimental period. Cover in control plots started at 11% (SE = 0.7) and declined gradually until August when it rose to 13.5% (SE = 1.3). By March 1991, cover was again 11%. *Endocladia muricata*'s decline in trampled plots was due to the loss of canopy cover of upright forms: low profile turf forms persisted near 4.5% (SE = 0.9) in trampled plots throughout the trampling phase (Fig. 2)

Total canopy cover in control plots increased gradually from 69% in April to 85% in August, due to increased abundance of all species. Canopy declined during fall and winter. Settlement and growth of *Iridaea cornucopiae* caused the large rise in canopy cover between January and February, 1991 (60–87%). All other foliose species declined slightly during this period, except for *Endocladia muricata*. The decrease in March was also due primarily to *Iridaea cornucopiae* loss, although the reason for this is unknown. Canopy cover in trampled plots did not show the same pattern as control plots except for a rise in February 1991. This increase again reflected a rise in *Iridaea cornucopiae* from 4 to 8%. In contrast to control plots, the subsequent drop in canopy cover was due to declines in *Fucus distichus*, *Pelvetiopsis limitata*, and *Iridaea cornucopiae*

In summary, canopy cover declined significantly in trampled plots. Foliose species appeared to be more susceptible to trampling, whereas the turf form of *Endocladia muricata* was more resistant. Non-trampled plots showed greater fluctuations in canopy cover than did trampled plots: trampled plots, on the other hand, after an initial decline, showed only small changes in cover.

Recovery. Algal cover steadily increased after trampling stopped (Fig. 1). Species recovering rapidly included *Iridaea cornucopiae*, *Mastocarpus papillatus* and *Endocladia muricata* (Fig. 2) In the case of *Endocladia muricata*, trampled plots increased in cover from 5.6% (SE = 1) in April 1991 to 19.5% (SE = 3) in April, 1992 [higher than the initial pre-trampling cover of 5% (SE = 1.5)].

3.1.2. Sessile invertebrates

Barnacles. Initial barnacle cover differed between sites (F = 81.78, p = 0.0001, df = 1). Therefore, sites were analyzed separately. Fogarty Creek trampled and control sites initially contained 66.6% (SE = 3.3) and 71% (SE = 7.7) respectively. At Little Whale Cove barnacles covered 21.3% (SE = 3.1) of primary substratum in trampled plots and 15% (SE = 2.3) in control plots. At each site there was no initial difference in barnacle cover between control and trampled plots (Fogarty Creek, F = 0.38, p = 0.56, df = 1;



Fig. 3. Primary cover of barnacles in trampled and control plots at Fogarty Creek (a) and Little Whale Cove (b) during trampling and recovery phases. * and ** indicates significant difference between trampled and control plots at p = 0.05 and p = 0.01 levels, respectively; error bars are standard error.

Little Whale Cove F = 2.88, p = 0.14, df = 1). Trampling significantly reduced barnacle cover at both sites (Fig. 3). Barnacle cover declined from 66.6 to 7.2% in 4 months at Fogarty Creek. At Little Whale Cove cover fell from 21.3 to 5.5% in 6 months. Barnacle cover in control plots did not vary much from initial levels. Barnacle cover on trampled plots was significantly lower than control plots until recruitment increased cover on trampled plots in March 1991. Barnacle density did not increase as much in control plots, because there was little available bare space.

Mussels. Small mussels (*Mytilus* spp) occupying primary space were scarce in all plots. Cover ranged from 1 to 3.5% in control plots during the study. Trampled plots initially had 2.5% (SE = 0.9) mussel cover. Within 4 months mussels were absent in all trampled plots and did not reappear.

3.2. Mussel-bed community

3.2.1. Primary space

There was no difference between mussel cover in control and trampled plots at the beginning of the experiment (Fogarty Creek, F = 0.679; p = 0.441, df = 1); Little Whale Cove, F = 0.028, p = 0.872 df = 1); mussel cover averaged 97% (SE = 2.8) at both sites. Because of the differences in mussel bed structure sites were analyzed separately.

At Little Whale Cove, there were large declines in mussel cover in trampled plots in April and May 1990 (Fig. 4). This was due mainly to mussel loss from one plot: on a single day 54% of the mussels were lost from one trampled plot. By May, a second trampled plot had begun to lose mussels. Mussel loss continued throughout the experimental period, so that by January 1991 two large patches had been created, one measuring 2700 cm² and the second measuring 450 cm². These patches were much larger than our original plot size. A third small patch had formed in another trampled plot by this stage, and 1% of the mussels were lost. Bare space occupied these patches.



Fig. 4. Primary cover of mussels *M. californianus* at (a) Fogarty Creek and (b) Little Whale Cove during trampling and recovery phases. * indicates significant difference between trampled and control plots at p = 0.05; error bars are standard error.

In August 1990 mean cover of mussels in trampled plots was 48% (sE = 28.0). Control plots lost no mussels during this period.

Trampled plots at Fogarty Creek also lost mussels (Fig. 4). However, Fogarty Creek has a two-layer mussel bed, and loss of the top layer did not create bare space as it did in Little Whale Cove. Consequently, primary percent cover remained high [97% (SE = 1.6)] on all plots. However, based on marked mussel counts taken through July 1990, we estimated that trampled plots lost at least 14.2% of the initially marked mussels between April and July 1990. We could not reliably measure mussel loss after July 1990, as some paint was lost from mussels in the plot. But byssal threads attached to matrix mussels (which were visible in trampled plots) indicate that top layer mussels continued to be lost from trampled plots.

3.2.2. Recovery

Mussel beds did not show marked recovery during the year following trampling (Fig. 4). In fact, mussels continued to be lost from trampled plots at both sites. At Little Whale Cove, bare patch continued to expand in all three trampled plots. By April 1992 mussel cover averaged 33.2% (SE = 23.5) in trampled plots (this does not include the large mussel loss peripheral to the plots) and mussel cover was unchanged in control plots (mean = 98%, SE = 1.6) (ANOVA for April 1992, F = 9.83, p = 0.02, df = 1). By May 1993, patches were still visible, and patch size had enlarged in two of the plots. No mussels had recruited to the patches. At the same time, mussel beds were still intact in the control plots (D.M. Brosnan, pers. obs.)

By April 1992, one year after trampling had stopped, trampled plots in Fogarty Creek had lost mussels to a point where patches of bare space were visible in two of the trampled plots, indicating that two layers of mussels had been removed. Control plots did not lose mussels during the recovery year. In May, 1993, two years after trampling ceased, patch size had increased further; one patch in a previously-trampled plot measured 1×0.5 m, no mussels had recruited into the patch. Between 1992 and 1993 control plots did not lose mussels (D.M. Brosnan, pers. obs.).

In summary, trampling causes mussel dislodgement. Dislodgement rates were higher in Little Whale Cove than at Fogarty Creek because mussels in Little Whale Cove were less tightly packed. Patches of bare space, resulting from mussel loss, continued to expand even a year after trampling had stopped.

3.2.3. Epibionts

Trampling significantly affected epibiont cover. Epibiont cover was measured until July 1990, and included barnacles and the red alga *Endocladia muricata*. Barnacle epibionts per mussel were significantly more abundant at Fogarty Creek than at Little Whale Cove, while the opposite was true for *Endocladia muricata*, This alga was rare at Fogarty Creek, but abundant on Little Whale Cove mussels.

At both sites, barnacle cover decreased significantly in the first month in response to trampling (Fogarty Creek, F = 25.95, p = 0.0001; df = 1; Little Whale Cove, F = 4.902, p = 0.034, df = 1) (Fig. 5). At Fogarty Creek, cover in trampled plots reached a minimum of 17.8% (SE = 2.8) in July. At the same time barnacles increased to 58% (SE = 6.1) in control plots. Although there were fewer barnacles at Little Whale Cove, barnacle



Fig. 5. Percent cover of barnacle epibionts per mussel at (a) Fogarty Creek and (b) Little Whale Cove during the trampling phase from March-July 1990. Mussel loss from trampled plots prevented us from gathering further data. * and ** indicates significant difference between trampled and control plots at p = 0.05 and p = 0.01 levels, respectively; error bars are standard error.

cover also declined in the trampled plots. These differences were significantly lower on 2 of 4 dates.

The epibiont *Endocladia muricata* decreased steadily on trampled plots at Little Whale Cove, from an initial cover of 15% (sE = 2.9) to 4% (sE = 1.5) in July (Fig. 6). *Endocladia muricata* cover on control plots increased slightly from 13.6% (sE = 2.8) in early April to 14.5% (sE = 4.0) in July. Cover on trampled plots was significantly lower than that of control plots in July (F = 5.76, p = 0.02, df = 1). We did not record recovery data for epibionts.



Fig. 6. Percent cover of the red algal epibiont *E. muricata* per mussel during the trampling phase from March-July 1990, Mussel loss from trampled plots prevented us from gathering further data. * and ** indicates significant difference between trampled and control plots at p = 0.05 and p = 0.01 levels, respectively; error bars are standard error.

In summary, trampling significantly reduces both barnacle and algal epibionts on mussel shells.

4. Discussion

Trampling affects both the uppershore algal-barnacle assemblage and the midshore mussel community by dislodging individuals and weakening their attachment strengths, making them vulnerable to wave shock. We did not study trampling effects on the low intertidal community, but we expect these to be minimal. At a heavily visited site, we found no difference in low tide communities in trampled and isolated areas (Brosnan & Crumrine, 1992a).

4.1. Effect of trampling on the upper shore algal-barnacles assemblage

Our results show that foliose algae are susceptible to trampling and that turf forms (mainly *Endocladia muricata*) are more resistant. This suggests that turf or low profile (e.g. crusts) species will dominate areas subjected to heavy trampling. Data from Yaquina Head, a heavily visited marine garden 10 km south of Little Whale Cove support this idea: trampled areas at Yaquina Head are dominated by algal turf (*Endocladia muricata* and *Gelidium* spp). Turf was replaced by foliose species (mainly *Iridaea cordata* and *Fucus distichus*) when trampling was prevented in experimental plots (Brosnan & Crumrine, 1992a,b; Brosnan, 1993).

Why are foliose forms more susceptible to trampling? Many foliose canopy species are attached at a single point or over a small area, e.g. the discoid holdfasts of some red algae and fucoids. Kicking off one discoid holdfast can result in significant canopy loss. In addition, because erect canopy protrudes more from the substrate than turf, it is more likely to be removed by foot traffic. In contrast, the turf form of Endocladia muricata is short and profusely branched; it spreads vegetatively over rocky substrata (Sousa, 1984), and is attached at many points. These characteristics are likely to make turf and possibly some crustose algae (e.g. Petrocelis) resistant to trampling, and dominant on heavily trampled shores. Other authors have also noted that certain species appear susceptible to trampling in marine intertidal communities. For example, Povey & Keough (1991) noted that foliose species are more readily removed than crusts or turf. Zedler (1976, 1987), and Beauchamp & Gowing, (1982) found that foliose species, notably Pelvetiopsis limitata, were less abundant at heavily visited sites in California. Boalche et al., (1974) noted that the large canopy forming species Ascophyllum nodosum became significantly rarer at a shore in SW England after construction of a parking lot and an increase in visitors. They attributed this loss to trampling impact. Interestingly, growth forms that are reasonably resistant to wave shock provide poor defense against foot traffic disturbance: a flexible stipe attached by a single point can allow a species to persist in areas of high wave action, but not in heavily trampled sites for reasons noted above. Species differences in trampling resistance have also been noticed in reef flat communities (Woodland & Hooper, 1977; Liddle & Kay, 1987; Kay & Liddle, 1989).

Barnacles on primary and secondary substrata were crushed by trampling. We noticed that after trampled plots lost algal canopy, barnacles recruited heavily into bare space. Control plots did not show large concurrent increases in primary barnacle cover. Though canopy can provide protection against desiccation, it can also prevent barnacle settlement through whiplash or space occupancy (Dayton, 1971, 1975; Menge, 1978). Individuals settling into trampled space eventually reach a size large enough to be susceptible to trampling. The net effect of trampling will depend on the timing of the disturbance. If trampling removes barnacles prior to sexual maturity, the population will suffer a steady decline. Therefore, the benefit in recruitment to primary surfaces may be offset by direct crushing mortality.

Mussels did not recruit into uppershore trampled plots during the experimental period, although they did recruit into non-trampled plots. Mussel recruitment tends to be sporadic along the Oregon coast (Petersen, 1983; B.A. Menge pers. comm.). Trampling can indirectly prevent mussel settlement. For example, mussels settle preferentially among algal fronds and holdfasts and onto barnacle tests, but rarely onto bare rock (Paine, 1974; Suchanek, 1978; Paine & Levin, 1981; Petersen, 1983). By removing algae and large barnacles, trampling will reduce settlement space. Trampling can also directly dislodge or kill mussels after settlement, as shown in this experiment.

4.2. Effect of trampling on mussel-bed community

Trampling removed mussels and disturbed the surrounding mussel bed. We cannot account for initial differences in numbers of layers of mussels between Fogarty Creek and Little Whale Cove. Wave exposure is similar at both sites, and substratum type does not seem to vary in irregularities, which might allow for stronger attachment at Fogarty Creek. One possible explanation is that recruitment may be higher at Fogarty Creek. In a separate study, barnacle recruitment was higher at Fogarty Creek than Little Whale Cove (Brosnan, unpubl. data). Differential predation may also be a factor, but we have not noticed more predators at Little Whale Cove. Tightly packed mussels, such as the plots in the Fogarty Creek study, were less susceptible to trampling-induced loss. However, the top mussel layer was lost from the bed, suggesting that on some trampled shores mussel beds may be restricted to a monolayer, or that trampling may first reduce a multi-layered bed to a single layer, and continued loss may lead to disappearance of the mussel-bed. In separate studies, at a heavily trampled site (Brosnan & Crumrine, 1992a,b; Brosnan, 1993), we found that mussels were not common, and were confined to crevices. This suggests that the presence of crevices and depressions in the rock surface is likely to be important to the persistence of mussels on trampled shores. Mussels aggregated into a loose monolayer are highly susceptible to trampling, as at Little Whale Cove. Once a patch had been created, natural forces (e.g. waves) caused further loss, and the patches expanded beyond the area that was trampled. This effect contrasts with the observations of Paine & Levin (1981) who noted that patches formed by storms did not enlarge. Our results may indicate that trampling weakens areas of mussel beds that would normally not be affected by storms. Thus, trampling makes mussels more susceptible to winter disturbances.

Once bare space has been created, continued trampling appears to prevent coloni-

zation and succession. We found little recruitment on patches in mussel plots until experimental trampling had stopped. Even then, it may take many years for mussels to recolonize the area; Paine & Levin (1981), estimate that it would take at least 7 years for large patches to recover to a stage where natural disturbances would once again affect them. Loss of mussel bed also includes the loss of species dependent on mussels (Suchanek, 1978) and therefore results in a decrease in diversity of the site.

Epibionts seem particularly susceptible to trampling. Even *Endocladia muricata*, which is resistant when it grows on primary substratum, was significantly affected. Epibionts on mussel shells protrude above the surface, and are the first organisms to be hit by a walking foot. This may account for their susceptibility. Initially, barnacle epibionts were more abundant at Fogarty Creek than at Little Whale Cove. *Endocladia muricata*, which is known to smother and kill barnacles (Farrell, 1989,1991; Brosnan, unpubl. data), is common at the latter site and may be partially responsible for the low barnacle abundance there. In a study conducted in Oregon, Lee & Ambrose (1989) showed that barnacles are more abundant as epibionts than on bare rock. Trampling removes barnacle epibionts and therefore may have major consequences for barnacle populations on frequently visited shores.

The effect of algal epibonts on mussels varies with environmental conditions. In cold weather, algal epibionts reduce mortality rates in mussels by insulating them (Brosnan, 1990, 1992). Trampling, by removing epibionts, may thus increase mussel mortality rate under harsh environmental conditions. Epibonts also increase drag and the risk of mussel dislodgement (Witman & Suchanek, 1984). By removing epibionts, trampling decreases drag on mussels. However, this effect may be small compared to the increased risk of dislodgement from trampling.

4.3. Trampling as a disturbance

Storms and waveswept logs create disturbance in the rocky intertidal which results in patches of bare space (Harger, 1970; Harger & Landenberger, 1970; Dayton, 1971, Sousa, 1979, 1984b, 1985; Paine & Levin, 1981). Such disturbances are generally seasonal (winter) and localized. Trampling also removes individuals and creates patches of bare space and can therefore be defined as a disturbance (*sensu* Sousa, 1985). However, unlike natural disturbances such as storms and logs, trampling is more likely to be chronic in nature. Trampling may also be more frequent during spring and summer, and less common in winter.

Many species have evolved in response to the natural disturbance regime. For instance, fugitive species (*sensu* Sousa, 1985) may time their reproduction to take advantage of bare space created by these winter storms. Changes in the frequency and intensity of disturbance can change the species composition and diversity of a community (Connell, 1978, 1979). On the Oregon shore, trampling is concentrated in the spring and summer months, at a time of peak algal and barnacle settlement and growth. Hence these species that have evolved to take advantage of bare space at these times, are now subject to a new disturbance.

Some species are resistant to trampling (Liddle, 1991). Resistant species such as *Endocladia muricata* appear to benefit from chronic trampling. On untrampled shores

this alga is often present as an understory species and covers about 10% of space (D.M. Brosnan, unpubl. data). Consequently, trampling may initiate a shift in community structure. Historic evidence of such changes has been noted not only in terrestrial systems (Liddle, 1975) but also on rocky shores in the US and England (Widdowson, 1971; Boalche et al., 1974; Thom & Widdowson, 1978; Brosnan & Crumrine, 1992a,b; Brosnan 1993).

Trampling interacts with natural forces, such as storms, to increase the extent of the disturbance. For example, in our plots, trampling created the initial disturbance by removing mussels and weakening the beds; patches subsequently continued to expand as more mussels were lost through wave action. Similarly, trampling damages algal holdfasts and thalli, and damaged plants are more susceptible to wave dislodgement (D.M. Brosnan, pers obs).

Recovery from trampling depends on the community involved. Algal abundance on the upper shore reached nearly control-level a year after trampling stopped. Similarly, high barnacle recruitment aided recovery of these organisms. The relative abundances of certain species differed between the initial pre-trampling level and recovery period. But in general, the upper shore algal-barnacle community seemed to be resilient. However, chronic trampling for many years might alter this conclusion. Shores that have low recruitment will also have slower recovery. The mussel community did not recover in the year following trampling, and did not show mussel recruitment by April 1993 (D.M. Brosnan, pers. obs.), 2 years after trampling stopped. In fact, some of the patches had enlarged further (D.M. Brosnan, pers. obs). Paine & Levin (1981) found that recovery in some mussel bed patches did not begin until 26 months after a natural disturbance. Chronic trampling will most likely prevent recovery.

In conclusion, trampling affects community structure on rocky shores and may shift the community to an alternate state. Based on these and other studies, we predict that at similar sites, trampled shores will be dominated by algal turf or crust, and that cover of foliose canopy species will be low. We also predict that mussels will be infrequent or at most in densely packed monolayers. In contrast, where trampling intensity is low, mussels and foliose algae will be more common. Because it mimics some aspects of natural disturbance, communities can recover from the effects of trampling; however, its frequency and intensity make it a particularly severe stress. Trampling also interacts with natural disturbance to increase the rate of dislodgement of organisms.

Marine parks and reserves have been set up in many areas of the world to protect sensitive areas of high diversity. A designated reserve in a biologically rich area is a prime attraction to visitors. Ironically this increased use may degrade the very resource that the reserve was set up to protect. Human impact on marine ecosystems will continue to increase and its effects will need to be factored into any reserve or conservation design.

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