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Human Trampling in the Upper Rocky Intertidal: Trampling and Recovery in Barnacle Mediated Succession

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THESIS APPROVAL

The abstract and thesis of Timothy Lawrence Grubba for the Master of Science in Biology were presented June 2, 1997, and accepted by the thesis committee and the department.

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ABSTRACT

An Abstract of the thesis of Timothy Lawrence Grubba for the Master of Science in Biology presented June 2, 1997.

Title: Human Trampling in the Upper Rocky Intertidal: Trampling and recovery in barnacle mediated succession.

Marine intertidal ecosystems are vulnerable to human interference, because trampling can be a significant problem. I studied the impacts of trampling on community patterns and succession in a rocky intertidal habitats. This study was divided into two phases: (1) a trampling phase and (2) a recovery phase. Both phases are focused on two barnacles, Balanus glandula and Chthamalus dalli, and on fucoid and red algae. The trampling phase tested the effects of trampling on these organisms. The effects of herbivores, primarily limpets (Collisella digitalis) were also tested to determine whether anthropogenic (trampling) and natural (herbivory and limpet bulldozing) disturbances had independent or additive effects. The recovery phase monitored the recovery of these species after trampling was stopped.

A randomized block design was set up at two sites on the Oregon coast. Light and heavy trampling regimes and herbivore inclusion and

exclusion treatments were applied, to permit comparisons with control plots. During the trampling phase, experimental plots were trampled monthly from November 1992 to July 1993. During the recovery phase, the experimental plots were not trampled and recovery was monitored from August 1993 to October 1994.

Trampling severely reduced the abundance of B. glandula, but the smaller C. dalli increased. This increased abundance was due both to resistance of C. dalli to trampling and to reduced competition from B. glandula. Herbivores reduced abundance of newly-settled B. glandula , but had no effect on C. dalli. Cover of algae declined rapidly under trampling. This was due both to direct effects and to removal of B. glandula, the settlement substrate. Trampling had severe effects on overall community composition. Some species were eliminated, and succession was prevented. In this study, light and heavy trampling had equally detrimental effects. Trampling swamped potential herbivore effects.

Recovery/succession after trampling was slow as B. glandula, a facilitative species was in low abundance. Chthamalus dalli abundance was high due to high recruitment and to release from competition. Chthamalus dalli individuals grew to unusually large sizes, which enabled them to function as a facilitative species. This occurrence enabled succession to proceed despite the absence of B. glandula. Because it has already established, C. dalli in this large form has a short term competitive dominance over B. glandula. With increased recruitment of B. glandula, over time, the pre-emptive competition will fail and B. glandula regain dominance.

HUMAN TRAMPLING IN THE UPPER ROCKY INTERTIDAL: TRAMPLING AND RECOVERY IN BARNACLE MEDIATED SUCCESSION

BY

TIMOTHY LAWRENCE GRUBBA

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INTRODUCTION

Human use of rocky intertidal areas alters the abundance of species, and also affects key processes and interactions in the communities (e.g., Castilla & Duran 1985, Olvia & Castilla 1986, Ortega 1987, Castilla & Bustamente 1989, Duran & Castilla 1989, Godoy & Moreno 1989, Keough & Quinn 1992, Osenberg & Schmitt 1994, Osenberg et al. 1994, Thrush et al. 1994). The effects of species reduction or removal by harvesting on community dynamics have been the focus of much attention (e.g., Moreno et al. 1984, Castilla & Duran 1985, Hockey & Bosman 1986, Olvia & Castilla 1986, Ortega 1987, Castilla & Bustamente 1989, Duran & Castilla 1989, Godoy & Moreno 1989, Underwood & Kennelly 1990). Human trampling is also known to affect community structure in many marine communities, including rocky intertidal shores (Zedler 1976, 1978, Beauchamp & Gowing 1982, Ghazanshahi et al. 1983, Castilla & Bustamente 1989, Povey & Keough 1991, Brosnan & Crumrine 1992a, 1994, Brosnan 1993, Elliott 1996) and coral reef flats (Liddle 1975, 1991, Liddle & Kay 1987, Kay & Liddle 1989). The impact of trampling on intertidal communities is likely to increase as more people visit the shore for educational, scientific and recreational use.

The effects of trampling on terrestrial communities have been much studied. (e.g., Jeffreys 1917, Shantz 1917, Bates 1934, 1935, Sun and Liddle 1993). Trampling also alters plant communities in alpine meadows, forests and sand dunes (Burden and Randerson 1972, Liddle 1975, Hylgaard and Liddle 1981, Nickerson and Thibodeau 1983, Sun and Liddle 1993). Certain species are susceptible to trampling, while others thrive in trampled areas (Sun and Liddle 1993). Trampling impacts on marine communities have, until recently, received less attention. In the 1970's, repeated surveys of marine areas showed that communities changed, as human population density and shore access increased (Widdowson 1971, Boalche et al. 1974, Thom and Widdowson 1978). Recently there have been more direct observational and comparative studies (Zedler 1976, 1978, Beauchamp and Gowing 1982, Ghazanshahi et al. 1983), and experimental studies on the effects of trampling on intertidal communities (e.g., Castilla and Bustamente 1989, Povey and Keough 1991, Brosnan and Crumrine 1992a, 1994, Brosnan 1993). Studies show that trampling has predictable effects on community patterns. Fucoid algae are particularly susceptible to trampling and are often rare at heavily visited sites (Zedler 1976, 1978, Beauchamp and Gowing 1982, Ghazanshahi et al. 1983, Povey and Keough 1991, Brosnan and Crumine 1992a, b, 1994, Brosnan 1993). Low-growing algal turf are more resistant to dislodgment (Povey and Keough 1991, Brosnan and Crumrine 1992a, b, 1994, Brosnan 1993, Elliott et al. unpublished manuscript). These studies establish the sometimes dramatic effects of trampling on competitive dominants and on later successional species. In this study, I extend the investigation of the effects of trampling to other organisms and its effects on successional pathways.

Most of the above experimental studies considered only a few groups, mainly algae (Povey and Keough 1991, Brosnan and Crumrine 1992a, b, 1994), and gastropods (Povey and Keough 1991) in high and mid-intertidal zones, and mussels in the mid intertidal zone (Brosnan and Crumrine 1992a, 1994). Few studies have focused on the direct effects of trampling on barnacles or on indirect effects on the community brought about by effects on the barnacles. Barnacles dominate or form mixed algal-barnacle assemblages in the upper intertidal zone of many temperate rocky shores (Lewis 1964, Connell 1961, Stephenson and Stephenson 1972). Barnacles often play a key role in succession, by facilitating the establishment of other species (e.g., Hawkins 1981, Hawkins and Hartnoll 1983, Lubchenco 1978, 1983, Hartnoll and Hawkins 1985, Navarette and Castilla 1990, Farrell 1991). Brosnan and Crumrine (1994) noted that barnacle abundance were reduced by trampling. However, they did not distinguish between barnacle species, or consider the indirect impacts of this on the community. In addition, no study that I am aware of, has examined at interactions between the effects of trampling and biotic disturbance, e.g. bulldozing effects of herbivores. If trampling and natural disturbances have additive effects, this may magnify the importance of human disturbance. In this study, I experimentally tested the effects of trampling intensity on species composition and abundance of barnacles, and algal species associated with barnacles. I also experimentally tested interactions between trampling and herbivores (Limpets, *Collisella digitalis*), and how they affect barnacles and algae.

Barnacles are often an essential link in the successional process (e.g., Hawkins 1981, 1983, Hawkins and Hartnoll 1983, Hartnoll and Hawkins 1985, Farrell 1989, 1991). Their tests provide a settlement site for algae and mussels. Recruitment of algae and mussels is often higher onto barnacle tests than onto bare rock (e.g., Burrows and Lodge 1950, Lubchenco 1978, 1983, Hawkins 1981, 1983, Petersen 1984a, b, Hartnoll and Hawkins 1985, Farrell 1989, 1991, Navarette and Castilla 1990). In studies on the Oregon coast, Farrell (1991) found that algal colonization and succession were dependent on barnacles. Brosnan (unpublished manuscript) confirmed that algae do not become established in the absence of barnacles. Similarly, Lubchenco (1983) found that barnacles were nearly essential for the establishment of algae on shores in New England. On rocky shores in England, the presence of barnacles plays a key role in determining the rate and trajectory of succession (Hawkins and Hartnoll 1983, Hartnoll and Hawkins 1985). Previous studies have shown that human trampling leads to reductions in abundance and diversity of barnacles and algae (e.g., Povey and Keough 1991, Brosnan and Crumrine 1992a, 1994). However, trampling effects on algae may be either by direct removal or by indirect removal of settlement substrate (barnacles). Thus by removing barnacles, trampling may also prevent algal recovery.

Abundance of barnacles and algae is also affected by herbivores. Limpets, for example remove barnacles by bulldozing them (Branch 1975, 1981). Thus, trampling and herbivory may have additive effects on barnacle abundance. Herbivores also reduce algal abundance directly (e.g., Branch 1975, 1981, Lubchenco 1978, 1983, 1985, Underwood 1980, Jernakoff 1983, Cubit 1984, Sousa 1984) and thus may retard succession (Farrell 1989, 1991). Again, the effects of trampling and herbivory may be additive; we may also expect both direct effects on algae, and indirect effects exerted through effects on barnacles.

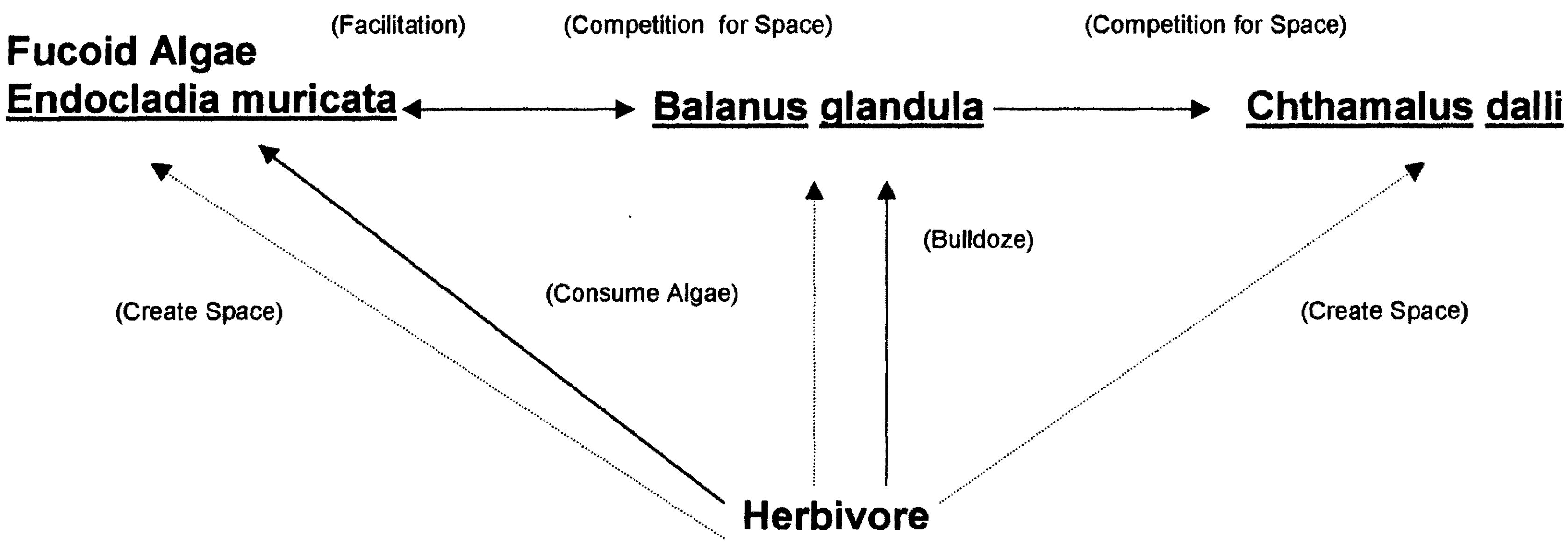
The Barnacle-Algal Assemblage

Experiments were carried out in the upper intertidal zone on shores of the Oregon, USA (Fig 1). Two species of barnacles co-exist in this zone, Balanus glandula and Chthamalus dalli (Kozloff 1973). Balanus glandula is the larger species and outcompetes C. dalli for space (Farrell 1989, 1991). Algal recruitment is largely dependent on facilitation by B. glandula (Farrell 1991, Brosnan unpublished manuscript). Facilitation by C. dalli is relatively unimportant (Farrell 1991). Limpets, as they graze on algae significantly reduce the abundance of B. glandula by bulldozing them (Farrell 1989, 1991, Brosnan in prep), but they have little effect on C. dalli (Farrell 1991). Thus, Coexistence of these barnacle species is, therefore partly facilitated by limpets (Farrell 1989). Figure 2, summarizes the main interactions that occur in the upper intertidal zone.

The upper intertidal zone is dominated by barnacles, or by a mixed assemblage of barnacles and algae. Algae often establish on barnacles, and spread to primary substrate (Farrell 1991, Brosnan personal observation). The main algal species on this part of the shore are fucoids (Pelvetiopsis limitata, Fucus distichus), red algae (Mastocarpus papillatus, Iridaea cornucopiae, Endocladia muricata, and Petrocelis, the tetrasporic crust phase of M. papillatus,), and the green alga Ulva sp. is occasionally common.

Figure 1. The position of the upper intertidal zone.

Figure 2. Main species interactions in the upper intertidal zone



Effects of Trampling and Herbivores on marine communities: Predictions

Trampling removes biomass and creates space (Brosnan and Crumrine 1994). If trampling removes key species in a community then community wide processes, including species colonization and abundance will be affected. Table 1 summarizes predictions in the trampling phase for changes in species abundance and composition under light and heavy trampling intensities, and in the presence or absence of herbivores. Table 2 summarizes predictions for the recovery phase. The predictions in Table 2 are based on no significant herbivore effects and no significant differences between trampling intensities.

Table1. Predicted outcomes of trampling.

	HERBIVORES PRESENT	HERBIVORS EXCLUDED
No TRAMPLING (CONTROL)	B. glandula will be the dominant barnacle: Percent cover of C. dalli will be low . Late successional algae (e.g., fucoids) will be common and many species will be associated with barnacles. Early successional species will be rare. Herbivore-resistant species will be present.	B. glandula will outcompete, and exclude C. dalli. Algae will be more abundant than in herbivore inclusion areas. Algae may overgrow and smother barnacles.
LIGHT TRAMPLING	There will be some reduction in biomass but no large changes in community composition. B. glandula will show some reduction from trampling and grazers, and this will lead to increased abundance of C. dalli. Algal turf and grazer-resistant species will be common. Algal canopy will be present, but reduced from non-trampled control levels.	B. glandula and foliose algae will be more abundant than in light trampling and the presence of grazers, and C. dalli will be less abundant. Herbivore-resistant algae will be uncommon. Algal canopy will be less abundant than in control areas, but will still be relatively common. Overall, I predict a reduction in the abundance of certain species under light trampling conditions, but I do not predict that these species will be reduced to near zero levels.
HEAVY TRAMPLING	B. glandula cover will be significantly reduced. Because it is smaller, C. dalli is less likely to be affected by trampling, and will be the most abundant barnacle species. Cover of fucoid algae will decrease dramatically. Cover will remain low, because B. glandula substrate will be unavailable. Algal turf and crusts which are resistant to trampling and herbivory will be abundant. The substrate will be dominated by C. dalli and algal turfs and crusts.	A low abundance of B. glandula, and foliose algae. Because the detrimental effects of trampling may be offset by the absence of herbivores. Small barnacles and algae may become established. Chthamalus dalli will be common and will co-exist with B. glandula. Under these conditions species that dominate in no-trampling conditions will persist: However, they will be significantly less common and subject to frequent disturbances from trampling.

Table 2. Predicted recovery pathway.

	HERBIVORES PRESENT AND EXCLUSION
No TRAMPLING (CONTROL)	B. glandula will be the dominant barnacle: Percent cover of C. dalli will be low . Late successional algae (e.g., fucoids) will be common and many species will be associated with barnacles. Early successional species will be rare.
LIGHT TRAMPLING AND HEAVY TRAMPLING	B. glandula abundance will be low while cover of C. dalli will be significantly greater initially. Over time, B. glandula abundance increases while C. dalli abundance decreases. The low abundance of B. glandula will retard establishment of late successional species such foliose algae.

STUDY AREA

Experiments were set up on two rarely visited sites on the central Oregon coast USA, Fogarty Creek (44.51^{o} N: 124.03^{o} W) and the south headland at Yaquina Head (44.41^{o}N: 124.04^{o}W). Plots were located in the high intertidal zone (1.5-2.0 m above mean lower low water). These sites were chosen so that trampling from others would not confound the study.

The Yaquina Head site is located at the base of a relatively inaccessible cliff. The area is frequented only by a few local fishermen. Their impact is restricted to small patches, which were not included in the experimental site. The shore consists of a narrow basalt platform and is exposed to a low to medium wave intensity from the southwest. The community at Yaquina Head is dominated by barnacles (Balanus glandula and Chthamalus dalli). Macroalgae are not common and tend to be patchily distributed.

The Fogarty Creek site is a basaltic headland which has extensive intertidal benches. Access to the shore is through private property. Apart from other researchers, visitors to the headland are rare. Experiments were set up on a small isolated northern headland. The community in this part of Fogarty Creek is composed of a mixed barnacle-algal assemblage.

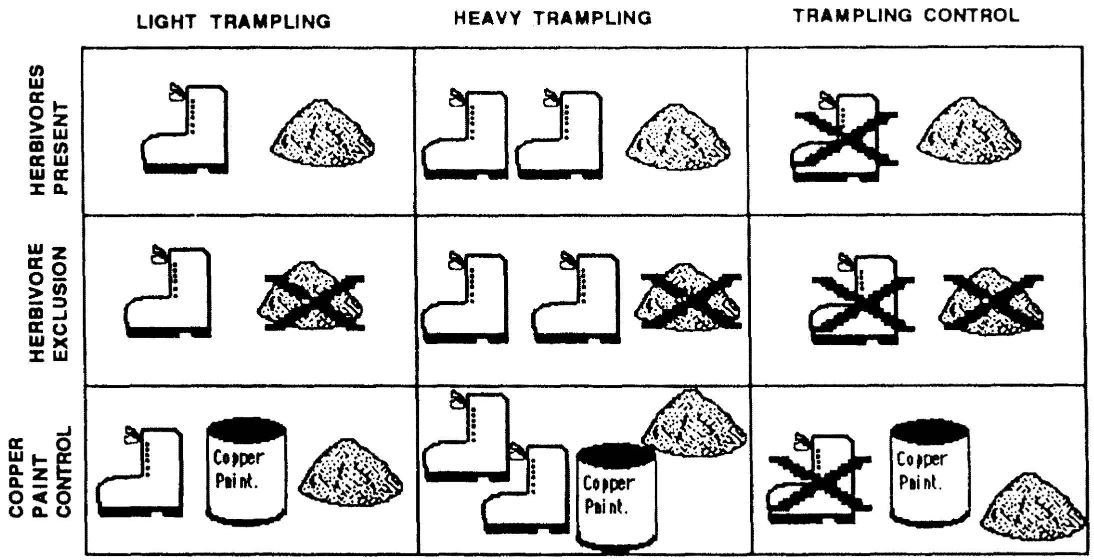
Barnacles (B. glandula and C. dalli) are less common at Fogarty Creek than at Yaquina Head. Algal species are more abundant at Fogarty Creek. The main species present include fucoids, mainly Pelvetiopsis limitata and Fucus. distichus, and the red algae (Iridaea cornucopiae, Endocladia muricata, and Mastocarpus papillatus).

METHODS

The study was divided into a trampling phase and a recovery phase. In both phases a randomized block design was used to test the effects of trampling, and herbivores on the marine community and on the successional pathway. The experimental design consisted of three trampling intensities, (light trampling, heavy trampling, and a non-trampled control treatment), and three herbivore treatments (herbivore exclusion, herbivore inclusion, and a copper-paint control treatment). In each block, one replicate of each of the nine possible combinations of trampling intensity and herbivore treatments was established (Fig 3). There were four blocks at each of the two sites making a total of 72 experimental plots. Plots measured 10cm by 10cm and were marked out at each corner with a marine epoxy (Z-spar).

During the trampling phase the control plots were not trampled. Trampled plots were trampled monthly for nine months from November

Figure 3. The layout of trampling and herbivore treatment combinations in one block..



1992 to July 1993. Light trampling consisted of 150 single footsteps per plot per month. Heavy trampling consisted of 300 single footsteps per plot per month. These intensities were based on previous studies at frequently visited sites on the Oregon coast. Brosnan and Crumrine (1992a) found that species on frequently used sites are trampled up to 228 times per hour. During the recovery phase the monthly application of trampling was stopped for 15 months, from August 1993 and October 1994.

Herbivores were excluded from herbivore exclusion treatments by painting a barrier of copper-based antifouling paint around the experimental plots (Cubit 1984). The paint was applied in a 5 cm wide band around the plots. Herbivore paint controls were used to test for any effects of copper-paint. Paint was applied in two 10 cm wide bands at opposite sides of the plots. This allowed herbivores access only through the two paint-free sides. Herbivores were removed from the herbivore-exclusion treatments by hand. Herbivore treatments were maintained through both the trampling and recovery phases. On each sampling date, herbivore-exclusion plots were searched for grazers and any present were removed. As paint barriers deteriorated they were repainted.

The trampling phase extended from November 1992 to July 1993. During this period nine monthly observations were made. The recovery phase extended from August 1993 and October 1994. During this period thirteen monthly observations were made, with no observations taken on two months (November 1993 and May 1994) due to adverse conditions. Data were collected during both phases on percent cover and identity of species occupying primary space and secondary (canopy) space. For algae and barnacles, primary percent cover is defined as direct attachment to the substrate. For algae, canopy cover is the percent of the rock surface that a species covers, although it may not be attached at that particular point. Percent cover was determined by using a transparent vinyl sheet (10 cm by 10 cm) marked with 100 randomly spaced dots. The sheet was laid directly over the plots, and any species under a dot was recorded.

Data Analysis

Data from the trampling and recovery phases was analyzed separately. Raw data were tested for homogeneity of variance using Hartley's test ($p< 0.05$) (Sokal and Rohlf 1981). Variances were not homoscedastic, and data were arcsine transformed to give homogeneity (Hartley's test $p< 0.05$). Transformed data were then analyzed using a repeated measures analysis of variance (RMANOVA) on the program Systat (Systat Inc. 1990) . RMANOVA were carried out on each species to test for significant changes in mean cover over time in the treatment combinations.

Special attention was given to trampling, herbivore and trampling herbivore effects. Also noted were block and site differences. As sites were so different in species composition, blocks were nested within sites during the RMANOVA. The Post Hoc test, Student-Newman-Keuls (SNK) was carried out on any treatments that showed significant results. The results of the RMANOVA are summarized in the results section.

RESULTS

TRAMPLING PHASE:

Barnacles

Balanus glandula (Table 3, Figs. 4 and 5)

Balanus glandula density and distribution were patchily distributed between sites and between blocks and plots within each site throughout the trampling phase (Table 3). Generally, B. glandula was more abundant at Yaquina Head with distribution between blocks heterogenic. Balanus glandula was less abundant at Fogarty Creek but more homogenously distributed among blocks.

Trampling significantly reduced barnacle abundance at Fogarty Creek and Yaquina Head (Table 3; Figs 4 and 5). This effect occurred within one month of the first trampling (Figs 4 and 5). At Fogarty Creek, where B. glandula was less abundant, mean cover in trampled plots declined from 37.6% in November to 9.2% in December 1992 (Fig 4), Balanus glandula mean cover in control plots during the same period declined from 46.7% to 25.0% (Fig 4). At Yaquina Head, B. glandula mean cover declined from 66% to 7.8% in trampled plots between November and December 1992 (Fig 5). At the same time, B. glandula mean cover in control plots declined from 67.3% in November to 58.6% in December 1992 (Fig 5).

Trampling continued to reduce B. glandula mean cover throughout the experiment. Mean cover in trampled plots remained lower than the mean cover in control plots in all cases except March 1993 at Fogarty Creek (Fig 4). There were no significant differences in mean cover between light trampling and heavy trampling on any date at either site (Table 3). Light trampling removed almost all B. glandula individuals, and additional trampling had no further effect.

Balanus glandula recruited in March 1993, as shown by an increase in mean cover, in all plots at both sites (Figs 4 and 5). At Yaquina Head, the level of recruitment did not compensate for the effects of trampling and mean cover in trampled plots remained significantly lower than mean cover in control plots (Fig 5). In contrast, at Fogarty Creek (where barnacle abundance is lower) recruitment into trampled plots was sufficient to compensate for trampling effects (Fig 4). However, subsequent trampling reduced B. glandula mean cover so that by April 1993, B. glandula mean cover was again significantly lower in trampled plots. However, B. glandula mean cover did not decline to pre-recruitment mean cover at either site (Figs 4 and 5). There were no further recruitment pulses during the trampling phase.

Figure 4. Effect of trampling on Balanus glandula at Fogarty Creek in the presence and absence of herbivores. Data points represent the mean, and vertical bars are ± 1 SE.

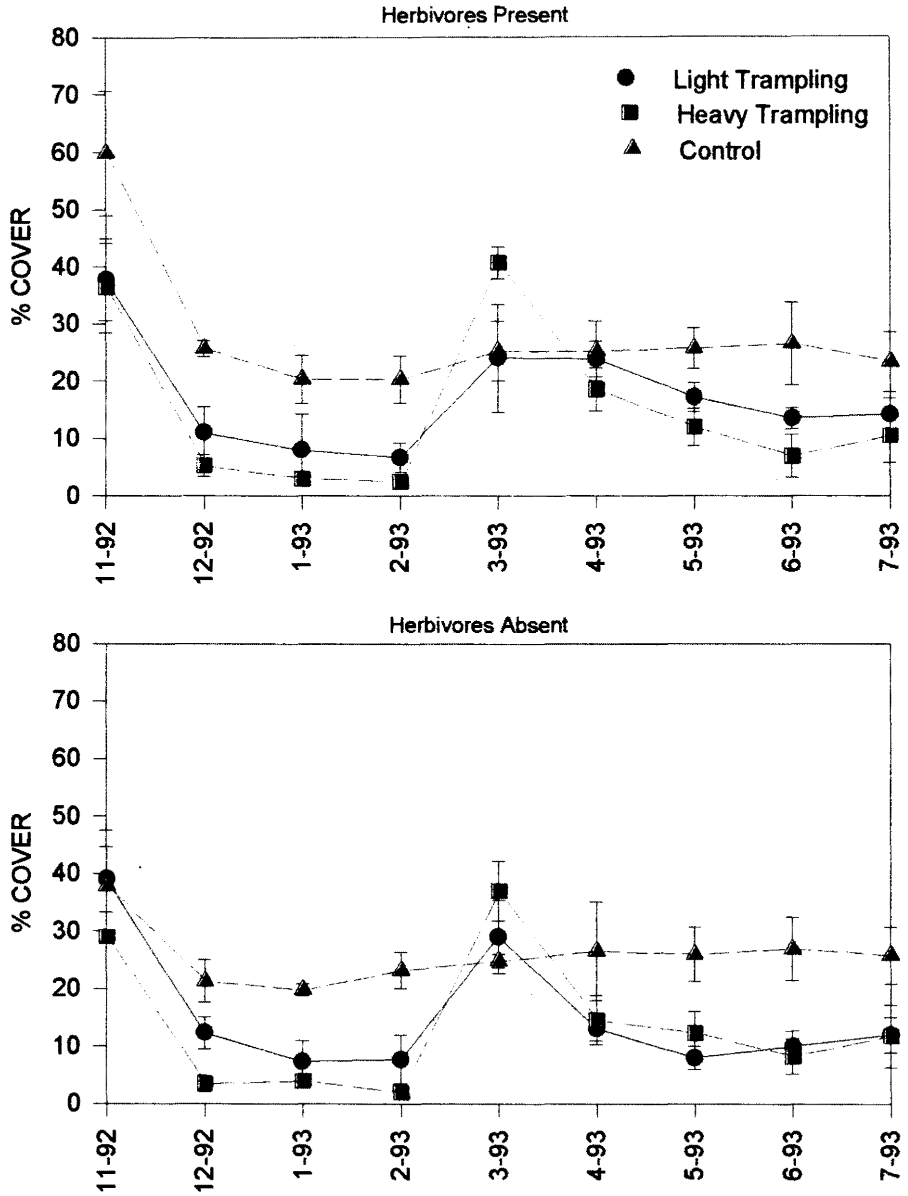


Figure 5. Effect of trampling on Balanus glandula at Yaquina Head in the presence and absence of herbivores. Data points represent the mean, and vertical bars are ± 1 SE.

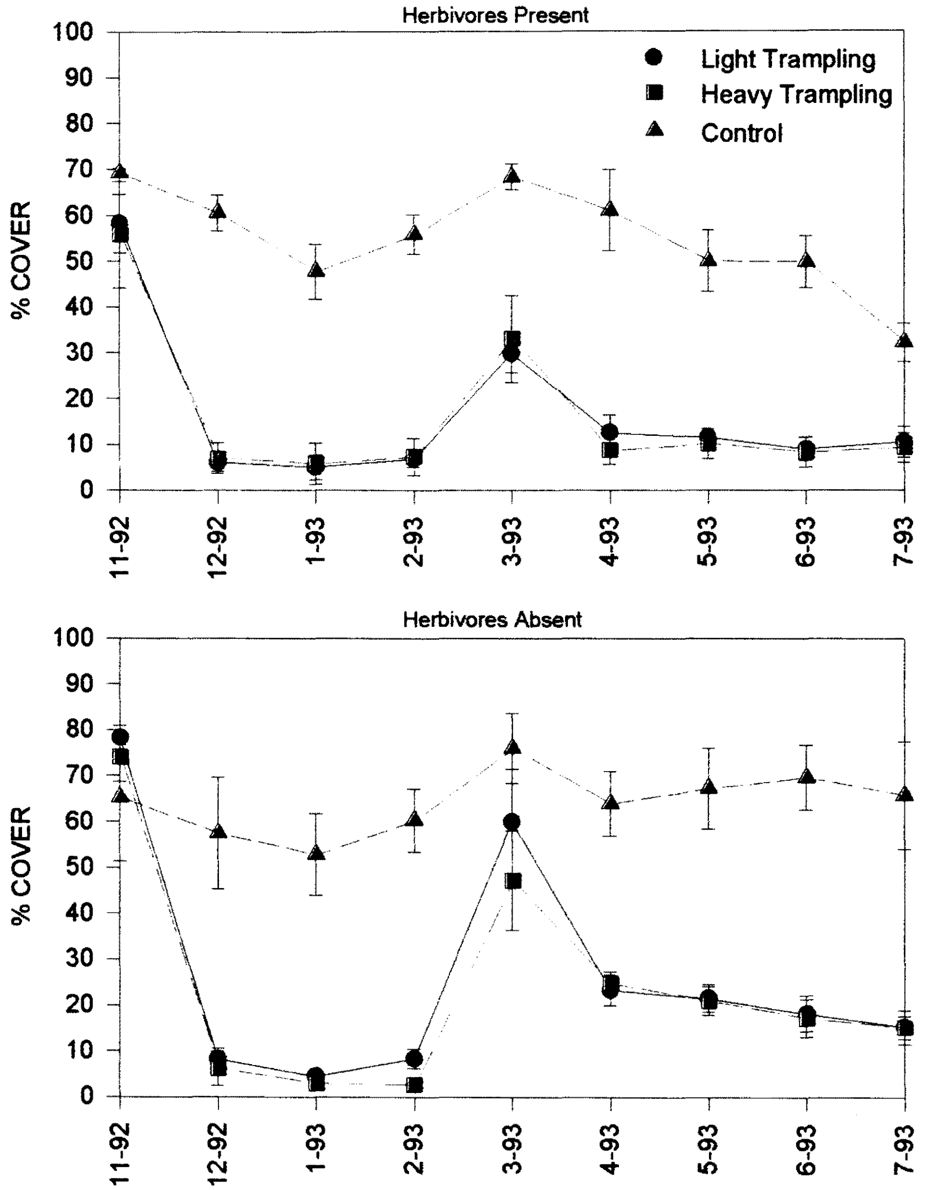


Table 3. Summary of RMANOVA on abundance of barnacles (Balanus glandula) in the trampling phase. Data were arcsine -transformed prior to analysis.

SOURCE	DF	MS	F	P
Between treatments				
Site	1	3.605	64.331	P <0.05
Block{Site}	6	0.140	2.496	P <0.05
Trampling{Site}	4	4.466	79.702	P <0.05
Herbivore{Site}	4	0.207	3.692	P <0.05
Trampling*Herbivore	4	0.006	0.115	0.976
Error	52	0.056		
Within treatments				
Date	8	1.816	142.473	P <0.05
Date*Site	8	0.058	4.568	P <0.05
Date*Block{Site}	48	0.027	2.096	P <0.05
Date*Trampling{Site}	32	0.106	8.291	P <0.05
Date*Herbivore{Site}	32	0.016	1.245	0.173
Date*Trampling*Herbivore	32	0.019	1.458	0.054
Error	416	0.013		

Greenhouse-Geisser Epsilon: 0.6158: Huyn-Feldt Episilon: 0.9366

Herbivores had no effect on B. glandula cover at Fogarty Creek (Table 3). However, at Yaquina Head herbivores had a significant effect on barnacle abundance, beginning when B. glandula recruited in March 1993. The rate of barnacle loss from trampled plots with herbivores present was higher than from trampled plots without herbivores. For instance, in April 1993, one month after recruitment, in trampled plots, mean cover was 14%

in herbivore inclusion plots and 27% in herbivore exclusion treatments (Fig. 5).

Herbivores continued to have a negative effect on B. glandula throughout the experimental period. Limpets as well as trampling reduced barnacle cover. Consequently, B. glandula cover was significantly lower in trampled plots with herbivores than in trampled plots without herbivores (Fig. 5).

Chthamalus dalli (Table 4, Figs 6 and 7)

Chthamalus dalli abundance was low prior to trampling at both sites, 1.3% at Fogarty Creek, and 0.03% at Yaquina Head (Figs 6 and 7). The distribution of C. dalli was also spatially heterogenic within each site (Table 4). For example, at Yaquina Head, C. dalli mean cover was higher in herbivore inclusion plots than in herbivore exclusion plots (Fig. 7).

Trampling had no negative effects on C. dalli abundance at either site. Instead, there were indirect positive effects with mean cover of C. dalli increasing as a result of the reduction B. glandula (Table 4). At Yaquina Head, C. dalli mean cover increased gradually in all plots. However, C. dalli was never abundant, and maximum mean cover was less than 15% (Fig. 7). At Fogarty Creek, C. dalli mean cover gradually increased and became more abundant than at Yaquina Head (Fig 6). At Fogarty Creek, C. dalli mean cover reached 35% in some trampled plots (Fig. 6). There were two discernable
recruitment pulses in February 1993, and a larger settlement pulse in July 1993 (Figs 6 and 7).

Chthamalus dalli mean cover in control plots increased slightly through the trampling phase. However, mean cover remained low (Figs 6 and 7). There were no herbivore effects at either site (Table 4). There was also no significant difference between light and heavy trampling.

Figure 6. Effect of trampling on Chthamalus dalli at Fogarty Creek in the presence and absence of herbivores. Data points represent the mean, and vertical bars are ± 1 SE.

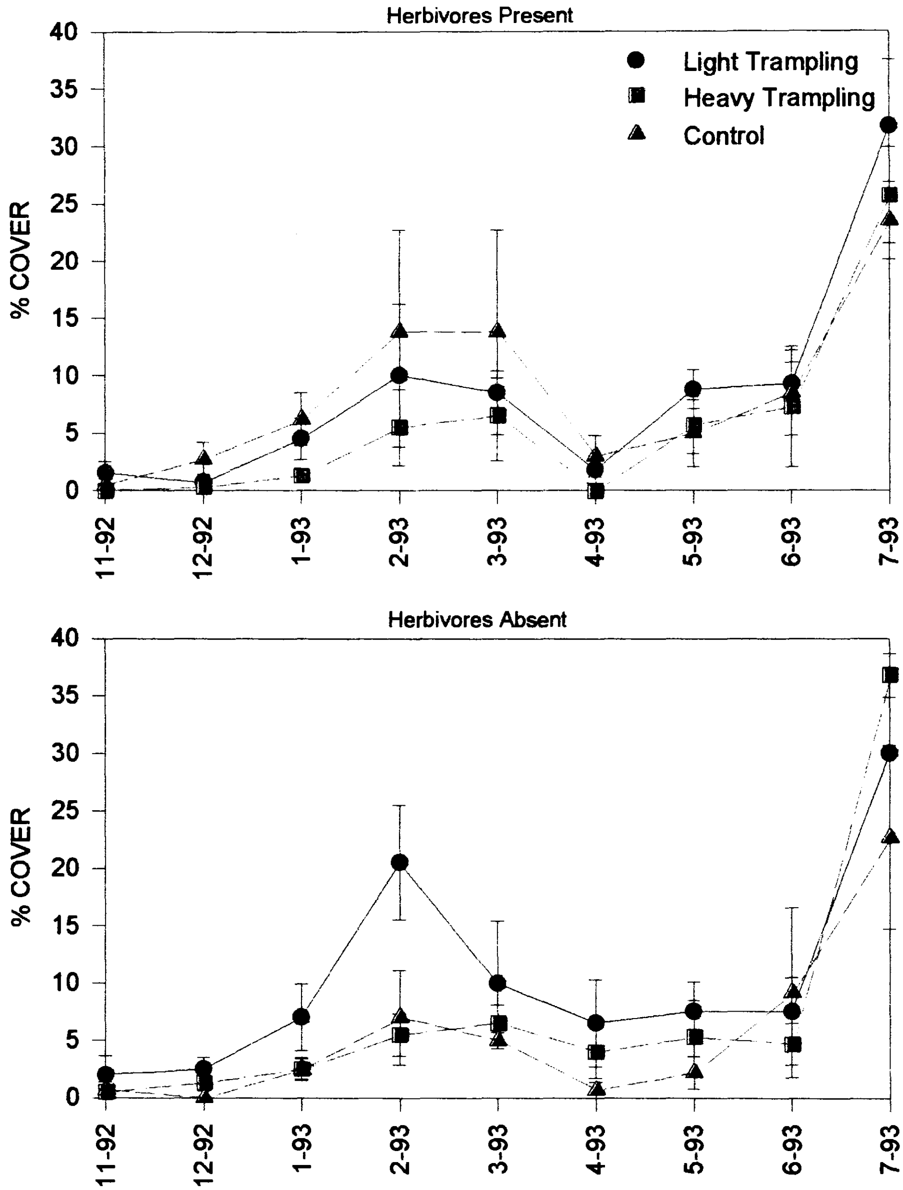


Figure 7. Effect of trampling on Chthamalus dalli at Yaquina Head in the presence and absence of herbivores. Data points represent the mean, and vertical bars are ± 1 SE.

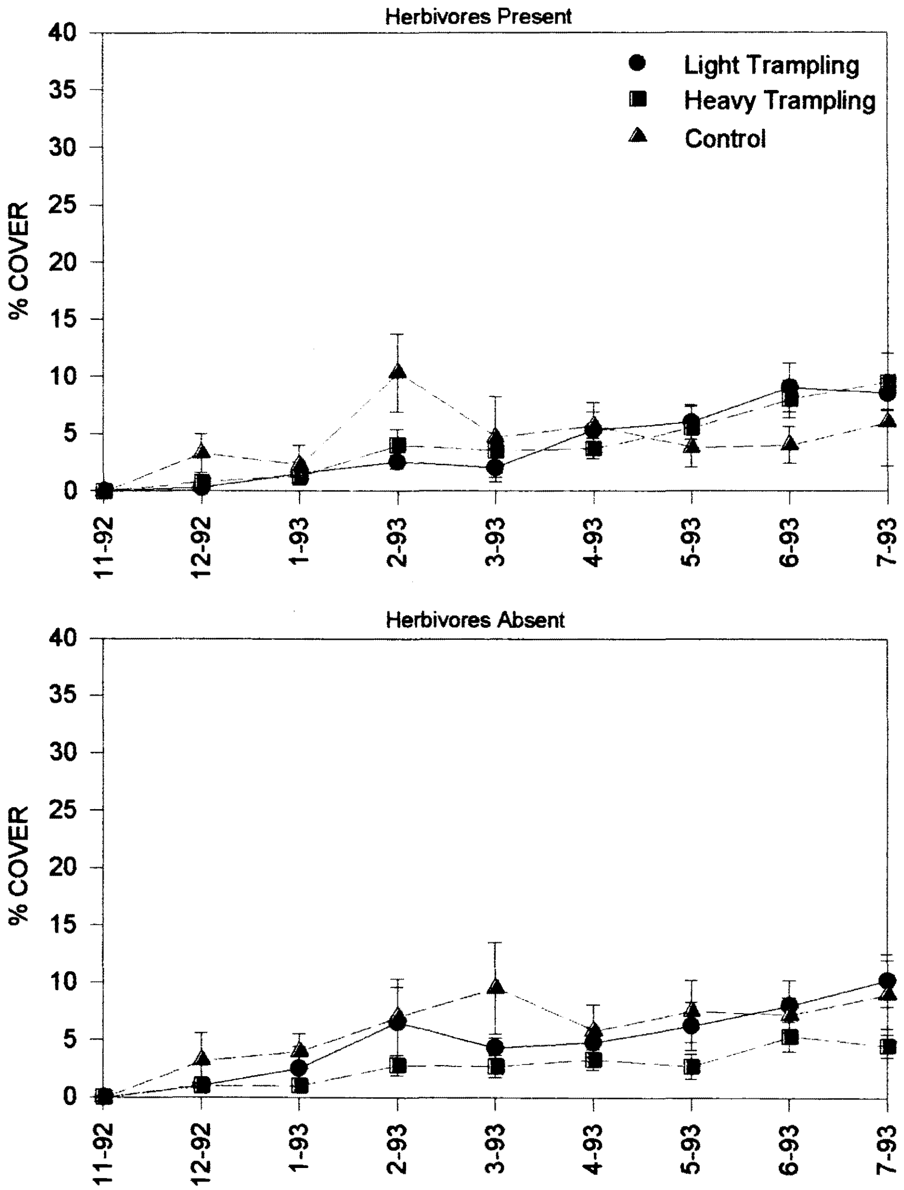


Table 4. Summary of RMANOVA on abundance of barnacles (Chthamalus dalli) in the trampling phase. Data were arcsine -transformed prior to analysis.

SOURCE	DF	MS	F	P
Between treatments				
Site	1	0.515	14.132	P <0.05
Block{site}	6	0.144	3.951	P <0.05
Trampling{site}	4	0.044	1.196	0.324
Herbivore{site}	4	0.027	0.742	0.568
Trampling*Herbivore	4	0.021	0.584	0.676
Error	52	0.036		
Within treatments				
Date	8	0.936	117.415	P<0.05
Date*Site	8	0.185	23.247	P<0.05
Date*Block{site}	48	0.024	3.057	P<0.05
Date*Trampling{site}	32	0.013	1.659	P <0.05
Date*Herbivore{site}	32	0.010	1.312	0.123
Date*Trampling*Herbivore	32	0.009	1.131	0.289
Error	416	0.008		

Greenhouse-Geisser Epsilon: 0.6909: Huyn-Feldt Episilon: 1.0000

Fucoid algae

Density and distribution of fucoid Algae were spatially heterogous between sites and between blocks and plots within each site throughout the trampling phase (Tables 5 and 6). Generally, fucoid algae were more abundant at Fogarty Creek compared to Yaquina Head. At Fogarty Creek, fucoid density and distribution were more spatially homogenic, while at Yaquina Head fucoid density and distribution were heterogenic to the extreme where blocks lacked fucoids. Fucoids are very susceptible to trampling. Results for canopy and primary cover are presented separately.

Canopy Cover (Table 5; Figs 8 and 9)

At Fogarty Creek in December 1992 (after one application of trampling), mean cover had declined from an average of 11.0% in November 1992 to 0.9% in December 1992 in herbivore inclusion treatments, and from 12.8% in November 1992 to 0.7% in December 1992 in herbivore exclusion treatments (Fig 8). There was no difference in canopy loss between light and heavy trampling (Table 5). Trampling and the lack of facilitative species prevented foliose algae from significant recovery.

At Fogarty Creek, canopy cover in control plots remained relatively high and showed seasonal fluctuations. Canopy mean cover ranged from

5.5% in November 1992 to 27% in March 1993 in herbivore inclusion plots (Fig 8). Canopy cover in control plots fluctuated more than canopy cover in trampled plots, which remained at <15% cover throughout the experimental period (Fig 8). At Fogarty Creek, canopy cover declined in herbivore inclusion plots between May and July 1993. These declines were the result of harbor seals, Phoca vitulina, using blocks 2 and 3 as haul-out areas. Herbivores did not significantly affect mean canopy cover of fucoids. In addition, there were no herbivore-trampling interactions: Trampling was the only significant factor (Table 5). This implies that trampling swamps any potential herbivore effects on recruitment or colonization of algae.

At Yaquina Head, canopy mean cover was low, 8.5% in November 1992 (Fig 9). Canopy cover in trampled plots declined to zero within two months of trampling. Canopy cover did not recover in herbivore inclusion plots during the trampling phase. Canopy cover in herbivore exclusion plots ranged from 0% to 3% (Fig 9). Canopy cover in the control plots increased throughout the spring, and declined in summer (Fig 9).

Canopy cover was most abundant in herbivore inclusion plots due to the heterogenic distribution of fucoids (Table 5; Fig. 9). Initial cover ranged from 14% to 40% in control, herbivore-exclusion plots. By chance, experimental plots that were randomly assigned as herbivore inclusion

Figure 8. Effect of trampling on Fucoid Algae (Canopy) at Fogarty Creek in the presence and absence of herbivores. Data points represent the mean, and vertical bars are ± 1 SE.

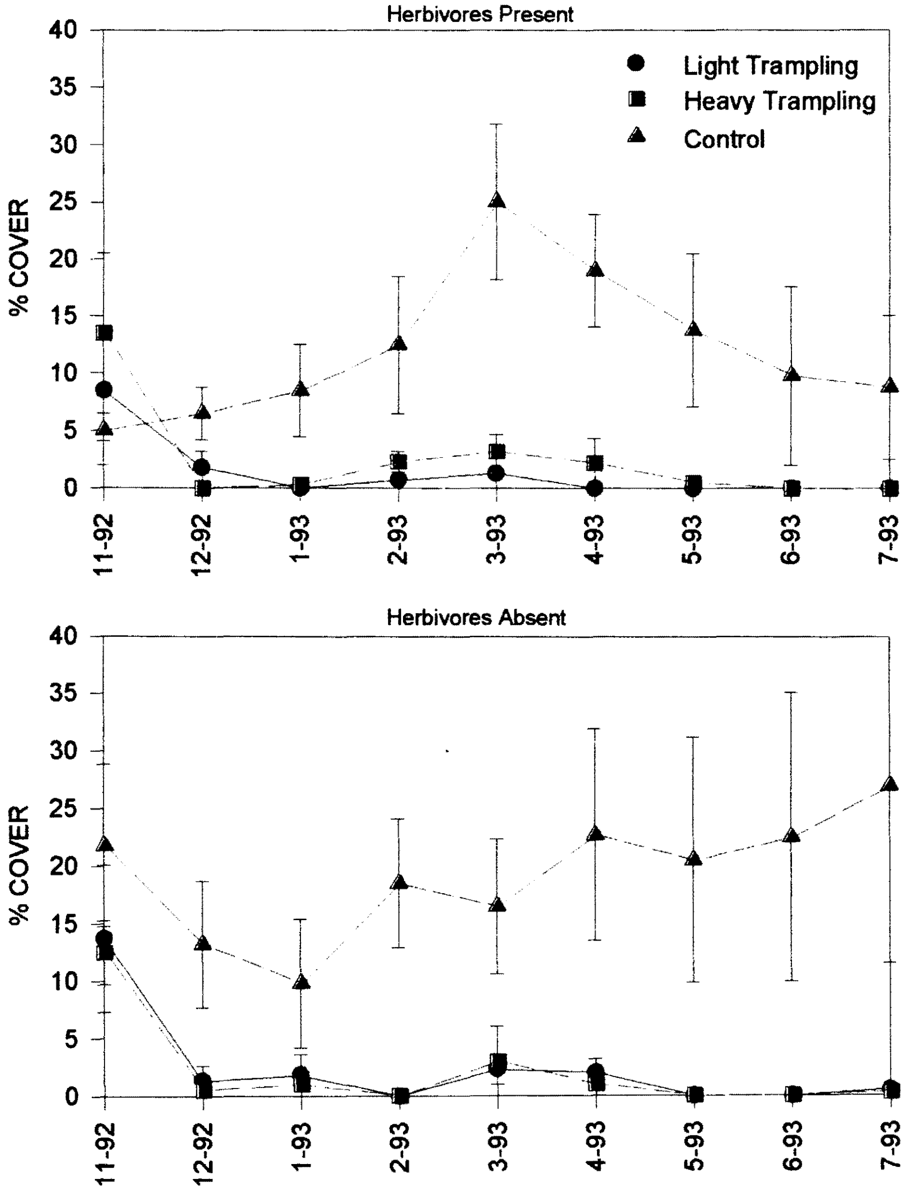


Figure 9. Effect of trampling on Fucoid Algae (Canopy) at Yaquina Head in the presence and absence of herbivores. Data points represent the mean, and vertical bars are ± 1 SE.

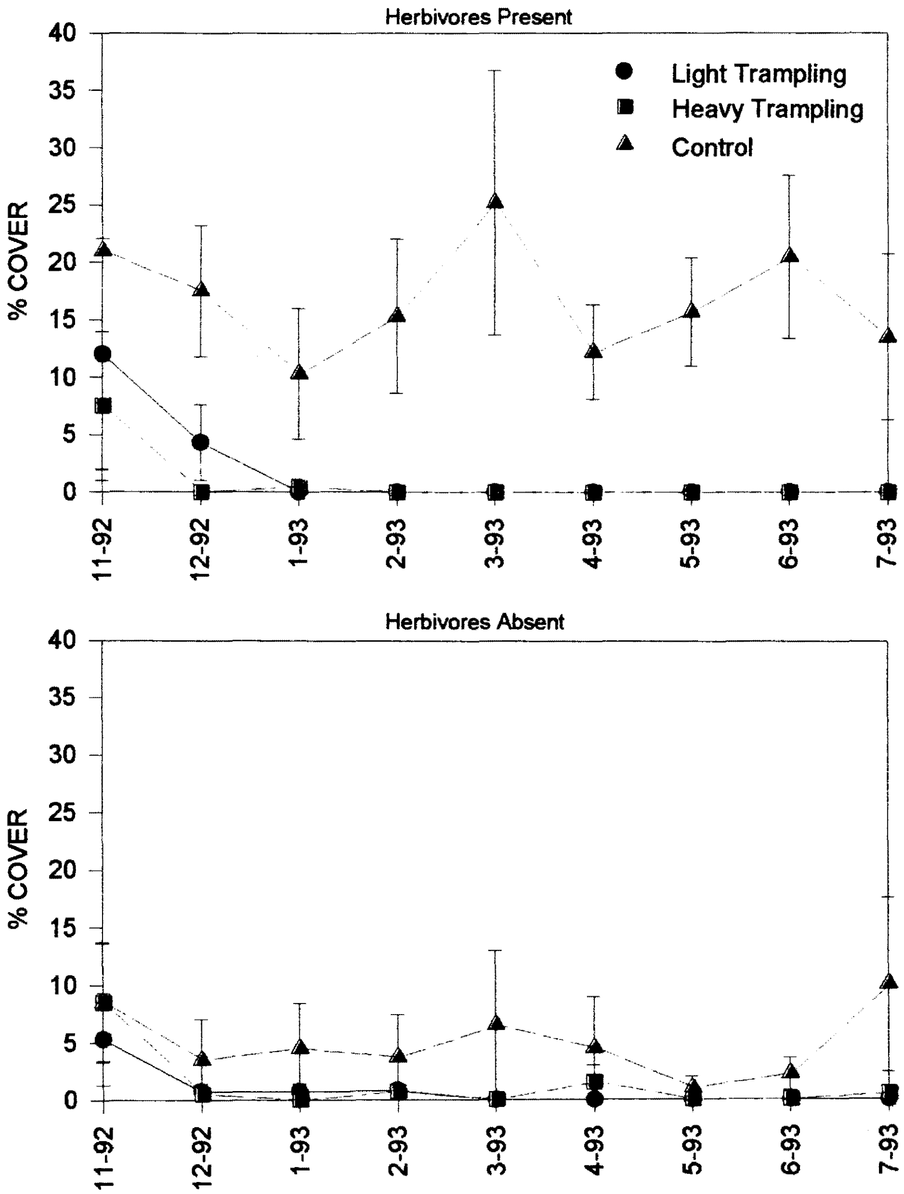


Table 5. Summary of RMANOVA on abundance of Fucoid Algae (canopy) in the trampling phase. Data were arcsine -transformed prior to analysis.

SOURCE	DF	MS	F	P
Between treatments				
Site	1	0.137	24.820	P <0.05
Block{Site}	6	0.013	2.282	P <0.05
Trampling{Site}	4	0.195	35.305	P <0.05
Herbivore{Site}	4	0.003	0.559	0.693
Trampling*Herbivore	4	0.004	0.659	0.623
Error	52	0.006		
Within treatments				
Date	8	0.004	1.631	0.114
Date*Site	8	0.012	5.259	P <0.05
Date*Block{Site}	48	0.006	2.489	P <0.05
Date*Trampling{Site}	32	0.005	1.989	P <0.05
Date*Herbivore{Site}	32	0.004	1.789	P <0.05
Date*Trampling*Herbivore	32	0.003	1.233	0.183
Error	416	0.002		

Greenhouse-Geisser Epsilon: 0.6254: Huyn-Feldt Episilon: 0.9529

treatments had a greater cover of fucoids. By contrast, in herbivore exclusion plots and paint control plots, initial fucoid mean cover was less than 10%.

There was no difference between control plots in herbivore exclusion plots and paint control (herbivore inclusion) plots during the experiment. This effect was carried through the trampling phase. So the significance of herbivores (Table 5) is actually not due to herbivore effects.

Primary cover (Table 6; Figs 10 and 11)

Two months after trampling was begun primary cover of fucoids declined significantly (Table 6; Figs 10 and 11). At Fogarty, Creek primary cover in trampled plots remained below 5% for the remainder of the trampling phase (Fig 10). By contrast, primary cover in control plots gradually increased during spring. At Fogarty Creek, there was no difference between the effects of light and heavy trampling. Both reduced fucoid primary cover to the same level. At the beginning of the experiment (prior to any trampling), algal cover was higher in the herbivore exclusion treatments (Fig 10). This was not due to any trampling effect. However, after trampling started, herbivores had no effect on trampled plots: Cover in herbivore inclusion and exclusion plots in trampled treatments was the same, and cover in herbivore inclusion and exclusion plots in control treatments was also the same (Table 6; Fig 10).

Primary cover of fucoid algae at Yaquina Head was low. Trampling reduced mean cover to 0% within two months of trampling (Fig 11). There was some recruitment in April in herbivore inclusion plots but these plants disappeared a month later (Fig 11). In control plots, fucoid primary cover increased and was most abundant in the herbivore inclusion plots (for reasons explained above).

Figure 10. Effect of trampling on Fucoid Algae (Primary) at Fogarty Creek in the presence and absence of herbivores. Data points represent the mean, and vertical bars are ± 1 SE.

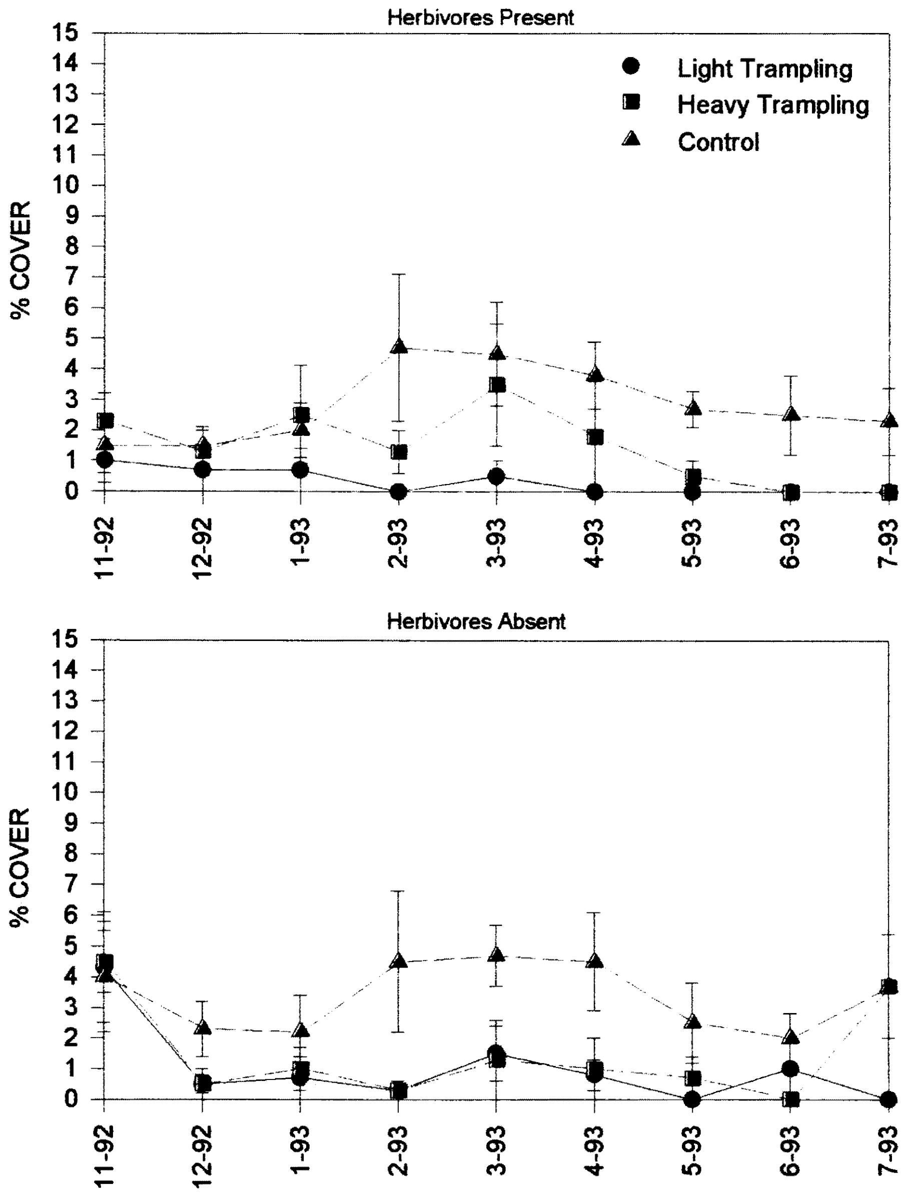


Figure 11. Effect of trampling on Fucoid Algae (Primary) at Yaquina Head in the presence and absence of herbivores. Vertical bars are ± 1 SE.

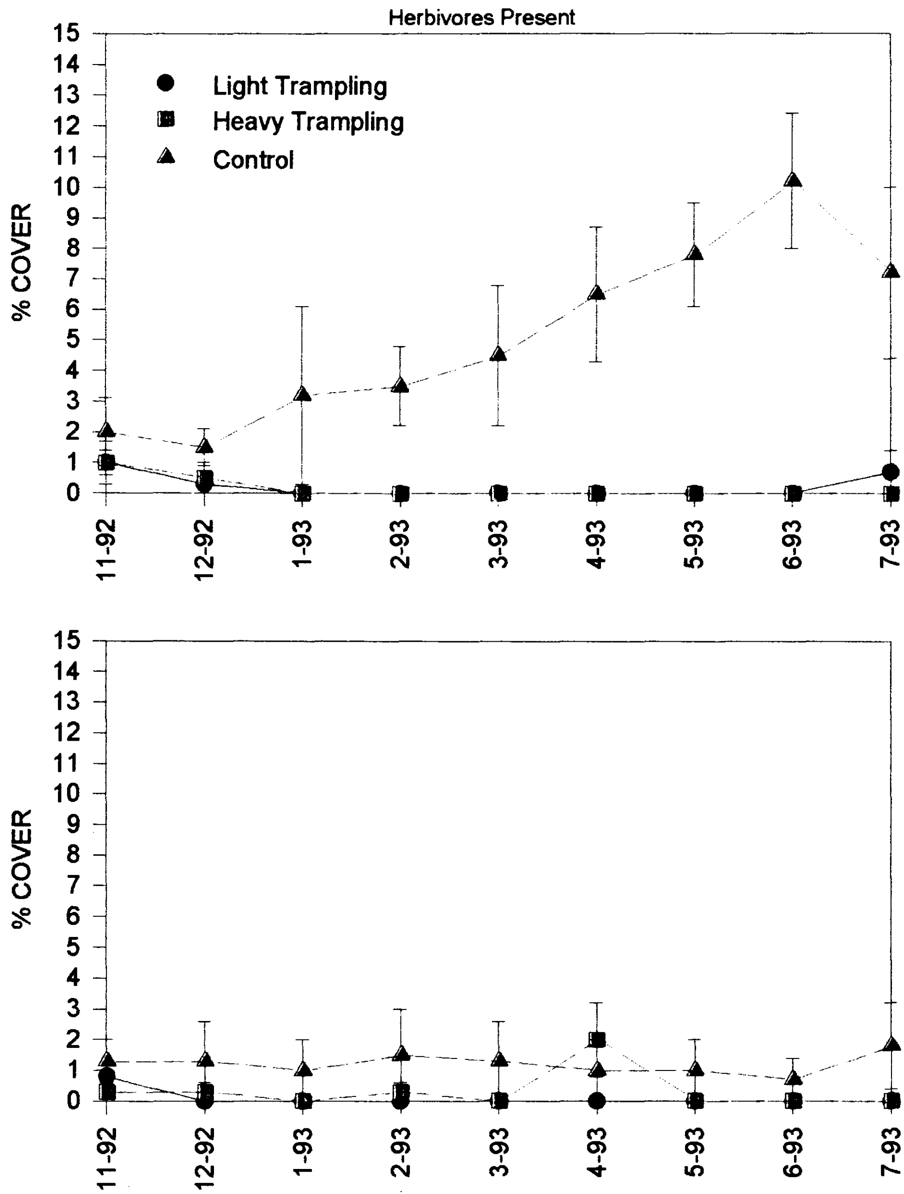


Table 6. Summary of RMANOVA on abundance of Fucoid Algae (primary) in the trampling phase. Data were arcsine -transformed prior to analysis.

SOURCE	DF	MS	F	P
Between treatments				
Site	1	0.151	24.861	P <0.05
Block{Site}	6	0.011	1.753	0.127
Trampling{Site}	4	0.118	19.442	P <0.05
Herbivore{Site}	4	0.001	0.207	0.934
Trampling*Herbivore	4	0.004	0.600	0.665
Error	52	0.006		
Within treatments				
Date	8	0.003	2.250	P <0.05
Date*Site	8	0.005	4.140	P <0.05
Date*Block{Site}	48	0.003	2.540	P <0.05
Date*Trampling{Site}	32	0.003	2.102	P <0.05
Date*Herbivore{Site}	32	0.002	1.447	0.058
Date*Trampling*Herbivore	32	0.001	0.546	0.980
Error	416	0.001		

Greenhouse-Geisser Epsilon: 0.6254: Huyn-Feldt Episilon: 0.9529

Endocladia muricata (Table 7, Figure 12)

Endocladia muricata abundance at Yaquina Head was very low and patchily distributed. For these reasons, data on this species at the Yaquina Head site are not included as they could not be analyzed or graphed. At Fogarty Creek, E. muricata was rarely attached directly to primary substrate. The majority of E. muricata individuals grew as epibionts on barnacles (predominantly B. glandula). Trampling significantly reduced E. muricata cover beginning in January 1993 (Table 7; Fig. 12). Canopy cover increased in control plots (up to 25% cover in herbivore inclusion plots), while cover in trampled plots remained low, >5% (Fig 12). The effect of trampling intensity on E. muricata was not significant. There were no herbivore effects (Table 7). Endocladia muricata was present only in trace amounts in plots at Yaquina Head, and cover was too low for analysis.

Figure 12. Effect of trampling on Endocladia muricata at Fogarty Creek in the presence and absence of herbivores. Data points represent the mean, and vertical bars are ± 1 SE.

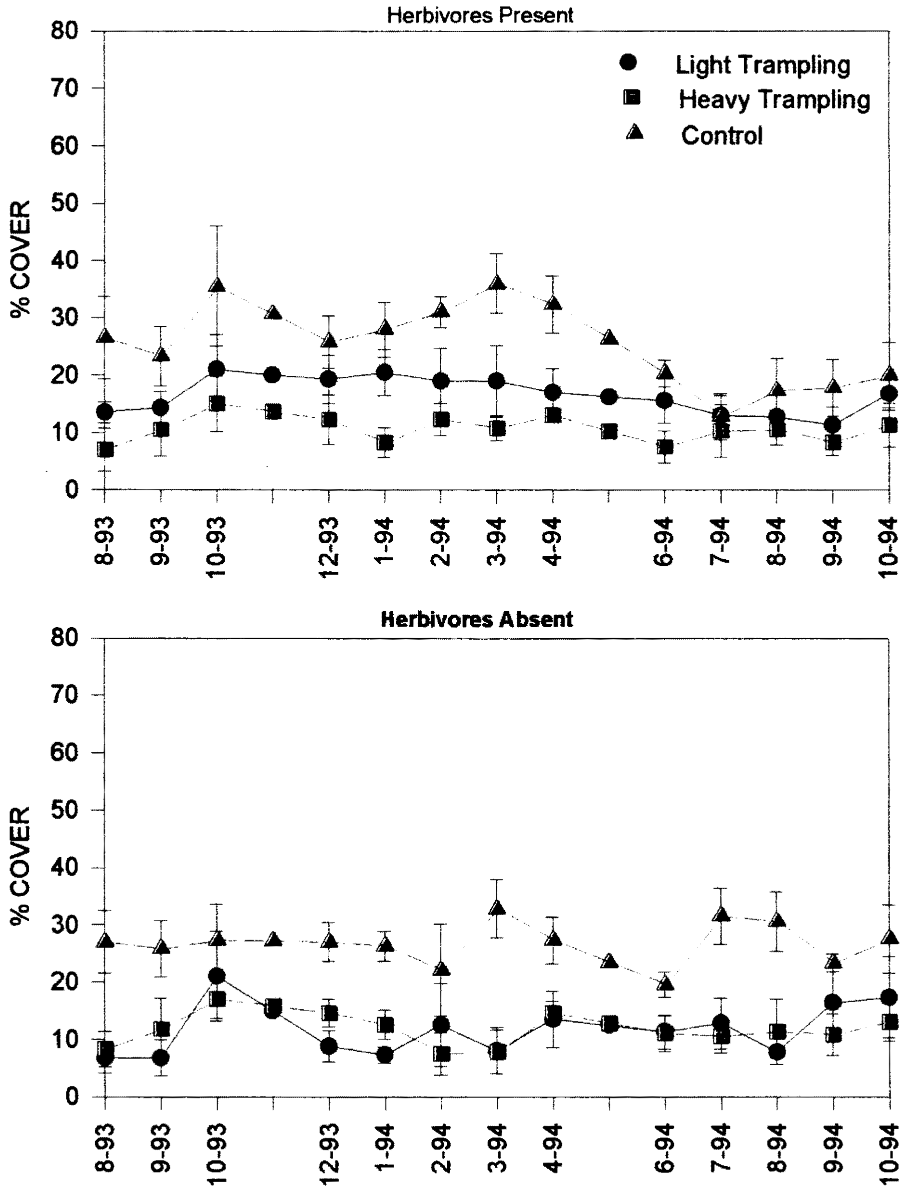


Table 7. Summary of RMANOVA on abundance of (Endocladia muricata) in the trampling phase. Data were arcsine -transformed prior to analysis.

SOURCE	DF	MS	F	P
Between treatments				
Block	3	0.079	2.025	0.137
Trampling	2	1.361	34.764	P <0.05
Herbivore	2	0.122	3.116	0.063
Trampling*Herbivore	4	0.075	1.911	0.141
Error	24	0.039		
Within treatments				
Date	8	0.062	6.782	P <0.05
Date*Block	24	0.017	1.836	P <0.05
Date*Trampling	16	0.057	6.180	P <0.05
Date*Herbivore	16	0.009	0.986	0.474
Date*Trampling*Herbivore	32	0.008	0.894	0.634
Error	192	0.009		

Greenhouse-Geisser Epsilon: 0.6211: Huyn-Feldt Episilon: 1.0000

RECOVERY PHASE

Barnacles:

Balanus glandula (Table 8; Figs 13 and 14)

The distribution and abundance of B. glandula is spatially heterogenic within sites and between sites (Table 8). Balanus glandula mean cover remained higher at Yaquina Head compared to Fogarty Creek. Balanus glandula mean cover varied throughout the recovery phase at both sites (Figs 13 and 14). There were no significant recruitment pulses during the recovery phase, unlike the recruitment pulses observed during the trampling phase. Initially mean cover of B. glandula in trampled plots during the recovery phase was below 15% at both sites Fogarty Creek: light trampling 9.9%, heavy trampling 9.7%; Yaquina Head: light trampling 13.3%, heavy trampling 12.7% (Figs 13 and 14). At Fogarty Creek, B. glandula mean % cover remained below 20% in light trampling treatments and below 16.5% in heavy trampling treatments (Fig 13). At Yaquina Head, B. glandula mean % cover remained below 36.9% in light trampling treatments and below 29.7% in heavy trampling treatments (Fig 14).

In the control plots (no trampling) B. glandula mean cover varied throughout the recovery phase but on average declined. At Fogarty Creek, the initial mean cover was 27.0%; by the conclusion of observations, mean cover was 21.3% (Fig 13). At Yaquina Head, the initial mean cover was

59.5%; by the conclusion of observations mean cover, was 52.8% (Fig 14). Generally, mean cover in the controls converged with mean cover in the trampling treatments.

There continued to be no significant differences in mean cover of B. glandula between light and heavy trampling. There was, however, one case on July 1994 at Yaquina Head where mean cover was greater in light trampling (42.1%) compared to heavy trampling (27.0%). At both Fogarty Creek and Yaquina Head there were significant differences in B. glandula mean cover between each of the trampling treatments (light and heavy) and the controls (Table 8).

There were no significant differences in mean cover of B. glandula between herbivores present and herbivore exclusion, and herbivores present/exclusion and paint control at Fogarty Creek and Yaquina Head (Table 8).

Figure 13. Recovery of Balanus glandula at Fogarty Creek in the presence and absence of herbivores. Data points represent the mean, and vertical bars are ± 1 SE.

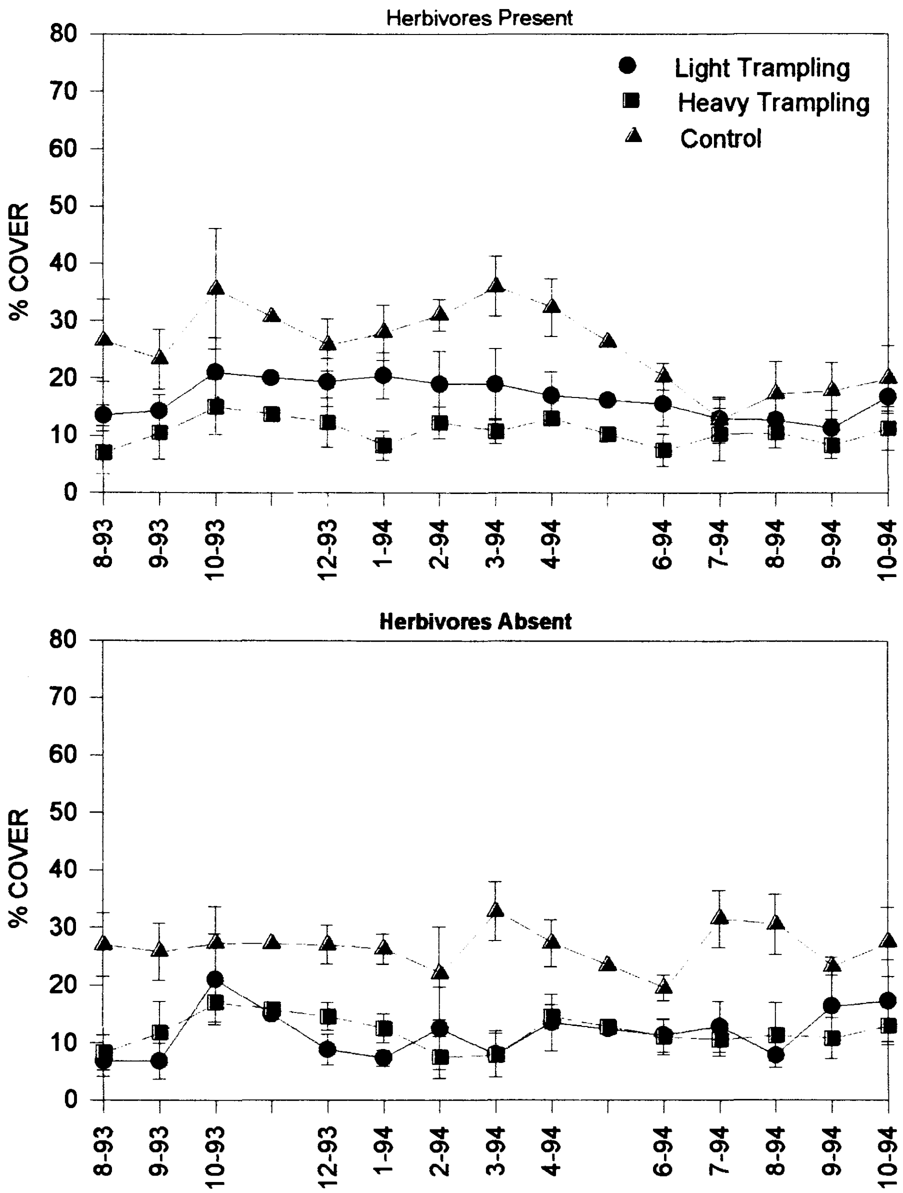


Figure 14. Recovery of Balanus glandula at Yaquina Head in the presence and absence of herbivores. Data points represent the mean, and vertical bars are ± 1 SE.

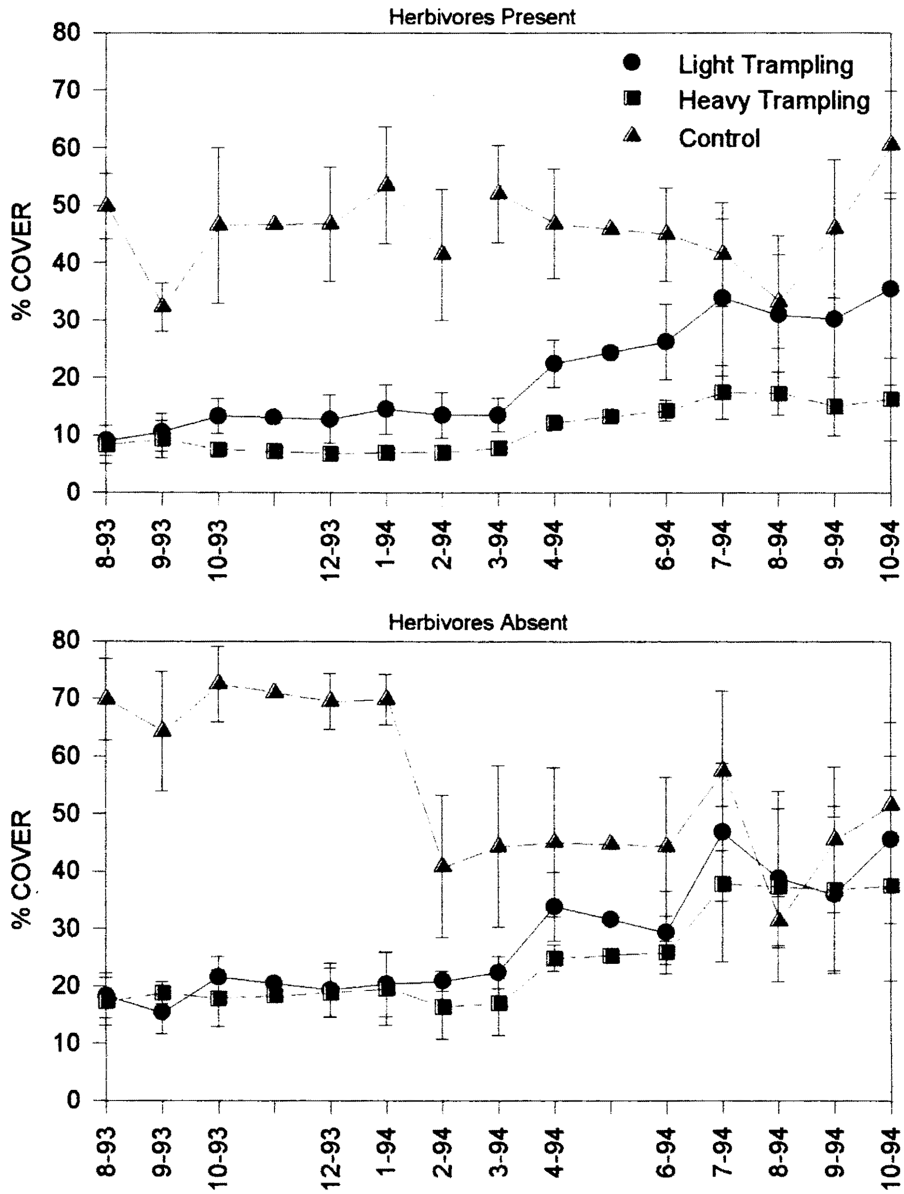


Table 8. Summary of RMANOVA on abundance of barnacles (Balanus glandula) in the recovery phase. Data were arcsine -transformed prior to analysis.

SOURCE	DF	MS	F	P
Between treatments				
Site	1	8.646	73.029	P <0.05
Block{Site}	6	0.390	3.297	P <0.05
Trampling{Site}	4	4.886	41.271	P <0.05
Herbivore{Site}	4	0.447	3.772	P <0.05
Trampling*Herbivore	4	0.188	1.587	0.192
Error	52	0.118		
Within treatments				
Date	12	0.080	5.508	P <0.05
Date*Site	12	0.123	8.469	P <0.05
Date*Block{Site}	72	0.066	4.549	P <0.05
Date*Trampling{Site}	48	0.054	3.707	P <0.05
Date*Herbivore{Site}	48	0.017	1.140	0.245
Date*Trampling*Herbivore	48	0.009	0.611	0.983
Error	624	0.015		

Greenhouse-Geisser Epsilon: 0.3342: Huyn-Feldt Episilon: 0.4979

Chthamalus dalli (Table 9; Figs. 15 and 16)

Chthamalus dalli abundance was low and spatially heterogenic (between sites and within sites) prior to this study (trampling and recovery phase); (Table 9). Chthamalus dalli continued to increase in abundance throughout the recovery phase and remained spatially heterogenic (Table 9). The increase in abundance was due to the near constant recruitment of C. dalli in the early stages of the recovery phase. At Fogarty Creek, mean cover was initially 10.0% in the light trampling treatments and 7.2% in heavy trampling treatments (Fig 15). There was a large recruitment on September 1993 which peaked by the October 1993 (Fig 15). By the conclusion of the recovery phase mean cover in light trampling was 49.6% and 42.8% in heavy trampling (Fig 15). After this point there was a slight decline in C. dalli cover. At Yaquina Head mean cover was initially 7.7% in light trampling treatments and 7.2% in trampling treatments. Chthamalus dalli recruitment was slow reaching a peak around July 1994 and August 1994 (Fig 16).

In general, mean cover of C. dalli in trampling controls was variable at both sites. At Fogarty Creek, C. dalli mean cover in the trampling treatments exceeded the mean cover in the trampling controls (Fig 15). At Fogarty Creek mean cover in the trampling controls increased from an initial mean cover of 9.3% to 13.9% by the end of the recovery phase (Fig 15). At

Yaquina Head, mean cover in the trampling control decreased from an initial cover of 6.6% to 1.7% by the end of the recovery phase (Fig 16).

Mean cover of C. dalli was significantly higher in light and heavy trampling treatments compared to the controls at all dates except the first date (August 1993) at Fogarty Creek (Table 9). At Yaquina Head, mean cover of C. dalli was significantly greater in light and heavy trampling treatments compared to the controls at all dates except the first two dates (August 1993 and September 1993). At Fogarty Creek there were no significant differences in C. dalli mean cover between light and heavy trampling at both sites. There were no significant differences in mean cover of C. dalli between herbivores present and herbivore exclusion on any dates and at both sites.

Figure 15. Recovery of Chthamalus dalli at Fogarty Creek in the presence and absence of herbivores. Data points represent the mean, and vertical bars are ± 1 SE.

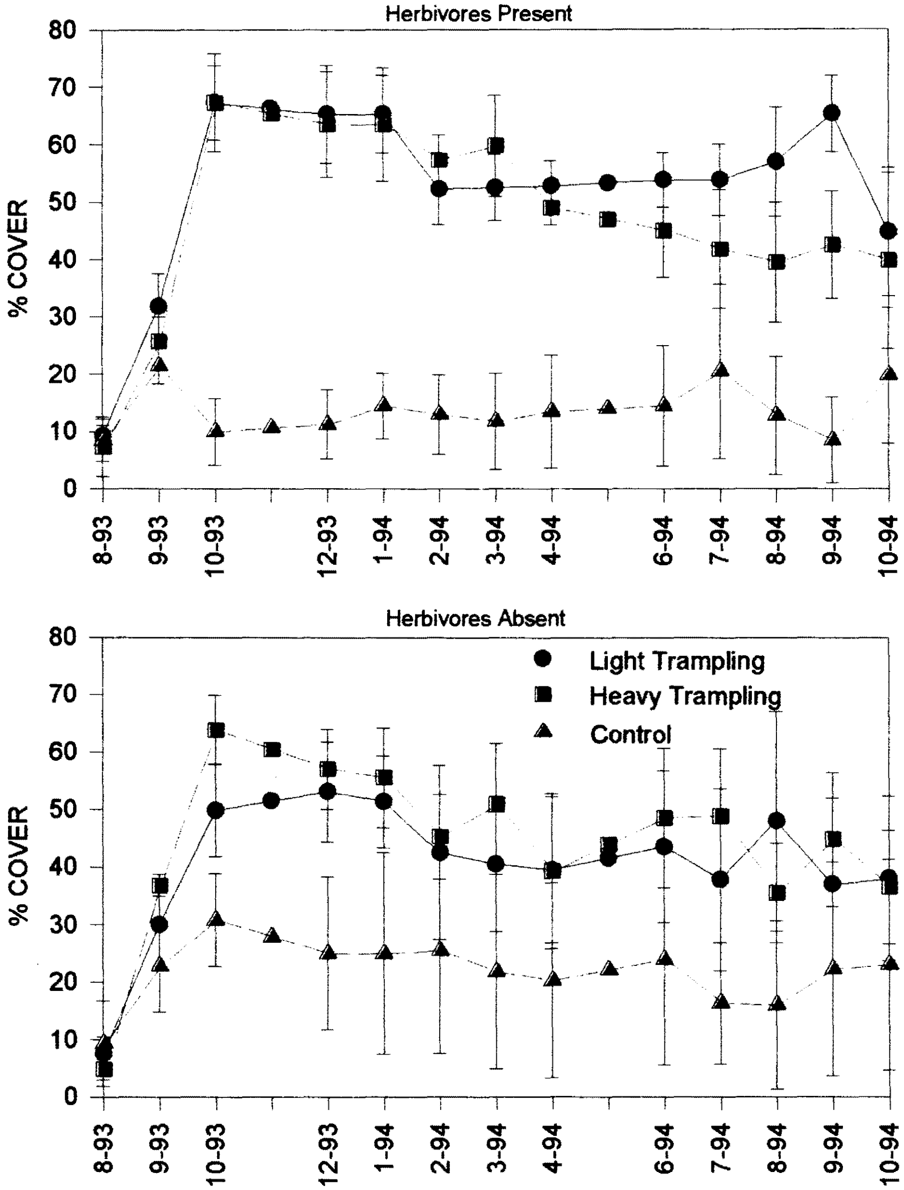


Figure 16. Recovery of Chthamalus dalli at Yaquina Head in the presence and absence of herbivores. Data points represent the mean, and vertical bars are ± 1 SE.

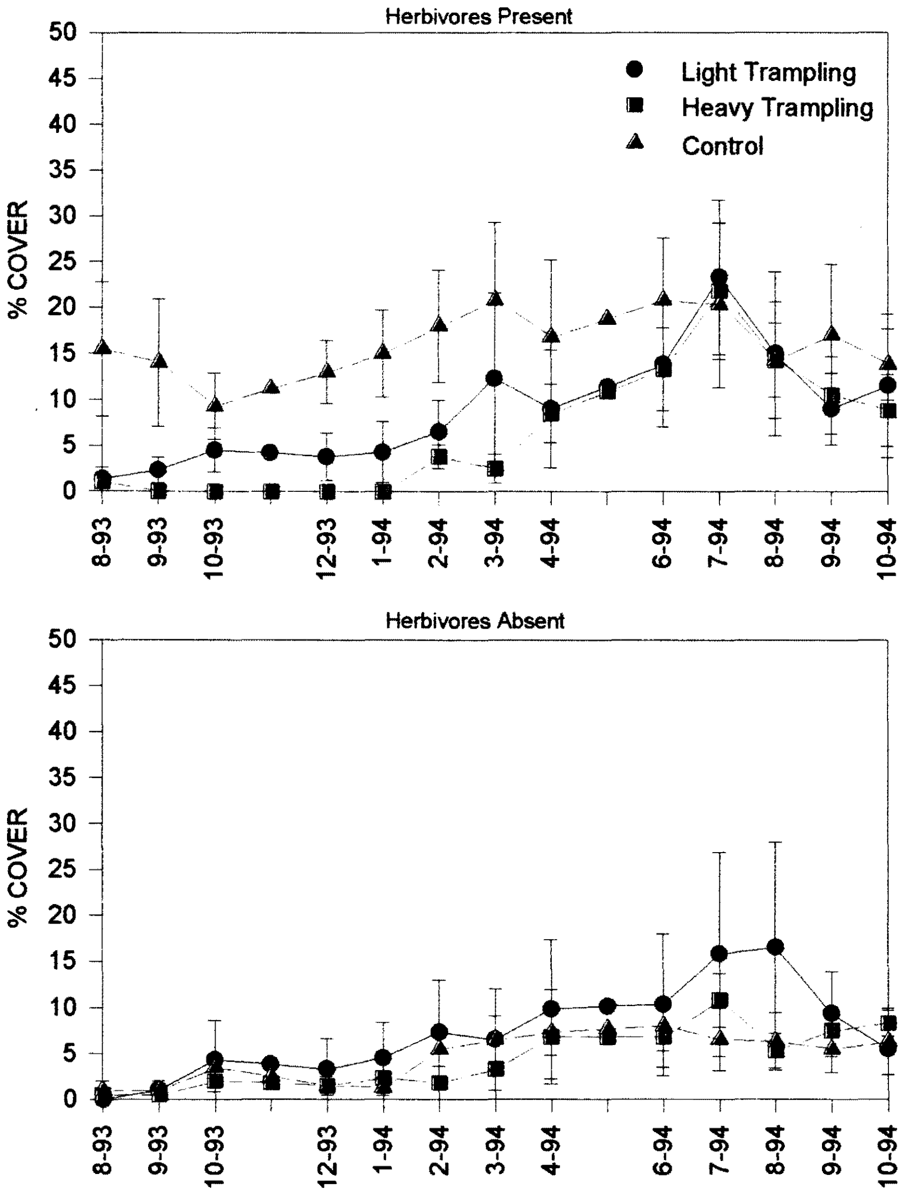


Table 9. Summary of RMANOVA on abundance of barnacles (Chthamalus dalli) in the recovery phase. Data were arcsine -transformed prior to analysis.

SOURCE	DF	MS	F	P
Between treatments				
Site	1	24.164	147.983	P <0.05
Block{site}	6	1.592	9.750	P <0.05
Trampling{site}	4	4.767	29.195	P <0.05
Herbivore{site}	4	0.023	0.138	0.967
Trampling*Herbivore	4	0.289	1.772	0.149
Error	52	0.163		
Within treatments				
Date	12	0.438	37.824	P <0.05
Date*Site	12	0.219	18.866	P <0.05
Date*Block{site}	72	0.036	3.114	P <0.05
Date*Trampling{site}	48	0.068	5.895	P <0.05
Date*Herbivore{site}	48	0.013	1.104	0.335
Date*Trampling*Herbivore	48	0.012	1.057	0.392
Error	624	0.012		

Greenhouse-Geisser Epsilon: 0.5335: Huyn-Feldt Episilon: 0.8387

Fucoid Algae

Canopy (Table 10; Figs 17 and 18)

During the trampling phase the fucoid canopy was completely removed. The recovery of the canopy was retarded in trampled plots at both sites (Figs 17 and 18) . By the conclusion of the recovery phase, mean canopy cover in trampled plots remained below 20%. There continued to be no difference between light and heavy trampling plots (Table 10). There was also no effect of herbivores at either site.

At Fogarty Creek, mean canopy cover in the controls was significantly greater than in the trampling treatments from August 1993 to September 1994. Mean canopy cover in the controls declined initially in the recovery phase following the downward trend seen in the trampling phase. In herbivore present plots mean canopy cover increased rapidly early in the recovery phase and reached a peak of 31% on October 1993. Canopy then declined to January 1994 after which it increased gradually, reaching a second higher peak of 36.3% on July 1994. After July 1994 mean canopy declined, reaching 23% by October 1994. In herbivore exclusion plots, mean canopy cover declined. rapidly between the trampling phase (22%) and the recovery phase (8%). Canopy cover then increased slightly through the recovery phase and reached 15.8% by October 1994,which was lower than pre-trampling cover.

At Yaquina Head, mean canopy cover in the controls was significantly greater than in the trampling treatments throughout the recovery phase (Table 10). Mean cover of the canopy increased steadily throughout the recovery phase reaching a peak by August 1994. In the herbivore present plots, the peak mean cover reached 100%, while in the herbivore exclusion plots the peak mean cover of 55%. The mean cover was significantly greater than the pre-experimental of November 1992.

Figure 17. Recovery of Fucoid algae (Canopy) at Fogarty Creek in the presence and absence of herbivores. Data points represent the mean, and vertical bars are ± 1 SE.

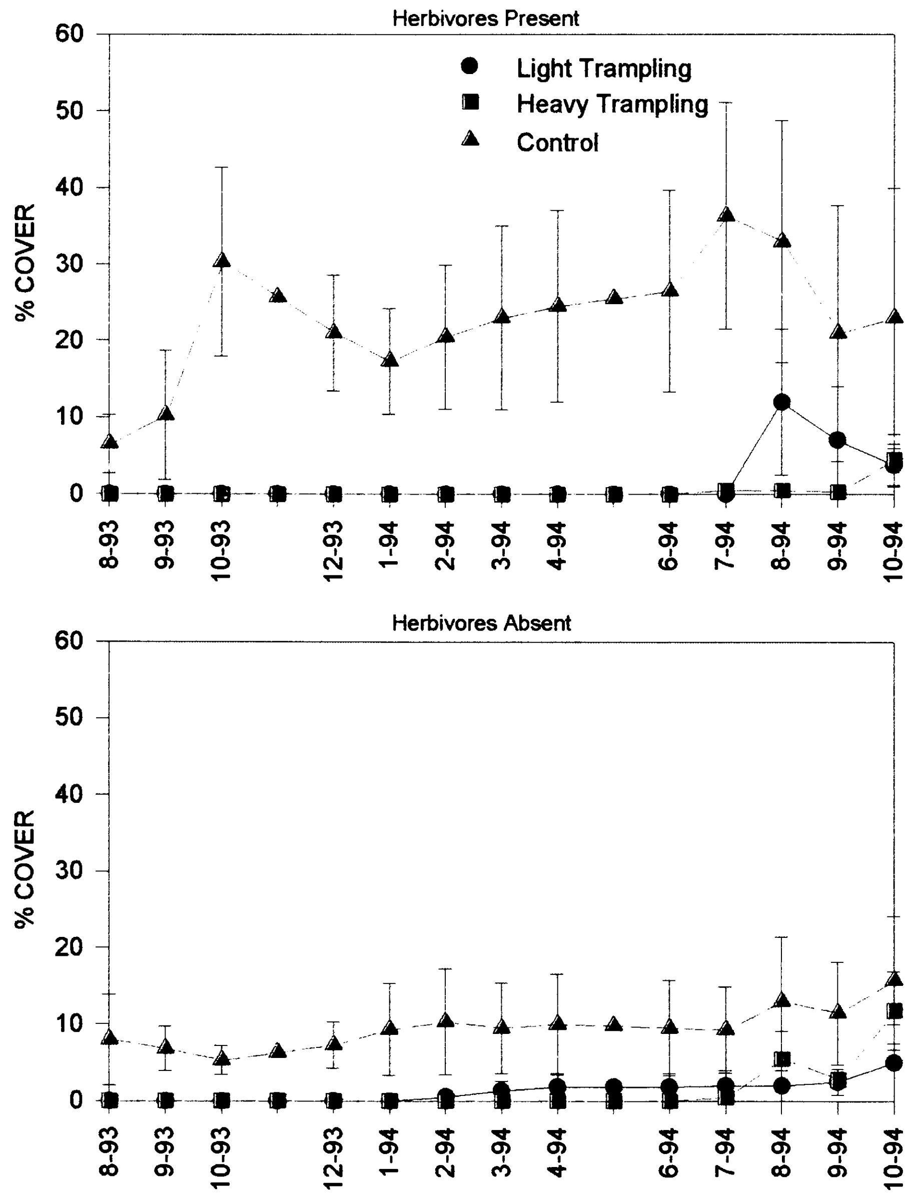


Figure 18. Recovery of Fucoid algae (Canopy) at Yaquina Head in the presence and absence of herbivores. Data points represent the mean, and vertical bars are ± 1 SE.

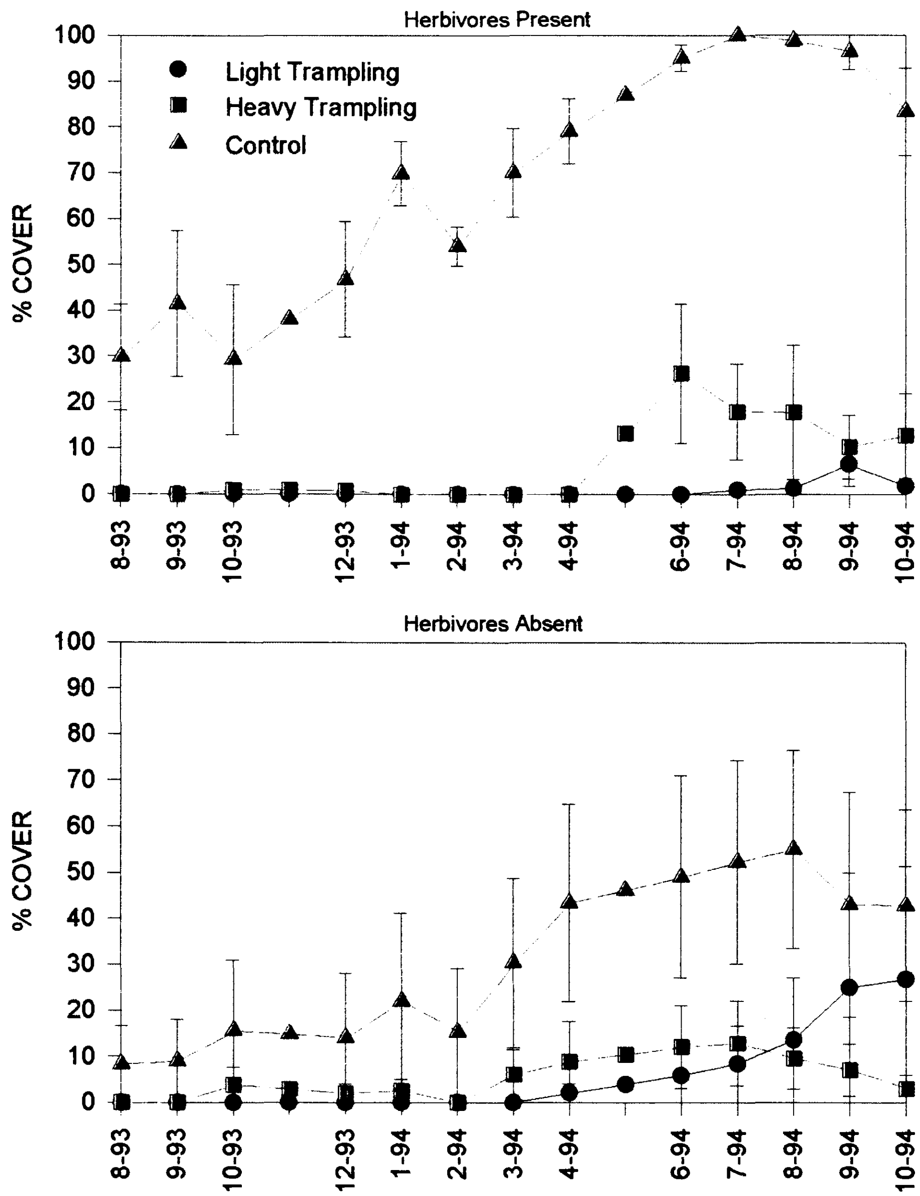


Table 10. Summary of RMANOVA on abundance of Fucoids (canopy) in the recovery phase. Data were arcsine -transformed prior to analysis.

SOURCE	DF	MS	F	P
Between treatments				
Site	1	6.880	13.564	P <0.05
Block{site}	6	2.188	4.314	P <0.05
Trampling{site}	4	11.458	22.588	P <0.05
Herbivore{site}	4	0.590	1.164	0.337
Trampling*Herbivore	4	1.486	2.930	0.290
Error	52	0.507		
Within treatments				
Date	12	0.865	39.748	P <0.05
Date*Site	12	0.366	16.810	P <0.05
Date*Block{site}	72	0.097	4.458	P <0.05
Date*Trampling{site}	48	0.148	6.804	P <0.05
Date*Herbivore{site}	48	0.015	0.688	0.946
Date*Trampling*Herbivore	48	0.017	0.797	0.835
Error	624	0.022		

Greenhouse-Geisser Epsilon: 0.6254: Huyn-Feldt Episilon: 0.9529

Primary (Figs 19 and 20)

The mean cover of fucoid primary cover was too low for statistical analysis. At Fogarty Creek, primary cover was zero until after April 1994 at which point it never exceeded mean of 4%. By the end of the recovery phase, mean cover was generally lower than the pretrampling levels of November 1992. Mean cover in control plots varied at Fogarty Creek, never exceeding 5%. Mean cover remained higher than in the trampling plots except on the September 1994 in herbivore present plots, and June 1994 and July 1994 in herbivore exclusion plots.

At Yaquina Head, mean primary cover remained under 2% in herbivore present plots, while in herbivore exclusion plots mean primary cover remained under 4%. In the controls in herbivore present plots, primary cover varied but continued on an upward trend that was observed in the trampling phase

Figure 19. Recovery of Fucoid algae (Primary) at Fogarty Creek in the presence and absence of herbivores. Data points represent the mean, and vertical bars are ± 1 SE.

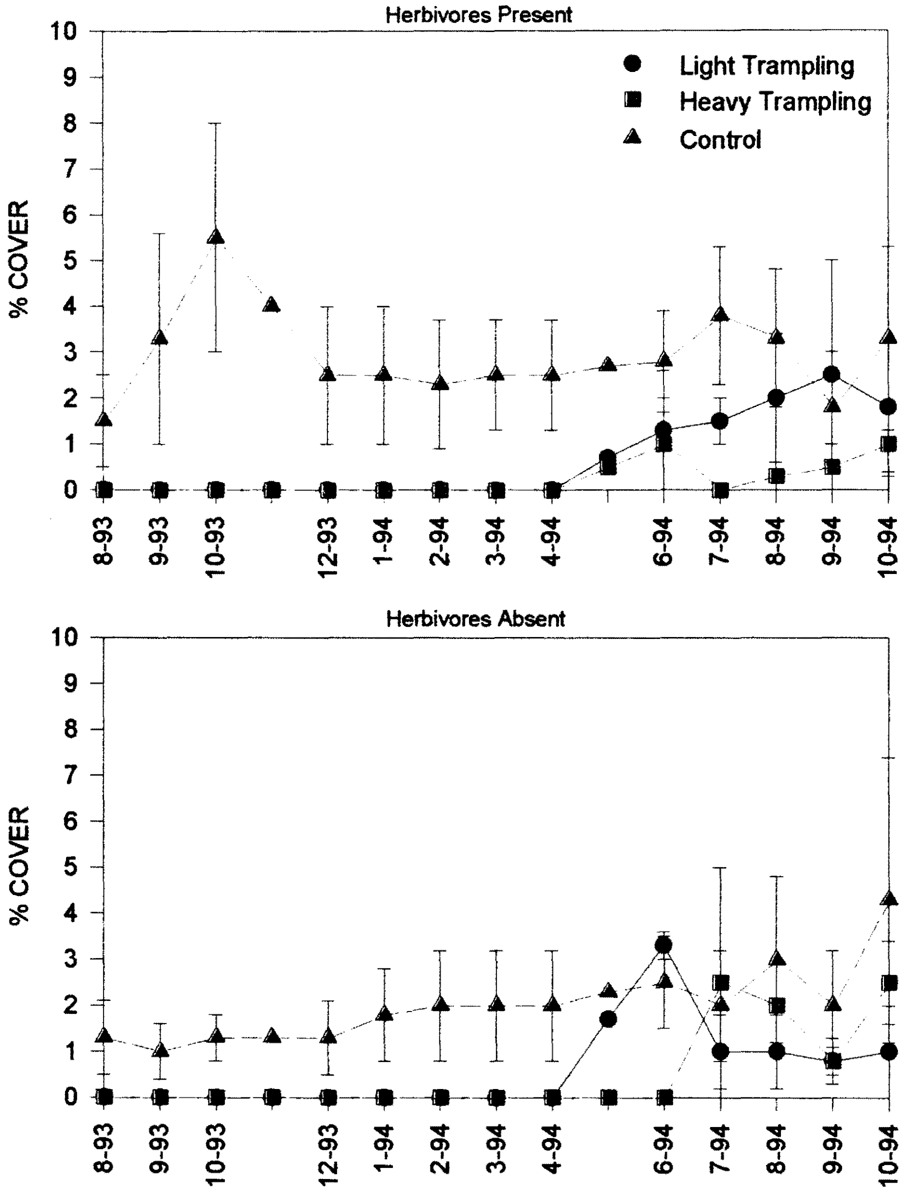
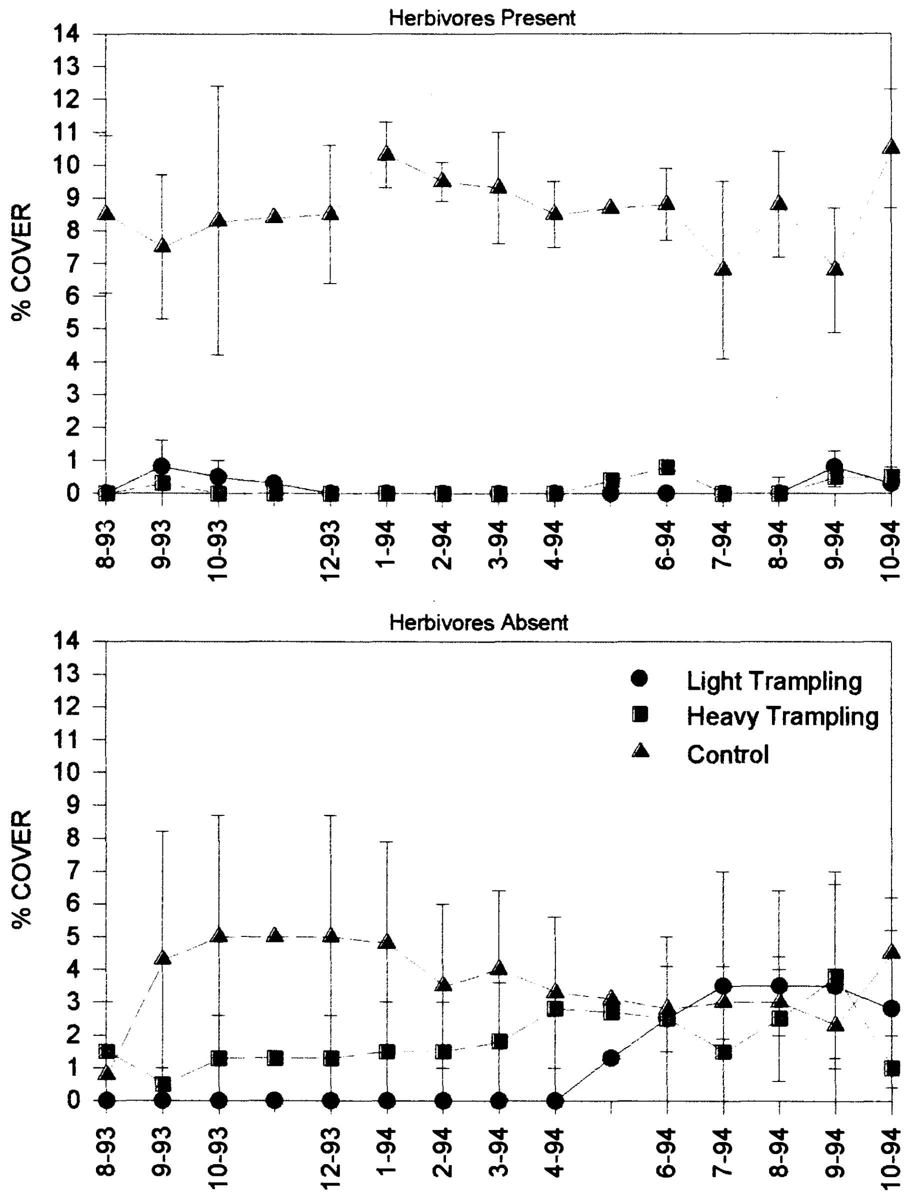


Figure 20. Recovery of Fucoid algae (Primary) at Yaquina Head in the presence and absence of herbivores. Data points represent the mean, and vertical bars are ± 1 SE.



Endocladia muricata (Table 11; Fig 21)

In general mean, cover of E. muricata increased throughout the recovery phase at Fogarty Creek (Fig 21). At Yaquina Head, E. muricata mean cover was very low throughout both the trampling phase and recovery phase and is not discussed in the this paper. The distribution of E. muricata was spatially heterogenic, within the site and blocks (Table 11). There was a peak in E. muricata cover at both sites between July 1994 and August 1994 (Fig 21). After this date E. muricata mean cover began to decline.

Mean cover of E. muricata in light and heavy trampling was significantly different than control on two dates. Mean cover of E. muricata in heavy trampling was significantly different than the control on a further four dates. Mean cover of E. muricata herbivore present treatments were significantly greater than herbivore exclusion on August 1993 (Table 11).

Figure 21. Recovery of Endocladia muricata at Fogarty Creek in the presence and absence of herbivores. Data points represent the mean, and vertical bars are ± 1 SE.

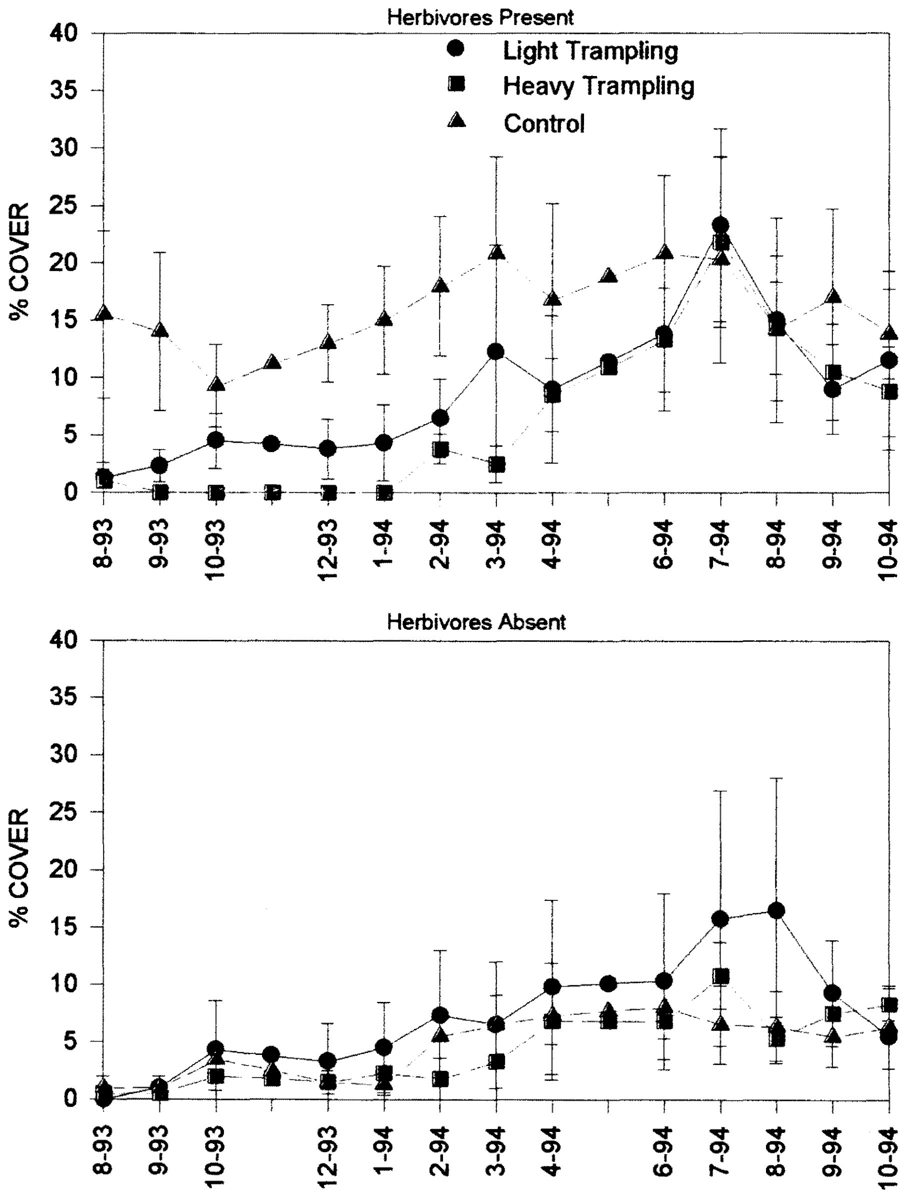


Table 11. Summary of RMANOVA on abundance of (Endocladia muricata) in the recovery phase. Data were arcsine -transformed prior to analysis.

SOURCE	DF	MS	F	P
Between treatments				
Block	3	1.187	8.600	P <0.05
Trampling	2	0.276	1.999	0.157
Herbivore	2	0.675	4.888	0.017
Trampling*Herbivore	4	0.228	1.649	0.195
Error	24	0.138		
Within treatments				
Date	12	0.424	32.002	P <0.05
Date*Block	36	0.032	2.430	P <0.05
Date*Trampling	24	0.025	1.910	P <0.05
Date*Herbivore	24	0.023	1.746	P <0.05
Date*Trampling*Herbivore	48	0.009	0.665	0.956
Error	288	0.013		

Greenhouse-Geisser Epsilon: 0.3484: Huyn-Feldt Episilon: 0.6248

DISCUSSION

The two phases of this study investigated a series of predictions on the effects of trampling, recovery from trampling and the presence or absence of herbivores on the upper shore barnacle-algal community (Tables 12, and 13). Some of these predictions were supported, trampling dislodged the larger barnacle species, and the smaller, competitively inferior barnacle became more abundant in trampled plots. Fucoid algae were highly susceptible to trampling. Fucoid algae and E. muricata recovered slowly in the absence of B. glandula. Other predictions were not supported, herbivores had little effect on the ability of communities to persist or to recover under trampling conditions. There was no difference between the effects of light and heavy trampling on most species in the community. Overall, trampling changed the community from one dominated by B. glandula and fucoid algae to one where the smaller barnacle C. dalli, algal crust, and bare space was more common. Succession was prevented because of direct effects of trampling on organisms and also because of indirect effects of the presence of barnacles. Balanus glandula recovery was slow due to low recruitment and competitive exclusion by C. dalli. Recruitment of C. dalli was high and individuals grew to a large size.

Table 12. Predictions/Results during the Trampling Phase

	HERBIVORES PRESENT	HERBIVORE EXCLUSION
No TRAMPLING (CONTROL)	**Predicted**: B. glandula abundant; C. dalli present at low density; Late successional algae abundant; herbivore resistant species present. **Observed**: supported, however algae were uncommon at Yaquina Head.	**Predicted**: B. glandula and foliose algae less common than in no trampling/ herbivores present; C. dalli coexists with B. glandula; Algal turf and Petrocelis more common than in no trampling/herbivores present. **Observed**: not supported; similar results to no trampling/herbivores present.
LIGHT TRAMPLING	**Predicted**: Reduction in biomass; no large changes in community composition; B. glandula less common; C. dalli more common; algal turf and grazer-resistant species more common; algal canopy present but lower than controls. **Observed**: not supported; B. glandula and fucoid algae reduced to near zero levels; increased C. dalli cover.	**Predicted**: B. glandula and fucoid algae more common than light trampling/herbivore present; C. dalli less common; algal canopy less abundant than in controls. **Observed**: not supported; B. glandula and fucoid algae reduced to near zero levels; increased C. dalli cover.
HEAVY TRAMPLING	**Predicted**: B. glandula significantly reduced; C. dalli more abundant; fucoid algae decrease; algal turf and petrocelis more. **Observed:** supported; reduction in B. glandula; increase in C. dalli; foliose algae removed; petrocelis and bare rock more abundant.	**Predicted**: B. glandula abundance low; fucoid algae abundance low; C. dalli more common and coexist with B. glandula; species dominant in no trampling will persist. **Observed**: B. glandula persist longer; trampling swamped herbivore effects - no difference between herbivore inclusion and exclusion plots.

Table 13. Predictions/Results during Recovery Phase.

	HERBIVORES PRESENT AND HERBIVORE EXCLUSION
No TRAMPLING (CONTROL)	**Predicted**: B. glandula abundant; C. dalli present at low density; Late successional algae abundant. **Observed**: supported, however algae were uncommon at Yaquina Head. C. dalli abundance increased due to high recruitment.
LIGHT AND HEAVY TRAMPLING	**Predicted**: B. glandula abundance low and C. dalli abundance significantly greater initially. By the conclusion B. glandula abundance increases while C. dalli abundance decreases. The low abundance of B. glandula would retard the re-establishment of latter successional algal species. **Observed**: B. glandula abundance low and C. dalli abundance significantly greater. High recruitment of C. dalli kept abundance high. Low recruitment of B. glandula and the newly established dominance of C. dalli keep B. glandula abundance lower than was expected. Recovery of latter successional algae retarded, however C. dalli observed to facilitate their settlement.

Trampling Intensity

It was predicted that light and heavy trampling would have different effects on the community. For instance, it was predicted that B. glandula and fucoid algae would be reduced but not removed in lightly trampled plots. These predictions were not supported, as there was no difference between light and heavy trampling in any of the experimental plots. Clearly the definition of light trampling was not "biologically light", as both light and heavy trampling had the same effect on the community. These intensities were chosen based on what was considered to be realistic light and heavy trampling regimes. Brosnan and Crumrine (1992a, b) found that at rarely-visited and relatively inaccessible sites on the Oregon coast, trampling ranged from 7-10 steps per hour. Organisms at two marine gardens (=reserves) were trampled 228 times per hour at one site, and 103 times per hour at the second. Povey and Keough (1991) found that algal species were much reduced by light and heavy trampling, but that heavy trampling caused a greater reduction. In their study, trampling was carried out daily for four months. Light trampling was defined as trampling twice per day, and intense trampling was 25 times per day. We did not trample daily, as most trampling occurs during low tide periods, and thus many species are not trampled every day. Nonetheless, light trampling had severe effects on the community. This is alarming, as it implies that in this community, trampling is a threshold phenomenon, and that the threshold for effects may be low. This will have important consequences for conservation of intertidal communities. It implies that simply reducing the numbers of visitors on a shore to moderate levels will not be sufficient to maintain species composition and abundance. This will need to be taken into account when decisions are made to increase access to intertidal zones, and to designate intertidal marine reserves.

Interactions between trampling and herbivore effects

It was predicted that trampling and grazing would have additive effects on species abundance. This prediction was supported only for B. glandula at Yaquina Head in the trampling phase. Herbivores decreased recruitment and increased the rate of loss of new barnacles in trampled plots. New recruits were susceptible to bulldozing before they were large enough to be dislodged by trampling. Barnacles that escaped bulldozing were subsequently dislodged by trampling. A corollary prediction was that under light trampling, and in the absence of grazers, B. glandula and algae would be able to establish itself. This prediction was not supported. The effects of trampling were intense enough to swamp any herbivore effect. In trampled plots, abundance of algae and B. glandula was the same in herbivore inclusion and herbivore exclusion treatments. There was no correlation between effects of trampling and abundance of herbivores, indicating that herbivore effects did not depend on the intensity of trampling. These results imply that communities do not recover while trampling is ongoing. Even when the detrimental effect of limpets was removed, barnacles and algae did not reestablish themselves successfully.

Effects of Trampling on Barnacles

It was predicted that B. glandula would be removed by trampling, and that the smaller C. dalli would be resistant to dislodgment. These predictions were supported. The abundance of C. dalli increased in trampled plots. Trampling removed B. glandula and created bare space which was subsequently colonized by C. dalli. At Fogarty Creek, cover of C. dalli increased from 0% to 40% in some plots over the nine month experimental period. During the same time B. glandula declined. Thus, trampling prevents competitive exclusion of C. dalli by B. glandula. Once C. dalli establish they may persist for some time. Farrell (1989) found that at Yaquina Head, it took three years for B. glandula to reach 70% cover in plots that were initially dominated by C. dalli. Dominance by C. dalli can slow the rate of succession and recovery in this community (Farrell 1989, 1991, and see below).

Size and profile of barnacles determine their susceptibility to trampling. B. glandula is a large barnacle with a high profile, and is easily dislodged by trampling. Young and newly settled individuals are smaller and flat, and are not as vulnerable to trampling. However, as they grow their risk of dislodgment increases. For instance, barnacle cover gradually declined in trampled plots following the settlement pulse in March 1993. Hummocking also increases susceptibility to dislodgment. At Yaquina Head, B. glandula was abundant and settlement was high. Clumps of hummocked barnacles were common at this site, and I found that they were easily removed by walking on them.

Effect of Trampling on Algae

As predicted, fucoid algae were susceptible to trampling, and cover dropped to near zero in many plots. This confirms the results of previous studies (Zedler 1976, 1978, Beauchamp and Gowing 1982, Povey and Keough 1991, Brosnan and Crumrine 1992a 1994, Brosnan 1993). Fucoid species are often attached at a single point and dislodgment at the point of attachment results in a large canopy loss (Brosnan and Crumrine 1994). Many fucoids are attached to barnacles (Farrell 1991; Grubba and Brosnan personal observation); by removing barnacles, trampling indirectly removes algae. When this happens, primary cover is also lost, and plants cannot regenerate from holdfasts.

E. muricata was removed by trampling. This was partly due to the settlement and growth patterns of E. muricata in the experimental plots. Most plants were growing as epibionts on the sides of barnacles. When barnacles were dislodged, the epibionts were lost too. The epibiont E. muricata often grows in upright clumps on mussels and barnacles (Brosnan and Crumrine 1994, Grubba personal observation). In this form, E. muricata is easily removed by trampling (Brosnan and Crumrine 1994). However, when E.

muricata grows as a prostrate, spreading turf, it is not easily dislodged by foot traffic (Brosnan and Crumrine 1992a, 1994). Endocladia muricata abundance increased in the presence of herbivores in control plots. This is despite the fact that barnacles (settlement substrate) were removed by herbivores. This effect has been previously noted by Brosnan (unpublished manuscript), but its causes are unknown.

Spatial Heterogeneity

Crevices in rocks are important spatial escapes from trampling. I did not document whether species were found in crevices or on horizontal surfaces. However, it was noted that species that are removed by trampling sometimes persisted in crevices (Grubba and Brosnan personal observation). This was true for B. glandula, fucoids, and E. muricata (on barnacles). In fact in trampled plots almost all of these individuals were found in depressions in the rock. If the crevices were small, they provided only temporary refuge. For instance, B. glandula grew out of small crevices and were subsequently dislodged by trampling. However, barnacles and algae persisted in larger crevices (Grubba and Brosnan personal observation). The presence of spatial refuges may be important to persistence of these species in highly disturbed shores. Refuges prevent local extinction of species, and individuals in refuges are a potential source of new recruits. Thus, recovery from trampling is likely to be faster on shores with high heterogeneity. By contrast, in areas where the rock surface is smooth (e.g., sandstone and metamorphosed sandstone) recovery may be slower.

Effect of trampling on successional pathway

By removing key species in the successional pathway, trampling can prevent succession. The barnacle B. glandula is essential to succession because it facilitates algae and mussels (Farrell 1989, 1991, D. M. Brosnan unpublished manuscript). Chthamalus dalli, if abundant and large in size can facilitate settlement of algae and mussels. However C. dalli even when large, are not as effective as B. glandula at facilitation. In other geographic areas barnacles are also key species in succession (e.g., Hawkins 1981, 1983, Hawkins and Hartnoll 1983, Hartnoll and Hawkins 1985). On temperate shores, disturbances often remove algae and invertebrates, and create patches of bare space (Harger 1970, Sousa 1979, 1984, Hartnoll and Hawkins 1985, Paine and Levin 1981, Farrell 1989). On some shores, this space is colonized by barnacles that facilitate succession to algae or mussels (Paine and Levin 1981, Hawkins and Hartnoll 1983, Farrell 1989, 1991). Trampling also removes organisms and creates patches of bare space (Brosnan and Crumrine 1994). However, B. glandula is removed by trampling, and does not recover while trampling continues. Many algal species depend on B. glandula for recruitment, and in the presence of trampling these species cannot recruit. This is true for species such as the turf form of E. muricata, which requires B. glandula in order to become established (Farrell 1991, Brosnan unpublished manuscript). Once it has spread to primary substrate, it is resistant to trampling and can thrive in trampled conditions (Brosnan and Crumrine 1992a, 1994). In addition, mussel recruitment is enhanced by barnacles (Navarette and Castilla 1990, Brosnan unpublished). Thus one effect of trampling on the community is to retard or prevent succession. This interpretation is supported by the observation that algae in trampled plots were only found on B. glandula in crevices.

Once trampling has stopped succession may be slow. This is because C. dalli becomes more abundant when the larger competitively dominant B. glandula is dislodged. Chthamalus dalli does not usually enhance succession (Farrell 1989, 1991) because it is too small and smooth for algae to recruit successfully. However to recruit successfully under the right conditions C. dalli can grow to large sizes that enable algae to recruit successfully. Under these conditions succession /recovery of the community may not be as retarded. It may take three years for B. glandula to replace mature C. dalli (Farrell 1989, 1991).

CONCLUSIONS

Trampling alters the community in the upper intertidal zone of rocky shores. Species composition changes from one that is dominated by the barnacle B. glandula or by a mixed B. glandula and algae assemblage, to a community where C. dalli is the most abundant barnacle, and algal crust is practically the only algal species present. Recovery of impacted communities is dependent on the presence of B. glandula, a keystone species in succession. Studies suggest that full recovery of an impacted community would take a minimum of three years.

Park and reserve managers will have to modify their management plans incorporating the ideas that 'light' trampling, has as detrimental effect as "heavy" trampling, recovery is a lengthy process, and for recovery there has to be a removal of impacts such as trampling. This presents the challenge of balancing the conservation of these areas with the ever-increasing visitation by humans, which is only going to increase in the future.

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