



## Effects of trampling on a rocky intertidal algal assemblage in southern New Zealand

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### Abstract

The effects of human trampling on a mid-intertidal assemblage dominated by the fuclean alga *Hormosira banksii* were tested experimentally on two rocky intertidal platforms on the east coast of the South Island of New Zealand. The major factors were Trampling intensity, Platforms and Timing of trampling. Seven trampling intensities (0, 10, 25, 50, 100, 150 and 200 passages per area) were used in 2-m long transects (0.6 m<sup>2</sup>) during single tides in Spring and Autumn on each platform. *H. banksii* initially had >96% canopy cover in all treatments. As few as 10 tramples reduced this cover by up to 25% after a single tide. Progressively greater reductions occurred at higher trampling intensities, with >90% of the *H. banksii* canopy removed at 200 tramples. There was recruitment into the Spring transects during the following summer months, and by five months after trampling all treatments had at least 50% cover of *H. banksii*. Treatments initiated in Autumn had similar reductions in *H. banksii* cover as Spring treatments, but the recovery was delayed by seven months until recruitment occurred during the following summer. Fifty percent recovery of the canopy took at least a year in most Autumn treatments. After 21 months the Spring treatments had recovered to control levels (>97% cover), while after 16 months the Autumn treatments were still recovering. Understory encrusting and turfing coralline algae were reduced in cover after trampling, with the greatest effects at the higher trampling intensities. The reduction of corallines was mostly due to burn-off after the *H. banksii* canopy was removed. By the end of the experiment, corallines had returned to control levels in both the Spring and Autumn treatments. Bare primary space increased significantly with up to 60% bare rock at the higher trampling intensities one year after trampling. By the end of the experiment, bare space was reduced to <10% in the Spring treatments but averaged as high as 24% in the higher trampling intensities of the Autumn treatments. There was an interaction between demographic processes, particularly recruitment, and coralline algae in the recovery of *H. banksii*. Up to 70% of cover at the 200-trample intensity was from new recruits, while most recovery in the 10 and 25 trampling intensities was from re-growth of damaged fronds. However, at one platform, composed of soft

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siltstone, recruitment of *H. banksii* occurred almost exclusively on the damaged encrusting and turfing coralline algae. Overall, this experiment showed that trampling intensity had variable effects and that the interaction of season, location, indirect effects of reduction in coralline algae, and facilitative processes in recruitment of *H. banksii* all contribute to recovery after disturbance. © 1999 Elsevier Science B.V. All rights reserved.

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## 1. Introduction

Rocky intertidal areas worldwide are subjected to considerable and increasing anthropogenic influences. Recreational and commercial harvesting of plants and animals, coastal development and recreational use can cause direct impacts on populations through selective removal of particular species or size classes of individuals (Beauchamp and Gowing, 1982; Ghazanshahi et al., 1983; Bally and Griffiths, 1989; Underwood and Kennelly, 1989; Povey and Keough, 1991; Brosnan and Crumrine, 1994), or indirect effects through chemical pollution, eutrophication and altered demographic processes and species interactions (Gray, 1982; Moreno et al., 1984; Castilla and Durán, 1985; Durán and Castilla, 1989; Kingsford et al., 1991).

The effects of human exploitation of the intertidal zone can be dramatic, but the results of perturbations depend on the trophic structure of particular areas (Menge, 1991). For example, where a top predator is present its removal can cause considerable changes in community structure and reduced diversity through the dominance of one or a few prey species (Castilla and Durán, 1985; Durán and Castilla, 1989; Paine, 1994). The scale, intensity and frequency of disturbances can greatly affect species diversity and competitive hierarchies (Connell, 1978; Connell and Keough, 1985; Sousa, 1985; Menge and Sutherland, 1976, 1987). Despite the great amount of work done in intertidal areas and the ecological theory generated (Underwood and Denley, 1984; Menge, 1991), however, there have been relatively few direct tests of the effects of human perturbations.

Comparisons of accessible areas to those with restricted access have provided useful insights into likely effects of protection (e.g., Alcalá and Russ, 1989; Beauchamp and Gowing, 1982; Moreno et al., 1984; Castilla and Bustamente, 1989; Durán and Castilla, 1989; Cole et al., 1990). Many of these types of studies, however, have limited replication of sites, few samples of sites before protection was initiated, or little information about the influences of a range of intensities of human usage, all of which may weaken conclusions about the overall effects of human disturbances (Hurlburt, 1984; Stewart-Oaten et al., 1986; Keough and Quinn, 1991; Underwood, 1991). Experimental tests, preferably over a range of intensities and spatial scales, provide the most powerful way of determining effects because of the variable nature of intertidal populations and the often variable consequences that follow disturbances (cf., Fairweather, 1991; Underwood and Petraitis, 1993). Recruitment variability both spatially and temporally (e.g., Reed et al., 1988; Vadas et al., 1990) may be of particular

importance in determining the recovery of disturbed populations. For example, populations of the intertidal fucalean alga *Fucus distichus* can be fertile for most of the year, yet recruitment occurs in discrete peaks; furthermore, high settlement rates are not always followed by successful recruitment (Ang, 1991).

Studies on the direct effects of trampling (i.e., pedestrian traffic) on intertidal areas have produced variable results. In South Africa, wave action may be of greater importance than pedestrian traffic on wave-exposed shores (Bally and Griffiths, 1989). Brosnan and Crumrine (1994) found the effects of trampling on the Oregon coast to be dependent on the community present, foliose algae being more susceptible than algal turfs and barnacles more susceptible than dense patches of mussels. Experimental studies in south-eastern Australia provide the most comprehensive information on the impact of trampling on intertidal platforms (Povey and Keough, 1991; Keough and Quinn, 1998). Of the three habitats tested by Povey and Keough (brown algal beds, coralline algal mats, and bare rock), the one dominated by the perennial furoid alga *Hormosira banksii* was most vulnerable to trampling. Individual plants lost about 20% of their biomass with a single footstep. Of the two intensities of trampling imposed for 33 days over four months, two tramples per day resulted in a 15% decline in the cover of *H. banksii* that took around 300 days to return to control levels, while 25 tramples per day resulted in a 75% reduction that had not recovered fully by 500 days, possibly due to an increase in grazing invertebrates. Recovery within the *Hormosira* habitat occurred through vegetative re-growth of existing holdfasts rather than from recruitment of young plants.

Platforms along the eastern coast of southern New Zealand can be hundreds of metres in extent with a dense cover of *H. banksii* and many associated species in the mid to lower intertidal zones (Raffaelli, 1979). They are superficially similar to those described by Povey and Keough (1991) and Keough and Quinn (1998). Our study was prompted by the observation of worn paths through the algal beds and obviously increasing pedestrian traffic due to tourism. Unlike the sites used in the Australian studies, however, where repeated human impacts occurred over several months, it is more common in the less densely populated areas of southern New Zealand to encounter intense trampling over short periods, for example when bus loads of tourists are let off at a single point and wander across a platform. In our study we specifically tested three major null hypotheses: that the intensity of trampling on platforms has no effect on intertidal algal assemblages; that there is no difference in trampling effects between different platforms; that there is no difference in trampling effects between different times of trampling.

## 2. Methods

### 2.1. Study sites

The two largest algal-covered intertidal platforms on the central eastern coast of the South Island were used. Wairepo flats, located on the Kaikoura peninsula (42°25'S, 173°41'E), is a gently sloping siltstone platform extending several hundred metres along the shore and around 200 m from the upper intertidal to the subtidal zones. It is partially

sheltered from wave action but is exposed to occasional severe swells (see Hickford and Schiel, 1995 and Woods and Schiel, 1997 for location descriptions). The other study site was a platform on the Moeraki peninsula (45°22'S, 170°50'E), 320 km southwest of Kaikoura. The site is a hard basaltic basement rock extending around 150 m from the upper intertidal to subtidal zones. The platform has similar exposure to the Kaikoura site, being generally protected by offshore reefs but occasionally subjected to severe oceanic swells.

Both study sites are dominated by the fuclean alga *Hormosira banksii* (Turner) Descaisne in the mid to lower intertidal zones, where it is densely layered at low tide with virtually 100% cover and a biomass of ca. 6 kg (wet mass) per m<sup>2</sup>. This species is dioecious and has a maximum frond length of ca. 30 cm on both study platforms. The understory is mostly encrusting and turfing coralline algae. Ephemeral algae are common seasonally and a few perennial algal species occupy the lowest part of the intertidal zone. The commonest herbivore present in the alga beds is the cat's eye turbinid gastropod *Turbo smaragdus* Gmelin. Both localities are near seal colonies and are popular tourist destinations, particularly during summer, but the experimental sites were at least 100 m away from where tourists usually wander, and interference with our experiments was unlikely to have occurred.

## 2.2. Experimental design

To test the effects of trampling intensity on *H. banksii*, seven treatments were used: 0 tramples (control), 10, 25, 50, 100, 150 and 200 tramples. A 2-m long transect about 30 cm wide was trampled by one of us (D.I.T., ca. 78 kg) wearing (size 9) standard gumboots. Short, even strides were used to pace back and forth over experimental areas during one low tide. Approximately 66% (S.E. = 12.6) of each transect was trod on during each passage of the walker; one traverse of a transect was considered one "trample". There were two transects per treatment. To test the effect of different platforms the same treatments were done at Kaikoura and Moeraki. Because there appears to be discrete recruitment periods for *Hormosira*, we tested the effects of different times of trampling; identical treatments were initiated during late Spring and late Autumn. Spring treatments were started during the last week of November (Moeraki) and the first week of December (Kaikoura) 1995. Autumn treatments were initiated in May 1996 on both platforms. All treatments and replicates were randomised within each site. The experiment was monitored approximately bi-monthly until September 1997. The Spring-initiated treatments, therefore, ran for 21 months and the Autumn-initiated treatments for 16 months.

Treatments were monitored prior to trampling, and again on the next low tide after trampling using a 25 × 25 cm quadrat sub-divided into 100 squares. Within each transect, three randomly positioned quadrats were visually assessed for the percentage cover of *H. banksii*, articulated corallines, encrusting corallines, bare rock and any algae present, and herbivores were counted. Five haphazardly chosen *H. banksii* plants were measured for total length within each quadrat.

Analysis of variance was used to test results. For the main model used, the main factors were Platforms, Time and Tramples. Platforms and Time were treated as random

factors. Transects within the other factors was treated as a random, nested factor to identify the variability between the two transects within treatments. Data were tested for homogeneity of variances using Cochran's test prior to analyses and were transformed when necessary. In the analysis of variance (ANOVA) model using Platform, Time of treatment initiation, Trampling intensity and Transects, there is no  $F$  test for "Tramples". In cases where either the Platform  $\times$  Trample or the Time  $\times$  Trample terms approached 0 ( $F$  value  $p > 0.25$ ), it was omitted; where both terms had  $p > 0.25$  they were pooled with the three-way interaction (cf., Underwood, 1997). In these cases, an appropriate  $F$ -test for Tramples was derived. Analyses were done using Statistica 5.0 (Statsoft Inc.). Initial pre-trampling data were tested to determine if there were differences among factors prior to trampling.

### 3. Results

#### 3.1. Characteristics prior to trampling

Prior to trampling, both platforms were similar in the percentage cover of *Hormosira* but there were differences among treatments in some of the other major taxa (Tables 1 and 2). The canopy of *Hormosira* formed virtually 100% cover at both platforms, but there was significant variation between transects within the treatments during Spring ( $F_{14,56} = 2.14$ ,  $p < 0.05$ ). Turfing coralline algae covered most of the primary substratum and were more abundant at Kaikoura during Spring and at Moeraki during Autumn (Table 1), although this effect varied between transects within the treatments during both seasons (Table 2). Encrusting coralline algae occupied most of the understory space not covered by turfing corallines and therefore showed similar pre-

Table 1

The percentage cover (standard deviation) of algal taxa present and bare space in treatment areas before trampling was done in the Spring and Autumn treatments at both platforms

Platform	Taxa	Spring	Autumn
Moeraki	<i>Hormosira</i>	99.1 (1.33)	96.1 (4.90)
Kaikoura		98.3 (2.61)	97.8 (3.06)
Moeraki	Turf	52.0 (10.39)	78.0 (18.67)
Kaikoura		97.4 (3.27)	64.9 (16.43)
Moeraki	Enc coralline	46.6 (10.21)	18.5 (13.14)
Kaikoura		1.7 (2.08)	28.3 (15.13)
Moeraki	Bare	1.4 (1.96)	3.5 (8.33)
Kaikoura		0.9 (1.59)	6.7 (5.65)
Moeraki	Other algae	0.9 (1.67)	1.8 (3.72)
Kaikoura		4.7 (3.16)	3.2 (4.54)

Turf = Turfing coralline algae, Enc coralline = encrusting coralline algae.

Table 2

Summary of ANOVA tests (*F* values) of percentage cover of major algal taxa and bare space before trampling was done in Spring (S) and Autumn (A)

Source	df	<i>Hormosira</i>		Turf		Enc coralline		Bare	
		<i>F</i> (S)	<i>F</i> (A) <sup>a</sup>	<i>F</i> (S) <sup>a</sup>	<i>F</i> (A)	<i>F</i> (S) <sup>b</sup>	<i>F</i> (A)	<i>F</i> (S)	<i>F</i> (A) <sup>c</sup>
Platform	1,14	1.83	2.81	377.39***	9.00**	587.25***	7.43*	1.55	22.34***
Tramples	6,6	0.85	2.43	0.44	1.55	0.58	1.37	0.17	1.22
P × T	6,14	0.61	0.60	1.08	1.68	1.26	1.32	2.15	2.72
Transect (P × T)	14,56	2.14*	1.40	2.78**	2.40**	2.17*	2.08*	1.36	0.73

Significance is denoted by \* (0.05), \*\* (0.01), \*\*\* (0.001). All Cochran's tests were n.s. "Turf": Turfing coralline algae; "Enc coralline": encrusting coralline algae.

<sup>a</sup> Arcsine transformed.

<sup>b</sup> Square root transformed.

<sup>c</sup> Square root arcsine transformed.

treatment effects. Bare primary space ranged from 0.9 to 6.7% between platforms and was greatest at Kaikoura during Autumn (Table 1). It was slightly greater in the 150 trampling intensity during Autumn at Moeraki (mean = 15.6%) compared to all other treatments (< 8.7%; cf., Fig. 4).

Other algae, such as the fucaleans *Cystophora torulosa* J. Agardh and *Carpophyllum maschalocarpum* Greville, and ephemeral species such as *Colpomenia peregrina* Derbes et Solier, *Ulva* spp., *Enteromorpha* spp., *Adenocystis utricularis* S. Kottsberg and *Pleonosporium hirtum* Laing occurred in small numbers and varied between platforms (Table 1).

Because of the small-scale variation in abundances of these taxa across platforms, it was impossible to have all treatments initially identical. Of most importance to the trampling experiment, however, was that the factors Tramples and Platform × Tramples were not significant (Table 2).

Only small numbers of the herbivorous snail *Turbo smaragdus* were observed in the general area of the experiments and only five were seen in all of the experimental transects at both sites during the course of the experiment.

### 3.2. Immediate effects of trampling

Trampled areas were clearly discernible after one tide at both sites (Fig. 1A Fig. 1B). The cover of *Hormosira* was affected by all trampling intensities with up to 30% of the canopy being removed after 10 tramples (Fig. 1B) and > 90% after 200 tramples (Fig. 1A Fig. 1B). Generally, there was a progression of damage from 10 to 200 tramples, although at both platforms the greatest damage (i.e., > 60% of the *Hormosira* canopy removed) occurred at 50 or more tramples. There was a large treatment effect due to trampling, but also significant variation between transects within the major factors (Table 3). Turfing coralline algae also showed a significant response to trampling after a single tide (Table 3). This was particularly evident at Moeraki where trampling intensities ≥ 25 resulted in a ca. 15% reduction in cover (Fig. 2A Fig. 2B). The pre-treatment variation between platforms and transects remained. Encrusting coralline

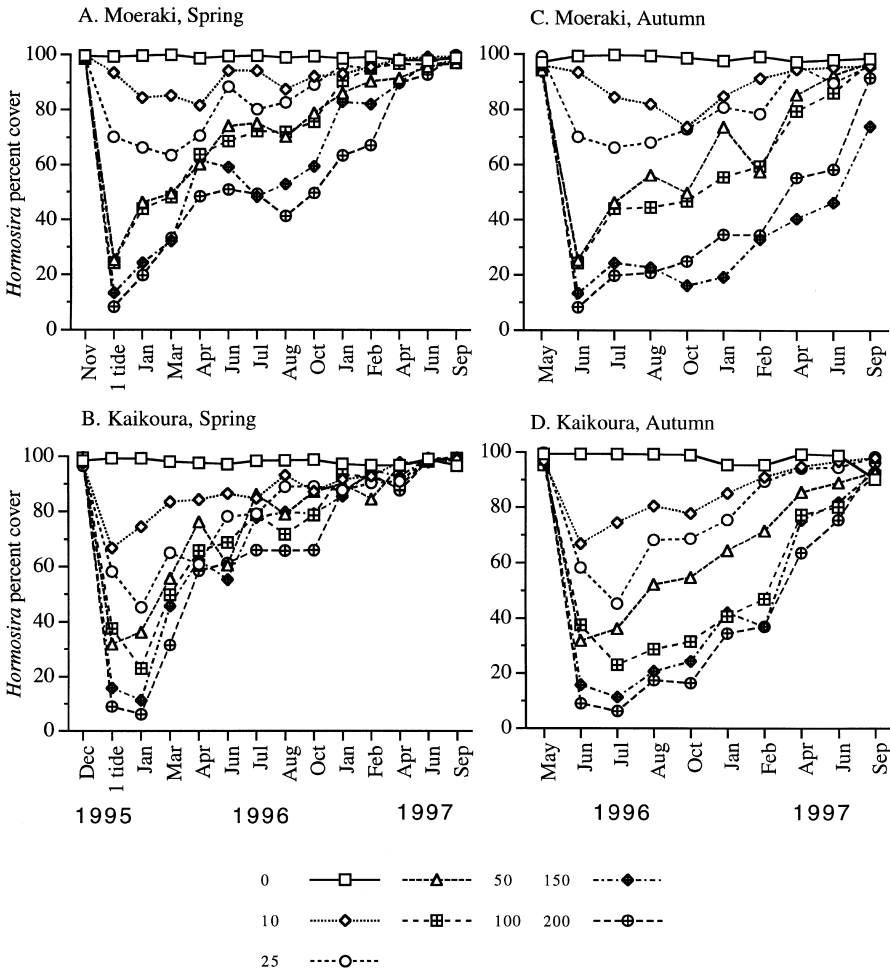


Fig. 1. The mean percentage cover of *Hormosira banksii* through time at all trampling intensities in the Spring-initiated treatments at Moeraki (A) and Kaikoura (B) and the Autumn-initiated treatments at Moeraki (C) and Kaikoura (D).

Table 3

Summary of ANOVA tests (*F* values) of percentage cover of major alga taxa and bare space in the Spring-initiated treatments after one tide

Source	df	<i>Hormosira</i>	Turf	Enc coralline	Bare
Platform	1,14	0.44	214.12***	315.41***	81.77***
Tramples	6,6	27.05***	20.93***	4.08	11.64**
P × T	6,14	1.25	0.08	0.19	0.45
Transect (P × T)	14,56	5.30***	7.86***	5.77***	2.07*

Significance is denoted by \* (0.05), \*\* (0.01), \*\*\* (0.001). Data were square root arcsine transformed; all Cochran's tests were n.s.

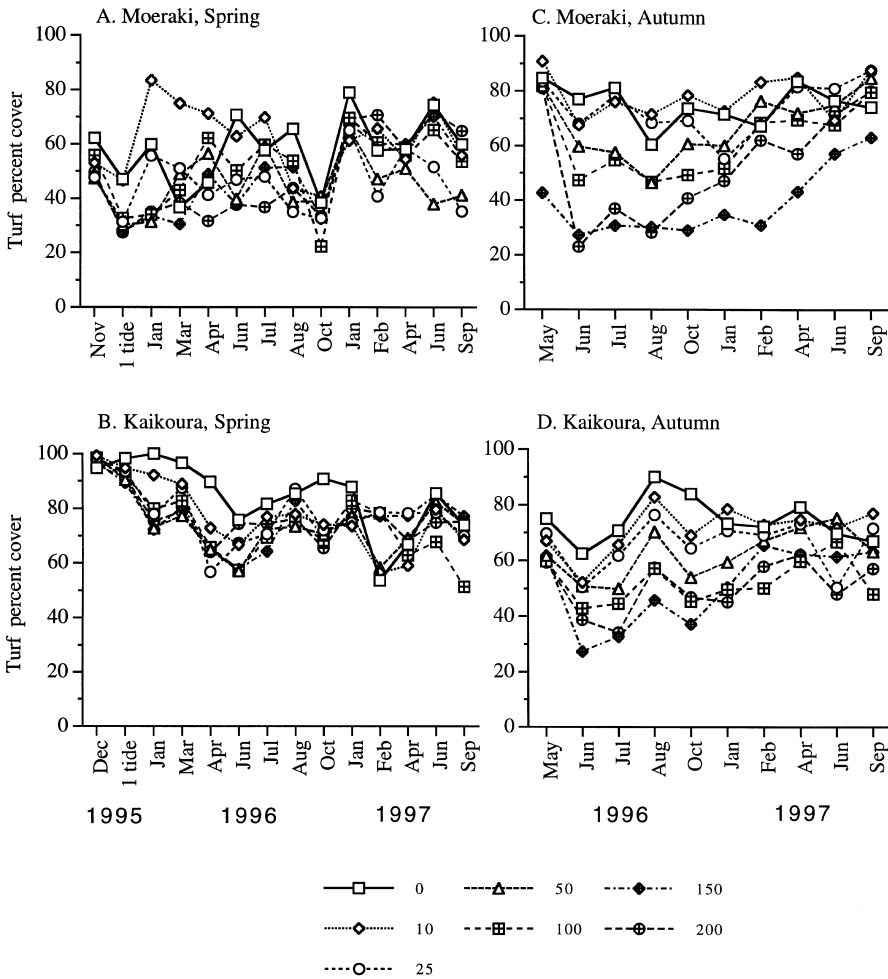


Fig. 2. The mean percentage cover of turfing coralline algae through time at all trampling intensities in the Spring-initiated treatments at Moeraki (A) and Kaikoura (B) and the Autumn-initiated treatments at Moeraki (C) and Kaikoura (D).

algae showed no significant response to trampling over a single tide (Table 3, Fig. 3A Fig. 3B). They were ca. 40% more abundant at Moeraki than at Kaikoura during Spring. Primary bare space increased due to trampling after a single tide (Table 3). This occurred mainly at > 100 tramples and was particularly noticeable at Moeraki (Fig. 4A Fig. 4B), although the Platform × Trample interaction was not significant. The increase in bare space was due to decreases in the combined cover of turfing and encrusting coralline algae.

Overall, *Hormosira* was the major component of the algal assemblage immediately affected by trampling, due to the crushing and dislodgement of fronds.

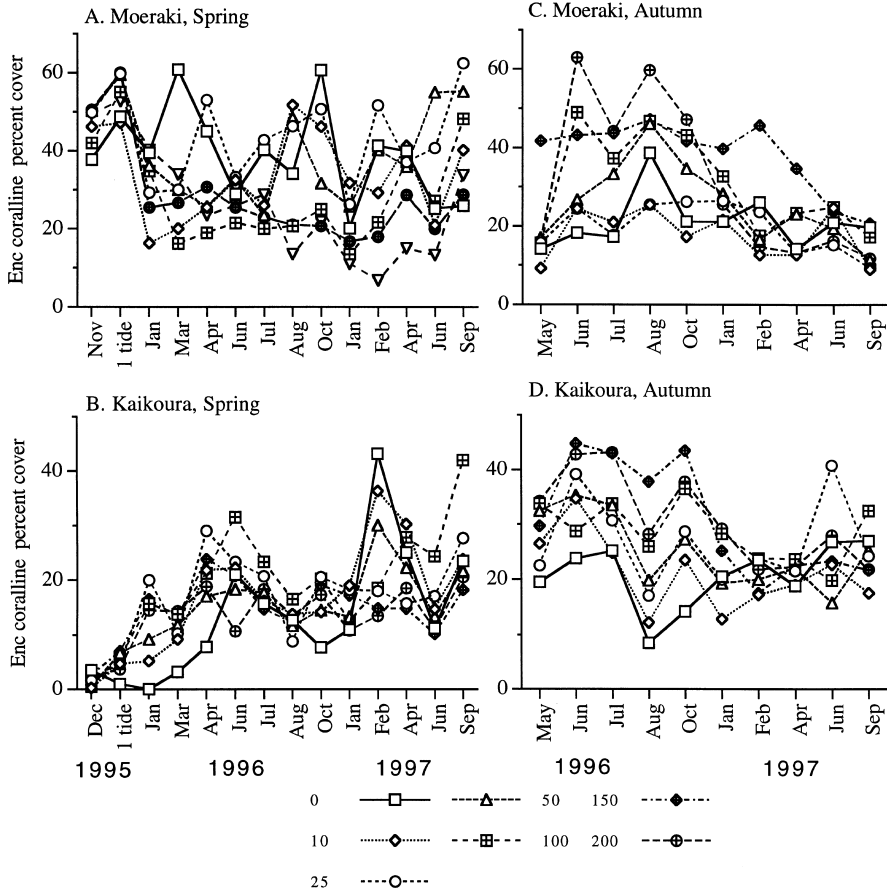


Fig. 3. The mean percentage cover of encrusting coralline algae through time at all trampling intensities in the Spring-initiated treatments at Moeraki (A) and Kaikoura (B) and the Autumn-initiated treatments at Moeraki (C) and Kaikoura (D).

### 3.3. Longer term effects and recovery

#### 3.3.1. *Hormosira*

Treatment effects due to trampling were generally greatest after one to two months (Fig. 1). The timing of trampling had no effect on the percentage cover of *Hormosira* (Table 4A). The damage tended to be greater at Kaikoura than at Moeraki, particularly at the 10 and 25 trampling intensities (Fig. 1). Damaged plants were easily dislodged from the soft siltstone reef of Kaikoura and initially damaged plants disappeared in the month following trampling. At Kaikoura, treatments with 25 or more tramples (Fig. 1B, D) were greatly affected during both seasons, while at Moeraki the greatest effects occurred at 50 or more tramples (Fig. 1A, C).

One year after the initial tramples (i.e., October 1996 for the Spring tramples and

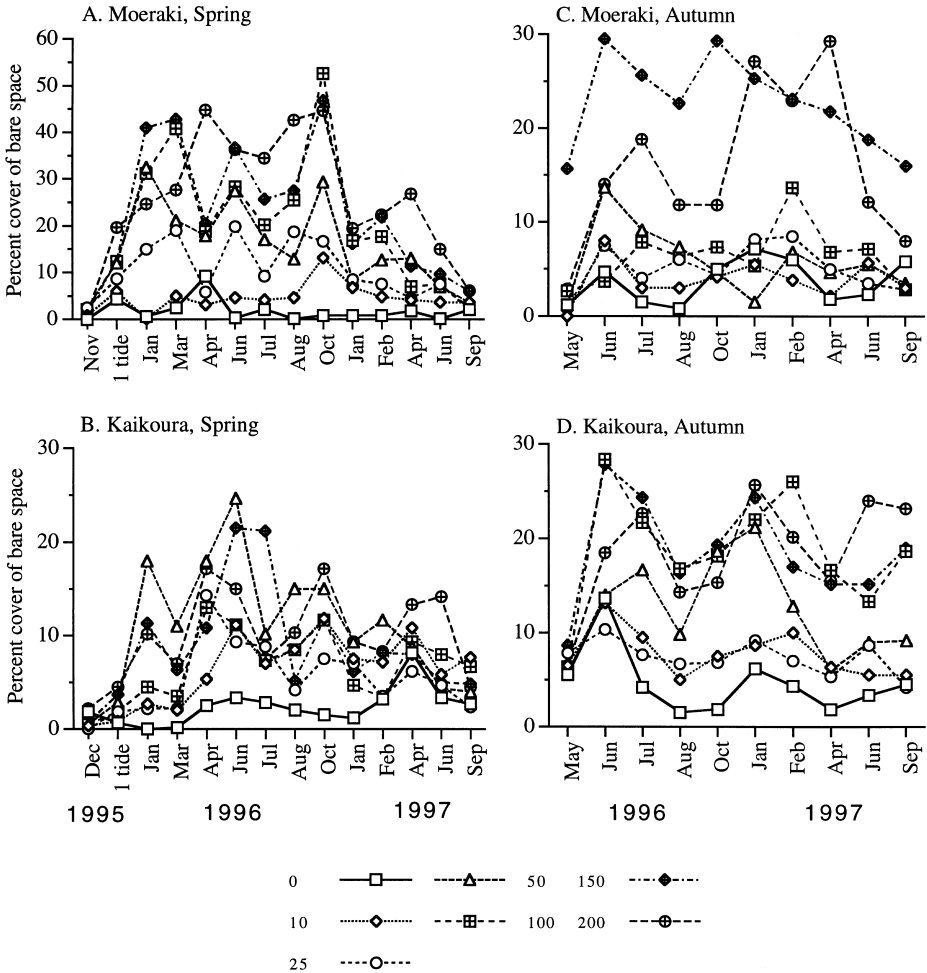


Fig. 4. The mean percentage cover of bare substratum through time at all trampling intensities in the Spring-initiated treatments at Moeraki (A) and Kaikoura (B) and the Autumn-initiated treatments at Moeraki (C) and Kaikoura (D).

April 1997 for the Autumn treatments), the effects of trampling were still evident (Table 4B, Fig. 1). There was still large variation among the trampling treatments but this varied between platforms ( $F_{6,6} = 4.60, p < 0.05$ ). In particular, the 150 and 200 trampling intensities had recovered only to 40–60% of control levels at Moeraki (Fig. 1A, C) but had reached 64–77% at Kaikoura (Fig. 1B, D) after one year. There was an effect of the different times of trampling (Table 4B) that reflected the different trajectories of recovery between seasons in the early stages. In the Spring-initiated treatments, there was a large recruitment of *Hormosira* during summer at both platforms. By April 1996, five months after trampling, significant recovery in the percentage cover

Table 4

Summary of ANOVA tests ( $F$  values) of percentage cover of major algal taxa and bare space at (A) one month after trampling and (B) one year after trampling (October 1996 for the Spring treatments, April 1997 for the Autumn treatments)

Source	df	<i>Hormosira</i> <sup>a</sup>	Turf	df	Enc coralline <sup>b</sup>	Bare <sup>b</sup>	Other algae <sup>b</sup>
<i>(A) After one month</i>							
Platform	1,1	26.41	0.46	1,1	0.89	0.06	94.82
Time	1,1	0.15	1.04	1,1	3.33	0.21	206.47***
Tramples	6,6	107.78***	No test	6,18	276.90***	4.52**	1.29
P × Time	1,28	1.15	41.97***	1,28	10.65***	32.40***	0.21
P × Tramp	6,6	(1.28) <sup>d</sup>	4.14				
Time × Tramp	6,6	2.58	7.19				
P × Tm × Tr	6,28	0.53	0.44	18,28	0.73	3.88**	1.42
Transect (P × Tm × Tr)	28,112	1.21	1.49	28,112	2.09	1.38	0.89
<i>(B) After one year</i>							
Source	df	<i>Hormosira</i>	df	Turf <sup>c</sup>	Enc coralline <sup>c</sup>	Bare <sup>c</sup>	
Platform	1,1	16 709**	1,1	0.79	0.55	0.55	
Time	1,1	1866*	1,1	0.60	0.22	0.21	
Tramples		No test	6,18	5.22**	0.22	0.22	
P × Time	1,28	0.01	1,28	85.97***	31.26***	31.30***	
P × Tramp	6,6	4.60*					
Time × Tramp	6,6	2.63					
P × Time × Tramp	6,28	0.57	18,28	1.65	3.31**	3.32**	
Transect (P × Tm × Tr)	28,112	3.10***	28,112	1.92*	2.64***	2.64***	

Significance is denoted by \* (0.05), \*\* (0.01), \*\*\* (0.001). Data were square root arcsine transformed; all Cochran's tests were n.s.

<sup>a</sup> "Tramples" tested over Time × Trample; P × Trample,  $p > 0.25$

<sup>b</sup> "Tramples" tested over P × Time × Trample; P × Trample and Time × Trample,  $p > 0.25$ .

<sup>c</sup> "Tramples" tested over P × Time × Trample; P × Trample and Time × Trample,  $p > 0.25$ , pooled with P × Time × Trample.

of *Hormosira* had occurred (Fig. 1A, B). Initial recovery was slower after the Autumn-initiated clearances (Fig. 1C, D). In the five months after trampling, increases in percentage cover of *Hormosira* were due to growth of the remaining fronds during the winter months. Recruitment occurred during the summer months (Jan–Feb 1997), eight to nine months after trampling, and the accelerated recovery after January 1997 was due mostly to the expanding cover of these recruits as they grew.

In September 1997, 21 months after trampling of the Spring treatments, there were no significant differences among any of the factors for *Hormosira* (Table 5). All trampled areas had around 98% coverage by the developing *Hormosira* canopy (Fig. 1). The Autumn treatments, however, still had significant differences in the Platform × Trampling interaction at the end of the experiment, 16 months after trampling (Table 5). At Moeraki, the 150 trampling treatment had 77% cover of *Hormosira* while the other trampling treatments varied between 94 and 97% cover (Fig. 1C). At Kaikoura, the final effects were more complicated because the controls (ca. 90% cover) had less cover than some of the trampling treatments (Fig. 1D).

Table 5

Summary of ANOVA tests (*F* values) of percentage cover of algal taxa and bare space in the Spring (S) and Autumn (A) treatments at the end of the experiment in September 1997

Source	df	<i>Hormosira</i>		Turf		Enc coralline		Bare	
		<i>F</i> (S)	<i>F</i> (A)	<i>F</i> (S)	<i>F</i> (A)	<i>F</i> (S)	<i>F</i> (A)	<i>F</i> (S)	<i>F</i> (A)
Platform	1,14	0.21	1.22	10.17**	42.89***	10.90**	15.94**	1.34	9.84**
Tramples	6,6	0.54	1.14	1.68	2.68	2.26	2.64	1.81	2.73
P × T	6,14	2.02	4.53**	0.70	2.16	0.55	0.60	0.86	1.80
Transect (P × T)	14,56	1.46	0.93	2.64**	0.99	4.08***	1.39	1.26	1.61

Spring treatments had run for 21 months and Autumn treatments for 16 months. Significance levels: \* (0.05), \*\* (0.01), \*\*\* (0.001). Data were arcsine transformed; all Cochran's tests were n.s.

### 3.3.2. Turfing and encrusting coralline algal cover

By one month after trampling there was a separation among the trampling intensities for coralline turf. Generally, 25 or more tramples resulted in a decrease in the cover of turf (Fig. 2). Turfing corallines declined over several months at Kaikoura as exposed corallines died and peeled off the soft rock surface (Fig. 2B). There was less evidence of bleaching and die-off at Moeraki over the same time period (Fig. 2A). There was significant variation among the different platforms and seasons (Table 4A), much of which may have been because of initial differences. Turfing coralline algae fluctuated in cover throughout the experiment and treatment effects remained after one year (Table 4B), when there were differences among trampling intensities and also significant variation between transects within the other factors. Overall, the Spring treatments at Kaikoura had a higher cover of turf than all other platform-season combinations (Fig. 2).

At the end of the observation period, the Spring-initiated treatments still varied between platforms (means: Moeraki = 52.2%, Kaikoura 70.0%), similar to their initial differences (cf., Table 1) and at the transect level, but the trampling treatments were no longer different (Table 5). The Autumn-initiated treatments varied among platforms after 16 months (Table 5) but there was no consistent difference among trampling intensities.

The cover of encrusting coralline algae was virtually reciprocal to that of the turfing corallines and showed generally similar treatment effects (Fig. 3) after one month and one year (Table 4). Encrusting corallines declined rapidly at Moeraki in the first two months following trampling, but some recovery was observed in the 10 and 25 trampling intensities during the following months (Fig. 3A). Encrusting corallines increased in all treatments and controls during the year following the Spring trampling at Kaikoura (Fig. 3B). Overall, there were wide fluctuations in cover throughout the year. By the end of the experiment, neither the Spring nor Autumn treatments showed trampling effects but the platforms were different (Table 5), similar to the start of the experiment except that the Spring treatments at Kaikoura had a greater coverage than initially (Fig. 3B).

### 3.3.3. Bare space

By one month after trampling, bare primary space increased dramatically (Fig. 4). This was due not only to the direct damage of trampling algae but also to the newly exposed coralline algae burning off. There was a significant trampling effect that

depended on both platforms and times of trampling (Table 4A). The Spring-initiated treatments at Moeraki (Fig. 4A) generally resulted in a greater amount of bare space than did the other platform–time combinations (Fig. 4B, D), most likely due to the intensified effect of the summer sun on the granitic rock at Moeraki. Generally, trampling intensities of 50 or more produced the greatest amount of bare space although this varied between platforms and times of trampling.

One year after trampling, there was significant variation among factor interactions (Table 4B). The percentage of bare space remained relatively high during the initial winter in the Spring-initiated treatments but decreased by the following summer (Fig. 4A, B). By September 1997, bare space in the Spring treatments returned to low levels (2 to 8%) and there were no longer treatment effects. The Autumn-initiated treatments, however, still had significant differences between platforms (Table 5). Bare space remained > 20% for the 100 to 200 trampling intensities at Kaikoura (Fig. 4D). The 150 trampling treatment was always higher at Moeraki (Fig. 4C).

#### 3.3.4. Other species

Other species of algae were patchy in space and time during the study and were found in small numbers throughout the experiment. There were differences between platforms and times after one month, but no treatment effects due to trampling (Table 4A). No mussels, barnacles or other invertebrates recruited into any treatments. There were never more than a few gastropods in or near the experimental transects and, because most treatments had no gastropods, no tests were possible using the ANOVA model.

#### 3.3.5. Species richness

Up to seven species of algae were seen within the trampling treatments at any one time. The number of these ephemeral species varied over several factors (Fig. 5). One month after trampling, there was an effect of trampling that varied both by platform and time (Table 6;  $F_{18,140} = 2.38$ ,  $p < 0.01$ ). Kaikoura treatments generally had one to two more species present than the Moeraki treatments (Fig. 5A, C). The Spring-initiated treatments at Kaikoura showed greatest species richness in the 50-trample treatment (Fig. 5A) but this trend was not seen during Autumn (Fig. 5C). There were no major differences among trampling intensities at Moeraki after one month. One year after trampling had occurred there were still significant effects between platforms and times of trampling, but no longer were there effects due to trampling (Table 6). Kaikoura remained higher in species richness with usually one more species present than at Moeraki (Fig. 5B, D). By this stage, ephemeral species still appeared but they did so indiscriminately among the trampling treatments.

#### 3.3.6. *Hormosira* sizes

Trampling had a great effect on the lengths of *Hormosira* plants (Fig. 6). One month after the initiation of the experiment, a few plants at the 10 trampling intensity were reduced to small sizes because of frond detachment but many plants lost only parts of their fronds. This effect was increasingly shown as the trampling intensity increased. At 100 to 200 tramples, virtually all plants were damaged and reduced in size, as evident in the skewness of size-frequencies. Almost all plants beyond 90 mm disappeared from the

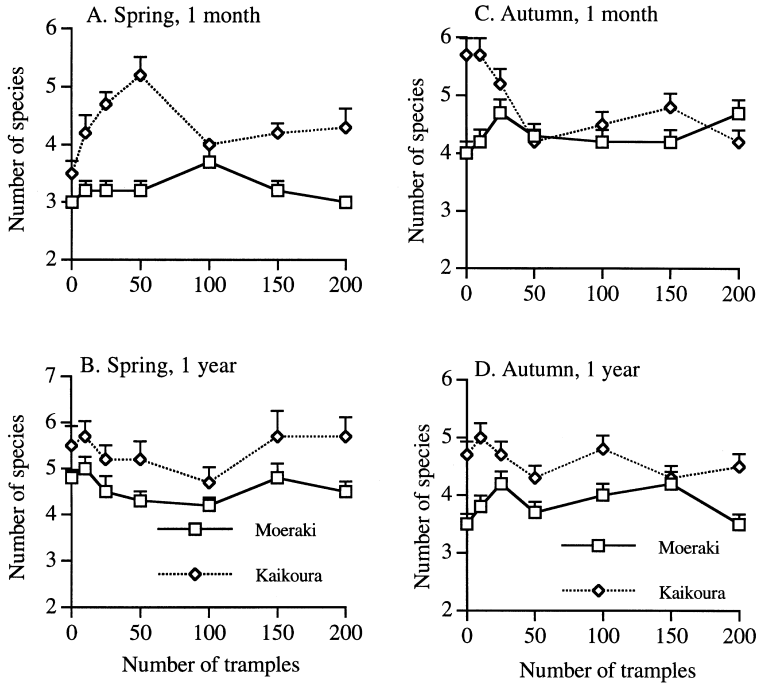


Fig. 5. The average number of species (+ 1 standard error) present at all trampling intensities at Moeraki and Kaikoura in the Spring-initiated treatments after one month (A) and one year (B), and the Autumn-initiated treatments after one month (C) and one year (D).

Table 6

Summary of ANOVA tests (*F* values) of the number of species in the trampling experiment after one month and one year

Source	df	One month <sup>a</sup>		One year <sup>b</sup>	
		<i>F</i>	df	<i>F</i>	df
Platform	1,1	> 3000***	1,1	4225**	
Time	1,1	0.11	1,1	3969**	
Tramples	6,18	0.15	6,6	0.76	
P × Time	1,140	0.01	1,140	0.01	
P × Tramp				(0.91) <sup>b</sup>	
Time × Tramp			6,6	3.47	
P × Time × Tramp	18,140	2.38**	6,140	0.37	

The nested factor (transects within all other factors) was non-significant ( $p > 0.50$ ) in both cases and was removed from the model. Significance levels: \* (0.05), \*\* (0.01), \*\*\* (0.001). Cochran's tests were n.s.

<sup>a</sup> "Tramples" tested over P × Time × Trample; P × Trample and Time × Trample,  $p > 0.25$ , pooled with P × Time × Trample.

<sup>b</sup> "Tramples" tested over Time × Trample; P × Trample,  $p > 0.25$ .

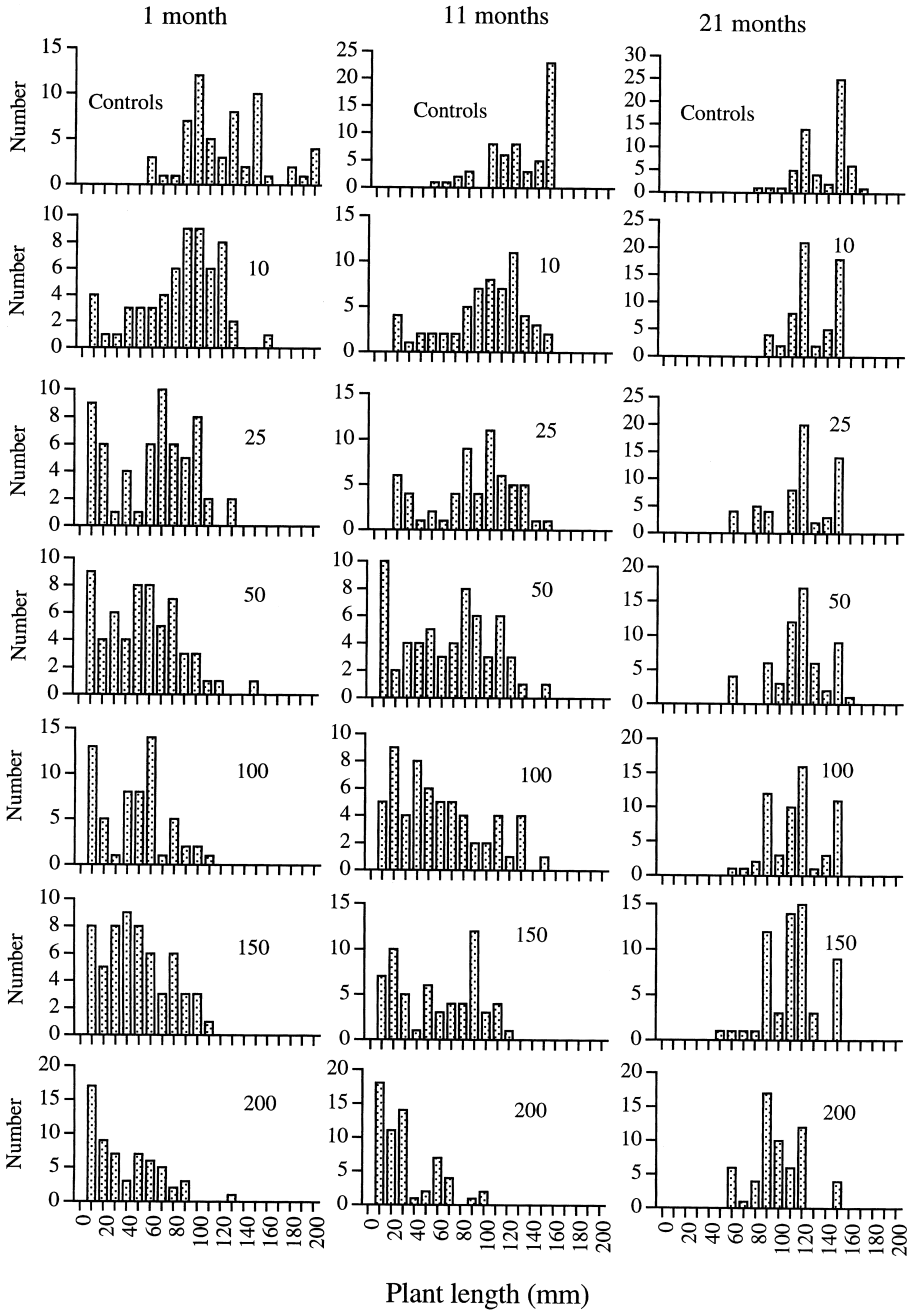


Fig. 6. The size-frequencies of *Hormosira banksii* at all trampling intensities at one month, 11 months and 21 months after trampling. Data are the combined Moeraki and Kaikoura sizes in the Spring treatment.  $N = 60$  for each histogram.

200 trampling treatments. One month after trampling, the average size of control plants was greater than in all trampling treatments for both Spring and Autumn (Fig. 7A, C). The reduction in frond size was most apparent from 100 to 200 tramples.

Recovery of trampled areas occurred in different ways among the trampling intensities. Controls had generally large plants (> 100 mm) throughout the experiment (Fig. 6). Most of the recovery within lower intensity treatments (10, 25 and 50 tramples) was through vegetative re-growth of existing fronds and holdfasts that had survived trampling. By 11 months after trampling, the 10 and 25 trampling treatments showed good re-growth of fronds. Only a few plants from the previous summer's recruitment were seen. While there was mostly re-growth of older fronds in the 50 treatment, there was also a relatively large recruitment of new plants (< 30 mm; Fig. 6) from the previous summer. The proportion of new recruits increased through the 200 trampling intensity, in which 70% of plants were recruits from the previous summer.

By 21 months after the Spring treatments, plants from most trampling intensities approached the larger sizes seen in controls (Fig. 6). At this stage, few small plants were present in any of the trampling intensities and a substantial canopy had reformed. By the end of the experiment, however, the average frond length had not returned to control

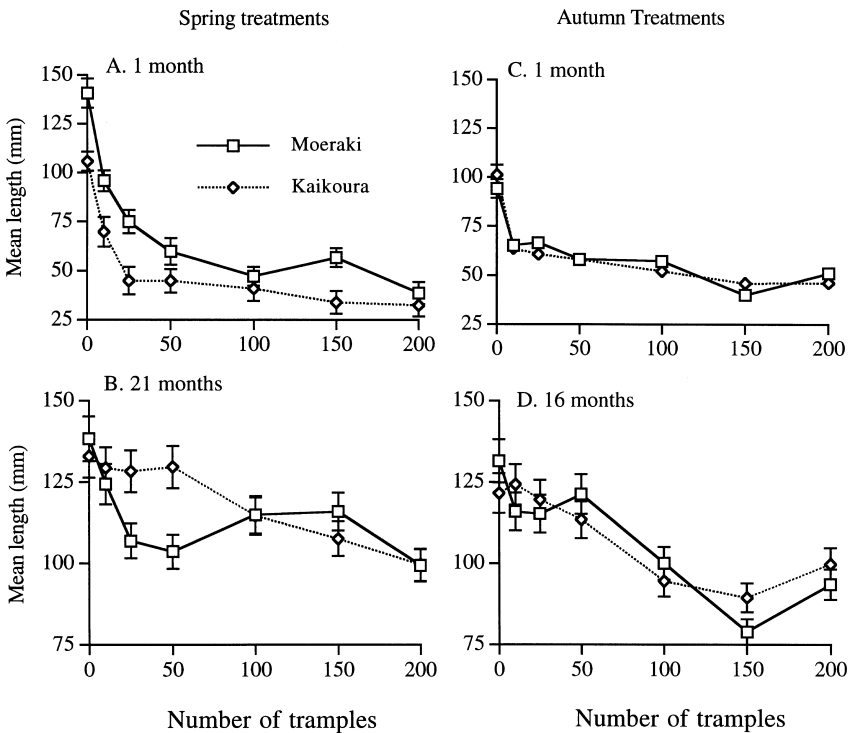


Fig. 7. The average length of *Hormosira banksii* ( $\pm 1$  standard error) across trampling intensities at Moeraki and Kaikoura in the Spring-initiated treatments after one month (A) and 21 months (B), and the Autumn-initiated treatments after one month (C) and 16 months (D).

levels. The Moeraki plants from  $\geq 25$  tramples averaged 20–25 mm less in length than controls, while plants from  $\geq 100$  tramples at Kaikoura were smaller on average than in all other treatments (Fig. 7B). In the Autumn treatments, plants from the 100 to 200 intensities averaged  $< 100$  mm length while plants in the other treatments were  $> 120$  mm (Fig. 7D).

#### 4. Discussion

This study showed that there were immediate and long-term effects of trampling and that these effects were both direct and indirect. The recovery process was affected by the timing of trampling and there was variation between the different platforms and often between replicates within treatments. The major factor in the recovery of trampled areas was the ability of *H. banksii* to recruit successfully and re-grow in the disturbed areas, processes influenced by the scale and intensity of the disturbances.

##### 4.1. Direct vs. indirect effects

*H. banksii* is particularly vulnerable to trampling, a conclusion both of our study and others (Povey and Keough, 1991; Keough and Quinn, 1998). After the highest intensity trampling, for example, the cover had decreased by  $> 90\%$  after one tide at both sites. Povey and Keough (1991) found after 33 days of high intensity trampling on Victoria shores that the percentage cover of *Hormosira* was reduced by ca. 75% of the control value. Fronds of this species are composed of strings of spherical, water-filled bladders. While this morphology enables plants to withstand heat stress and recover quickly from exposure (Dromgoole, 1980; Brown, 1987), it also makes frond separation from the substratum and partial loss of fronds a near certainty when these bladders are crushed or kicked. Fronds taper towards a small discoid holdfast, which is easily dislodged from the substratum. This species, therefore, is highly susceptible to both complete and partial removal when trod upon.

Indirect effects can encompass community-wide processes such as competition and predation which may be altered as direct effects reduce or remove dominant species and other species become more abundant (Underwood, 1989; Keough and Quinn, 1991, 1998). In our study, however, the major indirect effect of trampling was the reduction in both turfing and encrusting coralline algae. The removal of the dense *Hormosira* canopy increased the exposure of these understory algae and resulted in partial die-back following both the Spring and Autumn treatments. The algal turfs were reduced in both height and cover, and damage to them varied between platforms. As in the study by Povey and Keough (1991), the upright coralline algae were also damaged directly by intense trampling. Other studies have shown red algal turfs to be the least susceptible components of an assemblage. For example, in North America on exposed platforms dominated by mussels, algal turfs increased or were unaffected in response to the stress of human activities (Beauchamp and Gowing, 1982; Brosnan and Crumrine, 1994). The differences between our study and others may reflect not only the type and intensity of trampling but also species differences in susceptibility, differences in rock type, or

short-term effects in the recovery after disturbance. The subsequent increase in bare space can affect recovery through promoting suitable substratum for grazers and other invasive species. Povey and Keough (1991) and Keough and Quinn (1998) noted that grazers, particularly limpets, invaded some heavily trampled areas. No such movement of grazers was seen in our study. Several species of prosobranch and pulmonate limpets are common on elevated mounds within the mid-intertidal zone of both platforms but limpets have rarely been seen in the adjacent algal beds (cf., Underwood and Jernakoff, 1981). The turbinid gastropod *Turbo smaragdus* is common on coralline algal turfs on both platforms, is capable of affecting recruitment of low shore fucoids (Creese, 1988), but it is particularly abundant in the lower intertidal zone and was seen only occasionally in or near the experimental treatments. We conclude that grazers had little or no effect on the outcomes of trampling in our study.

There was no evidence that the provision of more bare space in heavily trampled areas resulted in greater diversity of algae. Ephemeral species were equally abundant in controls and in the transects of different trampling intensities. This may have been due to the small-scale patchiness of effects within transects and also to the surrounding *Hormosira* canopy remaining intact. Keough and Quinn (1991), (1998) also found that trampling affected neither the number of species present nor the overall species diversity (as measured by the Shannon Diversity Index  $H'$ ). The number of species encountered by Povey and Keough (1991), however, averaged 10–15 while our experiments had only three to six species on average at any given time. The discrepancy may lie not only in the general differences between Australian and New Zealand shores but also in the fact that molluscs were much less frequently encountered in our *Hormosira* areas than in the Australian study sites where many grazing species were seen in trampled areas.

#### 4.2. Scale, season and effects of other species

The size of disturbed areas clearly affects the recovery process. In our study, the corridor of disturbance was only about 30 cm wide and there was always at least a partial canopy of *Hormosira* plants overlaying the disturbed substratum. *Hormosira*, typically for an intertidal fucalcan, releases eggs directly into the surrounding water. After these are fertilised and sink to the substratum, they develop for several days before becoming firmly attached. Dispersal is unlikely to be very far from adults. In a species of *Fucus*, for example, Brawley and Johnson (1991) found that embryos survived better beneath a canopy of adult plants, which provided shade and a cooler moist environment compared to nearby areas where the canopy was removed. However, juvenile plants do not usually develop beneath an adult canopy because of shading (cf., Kennelly, 1987; Reed and Foster, 1984; Schiel, 1988). Gaps in the *Hormosira* canopy are likely to be swamped by zygotes, at least during late Spring and summer, while the light gap provided by canopy thinning would be conducive to growth and development.

The recovery process is clearly dependent on the timing of disturbance. Spring treatments had successful recruitment during the following three months and recovery of *Hormosira* to 50% of original cover occurred at around six months on both platforms. Although Povey and Keough (1991) found no recruitment of *Hormosira* to trampled areas, plants took a similar time of 270 days to recover to 50% of controls. Our Autumn

treatments, however, showed little recovery for eight months after trampling. It was only through successful recruitment the following summer that significant recovery occurred. Seasonal recruitment can be a major factor in determining which species captures space after a disturbance in subtidal algal assemblages in New Zealand (Schiel, 1988). However, the paucity of perennial brown algae capable of recruiting successfully into the mid-intertidal zone makes eventual recovery of *Hormosira* populations more likely.

There was clearly a facilitative relationship between successful recruitment of *Hormosira* and the nature of the substratum. On the hard basaltic rock at Moeraki, *Hormosira* recruited directly onto bare rock as well as onto thin encrusting coralline algae and into low-lying coralline turf. On the soft siltstone at Kaikoura, however, very few of the thousands of recruits encountered developed directly on bare rock but instead were seen almost exclusively on the corallines. It appears that at Kaikoura coralline algae provide a more physically stable substratum than the continually-eroding siltstone. The ability of *Hormosira* to recruit to coralline algae is mediated, however, by the reduction in thickness of the corallines that occurs after trampling when the algae become exposed to direct sunlight at low tide. Turfs were reduced to thin mats < 2 mm high while crusts were often reduced to thin layers. While heavy recruitment occurred on these surfaces, virtually none was seen on the older and more developed turfs and crusts nearby, a result also seen in another longer term experiment (Schiel, unpubl. data).

The damage to corallines and the relationship between them and recruitment of large perennial algae can be complex and variable. For example, Kendrick (1991) found turfs to be less resistant to scouring than encrusting corallines. In areas of high levels of scouring, encrusting algae recovered faster and covered greater areas than turfs. Camus (1994) suggested that encrusting corallines, through the shedding of epithelial cells, reduced the recruitment of *Lessonia nigrescens* in northern Chile. Worm and Chapman (1996) found that *Chondrus crispus* crusts inhibited recruitment of *Fucus evanescens*, most likely because surface sloughing did not allow permanent attachment of young plants. Turfing coralline algae, however, facilitated recruitment of furoid algae in several studies (Brawley and Johnson, 1991; Benedetti-Cecchi and Cinelli, 1992; Brawley and Johnson, 1993).

Early life history stages of fucoids seem most vulnerable to desiccation due to their high surface to volume ratio (Chapman, 1995). The microhabitat provided by turfing corallines may protect spores from desiccation, scouring and grazing. Brawley and Johnson (1993) found, using agarose beads to simulate the dehydration of microscopic zygotes, that survival of *Pelvetia fastigiata* zygotes was correlated with the protection from desiccation stress provided by coralline turf microhabitat. Turfing corallines may also trap sediments and prevent scouring, thereby increasing survival of algal recruits (Brawley and Johnson, 1991). Where herbivores are present, turfing corallines can facilitate recruitment of large brown algae by preventing successful grazing (Camus, 1994). The recruitment success of *H. banksii* may be affected by one or more of these interactions. Therefore, the burn-off of turfing corallines following trampling damage can have long term consequences on *Hormosira* recovery, particularly since turfs took longer to recover than did encrusting corallines. Overall, the recapture of space by *Hormosira* depends on recruitment windows where zygote availability coincides with suitable substratum and canopy gaps.

### 4.3. Trampling as a disturbance

Critical features of any community subjected to disturbance are its ability to withstand damage and to recover from it. These will depend not only on the nature of the community itself but also on the type, magnitude and frequency of disturbance (Underwood, 1989). Our experiment represented a “pulse” disturbance whereby trampling was done at different intensities and at two discrete times in different seasons. Most other similar studies, in several countries, are closer to “press” disturbances, whereby dominant species are repeatedly impacted over long periods (Beauchamp and Gowing, 1982; Castilla and Durán, 1985; Bally and Griffiths, 1989; Povey and Keough, 1991; Brosnan and Crumrine, 1994). Recovery, therefore, depends not only on a reduction or cessation of human disturbance but also on an adequate source of propagules and sufficient time to recover through recruitment and growth processes. The study of Keough and Quinn (1998) highlights the complex interactions of effects due to trampling and natural variation over several years. They found that repeated pulse disturbances do not necessarily lead to a press response but that this was variable among sites. Recovery from trampling at some of their sites generally occurred after nine months, and so repeated trampling acted as a series of pulse disturbances. At other sites, however, there was little recovery after repeated trampling and, therefore, a press response.

For *Hormosira*-dominated assemblages in New Zealand, the inertia is rather low. As few as 10 tramples produces discernible changes in percentage cover. The resilience, however, can be high provided there is sufficient time without further disturbance to recover. In the case of the southern New Zealand platforms, *H. banksii* is not only the major habitat-former of the algal beds on platforms, occupying up to 80% of the surface cover (Schiel, unpubl. data) but it is also the only perennial large brown alga capable of living extensively in much of the intertidal zone. No other species equivalent in canopy cover is able to invade, particularly in the mid-intertidal zone. Given this, and provided no new disturbance occurs, *Hormosira* is likely to recapture space eventually both through re-growth and recruitment episodes, especially when only small patches are disturbed in a canopy such as in our experiment.

Compared to most places and countries, the intertidal platforms in southern New Zealand have a relatively low frequency of human disturbance. As tourist numbers rise, however, the present pulse-type impacts may become more frequent, creating more and larger patches and allowing less time for undisturbed recovery. If this persists, the result will be more primary space and a reduction in one of the main intertidal habitats of the South Island.

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