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NON-LINEAR RESPONSE OF THE BROWN SEAWEED *FUCUS GARDNERI* TO THE INTENSITY OF DISTURBANCE REVEALS A DENSITY THRESHOLD

Markus G. Speidel

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Padilla Bay National Estuarine Research Reserve
10441 Bayview-Edison Road
Mount Vernon WA 98273-9668
(360)428-1558

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If you have special accomodation needs, please contact Linda Smith, Department of Ecology, at (360)428-1558 or (360)757-1549 (TDD).

Padilla Bay National Estuarine Research Reserve
Shorelands and Environmental Assistance Program
Washington State Department of Ecology
10441 Bayview-Edison Road
Mount Vernon WA 98273

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Abstract

The recovery of the brown seaweed *Fucus gardneri* to controlled pulse disturbances of different intensities were studied on a rocky shore in Padilla Bay, Washington, USA. The percent ground cover of this dominant alga was reduced by twenty-percent increments to simulate different levels of disturbance and examine the linearity of subsequent recovery. Abundance of invertebrate grazers and ephemeral algae were monitored as well to examine indirect effects on the community. The recovery of *F. gardneri* cover one year after the disturbance was markedly non-linear, with a threshold to disturbance observed between plots reduced to 20% and 0% *Fucus* cover. The abundance of invertebrate grazers and ephemeral algae did not vary significantly with the intensity of disturbance. These results add to the corpus of work demonstrating that ecological responses to disturbance are often non-linear, and suggest that manual removal of *Fucus* may be an effective method of cleaning oil from rocky shores following a spill without significantly impairing biological recovery.

Acknowledgements

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Introduction

Disturbance and the course of subsequent succession have long been shown important in shaping communities (Clements 1916), and are key to understanding the dynamics driving patterns of community structure. Given the ecological importance of disturbance, and the advantages of compressed spatial and temporal scales for studying such dynamics offered by intertidal systems, many aspects of disturbance have been extensively studied in marine and intertidal habitats (see references in Kim and DeWreede 1996). That the recovery of a community or population from disturbance may vary non-linearly with the frequency and intensity of that disturbance is not a new idea. In 1978 Connell presented the *Intermediate Disturbance Hypothesis* which predicted precisely this. The concept had been experimentally established independently that same year (Lubchenco 1978) and its theoretical ramifications were quickly explored (Huston 1979). Nonetheless, traditional studies of disturbance recovery utilizing a control/ impact design make the implicit assumption that communities respond linearly to different levels of disturbance. Such designs have the advantages of economy (only two treatments necessary) and greater statistical power, yet they cannot describe what occurs at intermediate levels of disturbance. Recent work examining nonlinear dynamics and threshold behavior in other ecological interactions (Ruesink 1998) has highlighted the importance of testing linear assumptions.

Fucus gardneri Silva (Phaeophyta: Fucaceae, formerly considered *Fucus distichus* in part; hereafter referred to as *F. gardneri*) is the dominant alga of the mid intertidal zone on rocky shores throughout the Northeastern Pacific. With respect to abundance, *F. gardneri* may be the most significant species in the mid to high intertidal zone, composing up to 90% of the algal biomass (Paine et al. 1996, Stekoll et al. 1996). Other species of *Fucus* hold similar dominance on temperate rocky shores around the Northern hemisphere. Population dynamics of various *Fucus* species have hence been the subject of much study (Ang 1991, Schonbeck and Norton 1978) as have their response to disturbance (removal) (Lodge 1948, Dayton 1971, Keser and Larson 1984, Ang and DeWreede 1992).

Among these studies focusing on disturbance, *Fucus* cover was either removed or left untouched. Interpolation of the response to intermediate levels of disturbance must thus assume *Fucus* behaves linearly to removal. There are, however, reasons to suspect that *Fucus* recovery may exhibit non-linear behavior due to intraspecific effects. First, *Halidrys* germlings (another intertidal alga genera belonging to the same family as *Fucus*) show a physiological threshold to heat stress at 20° C (Lee 1989), a temperature threshold lower than that experienced on bare rocks on Saddlebag during sunny summer low tides. Other studies provide indirect evidence that germling stages of *F. gardneri* may suffer mortality due to heat and desiccation during summer low tides (Ang 1991, Ang and Dewreede 1992, Highsmith et al. 1993, Kim and DeWreede 1996, Fukuyama et al. 1998), although they do not take the physiological approach of Lee and do not attempt to establish a temperature threshold. Second, the cover provided by larger *Fucus* individuals shades the substratum and retains moisture (personal observation) and hence may ameliorate the effects of heat and desiccation stress on germlings. At more intense levels of disturbance, recovery appears to depend increasingly on recruitment success and, if cover is important to recruitment, recovery may thus scale non-linearly with the degree of *Fucus* removal.

Knowing how *Fucus* recovers following disturbance is relevant to minimizing the effects of human caused pulse perturbations such as oil spills. The disturbance resulting from an oil spill takes two forms: the initial spill, and the chemical, biological, and physical aspects of cleanup that follow. On rocky shores, oil spill cleanup has often involved removing the intertidal community from large areas with subsequent lengthy and erratic recovery (Raffaelli and Hawkins, 1996). If there is a threshold level of *Fucus* cover above which *Fucus* recovery is substantially quicker, then there may be better ways that oil could be better removed from rocky shores.

I tested whether the recovery level of *F. gardneri* to a pulse disturbance varies nonlinearly with the intensity of that disturbance measured as the percentage of *F. gardneri* was removed. I also tested whether *F.gardneri* cover has a significant ameliorating effect on the microclimate of high intertidal algal beds. In addition to measuring the abundance of *F. gardneri* cover, adults, and germlings, I also monitored significant grazers and conspicuous other species of algae in order to see how the treatments affected other major components of the community.

Methods

Study sites

This research was conducted on Saddlebag Island in Padilla Bay, Washington, USA (Figure 1). Located at the East end of the Georgia-Puget Sound Basin, the island is very sheltered from waves. During the summer when the lower low tide occurs during the daytime, rock temperatures are high and frequent breezes further speed the rate of desiccation. The shores of the island are a mix of sand beaches, loose rock beaches, and dark bedrock. Sites were located in areas of primarily bedrock rather than boulder fields to avoid additional disturbances from boulder movements during storms. Available bedrock locations had broken and uneven surfaces, often containing cracks and small pools.

Figure 1. Location of Saddlebag Island.

F. gardneri was the most abundant alga on all rocky shores of the island in the upper middle intertidal region. Several other species of algae, both ephemeral and persistent, were found within the *F. gardneri* beds. The most conspicuous of these other algae were species of ephemeral *Ulva* and *Porphyra*. The grazer guild was represented predominantly by limpets (*Lottia digitalis, L. strigatella, L. pelta*) and littorine snails (*Littorina sitkana, L. scutulata*). Underneath the *Fucus* cover, crust-forming algae and barnacles were often found. Although *Fucus* clearly dominated the mid- and upper intertidal, its abundance was uneven and patches of thin or sparse *Fucus* cover were frequent.

Basic Experimental Design

Five experimental blocks were established each at a different site around the island (Figure 2). Six treatment levels were established at each site by reducing the cover of *F. gardneri* in six plots to varying initial levels (100, 80, 60, 40, 20, 0%, referred to as Tr100, Tr80, Tr60, Tr40, Tr20 and Tr0 respectively. Percent cover was reduced by trimming with scissors as described below. Cover was estimated using the point-intersect method in a 49 point, 20cm by 20cm quadrat. Percent cover of a species of algae was measured as the proportion of points in the quadrat lying over that species. Sites were named A—E beginning on the eastern shore and proceeding clockwise around the island. A sixth site, F, was established on the western shore where the macroscopic germlings were not removed. As the Tr0 at Site F behaved much differently from the other Tr0 replicates (see Results), the whole site was left out of the general analyses and was looked at separately as a single counter example.

Plots were 40 cm by 40 cm in size, with all variables measured in the interior 20 cm by 20 cm region. This left a buffer of 10cm width to reduce suspected edge effects[1]. Placement of plots was constricted by the unevenness of rock surfaces and the need for high initial *Fucus* cover. All plots selected had 80% or higher *Fucus* cover over the entire 40cm by 40cm plot area, and even higher cover for the interior subplot, prior to manipulation. Plot location was determined by selecting the spaces meeting the following criteria to the greatest extent: similar tidal height (to other plots within the given site), absence of large cracks, generally plane surface, and high surrounding *Fucus* density. All plots were in the upper half of the zone in which *F.*

[1] Suspected edge effects included refugia for littorine and limpet grazers under the cover of surrounding *Fucus*, as well as shading and whiplash effects of larger adults located outside of the plot boundaries. Trimming the fronds of exterior adults so that they could not reach over the plot boundaries further controlled for the later two concerns and assured that no fronds of exterior plants could reach the interior 20 cm by 20 cm subplot.

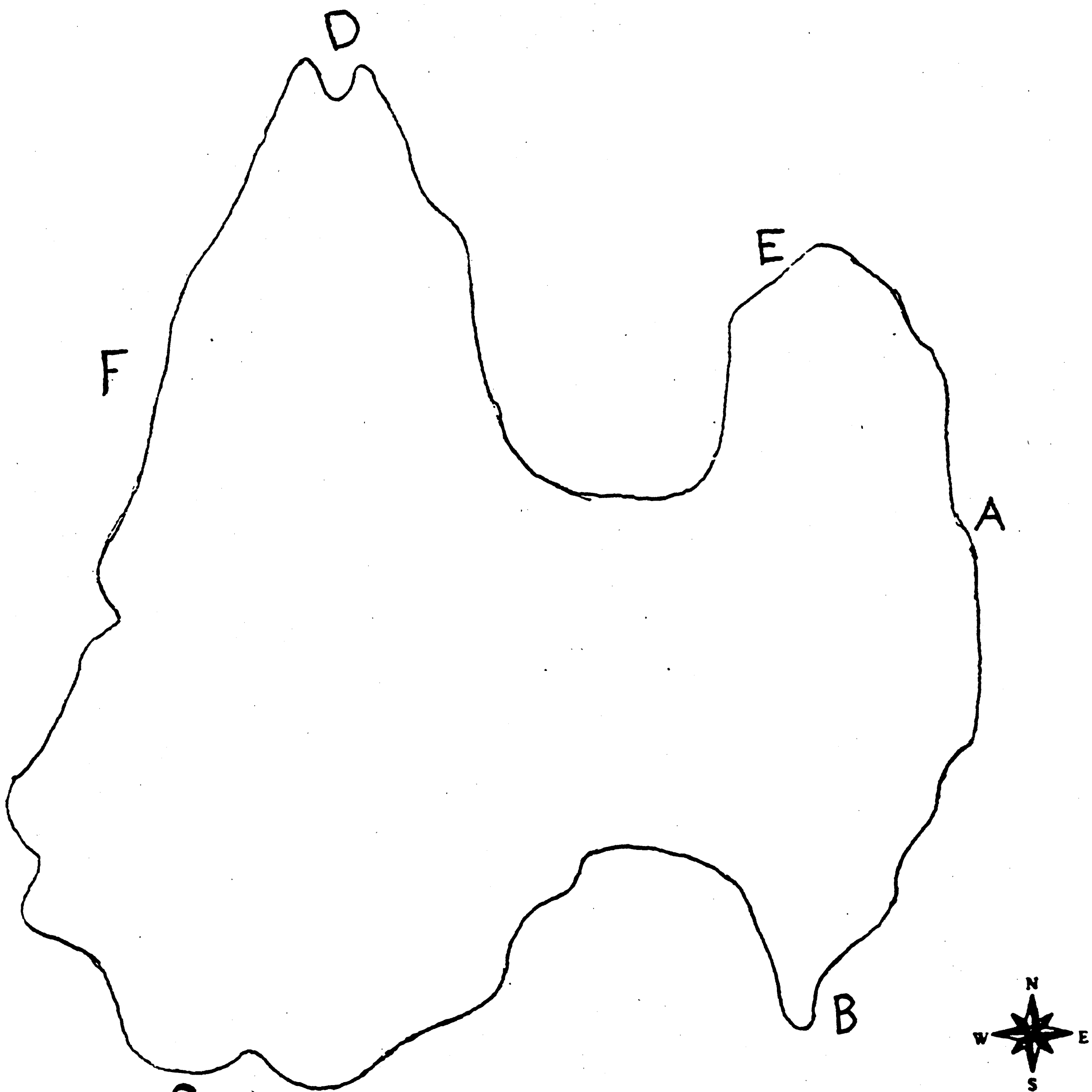


Figure 2. Saddlebag Island

gardneri is found. In this region *F.gardneri* is the clear dominant, while in the lower regions the abundance of other algal species increases and the stucture becomes more complex. Plot slopes ranged between 3 and 46 degrees with a mean of 19.6° +/- 10.64°.

Within a site, plots were separated by less than 15 meters (distances between sites were greater than 100 meters). As it was, compromises needed to be made and plots varied within a site in *Fucus* age structure, number of adults, and number of germlings before treatment. Plots were marked at all four corners using dime-size lumps of marine epoxy, which were replaced as necessary.

Treatment method

The experimental manipulations were performed during the week of July 8th, 1998, with one site, or block, being completed each successive day.

Plots were surveyed for initial *Fucus* cover, and number of germlings and adults present. (Germlings were defined as macroscopic recruits shorter than 1 cm in length). It is important to note that *F. gardneri* individuals exist in microscopic form (hereafter "microrecruits") for a period before growing to macroscopic size (Ang 1991). While sampling such microrecruits would have been informative, only macroscopic germlings were counted due to the difficulty of counting plants which cannot be seen unaided. Treatment level was then assigned to plots within a site. A conscious effort was made to get a good mix of the variation in initial conditions among treatment replicates. Assignment of the Tr100s was restricted to those plots that had very high initial cover (>95%), but an effort was made to not always assign it to the plot with the richest, densest *Fucus* growth in a site. This method was chosen over strict randomization since, given the sample size, it seemed to provide the most balanced division of natural variation among treatments.

Cover was reduced to the assigned level by trimming the distal end of fronds with scissors. An attempt was made to trim all plants within a plot evenly to retain the existing age-class structure and to remove the reproductive ends of adults in higher treatment plots to minimize initial differences in reproductive activity. This method of thinning was chosen over removing entire individuals because of the large variation in number and size of adults between plots. Some plots had just a few individuals supplying the majority of the cover and, had individual plants been removed, it would have been difficult to achieve the assigned level of cover. Percent cover in each plot was not maintained after manipulation but rather considered a response variable and its dynamics were recorded. The reduction was thus a pulse perturbation rather than a press perturbation.

It should be noted that the manipulation had a second effect restricted to the 0% treatment. In reducing plots to 0% cover, the germlings, the cohort of macroscopic recruits, were all plucked in addition to the adults, whereas in other treatments this potential wellspring of immediate regeneration was left intact. While this second effect may be seen as a natural consequence of reducing cover to 0% (and does not alter the central focus of this report, the non-linear response of *F. gardneri* to disturbance), it is a biologically significant distinction worthy of consideration. In order to gain some insight into the consequences of this second manipulation, a sixth block of treatments was established, Site F, at which the germlings were not removed from the T0 plot. An additional note: since the substratum was not sterilized, the "seed bank" of microscopic recruits proposed by Ang (1991) was not directly damaged by the treatment.

Monitoring methods

The plots were monitored over one year, from July 1998 to July 1999. Monitoring trips were made about every six weeks after the initial six weeks (Appendix 1). All plots were monitored each trip, with the exception of two trips. (Since data from these two trips was incomplete (n<5) they were not used in the analyses.) All six plots within a site were monitored during the same tide, and the order in which sites were sampled varied unsystematically. Early on, only one site was monitored per tide (day). After November 1998 two sites were generally monitored per tide. Summer lower low tides were during the day; during the winter, the lower low tide was monitored at night.

Seven response variables were measured, including three metrics of *Fucus* recovery: percent cover, number of adults, and number of germlings. To get a sense of the community response to the treatment, the most abundant grazers (*Lottia* spp. and *Littorina* spp.) were censused and the percent cover of other conspicuous algae species (*Ulva* and *Porphyra*) were estimated.

Relocation of several plots

Four weeks into the experiment an *Ulva* bloom occurred in a number of plots in several sites. The rapid appearance of *Ulva* in some plots but not in others within a given site seemed to be linked to differences in both treatment level and relative vertical height. Since *Ulva* can have negative impacts upon *Fucus*, subtle differences in relative height became a potentially confounding factor. To reduce the impact of differential *Ulva* growth due to plot height plots noticeably (if slightly) higher or lower than the others within a site were relocated. 13 of the 36 plots were moved in total (includes plots at Site F).

These 13 relocated plots (noted in Appendix 2) thus lagged four weeks behind the remaining plots. To minimize the influence of this difference in starting dates, five time points were chosen out of the dozen monitoring trips with the interval between time points being 10 or more weeks, far greater than the four weeks of the delay. By the second time point, September 1998, there were no significant differences in any of the response variables between the remaining initial plots and relocated ones. All data were analyzed by sampling date and were not adjusted for the time lag (except for pretreatment and initial data, which for the relocated plots was taken from a trip on October 12th, 1998).

Measurement of physical characteristics

Temperature and desiccation rate was measured for all six sites on August 26th 1999, which was a clear and hot day, with the low tide occurring around midday. Rock surface temperature was measured at each site both under dense *F. gardneri* cover and for a spot of bare rock at three different times during the tide. Air temperature was taken at the same time. For desiccation measurements a 40 cm by 40 cm location was chosen at each of the sites. Within the 40 by 40 area, *F. gardneri* cover was manipulated to 0, 50 and 100 percent in 10cm by 10cm subplots. A saturated wet sponge was placed in each subplot (beneath the *F. gardneri* cover in the 50% and 100% subplots) after being weighed with a spring scale. Sponges were 6cm x 6cm x 2cm in size. Sponges were reweighed during the middle of the tide, and again approximately five hours after first being set out.

Statistical methods

One-way ANOVAs ($\alpha = 0.05$) were run on all response variables for differences among treatment levels at each time point with n = 5 (each time point tested independently). The error term was reduced by blocking the data by site, thereby eliminating the variation due to Site differences. Census and percent cover data were transformed, using log transformation and arcsin-square root transformation respectively. Bonferroni post hoc analyses ($\alpha = 0.05$) were performed on significant tests using SPSS.

Results

Physical measurements

F. gardneri cover did ameliorate the microclimate below its canopy. Surface temperature of bare rock reached 26.6°C (+/- 1.67°C, n=5) on August 26th, while under thick *Fucus* cover rock surface temperature remained at 20.2°C (+/- 1.3°C, n=5), a difference of 6.4°C +/- 0.89°C (Table 1). Rock surface temperature increased much more rapidly in bare locations than below *Fucus* cover (Figure 3). Site F was significantly different from the other plots, remaining cooler throughout much of the day (Figure 4). Site F, the western most site, lies in the shadow of tall cliffs during the first part of the day, and receives the predominantly north-westerly breezes. Once direct sunlight reached Site F (after 9:45am), the temperature of bare rock rose rapidly (Figure 4a). Rock surface temperature below *Fucus* cover rose at the same lower rate as at other sites (Figure 4b). It was not until after 14:30 that the surface temperature of bare rock at Site F matched that of other sites (Figure 5). Thus the intertidal region at Site F experiences a cooler climate for most of a morning low tide. Because of the lower temperature of bare rock, the temperature difference between exposed and shaded rock surfaces remained less at Site F than at the other sites until after 13:30. Although there is a trend of increase with decreased *Fucus* cover, desiccation rates appear to have been unduly influenced by differences in rock slope and hence are only reported in Appendix 3.

Fucus cover

The level of cover of *Fucus gardneri* varied non-linearly with the intensity of canopy removal, showing a density threshold. On Saddlebag Island this disturbance threshold lay between 20 and 0% cover. After one year, the plots reduced to 0% had not yet recovered to their pre-disturbance level of cover while all other treatments had (Figure 6a). This non-linearity in recovery level was not reflected in two other metrics (number of adult, and germling *Fucus* individuals, Figure 6b and c respectively).

F. gardneri cover varied significantly with treatment at all five time points analyzed (One-way ANOVA, P = 0, <0.001, 0.005, 0.041, and 0.036 for July and September1998, and February, May, and July 1999 respectively, Table 2 and Figure 7). At the beginning of the experiment all treatment levels were significantly different (Table 3), reflecting the pulse disturbance. Ten weeks later a more complex pattern of differences had arisen. All treatments had declined (except Tr0), and variation among sites within treatments increased dramatically. Tr20 became statistically indistinguishable from Tr0, while Tr0 remain significantly lower than all other treatments. Tr20, Tr40, Tr60, and Tr80 became statistically indistinguishable. Cover Tr100 remained significantly higher than in all the other treatments.

Surface temperature of rocks with (shaded) and without (bare) *Fucus* cover

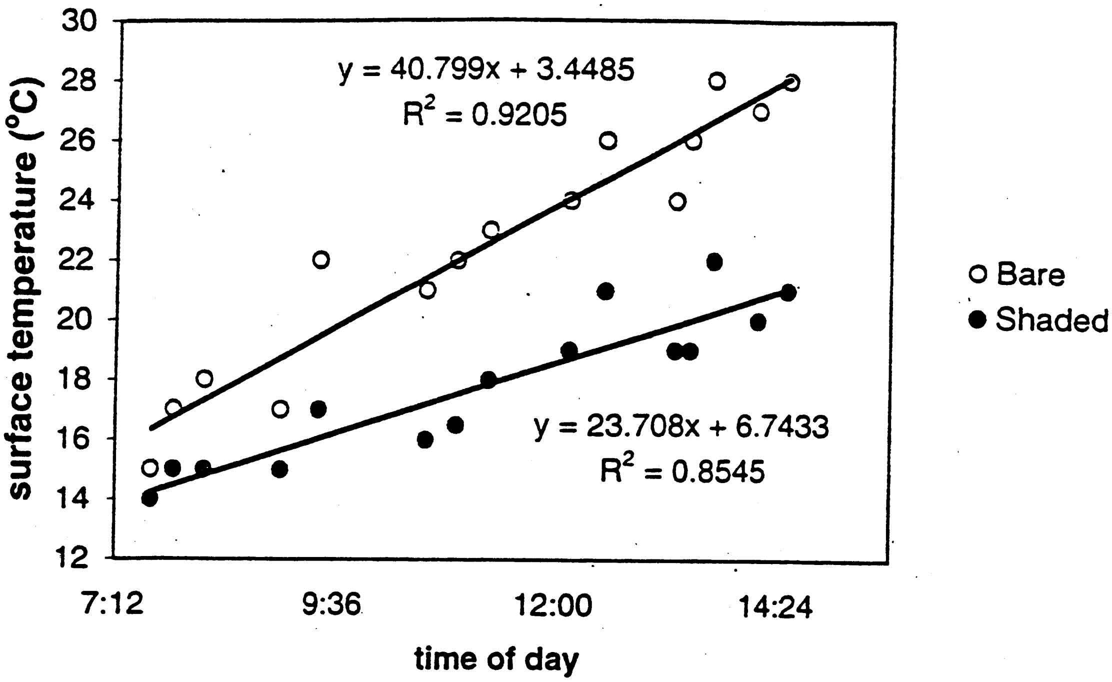


Figure 3. Comparison of surface temperatures over time for rocks with and without *Fucus* cover during low tide on August 25th, 1999. Rocks with Fucus cover remained cooler and the difference between bare and shaded rocks increased during the low tide. Rocks "with *Fucus* cover" had over 95% multi-layered cover.

Table 1: Rock surface and air temperatures (in °C) at Sites A-E (mean +/- 1 s.d.) and Site F on August 25, 1999.

a. With *Fucus* cover:

Time:	A-E:	St. dev.:	Site F:
7:35- 9:45	15.2	1.095	14
10:35-12:45	18.1	2.012	18
13:15-14:45	20.2	1.304	19

b. Without *Fucus* cover:

Time:	A-E:	St. dev.:	Site F:
7:35- 9:45	17.8	2.59	14
10:35-12:45	23.2	1.92	23
13:15-14:45	26.6	1.67	27

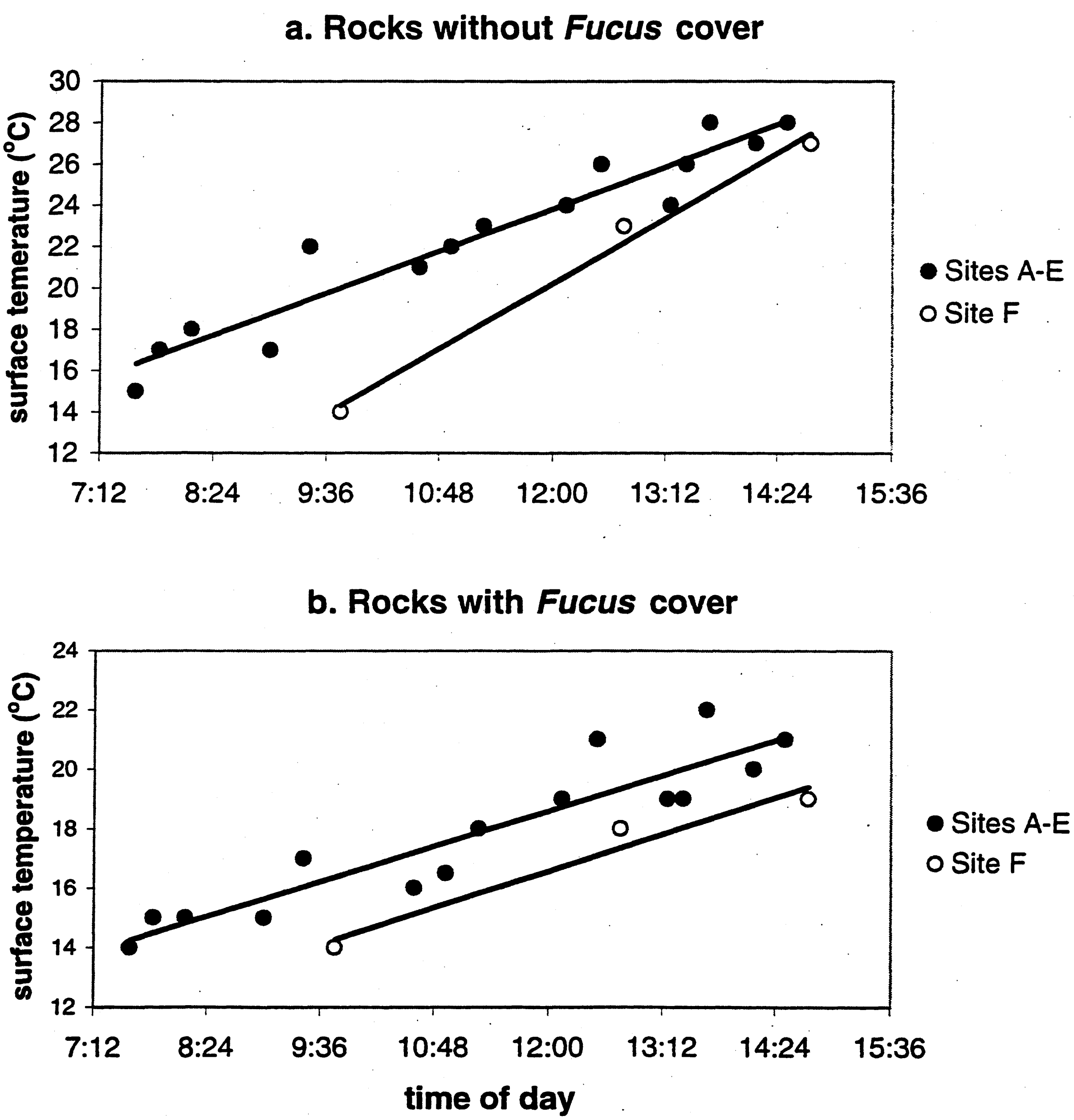
c. Temperature difference between with and without *Fucus* cover:

Time:	A-E:	St. dev.:	Site F:
7:35- 9:45	2.6	1.52	1.1
10:35-12:45	5.1	0.22	4.9
13:15-14:45	6.4	0.89	5.5

d. Air Temperature:

Time:	A-E:	St. dev.:	Site F:
7:35- 9:45	17.2	1.68	15.0
10:35-12:45	20.5	2.18	20.5
13:15-14:45	22.6	1.67	23.0

Figure 4. Comparison of surface temperatures between Sites A-E and Site F on August 25th, 1999 for:
A: Rocks without *Fucus* cover
B. Rocks with *Fucus* cover



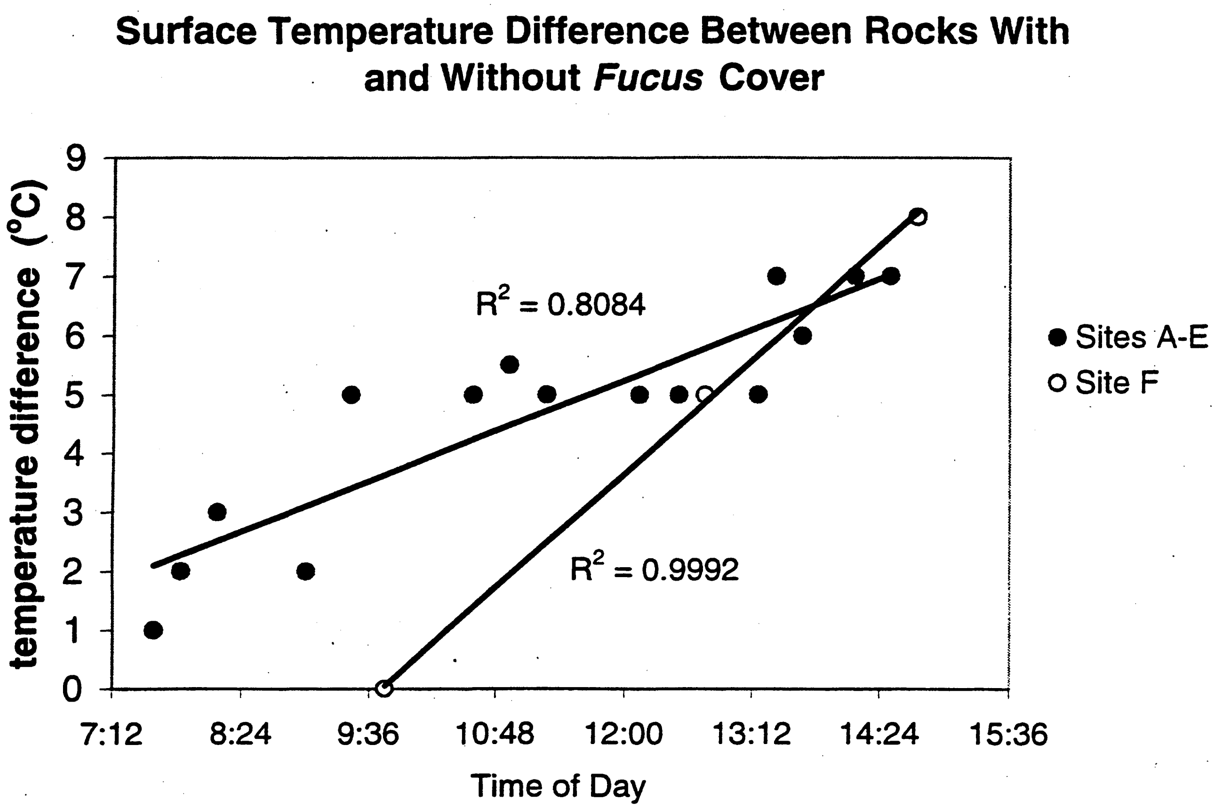


Figure 5. Difference in rock surface temperature between rocks with and without *Fucus* cover at Sites A-E and Site F on August 25th, 1999. The difference remained smaller at Site F until after 1pm.

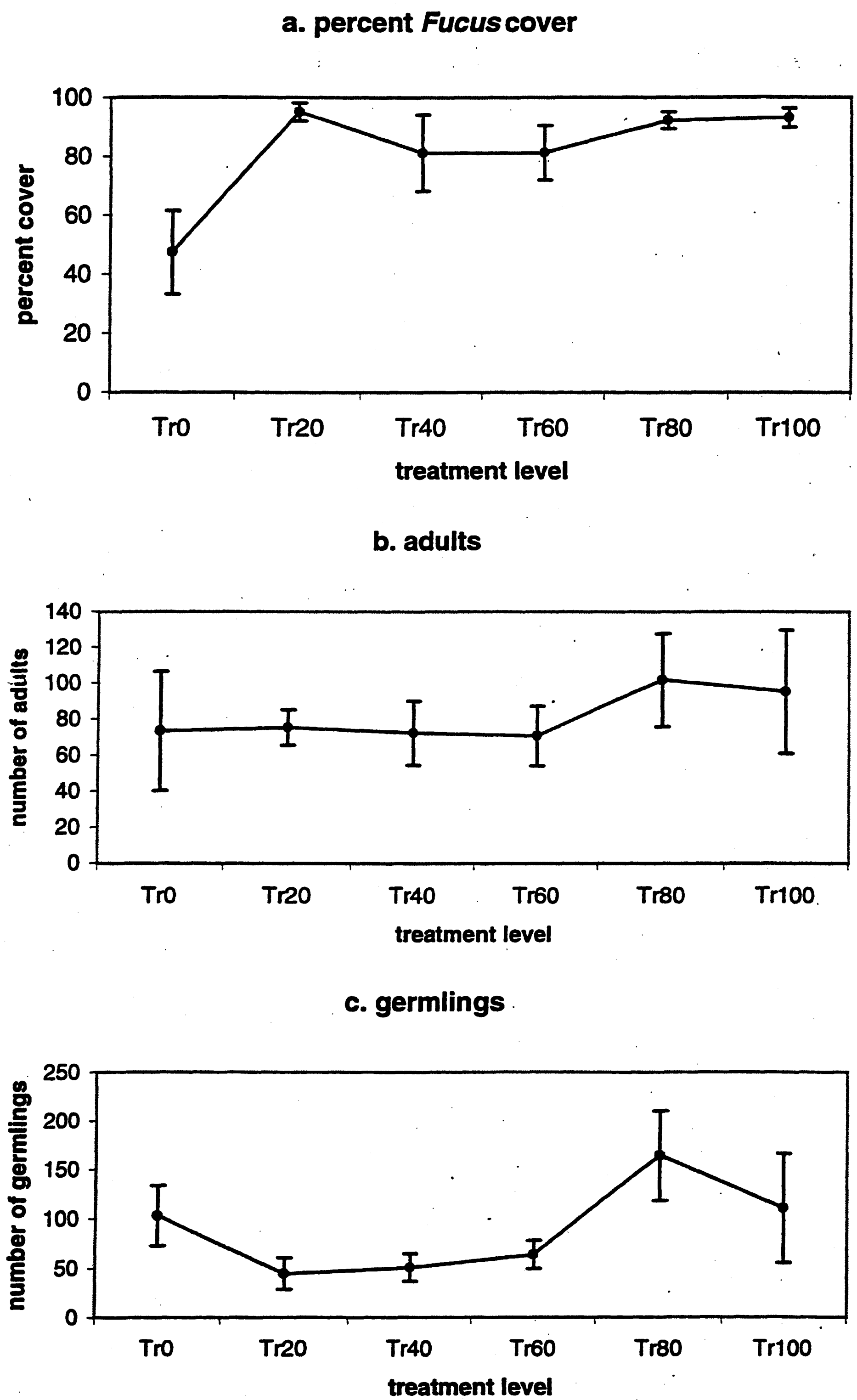


Figure 6. Recovery level of *Fucus* one year after manipulation in terms of a. percent cover, b. number of *Fucus* adults (> 1 cm), c. germlings (< 1 cm) for all treatment levels. Error bars denote standard error.

Table 2. Statistical significance among treatments for measured variables. (one-way ANOVA, blocked by site, α=0.05, bold denotes statistical significance):

	July 98	Sept. 98	Feb. 99	May 99	July 99
Fucus cover	**0**	**<0.001**	**0.005**	**0.041**	**0.036**
Number of Germlings	**0.017**	0.2	0.68	0.76	0.064
Number of Adults	**<0.001**	0.11	**0.001**	0.22	0.77
Ulva cover	--	0.065	0.96	0.58	0.44
Porphyra cover	--	--	0.21	0.32	0.51
Littorine abundance	--	0.26	0.58	0.092	**0.02**
Limpet abundance	--	0.33	0.43	0.55	0.54

Table 3. Bonferroni Corrected tests of between-subject effects (significance at α=0.05 denoted in bold). "Treatment a" and "treament b" are the two treatment levels compared.

Treatment a	**Treatment b**	**July 1998**	**Sept. 1998**	**Feb. 1999**	**May 1999**	**July 1999**
0	**20**	**.000**	.338	**.004**	**.034**	**.046**
	40	**.000**	**.040**	.997	1.000	.418
	60	**.000**	**.002**	.107	.645	.487
	80	**.000**	**.001**	.700	1.000	.136
	100	**.000**	**.000**	**.027**	.222	.080
20	**0**	**.000**	.338	**.004**	**.034**	**.046**
	40	**.000**	1.000	1.000	.639	1.000
	60	**.000**	.567	.337	1.000	1.000
	80	**.000**	.250	1.000	1.000	1.000
	100	**.000**	**.000**	.491	1.000	1.000
40	**0**	**.000**	**.040**	.997	1.000	.418
	20	**.000**	1.000	.337	.639	1.000
	60	**.000**	1.000	1.000	1.000	1.000
	80	**.001**	1.000	1.000	1.000	1.000
	100	**.000**	**.001**	1.000	1.000	1.000
60	**0**	**.000**	**.002**	.107	.645	.487
	20	**.000**	.567	1.000	1.000	1.000
	40	**.001**	1.000	1.000	1.000	1.000
	80	**.000**	1.000	1.000	1.000	1.000
	100	**.000**	**.011**	1.000	1.000	1.000
80	**0**	**.000**	**.001**	.700	1.000	.136
	20	**.000**	.250	.491	1.000	1.000
	40	**.000**	1.000	1.000	1.000	1.000
	60	**.000**	1.000	1.000	1.000	1.000
	100	**.000**	**.027**	1.000	1.000	1.000
100	**0**	**.000**	**.000**	**.027**	.222	.080
	20	**.000**	**.000**	1.000	1.000	1.000
	40	**.000**	**.001**	1.000	1.000	1.000
	60	**.000**	**.011**	1.000	1.000	1.000
	80	**.000**	**.027**	1.000	1.000	1.000

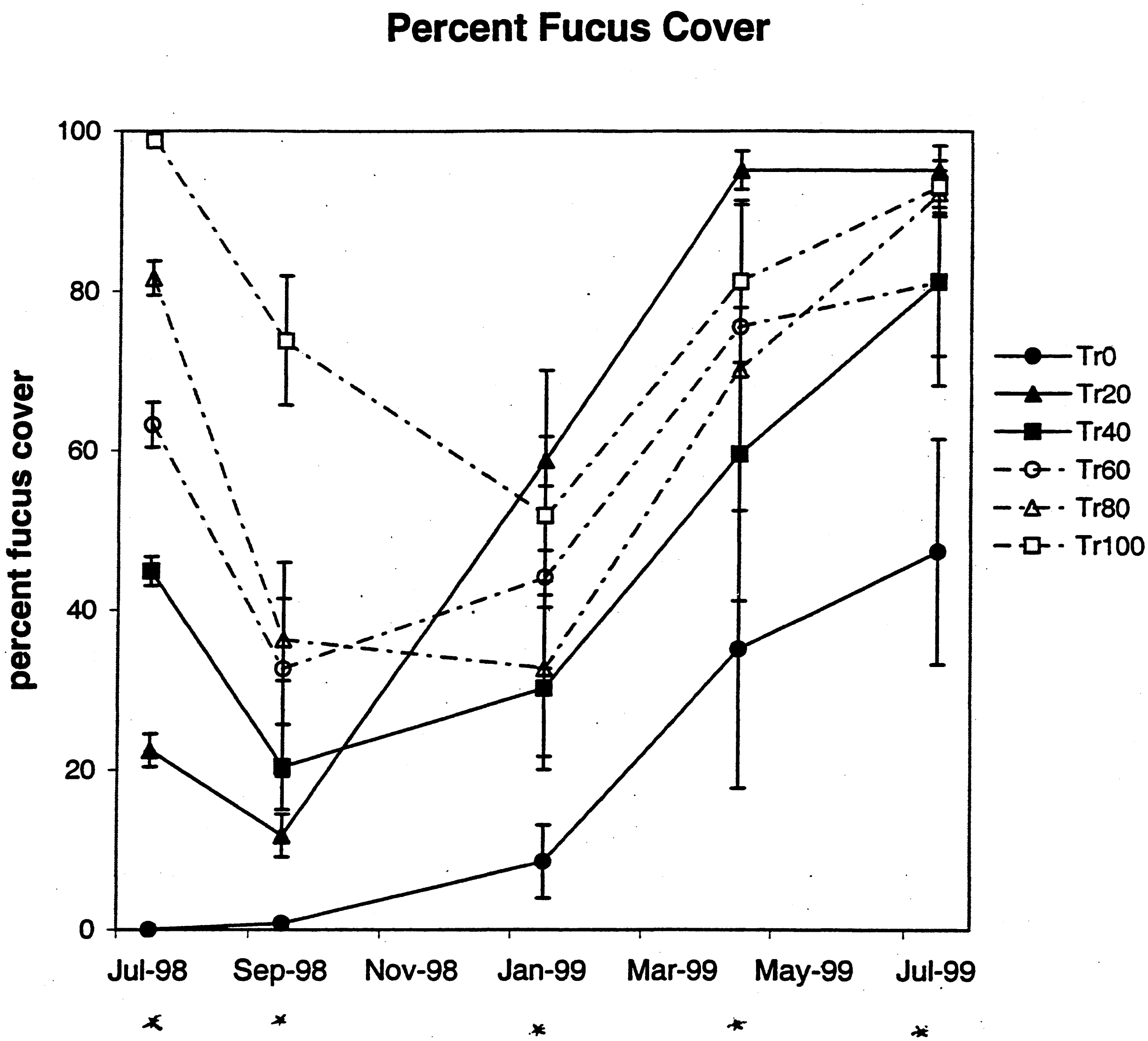


Figure 7. Mean percent *Fucus* cover over time for all treatment levels. Error bars denote standard error (n=5).Significant differences among treatments for a given sampling date denoted with a "*".

By February, all plots had converged with respect to cover and the only significant differences remaining were between Tr0 and both Tr100 and Tr20, which were higher (Bonferroni corrected, P=0.004 and 0.027). Tr20 had increased dramatically and become the treatment with the greatest amount of cover, which it remained through the end of the experiment. In both May and July Tr20 remained significantly higher than Tr0 (Bonferroni corrected, P= 0.034 and 0.046) and were the only pairs of treatments which remained statistically distinguishable (Table 3).

Other response variables

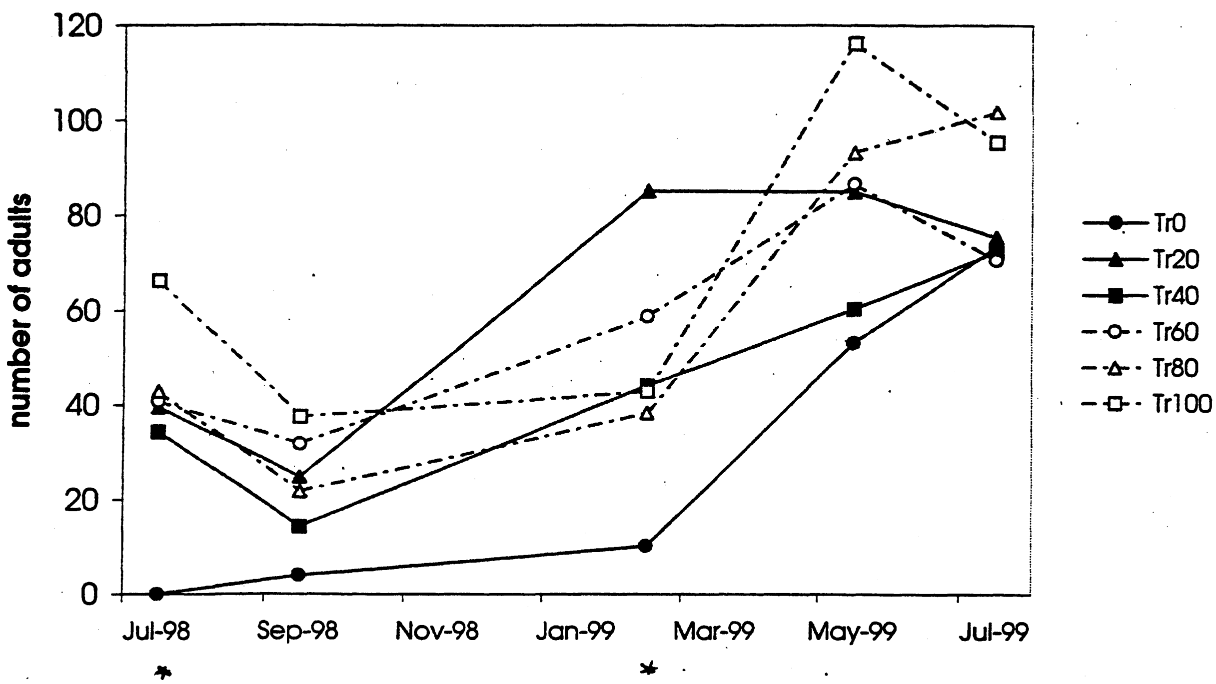
All P values, unless otherwise specified, are from one-way ANOVAs. After the manipulation, the number of adults per plot varied significantly, Tr0 having fewer than all other treatments since all adults had been removed in Tr0 (P<0.001, Figure 8). The statistical significance of this difference disappeared by September. A significant difference reemerged in February (P=0.001) among the treatments resulting from increased differences between Tr0 and all other treatments (P<0.03 for all Bonferroni pair-wise comparisons) with the greatest difference existing between Tr0 and Tr20. These differences in adult densities disappeared again by May. The number of germlings per plot differed among treatments only upon manipulation when they were completely removed in Tr0, causing Tr0 to be significantly less than all other variables (P=0.017, Table 1, Figure 9).

Abundance of ephemeral algae (*Ulva* and *Porphyra*), measured as % cover, never varied significantly among treatments although variation among and within sites was great. A relationship did exist between specific plots and abundance of ephemeral algae. Plots with high *Ulva* subsequently had high *Porphyra* (two-tailed paired t-test, P=0.033) although the presence of the two ephemerals did not coincide (Figs. 10 and 11). There was no significant relationship between treatment and limpet abundance (Figure 12). Littorine abundance only varied with treatment at the last time point (P= 0.02, Figure 13), with significant differences between Tr80 and both Tr60 and Tr0 (Bonferroni Corrected post hoc pairwise comparison, P= 0.046, 0.02).

Site F

The behavior of Tr0 at Site F was significantly different from that of the other five sites. In the weeks following the initial manipulations, there was a very large recruitment bout in the Tr0 at Site F which did not occur in Tr0 plots at Sites A-E (Figure 14). Two weeks after the experiment began the number of adults and germlings in Tr0 at Site F had gone from 0 and 30, to 64 and 98, respectively. At the other sites there was still not more than 1 adult and 6 germlings. A

Number of *Fucus* Adults



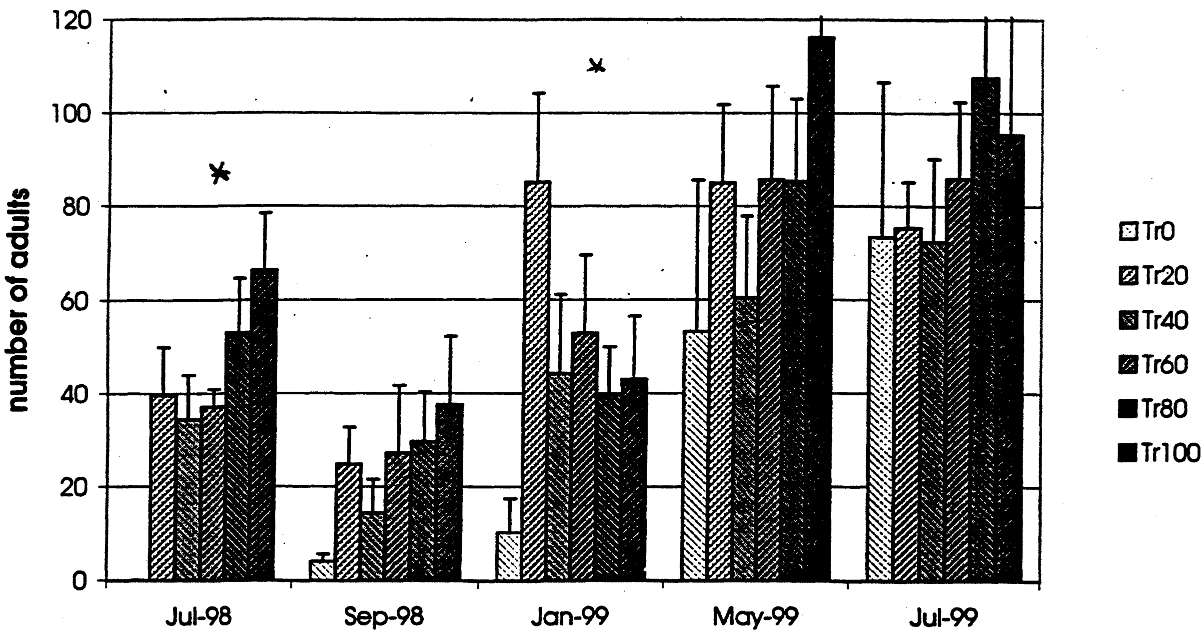
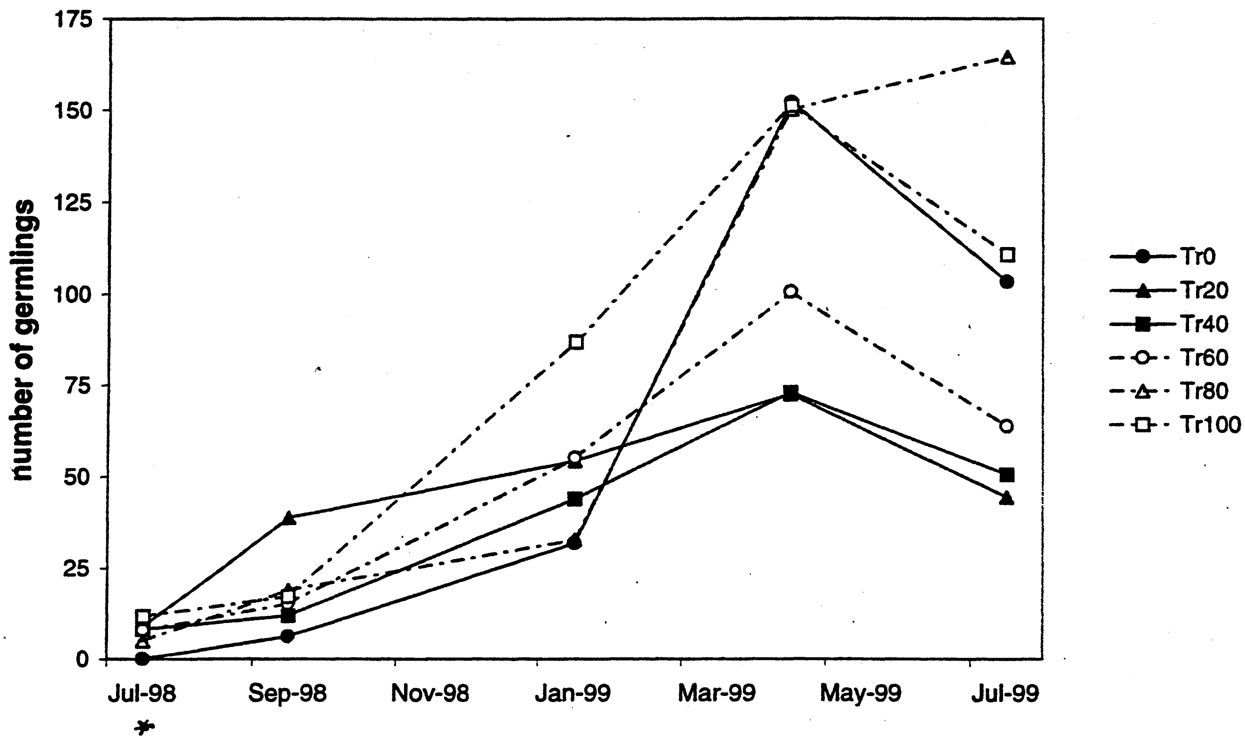


Figure 8. Number of *Fucus* adults by treatment level over time. Error bars equal standard error (n=5). Eror bars not shown on top graph to avoid confusion due to heavy overlap. Significant differences among treatments at a given sampling date denoted with an *.

Number of *Fucus* Germlings



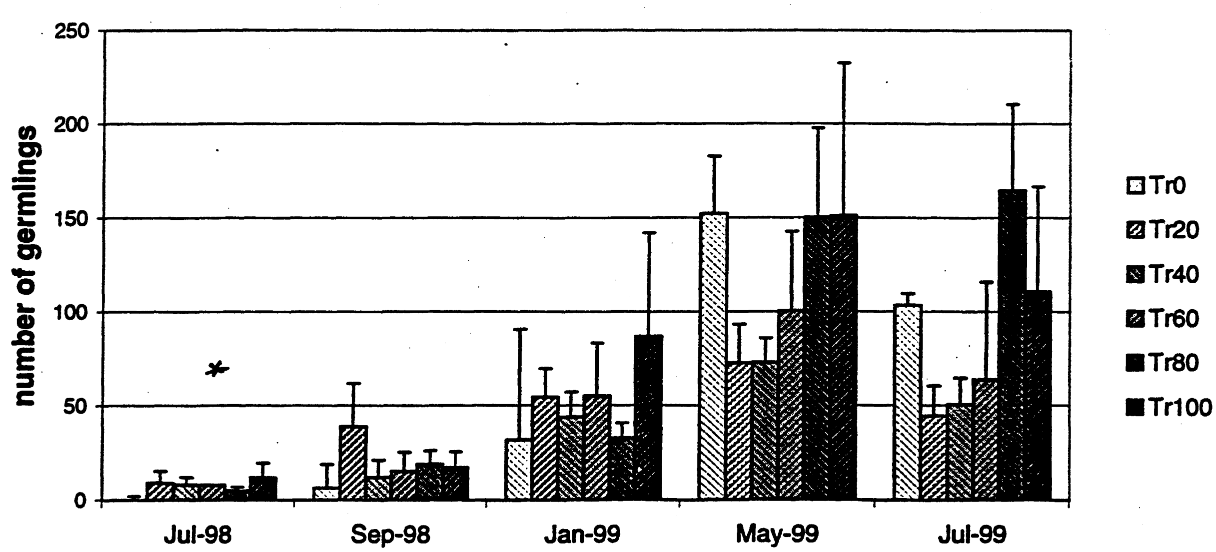


Figure 9. Number of *Fucus* germlings by treatment level over time. Error bars equal standard error (n=5). Significant differences among treatments for a given sampling date denoted with an *.

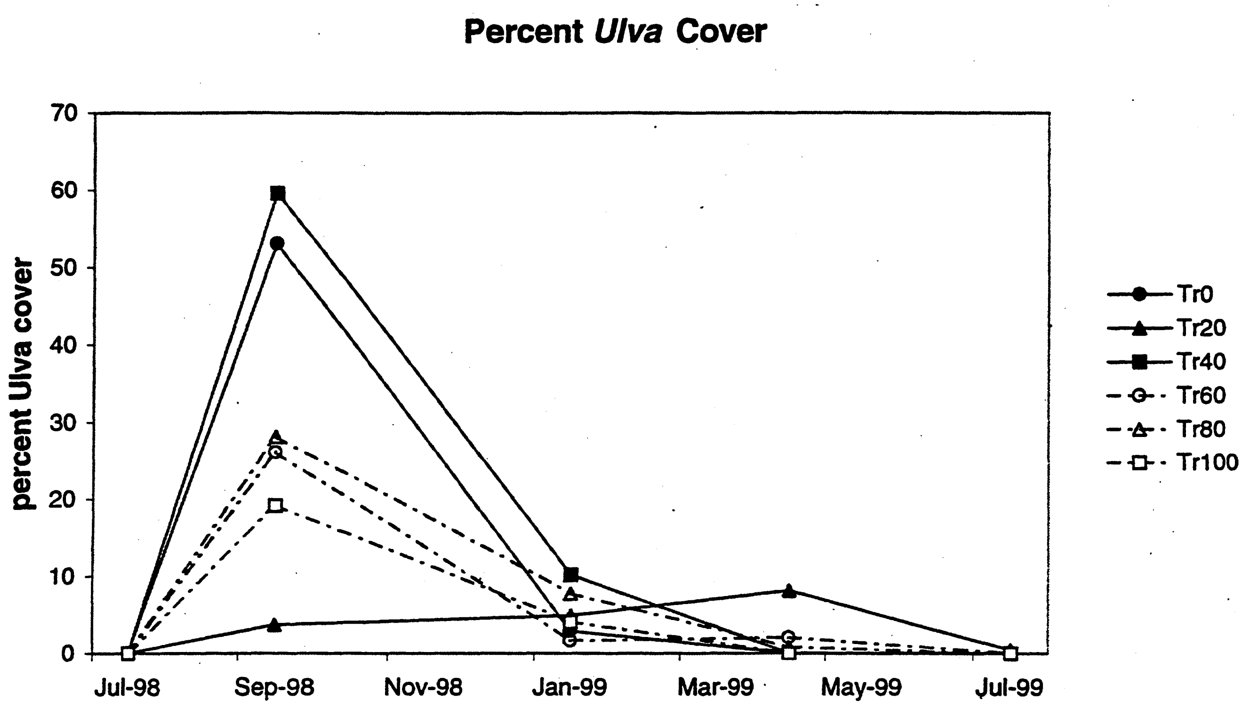


Figure 10. Percent cover of *Ulva* by treatment level over time. Significant differences among treatments for a given sampling date denoted with an"*"(n=5).

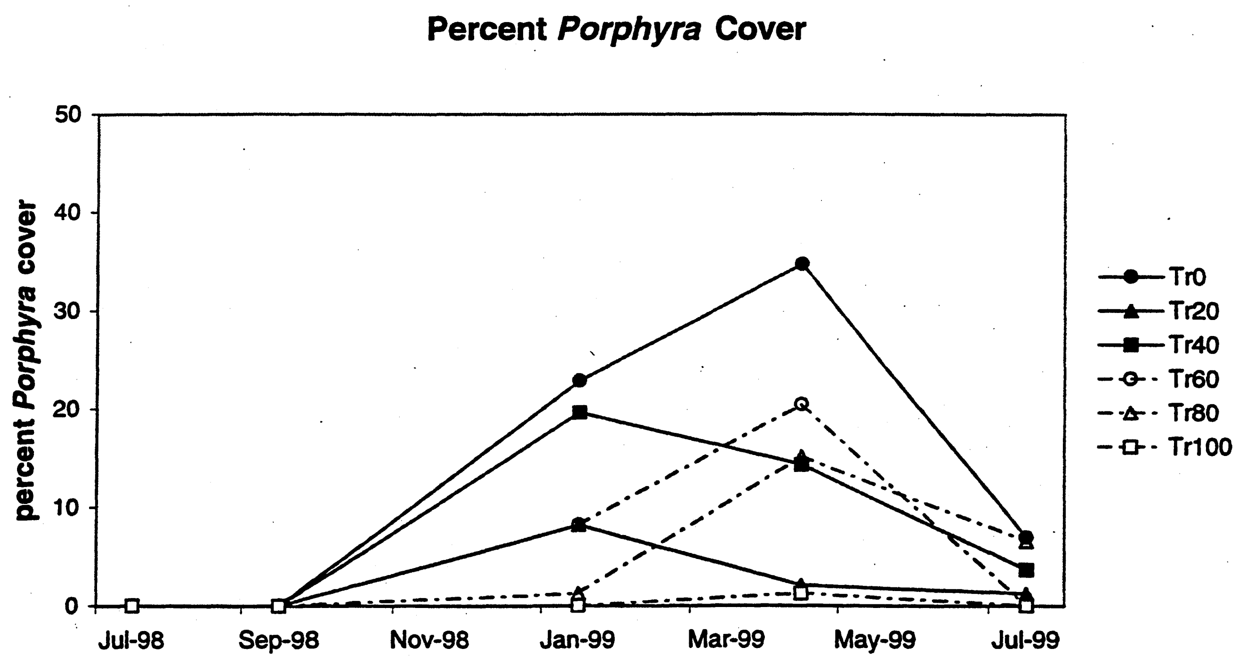
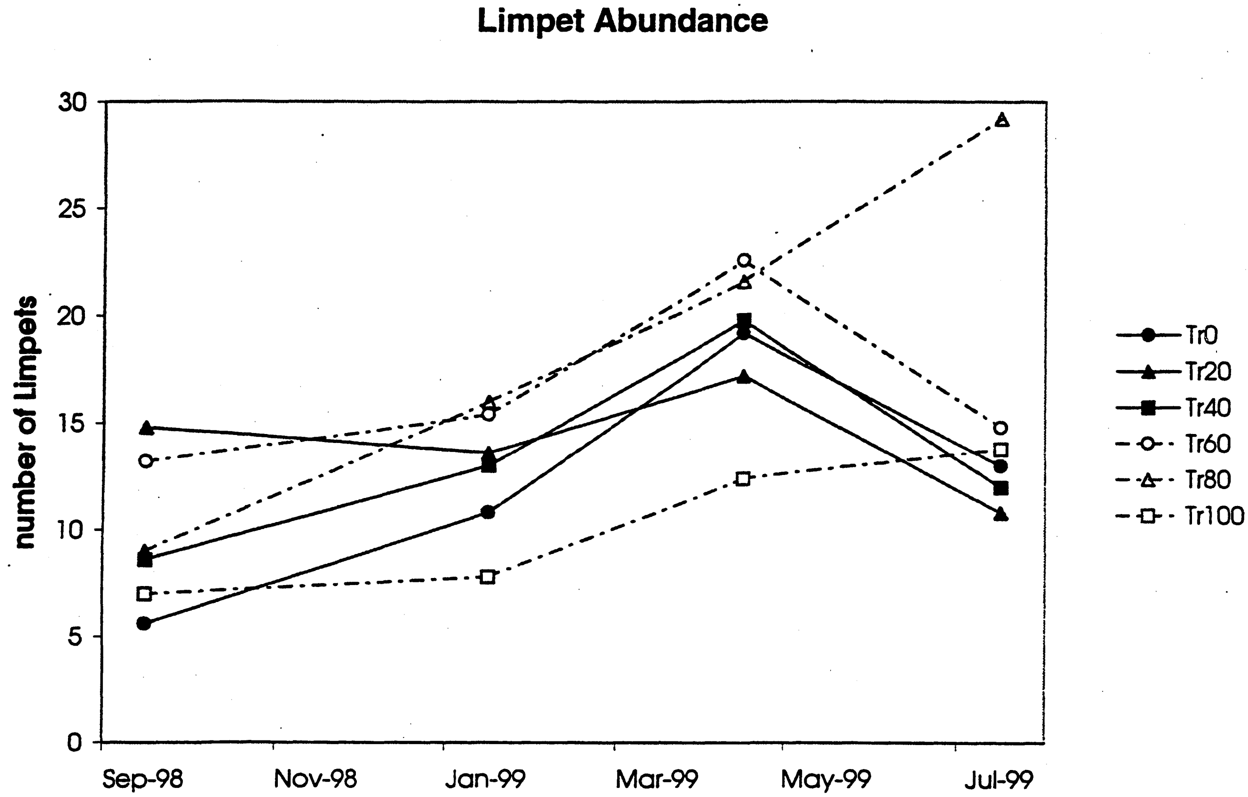


Figure 11. Percent *Porphyra* cover by treatment level over time. Significant differences among treatments for a given sampling date denoted with an"*"(n=5).

Limpet Abundance



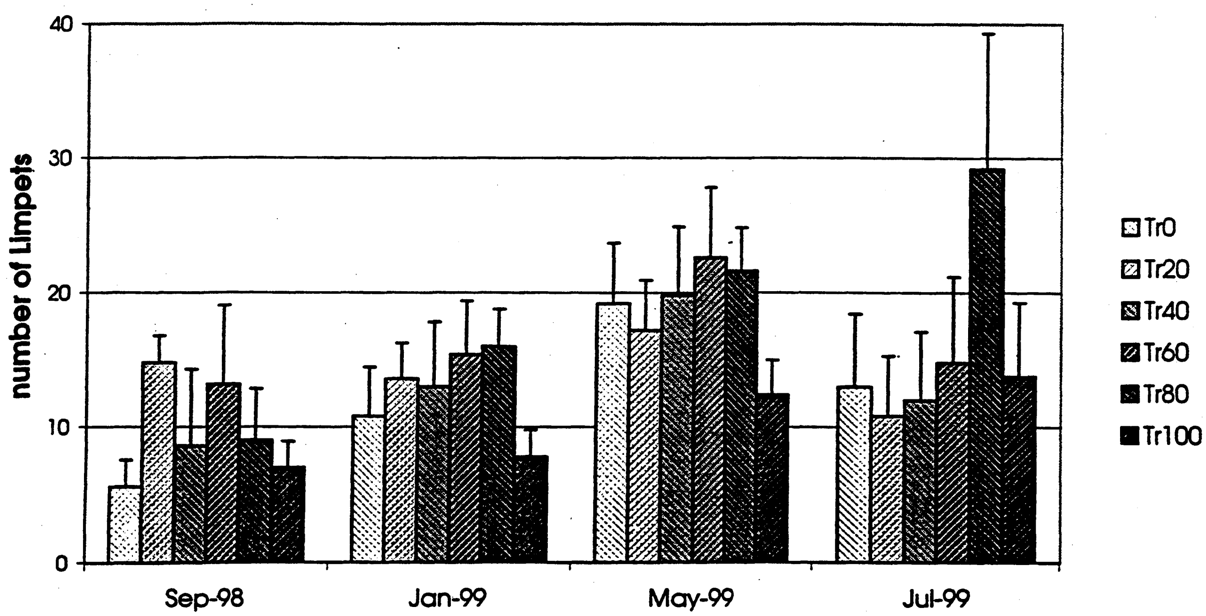


Figure 12. Number of Limpets by treatment level over time. Error bars equal standard error (n=5). Significant differences among treatments for a given sampling date denoted with an "*."

Littorine Abundance

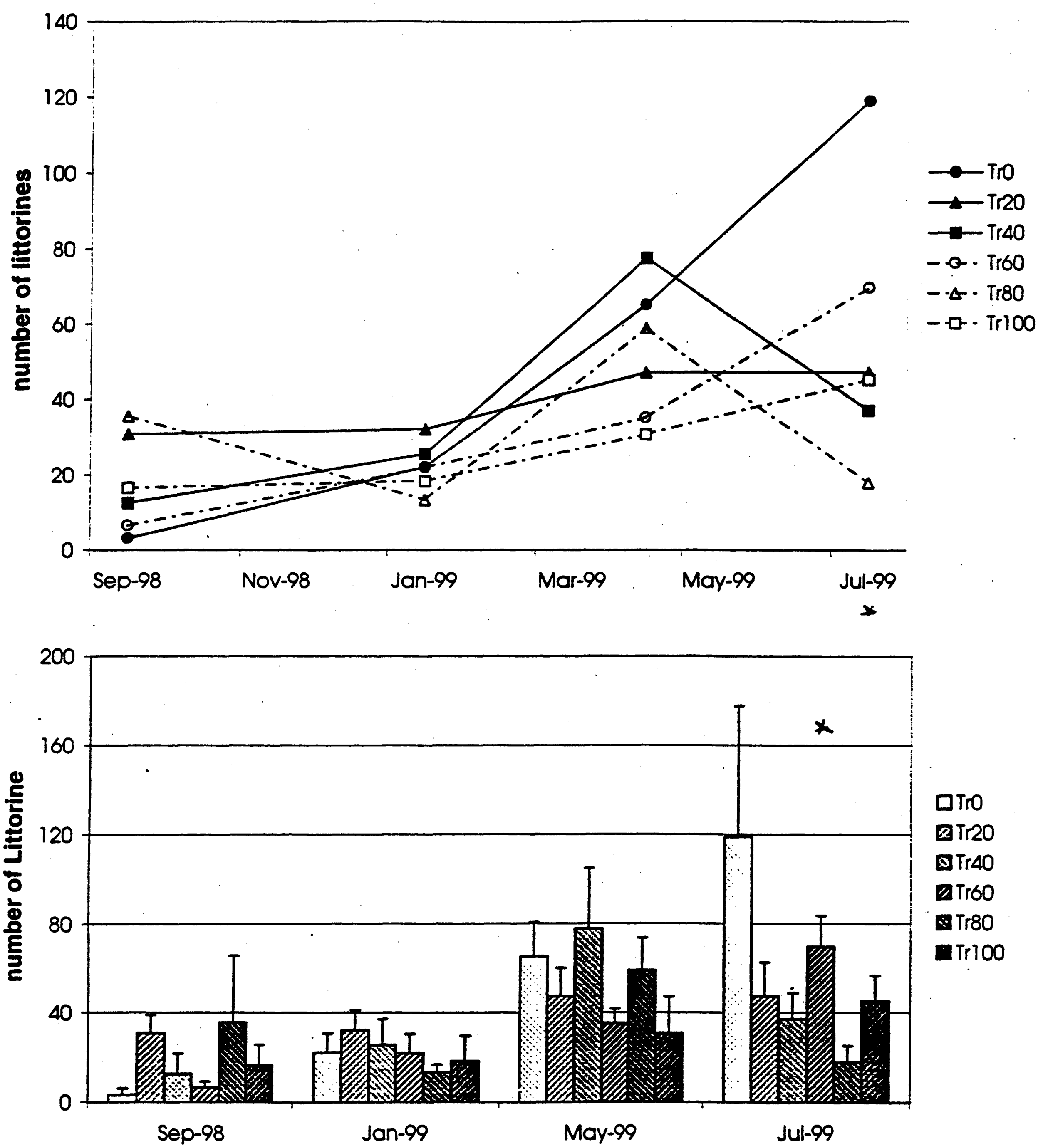


Figure 13. Number of Littorine snails by treatment level over time. Error bars equal standard error (n=5). Significant differences among treatments for a given sampling date denoted with an "*".

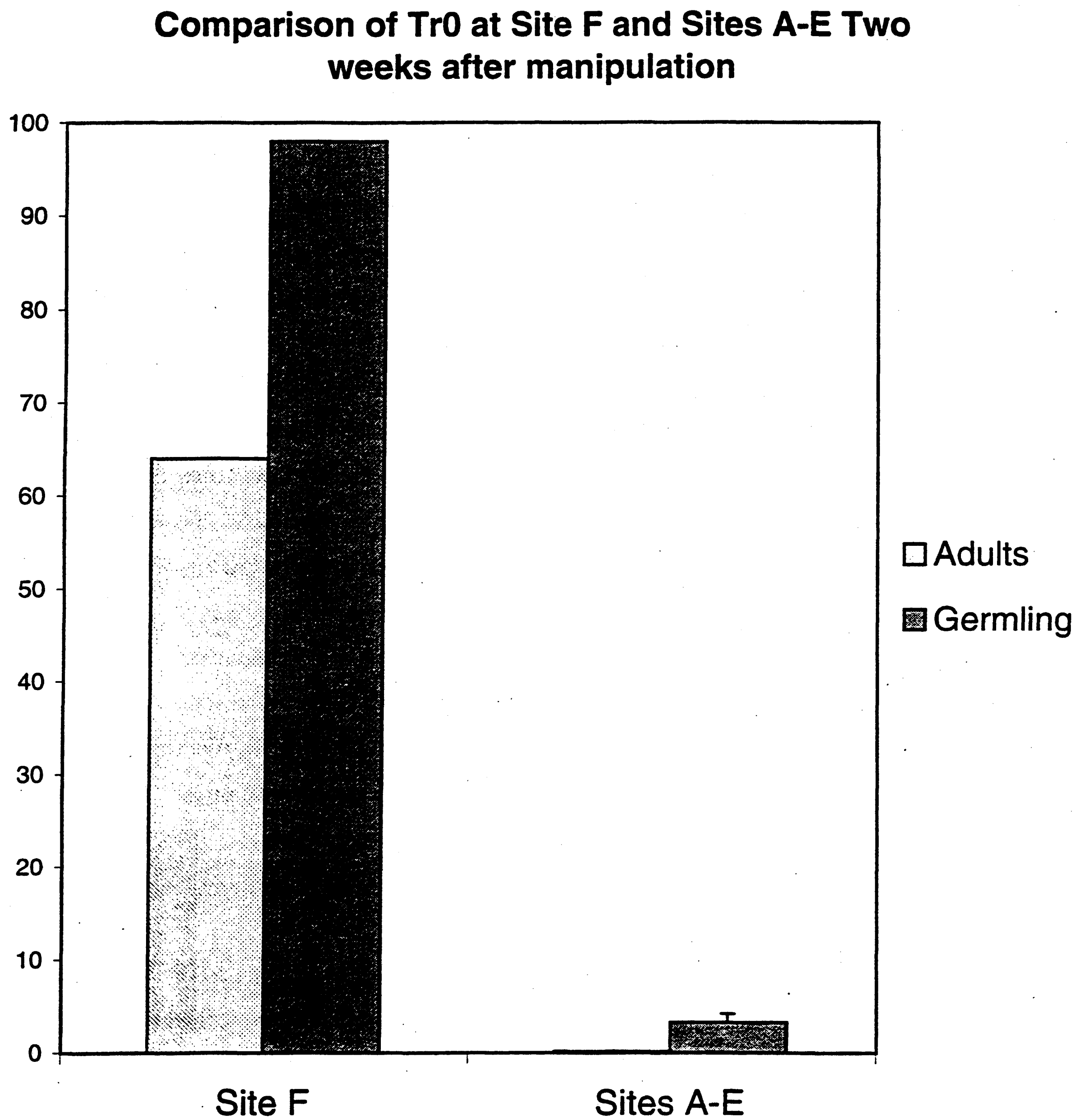


Figure 14: Comparison of the 0% treatment plot (Tr0) at Site F and Sites A-E two weeks after the experimental manipulation showing the difference in the number of Fucus adults and germlings between Site F and the other sites. Error bars equal standard error.

visible difference in the level of cover regeneration followed, while the differences in number of adults and germlings disappeared (Figure 15).

Discussion:

Non-Linear recovery

I found a density threshold for patches of *F. gardneri* below which recovery from disturbance was slowed. The level of recovery in *Fucus* cover one year after removal varied non-linearly with the degree of removal. Although *Fucus* patches recovered quickly from extensive trimming, under some conditions the ability to do so required a minimum density of *Fucus* cover; when the severity of disturbance exceeded this limit regeneration was significantly delayed. In this case the non-linear response to disturbance intensity exhibited a threshold between 20% and 0% *Fucus* cover: after one year the 0% treatment remained significantly lower than the 20% treatment while no other significant differences remained among treatments. Interestingly, such a non-linear response was not observed in the density of adults, germlings or total number of individuals.

The degree of non-linearity in this response seems to be context dependent based on comparisons with Site F and Sun's 1999 study (discussed below), being more intense in locations of higher environmental stress. The findings of this project are interesting for two reasons: both for increasing our understanding of how this particular, dominant species responds to disturbance, and for contributing to our general understanding of ecological interactions.

Comparison to a similar study on Tatoosh

A similar study was conducted by Adrian Sun (during the same year) on the wave-exposed island of Tatoosh which marks the West end of the Puget Sound system where the Strait of Juan de Fuca meets the Pacific ocean. A. Sun performed his manipulation at a later date (mid September). Because of its geographical location, Tatoosh has a much cooler and moister climate than Saddlebag. A. Sun likewise reduced *F. gardneri* cover in increments of 20% in 40cm by 40cm plots, but did not remove the existing macroscopic germlings in the 0% treatments. These two differences, climate and retention of standing germlings, were likely very influential in causing the different outcomes of the two studies.

Only qualitative results are available at this time from the study by Adrian Sun. With respect to *F. gardneri* cover, A. Sun found that all treatments including Tr0 converged and became indistinguishable by early winter (approximately January). There was thus no visible

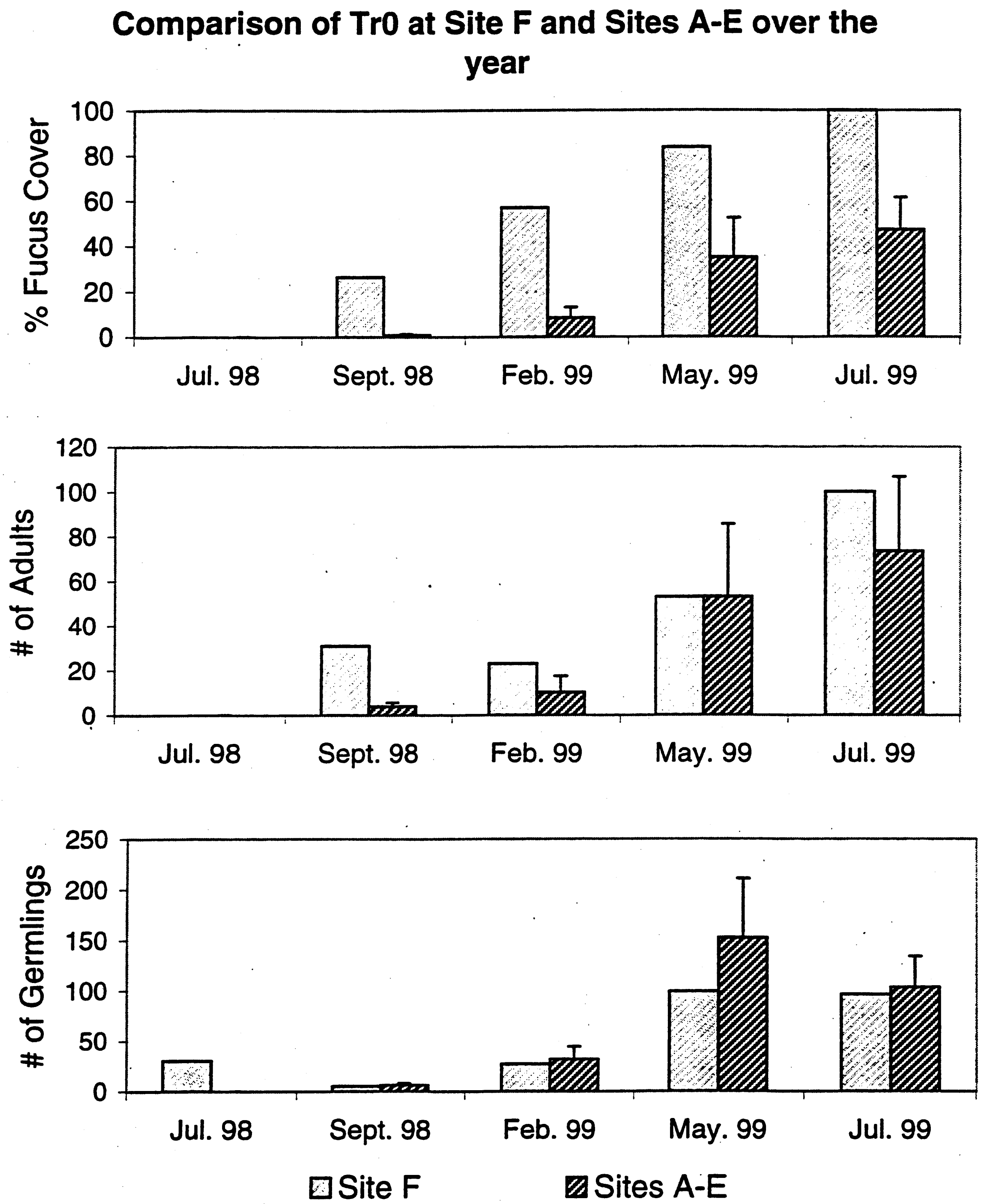


Figure 15: Comparison of the 0% treatment plot (Tr0) at Site F and Sites A-E over the course of one year following the experimental manipulation with respect to: percent Fucus cover, census number of adult and germling Fucus individuals = Error bars equal standard error.

threshold effect observed in the Tatoosh study (personal comment). Though his results cannot be used in direct comparison, they do provide insight into those of this study.

Cause of the non-linear recovery, a hypothetical mechanism

The difference in recovery level one year after the manipulated disturbance clearly shows a threshold between the 20% and 0% treatments. The cause for the delay in the 0% treatment is less clear, confounded by the treatment having two simultaneous effects over the interval in which the threshold appeared. In reducing the cover from 20% to 0% both the last of the cover provided by adults and existing macroscopic germlings were removed. In all other treatments, germlings were left in the plots. Hence, in the 0% treatment germlings first had to be recruited from microscopic individuals. There are thus two explanations, which are not necessarily mutually exclusive, for the delayed recovery of the 0% treatment plots compared to that of the 20% treatment. The first is that the quicker recovery of the 20% treatment was due to the head start (over the 0% treatment) given to them by the retention of the macroscopic germlings. The second explanation is that *Fucus* cover is important in ameliorating the microclimate for microrecruits, and without cover the growth of these individuals to macroscopic size was delayed. The rapid appearance of macroscopic germlings at Site F (130+ new individuals in two weeks time) shows that the delay observed at Sites A-E cannot be explained purely as the consequence of an inherently constrained growth rate of the microrecruits. The significantly cooler rock temperatures at Site F suggest that rock surface temperature may have been the factor driving the observed threshold.

The differential recovery of Tr20 and Tr0 was probably a consequence of both effects of the manipulation: removing the germlings and decreasing the *Fucus* cover below the threshold density necessary for sufficient ameliorating effects. Had the macroscopic germling been left, recovery would likely have been much more swift, as in the Tr20. Retention of germlings provides not only a head start in the recovery process, but also reduces the negative consequences of greater heat stress following severe reduction in *Fucus* cover. The ability of *F. gardneri* to endure heat and desiccation stress apparently increases with size making germlings less dependent on sheltering cover than microrecruits (Highsmith et al. 1993). When macroscopic germlings were left (Tatoosh and Site F) recovery of the Tr0 plots were much faster, converging with the other treatments by winter. Retaining established macroscopic germlings thus appears to significantly accelerate recovery. Both of these sites were also cooler, which could also have facilitated the recovery.

While retention of macroscopic germlings may explain, at least in part, the quick recovery at Site F and on Tatoosh, their removal is insufficient to explain the lag of Tr0 at the five sites (A-E) on Saddlebag. Tr0 at Site F showed that a large and rapid increase in germling abundance can occur if the conditions are right: 130 macroscopic germlings appeared during the first two week period. If over 130 microscopic individuals were capable of growing to macroscopic size or even larger in a mere two weeks, then one must explain why such recruitment of germlings did not occur in the other sites. The delay in the other sites was thus clearly not due to an inherently slow rate of recruitment of microscopic individuals. Assuming the other Tr0 plots had a similar number of microrecruits, the conditions must have been wrong in the other five sites for such a major recruitment; the growth of microrecruits must have been suppressed. The failure of large-scale recruitment at the other sites following the removal of all adults and macroscopic germlings strongly suggests the importance of existing cover to the quick recruitment of germlings.

Several other studies suggest that *F. gardneri* cover plays an important role in ameliorating heat and desiccation stress during daytime low tides (Ang 1991, Ang and De Wreede 1992, Highsmith et al. 1993, Fukuyama et al. 1998). Physiological study of a related genus suggest *Fucus* eggs may have a temperature tolerance below that of bare rock on Saddlebag's rocky shore; the eggs of *Halidrys*, another genera in the Fucales family, will not germinate in temperatures above 20° C (Lee, 1989). If *F. gardneri* has a similar temperature threshold for germination, then the absence of *Fucus* cover would explain the suppressed rate of recruitment. Even in mid-August the temperature of bare rock reached 26.6° C by early afternoon whereas it lingered around 20.2° C under thick *Fucus* cover. Thus the threshold density necessary for quick recovery may stem from a physiological threshold tolerance for heat stress and be regulated at a given site by the degree of physical stress.

Implications for oil spill cleanup

Knowing that the recovery of *Fucus* is relatively rapid above a threshold density, as well as the site-specific density of the threshold, is relevant to management decisions made in the event of an oil spill. The possibility of a sizable spill occurring in Padilla Bay is a real concern given the active use of the Anacortes refineries. Given the proximity of the refineries, sitting directly across from the southern shores of Saddlebag Island in good view, and oil tankers passing within 600 meters of the island (ships pass between Saddlebag and Huckleberry Islands) there is a high probability that in the event of a spill oil would reach the shores of Saddlebag, as well as those of the other neighboring islands, should containment efforts failed. Given the degree to which *Fucus* dominates the mid and upper rocky intertidal in Padilla Bay, it would undoubtedly be heavily oiled if oil reached such rocky shores. In the Exxon Valdez spill *F. gardneri* was severely impacted by oil (Highsmith et al. 1993, Paine et al. 1996).

In light of this project and the lessons learned from studies of past spills, manual removal of oiled mats of *Fucus* may be an effective and ecologically sound way to clean spilt oil from rocky shores. Reaction to past spills has shown that public demand for action is frequently very high (Raffaelli and Hawkins 1996, Paine et al. 1996). Without a more sound alternative such pressures to "do something" have driven cleanup crews to use oil removal methods such as high pressure hot water washing, even though the methods exacerbated the ecological damage (Fukuyama et al. 1998, and see references in Paine et al. 1996).

High intensity cleanup efforts causing the complete removal of intertidal organisms and sterilizing the substratum should be avoided as they can cause *Fucus* to return in an even age structure in turn leading to subsequent boom-bust cycles which may linger for up to a decade (Raffaelli and Hawkins 1996, Driskell et al. unpublished). Raffaelli and Hawkins (1996) suggest that when such techniques are used, recovery may take 10 to 15 years depending on the organisms. High pressure washing is particularly damaging to *Fucus*, removing the organisms along with the oil and sterilizing the rocks, and is generally unadvisable (Highsmith et al. 1993, Paine et al. 1996, Fukuyama et al. 1998).

Using methods of removing oil from rocky shores with less impact on intertidal communities thus seem a preferable alternative. Indeed the American Petroleum Institute recommends "natural cleansing" as the preferred method. Yet particular circumstances and public pressure for some form of visible action may mandate some cleanup operation be taken after a spill. Alternative methods must therefore be found. After an intensive study on the effects of the 1989 Valdez spill, Highsmith et al. (1993) recommended use of "low to moderate intensity treatment methods to remove the thickest mats of oil while still leaving as much of the intertidal community intact as possible". Manual removal of oiled *Fucus*, through cutting or raking, meets this recommendation and promises to be effective. Oil will settle on exposed surfaces of *Fucus* and heavy *Fucus* cover can "effectively shield the underlying biota and substrate from heavy exposure" (Fukuyama et al. 1998) The NOAA team examined the feasibility of "harvesting" *F, gardneri* as a cleanup method in the Northeastern Pacific. While the study found that large-scale cutting of *Fucus* offered a "fairly rapid oil removal with little need for specialized equipment", they did not recommend it for stands of *Fucus gardneri* on the basis of the "limited regenerative capabilities" of the species.

The findings of my study contradict this conclusion since recovery was swift from all but complete removal. The cause of our different findings is unclear, the memorandum giving few details. Given the rapid rate of recovery of *F. gardneri* that I found, even on relatively physically stressful Saddlebag Island, manual trimming seems a viable alternative method. Another option for manual removal may be raking. Raking should primarily remove the larger adult plants that are heavily oiled while leaving small adults, macroscopic germlings and the microrecruit bank intact. Leaving patches of less oiled *Fucus* untouched, to serve as sources of propagules, would further increase the likelihood of quick regeneration. A more costly additional step would be to deploy coarsely woven fabric mats in the upper intertidal to ameliorate the microclimate by increasing moisture retention and decreasing solar radiation (Stekoll and Deysher 1996, cited in Fukuyama et al. 1998).

General importance of thresholds to ecology and disturbance studies

This study adds further evidence that ecological interactions at the population level may be non-linear and can exhibit thresholds, in this case resulting in part from physiological thresholds to environmental variables (e.g. heat stress). Thresholds in ecological interactions at the population and community level are importance since they mark a sudden, sharp change in the response to a slight change in the driving factor. In other words, crossing a threshold elicits a strongly disproportional response. Non-linear dynamics have important ramifications for conservation and management plans at higher levels of ecological organization. For example, visibly healthy populations or communities, if on a threshold may be dramatically altered by even slight perturbations.

Thresholds at lower levels of ecological organization, such as autecology or physiological ecology, are very well established and widely recognized. Mammals have very specific temperature thresholds above or below which they quickly die. Plants frequently have a threshold tolerance to drought, beyond which they quickly wither. Yet although non-linear dynamics and thresholds were extended to interactions between individuals and even species in the seventies, and set on firm ground both experimentally and theoretically (Lubchenco 1978, Huston 1979, Menge and Sutherland 1987) such higher level ecological interactions are still often implicitly assumed to be linear (Ruesink 1998). This assumption of linearity is often seen in disturbance studies, which frequently utilize a control/ impact design. The present study strongly suggests not only that the response of *F. gardneri* to a pulse disturbance can vary non-linearly with the intensity of the disturbance, but that this disturbance threshold is the manifestation of a physiological threshold being expressed in population level dynamics. Although such a physiological threshold is likely relatively constant within a species, its manifestation in the response of a population to disturbance may be dependent on the physical environment. In other words the density at which the disturbance threshold occurs and the intensity of the non-linear response may vary with location according to the degree of physical stress. The greater level of recovery of *F. gardneri* at Site F and on Tatoosh compared to Sites A-E support this view of a context dependent disturbance threshold.

While further, refined comparative studies are required, the results of this study in combination with the independent work of Sun (unpublished), suggest that the strength of *F. gardneri's* non-linear response to disturbance varies predictably with environmental stress. Understanding and predicting how interactions change from place to place is arguably the most pressing challenge facing ecologists and managers alike. This understanding is fundamental to creating meaningful general ecological models of community and ecosystem dynamics. Only by understanding the way mechanisms vary spatially and temporally can one devise management plans and conservation solutions that are not restricted to specific locations.

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Appendix 1. Monitoring schedual showing all trip dates and which trips used in analyses:

	Week	Trip dates:	Notes:
*	w0	Jul. 8, 1998	-Initial measurements taken and manipulation performed
	w2	Jul. 28, 1998	
	w4	Aug. 13, 1998	-Highest and Lowest plots in each site relocated
	w6	Aug. 25, 1998	-One site monitored at night (C)
*	w10	Sep. 23, 1998	-Monitoring at night begins
	w16	Jun. 11, 1998	-Incomplete: Site E and F not sampled
	w22	Dec. 16, 1998	
*	w28	Jan. 30, 1999	
	w36	Apr. 12, 1999	-Incomplete: Site E, no littorine or limpet data at Site D
*	w42	May 1, 1999	
	w48	Jun. 19, 1999	
*	w52	Jul. 11, 1999	

* denotes a trip used in analysis

Appendix 2. Specification of treatments relocated at each site four weeks after initial manipulation:

Site:	Treatments relocated:
A	Tr0, Tr20
B	Tr20, Tr40, Tr100
C	Tr0, Tr60
D	Tr40, Tr60
E	Tr0, Tr20
F	Tr60, Tr80

Appendix 3. Desiccation Rates (taken on August 25, 1999):

Site	% Cover level	start	finish	Initial Weight (grams)	Inter-mediate (grams)	Final Weight (grams)	total loss (grams)	time elapsed (hrs)	Desicca-tion rate (grams/hr)
E	0	7:35	13:15	55	45	39	16	5:40	2.82
A	0	7:50	13:20	38	26	20.5	17	5:30	3.09
B	0	8:10	13:40	47	45	40	7	5:30	1.27
C	0	9:00	14:10	50	42	38	12	5:10	2.32
D	0	9:25	14:30	56	46	41	15	5:05	2.95
E	50	7:35	13:15	45	40	34	11	5:40	1.94
A	50	7:50	13:20	37	36	32	5	5:30	0.91
B	50	8:10	13:40	52	50	45	7	5:30	1.27
C	50	9:00	14:10	45	36	29	16	5:10	3.10
D	50	9:25	14:30	56	47	46	10	5:05	1.97
E	100	7:35	13:15	34	33	30.5	3	5:40	0.53
A	100	7:50	13:20	50	45	43	7	5:30	1.27
B	100	8:10	13:40	45	45	43	2	5:30	0.36
C	100	9:00	14:10	55	51	51	4	5:10	0.77
D	100	9:25	14:30	55	50	47	8	5:05	1.57
F	100	9:45	14:45	55	50	47	8	5:00	1.60
F	50	9:45	14:45	56	50	46	10	5:00	2.00
F	0	9:45	14:45	57	53	46	11	5:00	2.20

Mean Desiccation Rates (in grams of water lost/hour):

Treatment	Mean	St. Dev
0%	2.49	0.74
50%	1.84	0.84
100%	0.90	0.51

Appendix 4: Raw data

Percent *Fucus* cover:

Date: (mm/dd/yr)	Week	Treatment	Site A	Site B	Site C	Site D	Site E	Site F
07/08/98	0	Tr0	0	0	0	0	0	0
07/08/98	0	Tr20	14	24	24	24	24	24
07/08/98	0	Tr40	49	47	47	39	43	35
07/08/98	0	Tr60	55	71	61	67	61	65
07/08/98	0	Tr80	73	86	82	84	84	80
07/08/98	0	Tr100	100	100	98	96	100	98
09/23/98	10	Tr0	0	0	2	2	0	27
09/23/98	10	Tr20	10	10	14	20	4	20
09/23/98	10	Tr40	24	6	27	10	35	43
09/23/98	10	Tr60	86	12	22	22	20	61
09/23/98	10	Tr80	27	35	45	51	24	100
09/23/98	10	Tr100	86	61	96	51	76	12
01/30/99	28	Tr0	27	6	2	2	6	57
01/30/99	28	Tr20	65	49	100	39	41	24
01/30/99	28	Tr40	59	6	20	16	49	63
01/30/99	28	Tr60	78	10	59	39	35	49
01/30/99	28	Tr80	29	4	24	35	71	96
01/30/99	28	Tr100	69	37	27	47	80	27
05/01/99	42	Tr0	100	33	4	33	6	84
05/01/99	42	Tr20	100	88	100	96	92	43
05/01/99	42	Tr40	100	10	82	86	20	94
05/01/99	42	Tr60	98	16	98	78	88	90
05/01/99	42	Tr80	98	35	76	82	61	96
05/01/99	42	Tr100	84	100	45	100	78	76
07/11/99	52	Tr0	100	53	29	33	22	100
07/11/99	52	Tr20	100	94	100	84	98	90
07/11/99	52	Tr40	100	31	100	92	84	71
07/11/99	52	Tr60	100	51	100	71	84	98
07/11/99	52	Tr80	94	86	100	96	86	96
07/11/99	52	Tr100	88	100	84	100	94	98

Number of *Fucus* Adults (individuals > 1cm):

Date: (mm/dd/yr)	Week	Treatment	Site A	Site B	Site C	Site D	Site E	Site F
07/08/98	pretreatment	Tr0	33	7	39	9	33	67
07/08/98	0	Tr0	0	0	0	0	0	0
07/08/98	0	Tr20	34	20	26	79	39	49
07/08/98	0	Tr40	20	18	20	49	65	29
07/08/98	0	Tr60	50	34	49	32	39	19
07/08/98	0	Tr80	38	17	35	38	87	103
07/08/98	0	Tr100	110	52	44	51	75	50
09/23/98	10	Tr0	7	1	4	8	0	31
09/23/98	10	Tr20	34	11	50	23	6	51
09/23/98	10	Tr40	17	5	8	1	41	26
09/23/98	10	Tr60	85	1	38	19	16	17
09/23/98	10	Tr80	5	1	17	25	61	117
09/23/98	10	Tr100	76	15	3	26	68	11
01/30/99	28	Tr0	39	6	4	1	1	23
01/30/99	28	Tr20	122	36	137	63	68	12
01/30/99	28	Tr40	107	6	35	45	28	32
01/30/99	28	Tr60	79	3	104	54	54	23
01/30/99	28	Tr80	69	9	24	46	44	46
01/30/99	28	Tr100	30	29	19	95	42	8
05/01/99	42	Tr0	180	42	19	24	1	53
05/01/99	42	Tr20	42	60	128	120	75	59
05/01/99	42	Tr40	124	25	67	52	34	81
05/01/99	42	Tr60	54	65	163	60	91	81
05/01/99	42	Tr80	119	58	136	108	45	46
05/01/99	42	Tr100	35	303	29	171	43	244
07/11/99	52	Tr0	195	90	47	18	17	100
07/11/99	52	Tr20	77	45	90	101	64	58
07/11/99	52	Tr40	98	39	130	49	46	60
07/11/99	52	Tr60	43	85	129	42	54	123
07/11/99	52	Tr80	51	74	125	193	66	32
07/11/99	52	Tr100	70	219	37	117	34	240

Number of *Fucus* germlings (individuals <1cm):

Date: (mm/dd/yr)	Week	Treatment	Site A	Site B	Site C	Site D	Site E	Site F
07/08/98	pretreatment	Tr0	11	3	1	6	3	30
07/08/98	0	Tr0	0	0	0	0	0	30
07/08/98	0	Tr20	34	3	5	1	2	3
07/08/98	0	Tr40	15	1	1	4	20	4
07/08/98	0	Tr60	12	1	16	0	11	1
07/08/98	0	Tr80	7	2	3	11	2	12
07/08/98	0	Tr100	42	3	1	2	11	3
09/23/98	10	Tr0	12	8	4	6	1	5
09/23/98	10	Tr20	45	9	126	8	6	4
09/23/98	10	Tr40	48	0	5	1	6	6
09/23/98	10	Tr60	27	0	22	24	3	11
09/23/98	10	Tr80	22	4	11	45	13	51
09/23/98	10	Tr100	49	7	3	13	14	7
01/30/99	28	Tr0	64	26	58	11	0	27
01/30/99	28	Tr20	56	22	45	111	38	15
01/30/99	28	Tr40	79	3	65	41	32	62
01/30/99	28	Tr60	35	33	121	48	39	48
01/30/99	28	Tr80	33	60	34	12	25	42
01/30/99	28	Tr100	24	297	14	96	4	153
05/01/99	42	Tr0	348	105	48	221	39	99
05/01/99	42	Tr20	120	32	21	118	72	64
05/01/99	42	Tr40	112	53	94	46	60	104
05/01/99	42	Tr60	27	170	101	88	117	228
05/01/99	42	Tr80	56	119	196	313	67	71
05/01/99	42	Tr100	461	92	42	154	7	271
07/11/99	52	Tr0	136	45	39	203	94	96
07/11/99	52	Tr20	21	23	13	94	71	18
07/11/99	52	Tr40	27	21	51	54	100	84
07/11/99	52	Tr60	29	104	34	81	71	69
07/11/99	52	Tr80	191	70	52	297	213	112
07/11/99	52	Tr100	327	33	82	92	20	100

Percent *Ulva* cover:

Date: (mm/dd/yr)	Week	Treatment	Site A	Site B	Site C	Site D	Site E	Site F
09/23/98	10	Tr0	0	90	65	39	71	96
09/23/98	10	Tr20	0	0	0	18	0	98
09/23/98	10	Tr40	0	100	98	0	100	22
09/23/98	10	Tr60	0	100	29	0	2	14
09/23/98	10	Tr80	0	100	41	0	0	49
09/23/98	10	Tr100	0	96	0	0	0	98
01/30/99	28	Tr0	0	2	8	4	0	2
01/30/99	28	Tr20	0	0	0	24	0	0
01/30/99	28	Tr40	0	49	2	0	0	0
01/30/99	28	Tr60	0	6	0	0	2	0
01/30/99	28	Tr80	0	37	0	2	0	0
01/30/99	28	Tr100	0	12	0	8	0	55
05/01/99	42	Tr0	0	0	0	0	0	37
05/01/99	42	Tr20	0	0	0	41	0	0
05/01/99	42	Tr40	0	0	0	0	0	0
05/01/99	42	Tr60	0	8	0	0	2	0
05/01/99	42	Tr80	0	0	2	0	2	0
05/01/99	42	Tr100	0	0	0	0	0	24
07/11/99	52	Tr0	0	0	0	0	0	10
07/11/99	52	Tr20	0	0	0	2	0	8
07/11/99	52	Tr40	0	0	0	0	0	0
07/11/99	52	Tr60	0	0	0	0	0	0
07/11/99	52	Tr80	0	0	0	0	0	6
07/11/99	52	Tr100	0	0	0	0	0	0

Percent *Porphyra* cover:

Date: (mm/dd/yr)	Week	Treatment	Site A	Site B	Site C	Site D	Site E	Site F
01/30/99	28	Tr0	0	27	0	20	67	0
01/30/99	28	Tr20	6	0	0	2	33	0
01/30/99	28	Tr40	0	0	0	51	47	0
01/30/99	28	Tr60	0	41	0	0	0	0
01/30/99	28	Tr80	0	6	0	0	0	0
01/30/99	28	Tr100	0	0	0	0	0	0
05/01/99	42	Tr0	0	39	0	82	53	0
05/01/99	42	Tr20	0	0	0	4	6	0
05/01/99	42	Tr40	0	4	0	27	41	0
05/01/99	42	Tr60	0	98	0	0	4	0
05/01/99	42	Tr80	0	69	4	0	2	0
05/01/99	42	Tr100	0	6	0	0	0	0
07/11/99	52	Tr0	0	0	0	27	8	0
07/11/99	52	Tr20	4	0	0	2	0	0
07/11/99	52	Tr40	0	0	0	0	18	0
07/11/99	52	Tr60	0	0	0	0	0	0
07/11/99	52	Tr80	0	29	0	0	4	0
07/11/99	52	Tr100	0	0	0	0	0	0

Number of Littorines:

Date: (mm/dd/yr)	Week	Treatment	Site A	Site B	Site C	Site D	Site E	Site F
09/23/98	10	Tr0	15	0	0	0	1	0
09/23/98	10	Tr20	0	36	46	31	41	0
09/23/98	10	Tr40	3	1	11	48	0	0
09/23/98	10	Tr60	8	0	7	15	3	0
09/23/98	10	Tr80	15	0	1	155	7	3
09/23/98	10	Tr100	3	1	2	35	42	0
01/30/99	28	Tr0	26	10	54	13	8	0
01/30/99	28	Tr20	13	49	47	8	44	1
01/30/99	28	Tr40	18	5	67	33	5	20
01/30/99	28	Tr60	16	1	41	43	9	7
01/30/99	28	Tr80	4	19	22	7	15	2
01/30/99	28	Tr100	1	2	2	29	58	0
05/01/99	42	Tr0	31	96	49	42	108	1
05/01/99	42	Tr20	10	79	65	25	57	2
05/01/99	42	Tr40	16	170	99	35	68	88
05/01/99	42	Tr60	38	17	37	56	28	38
05/01/99	42	Tr80	28	81	80	87	19	3
05/01/99	42	Tr100	0	13	35	14	92	3
07/11/99	52	Tr0	45	345	83	16	106	0
07/11/99	52	Tr20	46	100	55	11	25	2
07/11/99	52	Tr40	28	37	82	21	18	71
07/11/99	52	Tr60	30	73	48	100	98	11
07/11/99	52	Tr80	6	15	14	9	46	0
07/11/99	52	Tr100	19	66	21	75	46	11

Number of Limpets:

Date: (mm/dd/yr)	Week	Treatment	Site A	Site B	Site C	Site D	Site E	Site F
09/23/98	10	Tr0	10	3	0	10	5	0
09/23/98	10	Tr20	18	13	11	11	21	0
09/23/98	10	Tr40	30	0	2	11	0	17
09/23/98	10	Tr60	24	0	4	8	30	3
09/23/98	10	Tr80	13	0	6	4	22	0
09/23/98	10	Tr100	2	3	9	12	9	0
01/30/99	28	Tr0	24	3	6	13	8	2
01/30/99	28	Tr20	9	16	7	14	22	10
01/30/99	28	Tr40	26	2	8	23	6	13
01/30/99	28	Tr60	10	18	9	10	30	4
01/30/99	28	Tr80	21	8	23	16	12	1
01/30/99	28	Tr100	2	8	11	13	5	2
05/01/99	42	Tr0	10	34	14	13	25	6
05/01/99	42	Tr20	20	15	4	21	26	16
05/01/99	42	Tr40	17	11	38	23	10	23
05/01/99	42	Tr60	12	17	14	38	32	24
05/01/99	42	Tr80	16	25	32	21	14	2
05/01/99	42	Tr100	7	19	18	11	7	8
07/11/99	52	Tr0	18	32	7	4	4	0
07/11/99	52	Tr20	0	12	1	22	19	14
07/11/99	52	Tr40	3	3	24	25	5	21
07/11/99	52	Tr60	5	3	7	36	23	11
07/11/99	52	Tr80	66	34	21	8	17	0
07/11/99	52	Tr100	7	3	29	5	25	21