

EXPERIMENTAL HARVESTS OF MACROALGAE ALONG THE OREGON COAST
WITH AN ANALYSIS OF ASSOCIATED EPIPHYTIC DIATOM COMMUNITIES

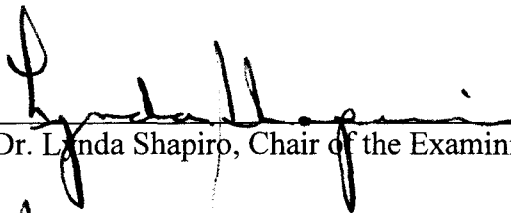
by
JOHN J. YOUNG

A THESIS

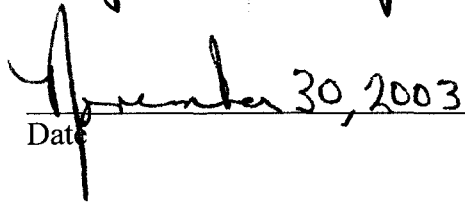
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“Experimental Harvests of Macroalgae along the Oregon Coast with an Analysis of Associated Epiphytic Diatom Communities,” a thesis prepared by John J. Young in partial fulfillment of the requirements for the Master of Science degree in the Department of Biology. This thesis has been approved and accepted by:



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CHAPTER I

GENERAL INTRODUCTION

Marine algae are harvested commercially worldwide resulting in a multi-billion dollar industry annually (Zemke-White and Ohno 1999). Macrophyte harvesting along the west coast of the United States is included in these figures. Oregon, however, does not permit the commercial harvesting of its algal resources due to a lack of knowledge regarding seaweed recovery. Yet, with the potential for commercial harvest, it is necessary to examine the effects harvesting would have on Oregon's seaweed.

Studies that have experimentally tested the effects of harvesting on macrophyte populations provide the best basis for management plans (Nelson and Conroy 1989; Ang *et al* 1996; Griffen *et al* 1999; Lavery *et al* 1999). Chapter II of this thesis describes various harvest experiments to test the effects of (1) harvesting during different seasons, (2) different harvest amounts and (3) different removal methods on five perennial species of macroalgae. The data from these experiments are used in Chapter III to recommend a management strategy for the tested species. This work will be useful in drafting a management plan for the regulation of seaweed harvest in Oregon.

Chapter IV compares the epiphytic diatom community upon *Mastocarpus papillatus* (C. Agardh) Kützing, one of the species used in the harvest study, over a growing season. Epiphytic diatoms are used as environmental indicators because the

silicified frustules are taxonomically distinct, easily preserved, and variations in community composition track environmental conditions (Christie and Smol 1993). This study provides baseline data on *M. papillatus* epiphytes that will aid in assessing recovery from disturbance events such as harvesting. The chapter also provides basic information on epiphyte diatom communities in the rocky intertidal.

CHAPTER II

EXPERIMENTAL HARVESTS OF FIVE SPECIES OF MACROALGAE
ALONG THE OREGON COAST

Introduction

The harvest of seaweed is a major industry worldwide. Global harvesting of seaweed for use as food products is estimated to value over 3.6 billion US dollars annually (Zemke-White and Ohno 1999). Additionally, the annual estimated value of the production of phycocolloids (i.e., alginates, agar, and carrageenan) from seaweed is 2.6 billion US dollars (Zemke-White and Ohno 1999). These data do not include seaweed harvested for medicinal purposes because accurate figures are difficult to compile. Aquaculture is an important method of producing seaweed resources accounting for 52% of commercial production (Zemke-White and Ohno 1999). The remaining 48% is, therefore, collected from wild stocks. Due to the large scale of world seaweed harvest, studies have experimentally examined the impacts of harvesting activities on macrophyte populations (Nelson and Conroy 1989; Ang *et al* 1996; Griffen *et al* 1999; Lavery *et al* 1999). Based on these studies, management plans have been developed (Westermeier *et al* 1987; Westermeier *et al* 1999; Vásquez and Vega 2001).

The harvesting of marine algae for human use has been recorded before the 14th century in Portugal. This practice began by collecting beach cast seaweed for use as fertilizer. Today, the exploitation of its seaweed in Portugal continues with Portugal being the world's fifth largest agar producer (Santos and Duarte 1991). China, France, U.K., Korea, Japan, and Chile are responsible for 90% of the world's seaweed production.

Comparatively, the US is not a major contributor to world seaweed production (Zemke-White and Ohno 1999). Furthermore, with the exception of *Macrocystis* harvest, the west coast of the US has a negligible production of commercial seaweed (Merrill and Waaland 1998; Zemke-White and Ohno 1999). Most harvesting that does occur on the Pacific Coast of the US is by small cottage industries which take relatively small amounts of seaweed from the wild (Zemke-White and Ohno 1999). Yet, since 1984 the production of commercially important seaweeds has grown by 119% (Zemke-White and Ohno 1999). The increasing value of seaweed as a food and industrial resource makes large-scale harvesting in the Pacific States likely in the near future.

To remove marine algae from the Oregon intertidal zone requires a permit issued by the state. Historically, the issuing of these permits has been rare. Recently the state has, however, received an increase in requests for such permits. Permits are also required to harvest marine algae in the states of Washington, Alaska, and California. With the potential for a growing industry of seaweed harvest in Oregon, it is necessary to examine the effects harvesting will have on wild stocks of marine algae.

This study was designed to assess the effects of commercial harvesting on algal resources and to provide information useful in drafting a management plan for seaweed harvesting in Oregon. The study had two goals: to assess (1) the within and between year recovery of seaweeds harvested during different seasons and (2) the recovery in subsequent years following different removal methods and amounts. Within-year recovery was defined as reaching pre-harvest lengths or biomasses and second recovery was defined as reaching pre-harvest plot density.

The five species chosen for study were *Alaria marginata* Postels et Ruprecht, *Laminaria setchellii* Silva, *Fucus gardneri* Silva, *Mastocarpus papillatus* (C. Agardh) Kützing, and *Mazzaella splendens* (Setchel et Gardner) Fredericq in Hommersand, Fredericq et Freshwater. All five species are perennials and are harvested either for food or dietary supplements (Abbott and Hollenberg 1976; Zemke-White and Ohno 1999). They are found in the mid to low intertidal zone of rocky shores all along the Oregon coast. Species will be referred to by genus henceforth.

Materials and Methods

Three sites were chosen for experimentation. South Cove (43°18.13'N, 124°23.91'W) is part of Cape Arago State Park, Oregon, USA, Hooskanaden Creek (42°13.17'N, 124°22.73'W) and Lone Ranch Creek (42°05.98'N, 124°20.82'W) are located in Samuel H. Boardman State Park, Oregon, USA (Fig. 1). *Laminaria*, *Alaria*, and *Mazzaella* were harvested from Hooskanaden Creek. *Mastocarpus*, and *Fucus* were

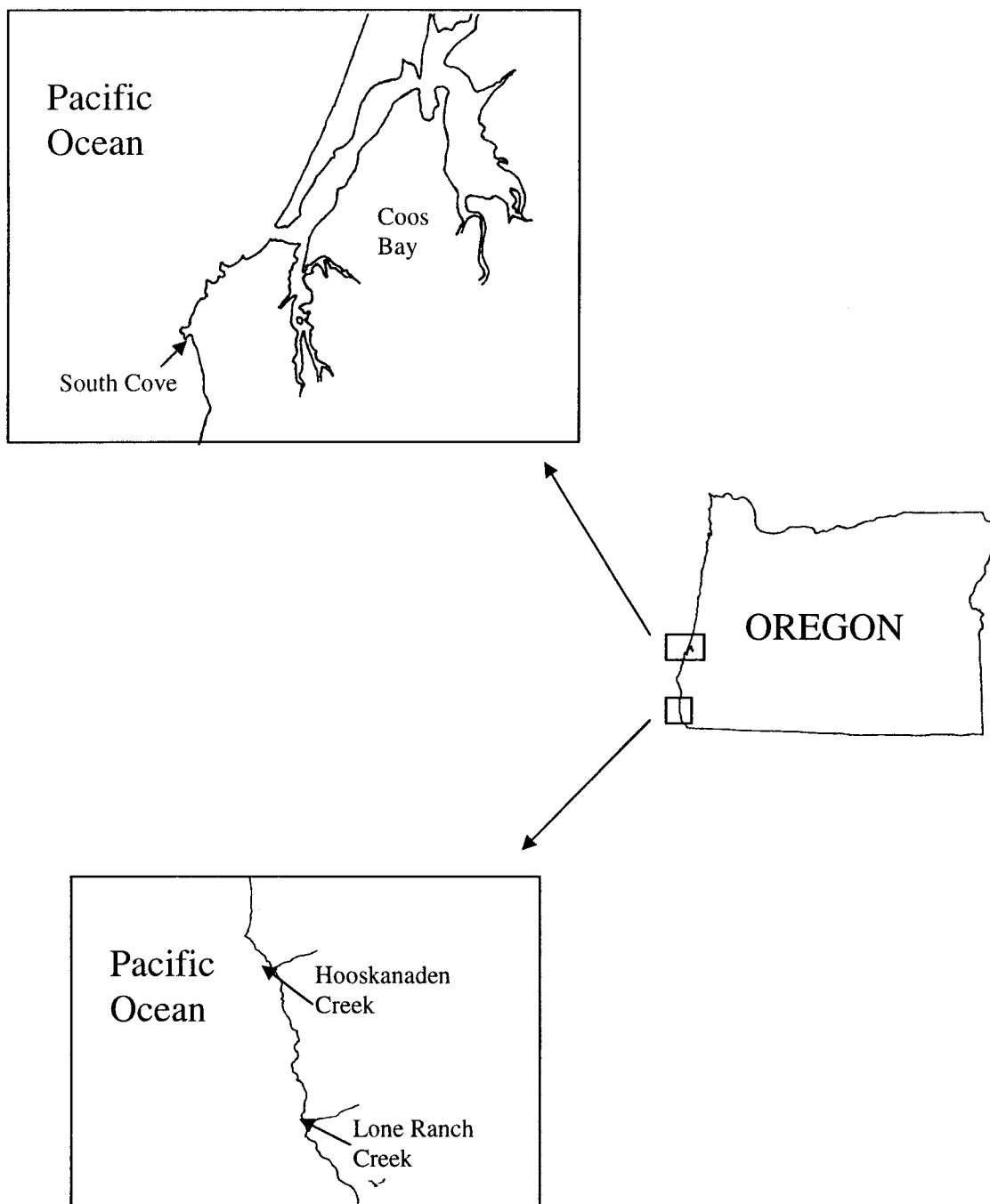


Figure 1: Selected Study Sites Along the Oregon Coast. *Alaria* and *Laminaria* were collected from South Cove and Hooskanaden Creek. *Fucus* and *Mastocarpus* were taken from Lone Ranch Creek. *Mazzaella* was collected from Hooskanaden Creek.

studied at Lone Ranch Creek. Experiments with *Laminaria* and *Alaria* were repeated at South Cove. All three sites are characterized by rocky substrata.

Preliminary studies at the southern sites (i.e., Hooskanaden Creek and Lone Ranch Creek) were done by randomly placing a 0.5M x 0.5M quadrat along transects parallel to shore and estimating species abundance via percent cover. Transects were placed at tidal levels supporting the zonal distribution of each individual species. Algal cover at Hooskanaden Creek averaged over 90%. *Alaria* and *Laminaria* were the dominant species in these measurements. *Mazzaella* was abundant at higher tidal elevations at Hooskanaden Creek. Lone Ranch Creek was estimated to have about 50% algal cover with *Fucus* and *Mastocarpus* being the most abundant.

Permanent transects and marked plots were placed through or in areas densely covered by the target species because such areas are chosen for harvesting. Bolts and bolt anchors drilled into the rock marked the endpoints of permanent transects. Some transects passed through areas covered with two target species. Areas along these transects were selected as harvest plots if they were densely covered (approximately 100%) with one target species. A numbered tag anchored to the rock with a screw and screw anchor marked the center of each plot. Quadrats were centered on the tag and an attached compass assured one edge of the quadrat was parallel to the transect. This allowed exact return to marked areas. Plots of *Laminaria* and *Alaria* were 0.5m x 0.5M and plots of *Fucus*, *Mastocarpus*, and *Mazzaella* were 0.2M x 0.2M.

Season of Harvest Experiments

Experimental harvests were conducted in May and June to compare the effects of harvesting during the spring and summer seasons, respectively. Three experimental plots were randomly assigned for each seasonal harvest. The first experiment occurred during the spring tide series between 25 and 30 May 2002. Harvests were performed on target species at all sites with the exception of *Mazzaella* and *Alaria* at South Cove. Large swells and high tides prevented these harvests. A summer harvest was performed on all species at all sites between 24 and 29 June 2002.

Experimental plots of *Alaria* and *Laminaria* had all harvestable quality plants (>50cm) marked through the stipes with numbered spaghetti tags (Floy Tag & Mfg., Inc. Seattle, Wa). Tagged plants were cut 6-10 cm above the meristems, and lengths recorded. Cutting above the meristems was chosen for *Laminaria* and *Alaria* because both show intercalary growth (Abbott and Hollenberg 1976). Furthermore, sporophylls of *Alaria* were spared. *Fucus*, *Mastocarpus*, and *Mazzaella* all possess apical meristems (Abbott and Hollenberg 1976), therefore, plants were cut 2-5 cm above the holdfast. All harvestable plants in experimental plots were tagged, cut and measured. Harvested plants were remeasured monthly during spring tides until August of 2002. Control plots (n=4 or more) were randomly assigned for each species at each site. Two of the control plots were tagged, measured, but left uncut. The other control plots were left untouched for subsequent year comparison. All tagged plants were then measured monthly through August 2002 during spring tides. All algae in experimental and tagged control plots were collected during the first spring tide in August 2002. Within-season controls were then

used as experimental August harvest plots in subsequent years. Collection was done according to the methods described above.

Selective/Method of Harvest Experiment

Plots of the same sizes were randomly selected along the same transects used in the season of harvest experiments. Selected plots were randomly assigned a treatment of either 25% frond removal, 25% entire alga removal, 50% frond removal, 50% entire alga removal, or control. All treatments were replicated three times. In plots chosen for frond removal, the algae were cut in the same manner as in the season of harvest experiments. Plots chosen for entire alga removal had the designated number of algae removed from the substrate by prying off their holdfasts. Controls were left undisturbed and used for reference in all experiments during subsequent years.

Plots of *Alaria* and *Laminaria* had all holdfasts counted in the quadrat prior to any removal. Then all harvestable quality plants (>50cm) were counted. Either 50% or 25% of plants >50cm were removed according to the treatment assigned. In plots where an even number could not be taken, we rounded up to the next whole number. Plots of *Fucus*, *Mastocarpus*, and *Mazzaella* were not counted prior to removal. These plots were usually 100% full of the target species. A quadrat equally divided into four sections was used and algae were removed from one or two squares depending on the assigned treatment. Algae were always removed from the same squares to ensure consistency.

Experiments were performed on *Alaria* and *Laminaria* in both Hooskanaden Creek and South Cove over the first spring tide series in July 2002. The experiments

were performed on *Mazzaella*, *Fucus*, and *Mastocarpus papillatus* during the second spring tide series in July 2002.

Experimental and control plots from both experiments were monitored during spring tides beginning in April 2003 through August of 2003. Recruitment in plots of *Alaria*, *Laminaria*, and *Fucus* was measured by counting the total number of holdfasts in the quadrat and the number of germlings. *Alaria* plants were scored as germlings if no sporophylls were present (typically < 50cm). *Laminaria* < 50cm were considered germlings and *Fucus* plants < 1cm in length were scored as germlings (Speidel *et al.* 2001). Percent cover was visually estimated with a subdivided quadrat for *Mazzaella* and *Mastocarpus*.

Collected algae were rinsed in freshwater to remove all epifauna previous to recording wet weight. The rinse water was passed through 150 μ m mesh and collected epifauna was preserved and cataloged. Algal samples were placed in a drying oven set at 60°C for 14 days prior to measuring dry weight. Aliquot samples from dried material of approximately 0.5g were placed in a muffle furnace set at 500°C for 14hrs to measure ash free dry weight (AFDW) and organic dry weight of the samples. Biomass was estimated by measuring the mass lost from the aliquot after heating and back calculating to determine organic dry weight of the plot. This figure was then multiplied by a constant derived from plot size to estimate organic dry weight per square meter.

Non-parametric Man-Whitney U-tests were used to compare final lengths of May and June harvested plants to control lengths. Within site biomasses and second year density data from the season of harvest experiments were compared with one-way

ANOVAs. When control replication was adequate (> 4), data from the selective harvest/method of removal experiments were analyzed using a factorial ANOVA design with method of removal (frond or entire alga) and amount of removal (25%, 50%, or control) as factors. One-way ANOVAs were used when a factorial design wasn't possible because control plot loss. A *post-hoc* Bonferroni test was performed on all significant results. All data were square root transformed if Cochran's C-test for homoscedasticity was significant. Furthermore, if transformations still failed Cochran's C-test, a non-parametric Kruskal-Wallis test was used. Statistical analyses were performed using the software package STATISTICA 6.0 (Statsoft).

Results

Season of Harvest Experiments

Alaria marginata

The lengths of plants harvested in May from Hooskanaden Creek were not significantly different from the lengths of control plants when the experiment ended in August (Fig. 2a; $p=0.620$; Appendix A: Table 2). The same result was obtained when June harvested plants were compared to controls ($p=0.522$; Appendix A: Table 2). However, a June harvest only, performed at South Cove (Fig. 2b) showed a significant difference between lengths at the end of August ($p<.001$; Appendix A: Table 2).

The ANOVA indicated that there were no significant differences between the final biomasses of experimental and control plots (Fig. 3a; $p=0.591$; Appendix A: Table

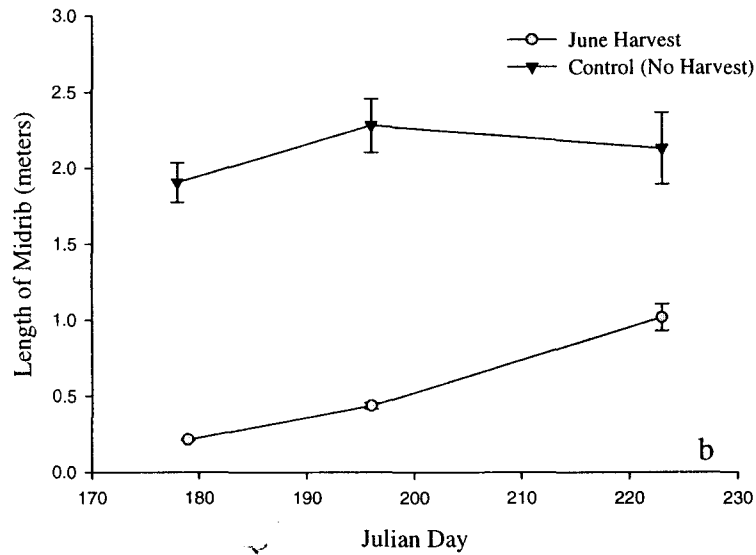
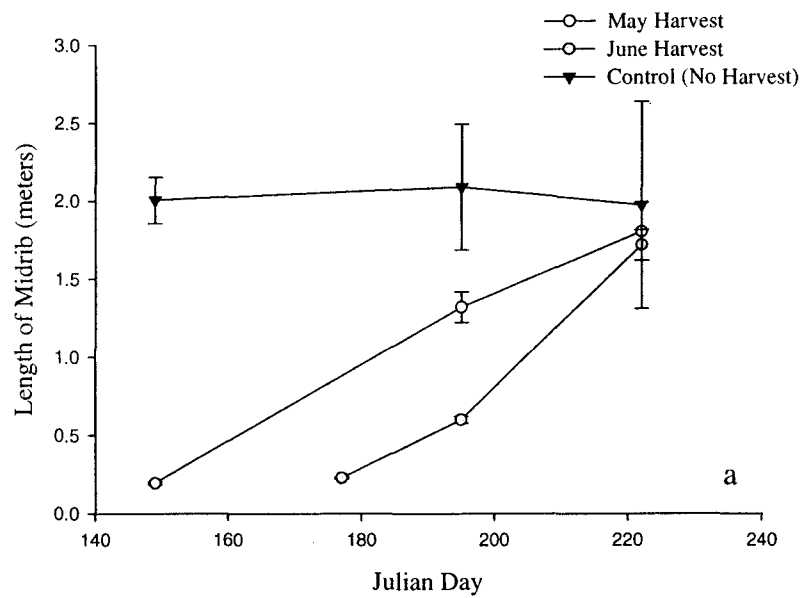


Figure 2: Season of Harvest Experiments for *Alaria*. Data points show the mean midrib lengths of *Alaria* from (a) Hooskanaden Creek and (b) South Cove. Error bars show one standard error from the mean.

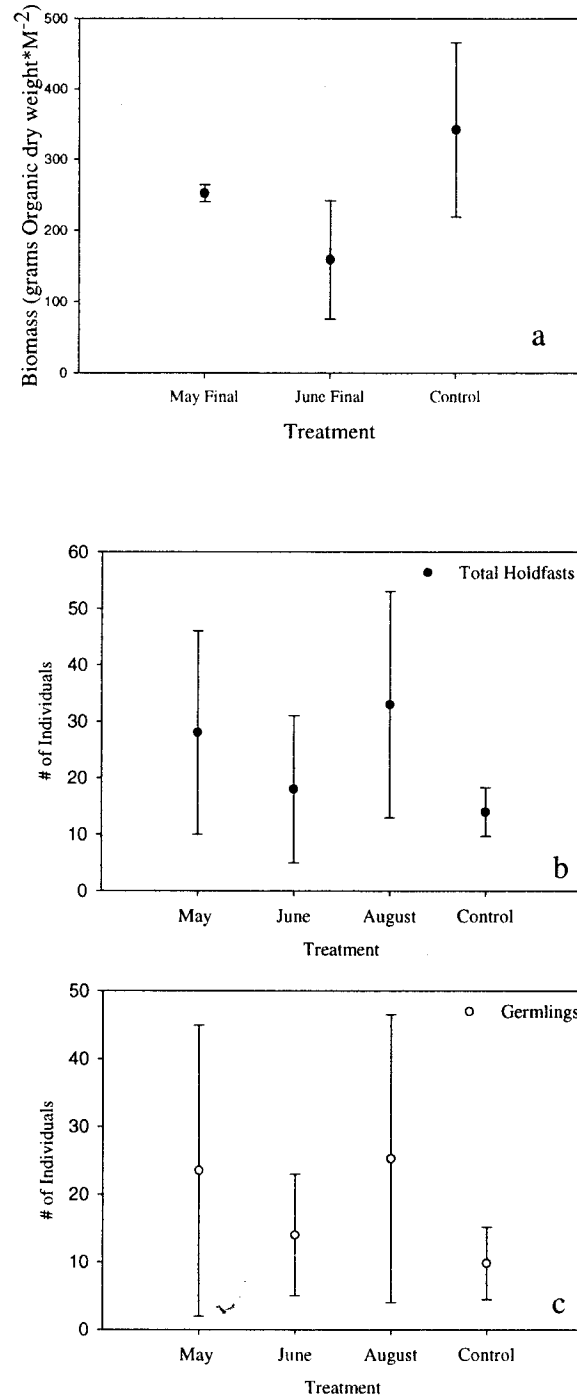


Figure 3: Recovery of *Alaria* from Hooskanaden Creek after the Season of Harvest Experiments. Within-year recovery (a) is represented by plot biomass. Second year recovery is shown by total(b) and germling(c) holdfast density. Error bars show one standard error from the mean.

3). Total and germling holdfast counts per plot in 2003 also showed no significant differences between all treatments (Figs. 3b and 3c; $p=0.731$ and $p=0.847$, respectively; Appendix A: Table 4). South Cove produced similar results (Fig. 4a and Figs. 4b and 4c).

Laminaria setchellii

The effects of both May and June harvests at Hooskanaden Creek were detected in August. There were significant differences in overall lengths between May harvested plants ($p=0.001$) and June harvested plants ($p=0.005$) and the controls (Fig. 5a; Appendix A: Table 2). The results of the same experiments performed at South Cove also produced significant differences ($p=0.008$ and $p<0.0001$) between the two harvests and the controls (Fig. 5b; Appendix A: Table 2).

The biomasses of all plots harvested in August were square root transformed to satisfy the assumption of homoscedasticity required for an ANOVA (Fig. 6a; Appendix A: Table 3). There is a significant difference between the August biomass of experimental and control plots ($p=0.001$). *Post hoc* tests revealed significant differences between control and May ($p=0.006$) and June ($p=0.001$) biomasses. Total and germling holdfast counts per plot in 2003 were not significantly different ($p=0.642$; $p=0.595$) between all treatments (Figs. 6b and 6c; Appendix A: Table 4).

In the ANOVA comparing final biomasses of plots from South Cove, treatment effects were not significant (Fig. 7a; $p=0.076$; Appendix A: Table 3). Furthermore, there

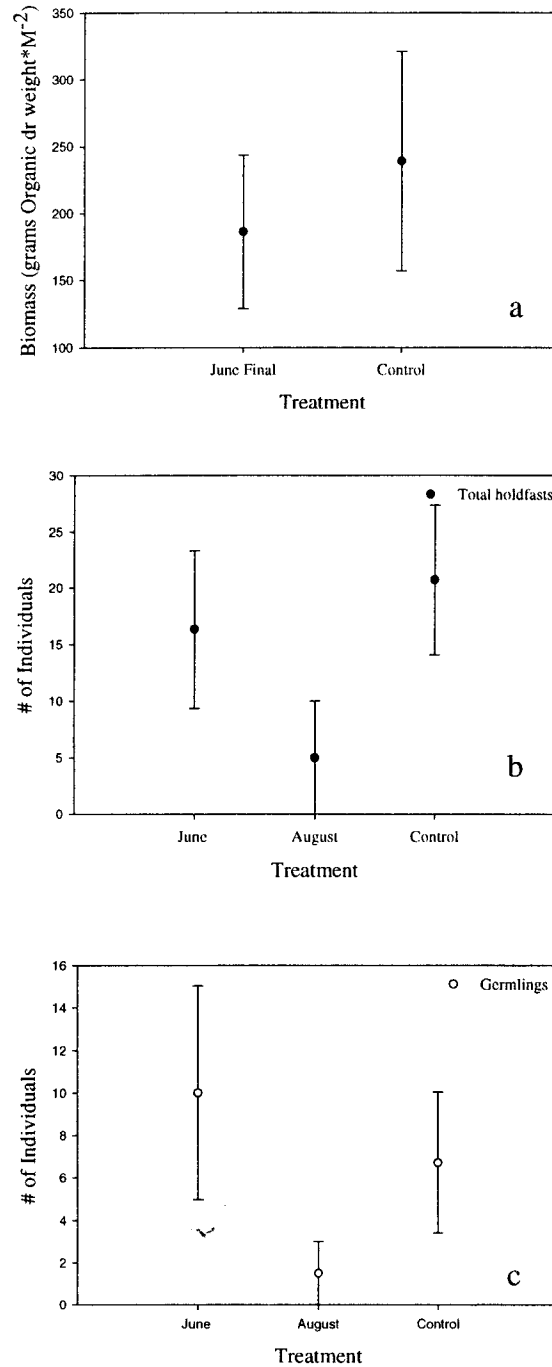


Figure 4: Recovery of *Alaria* from South Cove after the Season of Harvest Experiments. Within-year recovery (a) is represented by plot biomass. Second year recovery is shown by total(b) and germling(c) holdfast density. Error bars show one standard error from the mean.

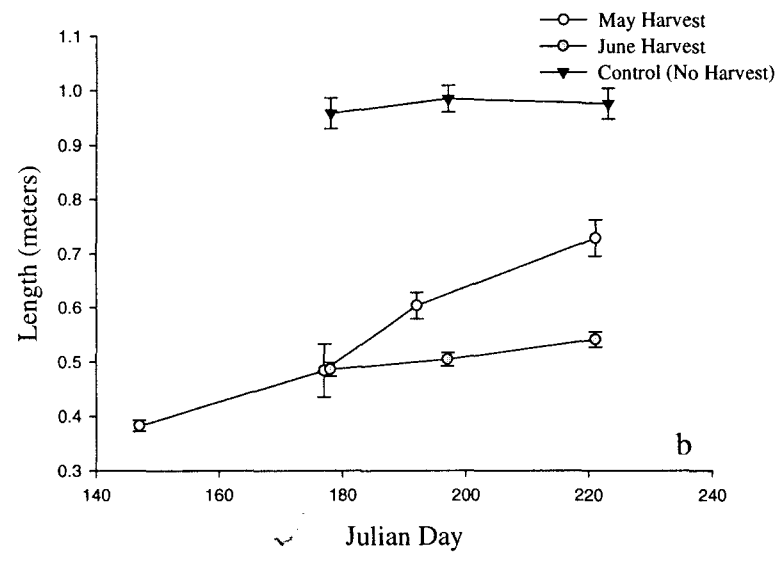
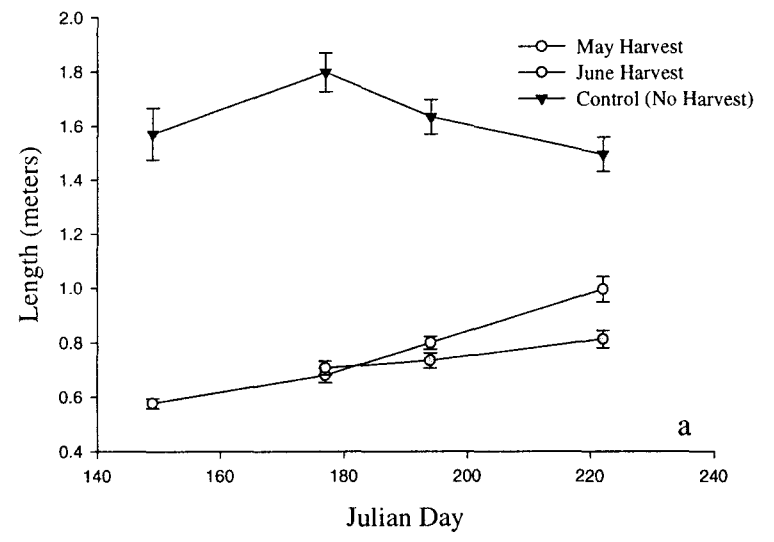


Figure 5: Season of Harvest Experiments for *Laminaria*. Data points show the mean lengths of *Laminaria* from (a) Hooskanaden Creek and (b) South Cove. Error bars show one standard error from the mean.

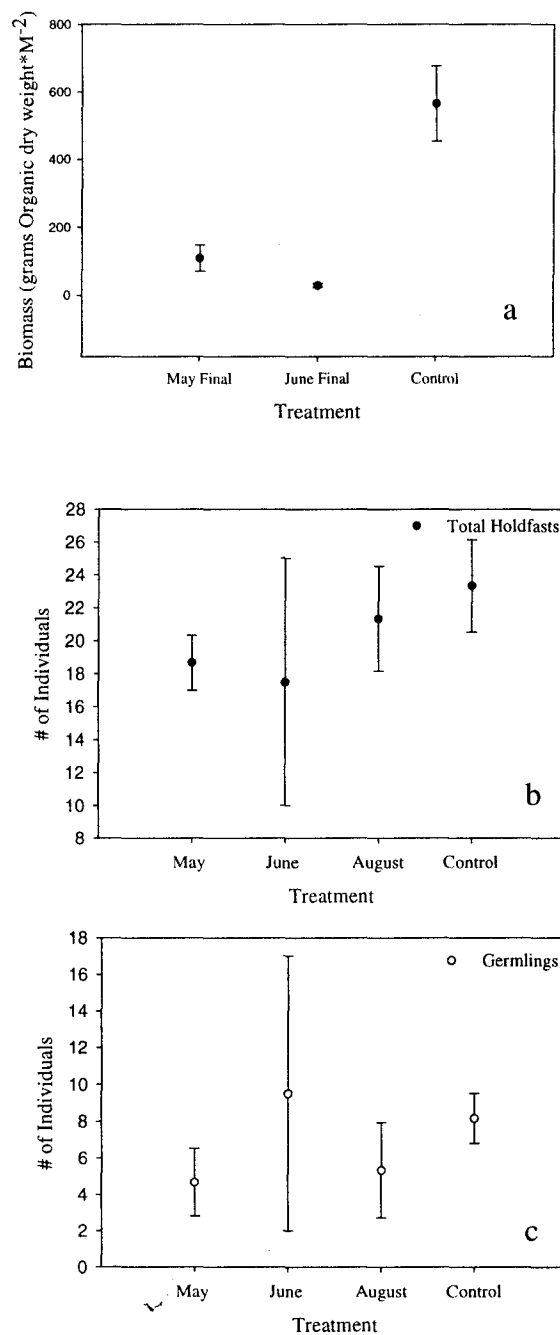


Figure 6: Recovery of *Laminaria* from Hooskanaden Creek after the Season of Harvest Experiments. Within-year recovery (a) is represented by plot biomass. Second year recovery is shown by total(b) and germling(c) holdfast density. Error bars show one standard error from the mean.

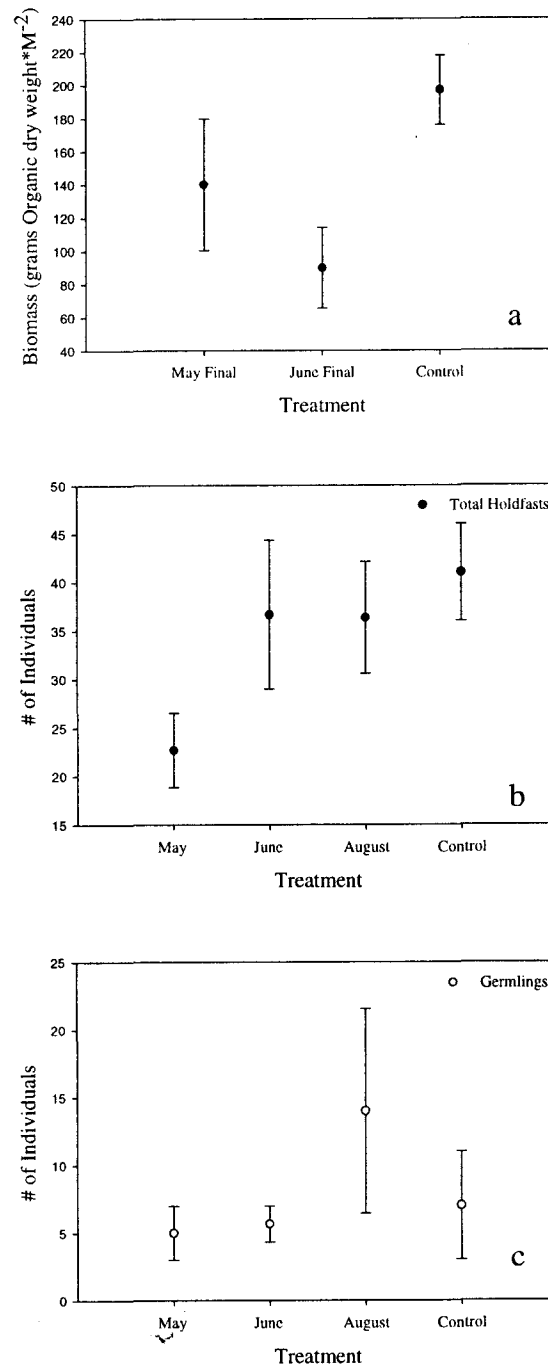


Figure 7: Recovery of *Laminaria* from South Cove after the Season of Harvest Experiments. Within-year recovery (a) is represented by plot biomass. Second year recovery is shown by total (b) and germling (c) holdfast density. Error bars show one standard error from the mean.

were no significant differences in total and germling holdfasts between experimental and control treatments (Figs. 7b and 7c; Appendix A; Table 4).

Fucus gardneri

In all of the tested seasons, *Fucus* did not grow appreciably following harvest (Fig. 8). Plants cut in May and June both had lengths significantly shorter than control lengths by August ($p=0.002$ and $p=0.002$, respectively; Appendix A: Table 2). The biomass data followed a similar pattern with significant differences in total organic dry weight (Fig. 9a; $p=0.01$; Appendix A: Table 3). The *post hoc* test revealed a significant difference between the June harvested and control plots ($p=0.02$), but no significant differences were found between the May harvest and control lengths. There were no significant differences in total and germling holdfast counts by harvest season in the 2003 season (Fig. 9b and 9c; $p=0.743$ and $p=0.829$, respectively; Appendix A: Table 4).

Mastocarpus papillatus

Following harvest, *Mastocarpus* grew little or not at all (Fig. 10a). The plants harvested in both May and June were significantly smaller than the control plants ($p=0.004$ and $p=0.014$, respectively; Appendix A: Table 2). The comparisons of the August biomasses from both experimental plots were not significantly different from that of the control plots (Fig. 10b; $p=0.805$; Appendix A: Table 3). No significant differences

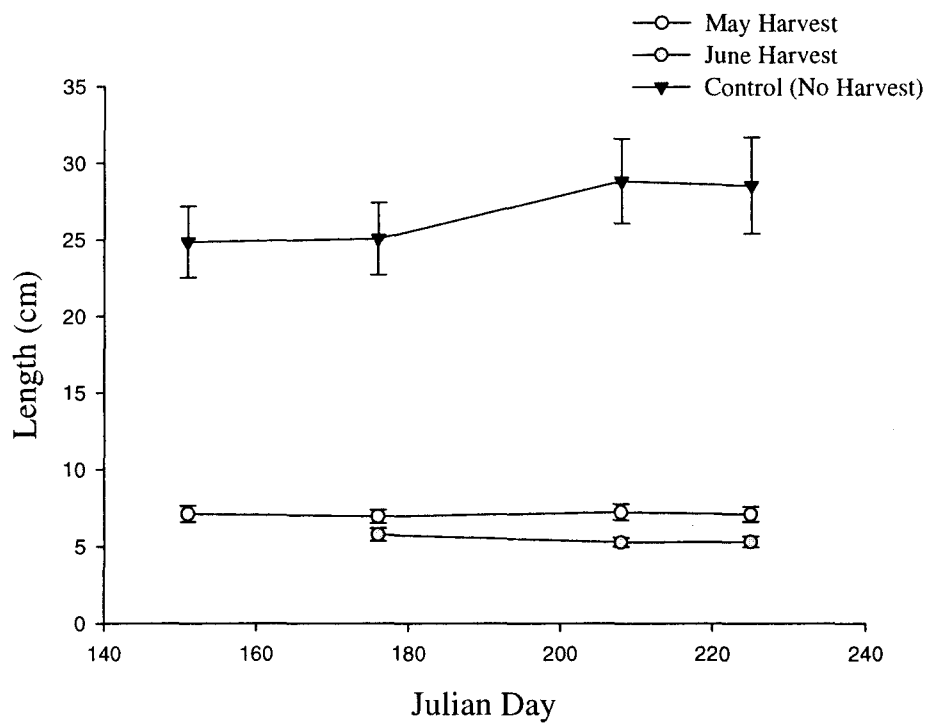


Figure 8: Season of Harvest Experiments for *Fucus*. Data points show the mean lengths of *Fucus* from Lone Ranch Creek. Error bars show one standard error from the mean.

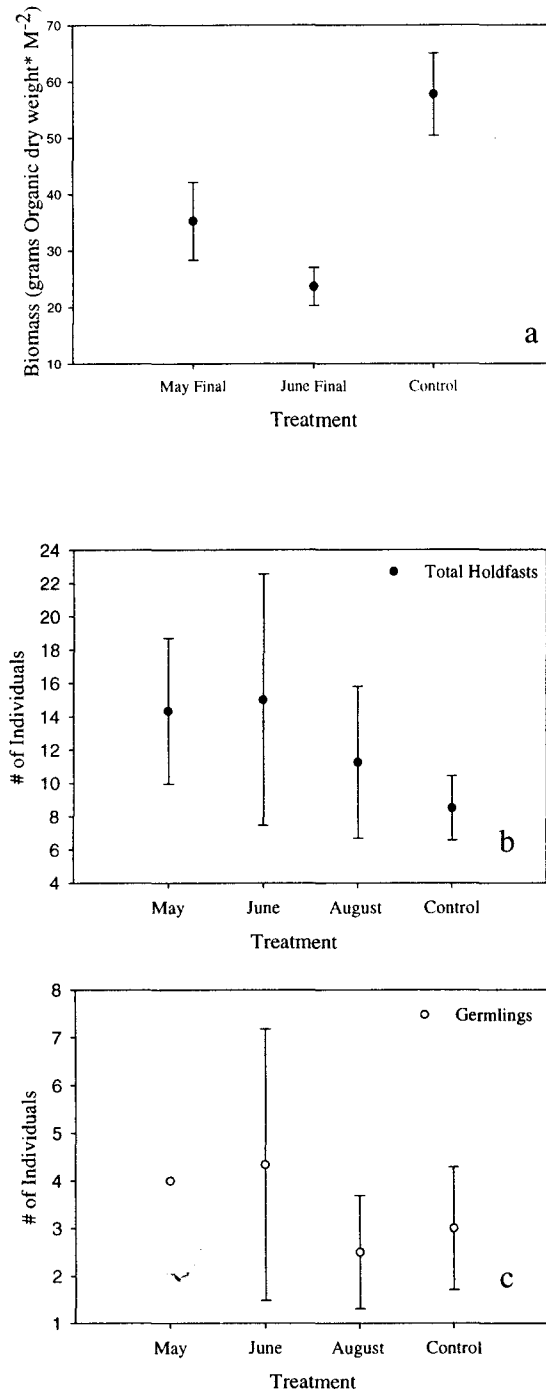


Figure 9: Recovery of *Fucus* from Lone Ranch Creek after the Season of Harvest Experiments. Within-year recovery (a) is represented by plot biomass. Second year recovery is shown by total(b) and germling(c) holdfast density. Error bars show one standard error from the mean.

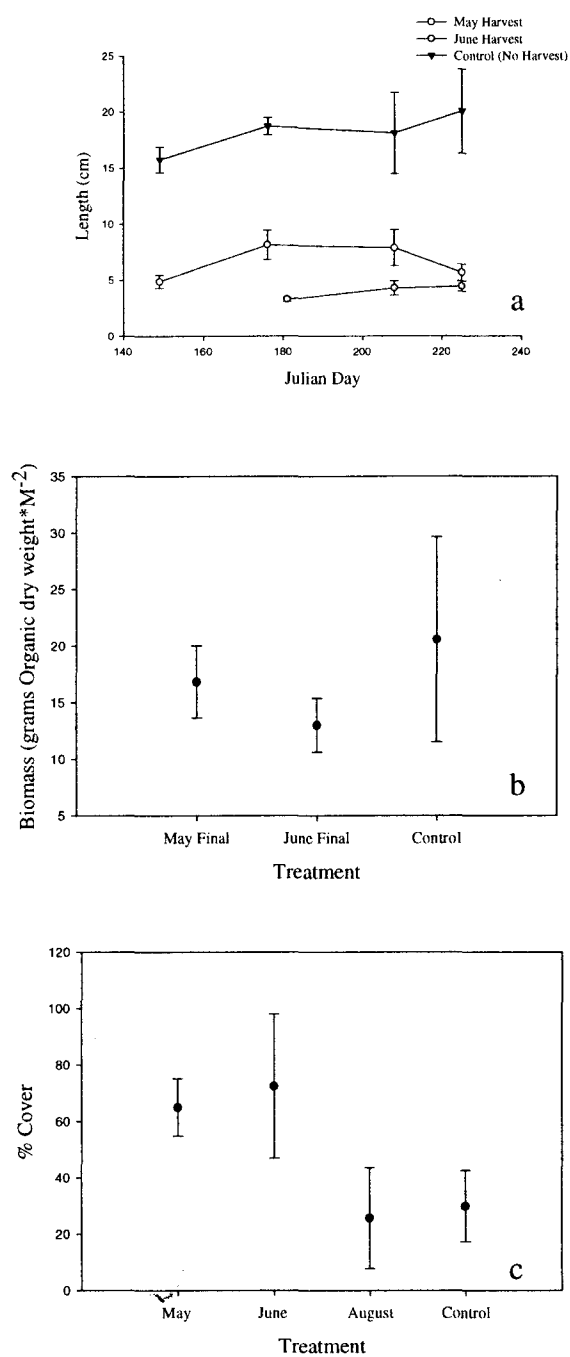


Figure 10: Season of Harvest Experiments with *Mastocarpus* at Lone Ranch Creek. Within-year recovery is shown by (a) lengths and (b) biomass. Second year recovery (c) is shown with percent cover. Error bars show one standard error from the mean.

($p=0.177$) were found between the percent cover of the experimental plots and the control plots (Fig. 10c; Appendix A: Table 4) in 2003.

Mazzaella splendens

Mazzaella failed to increase in length following the single June harvest (Fig. 11a). Harvested thalli lengths in August were significantly smaller than control thalli lengths ($p=0.0008$; Appendix A: Table 2). The August biomass of the June harvested plots were not significantly different from the biomass of the control plots (Fig. 11b, $p=0.369$; Appendix A: Table 3). There were no significant differences between the percent cover of harvested and control plots (Fig. 11c; $p=0.07$; Appendix A: Table 4) in 2003; however, there was a trend of lower percent cover in plots harvested in June.

Selective/Method of Harvest Experiment

Alaria marginata

There were no significant differences in total *Alaria* holdfasts whether removal amount or method was considered (Fig. 12a; $p=0.766$ and $p=0.433$, respectively; Appendix A: Table 5). The interaction between the two factors (removal amount and method) also proved to be not significant ($p=0.06$). However, removal of fifty percent of the frond produced the largest mean plot density, nearly twice that of the controls.

The pattern was the same for the density of germlings except there was a significant interaction between removal amount and method of removal (Fig. 12b;

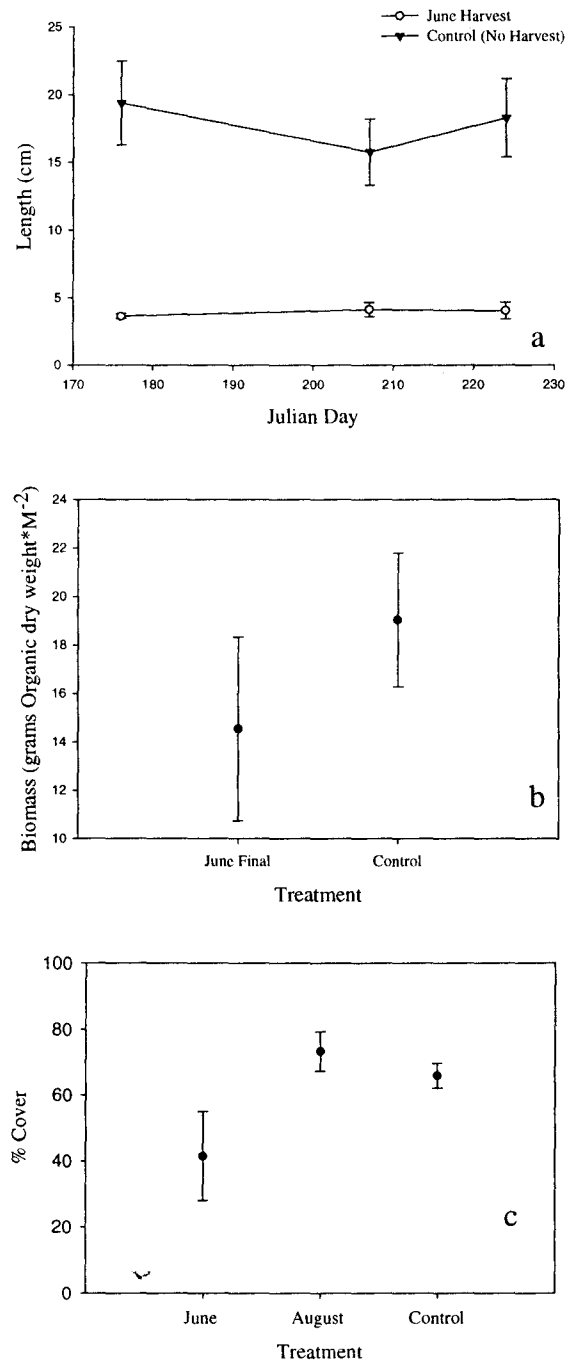


Figure 11: Season of Harvest Experiments with *Mazzaella* at Hooskanaden Creek. Within-year recovery is shown by (a) lengths and (b) biomass. Second year recovery (c) is shown with percent cover. Error bars show one standard error from the mean.

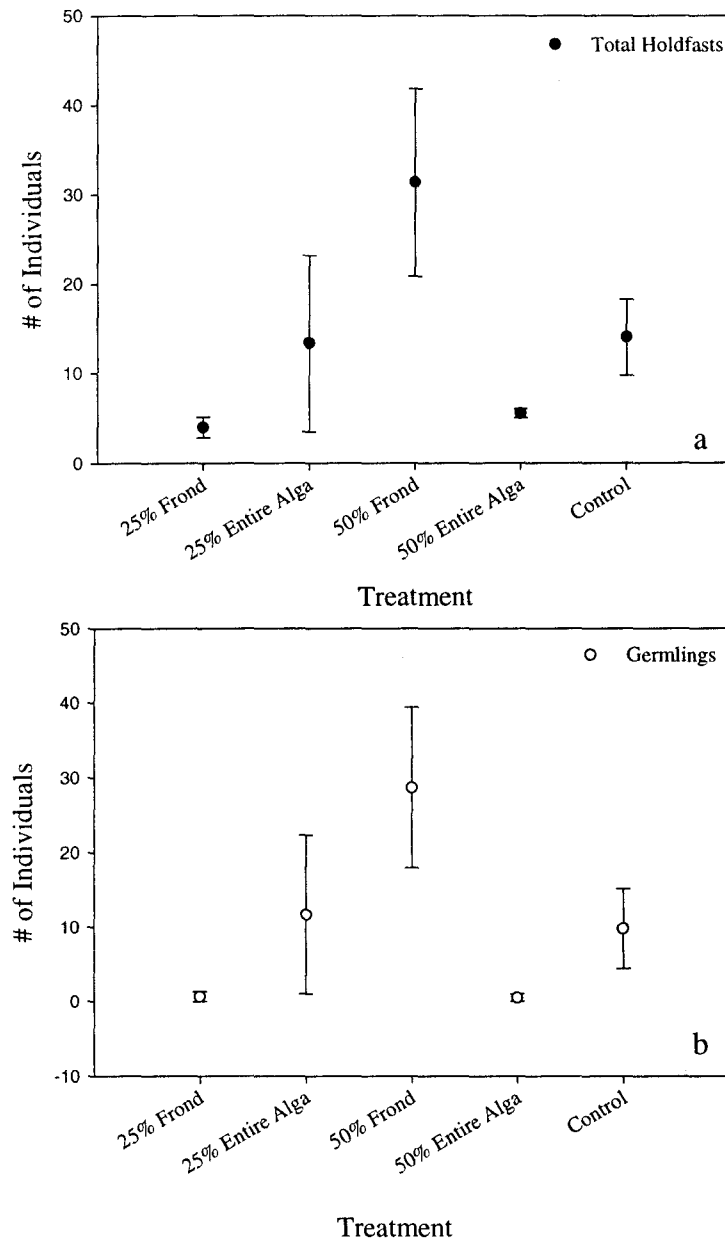


Figure 12: Recovery of *Alaria* from Hooskanaden Creek after the Selective/ Method of Harvest Experiments. Data points show the mean (a) total and (b) germling holdfast density. Error bars show one standard error from the mean.

$p=0.03$; Appendix A: Table 5). Again removal of fifty percent of the fronds in the plot yielded the greatest number of recruits. Removing 25% of the algae yielded second year density close to that of the controls. The treatments of 25% frond and 50% entire alga removal had the lowest plot densities. South Cove differed in that there were no significant differences between all effects, however, the trends were similar (Figs. 13a and 13b; Appendix A: Table 5).

Laminaria setchellii

A Kruskal-Wallis test revealed that removal of 25% of *Laminaria* present in plots produced significantly lower holdfast densities one year after the treatment (Fig. 14a; $p=0.020$; Appendix A: Table 6). Control plots, however, had the highest mean density of all treatments. Removing 50% of the fronds produced the second highest mean density.

There were no significant differences in germling density across treatments (Fig. 14b; Appendix A: Table 5). The one-way ANOVA comparing total and germling holdfast density differences at South Cove were not significant (Figs. 15a and 15b; Appendix A: Table 7). The removal of 50% of the fronds produced a larger mean total holdfast density than in the control plots, however, the variance was large.

Fucus gardneri

No significant treatment effects were found on total holdfast density (Fig. 16a) or germling density (Fig 16b). Statistical tables are shown in Appendix A: Table 5.

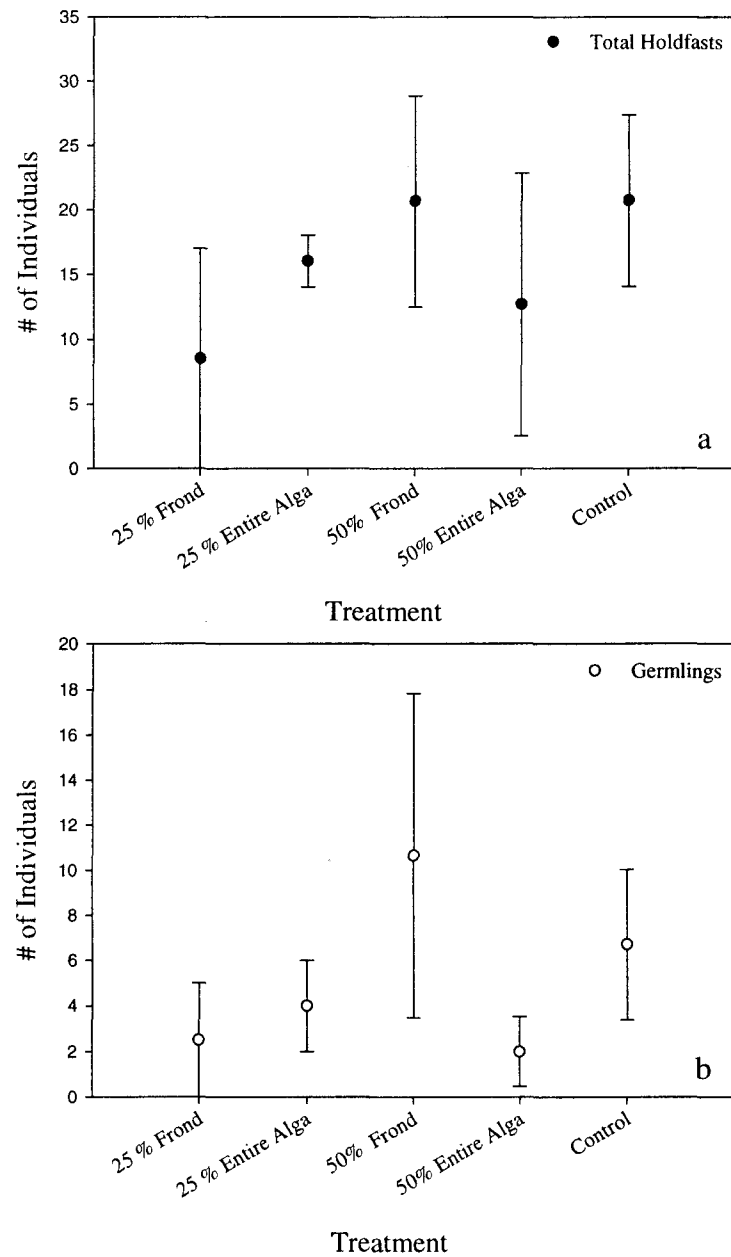


Figure 13: Recovery of *Alaria* from South Cove after the Selective/ Method of Harvest Experiments. Data points show the mean (a) total and (b) germling holdfast density. Error bars show one standard error from the mean.

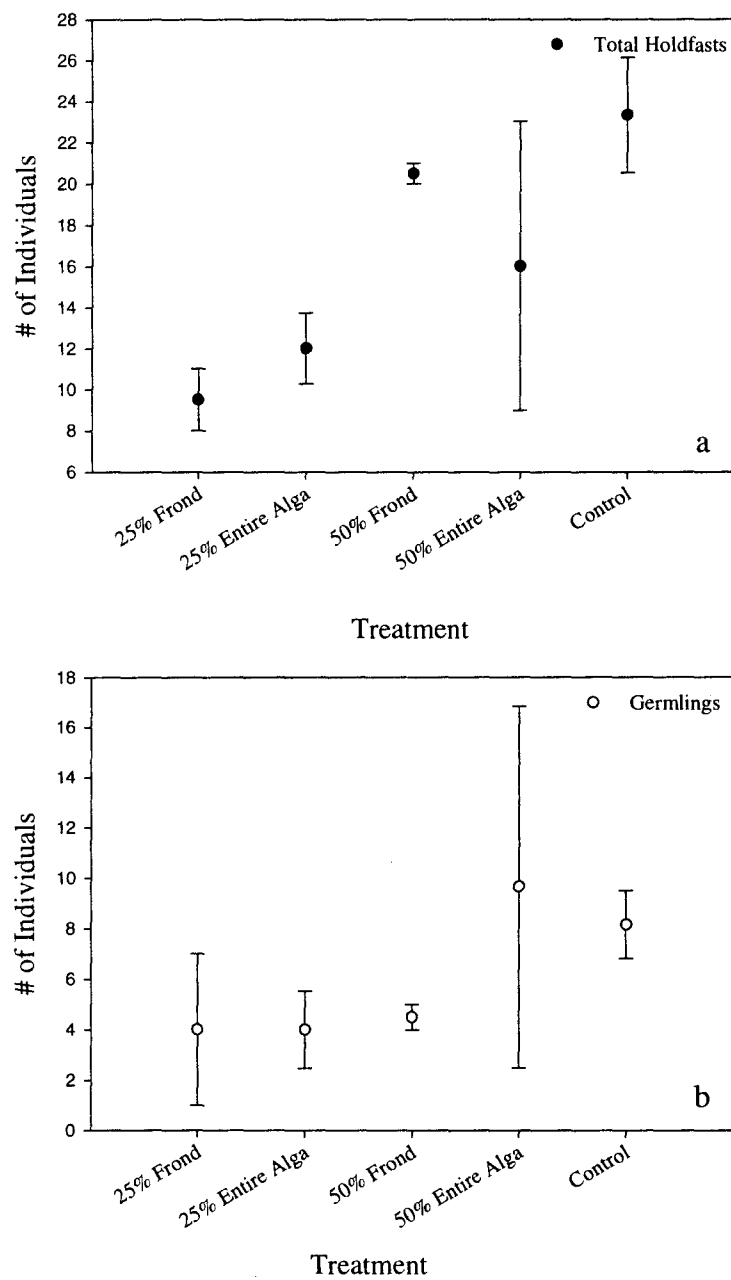


Figure 14: Recovery of *Laminaria* from Hooskanaden Creek after the Selective/ Method of Harvest Experiments. Data points show the mean (a) total and (b) germling holdfast density. Error bars show one standard error from the mean.

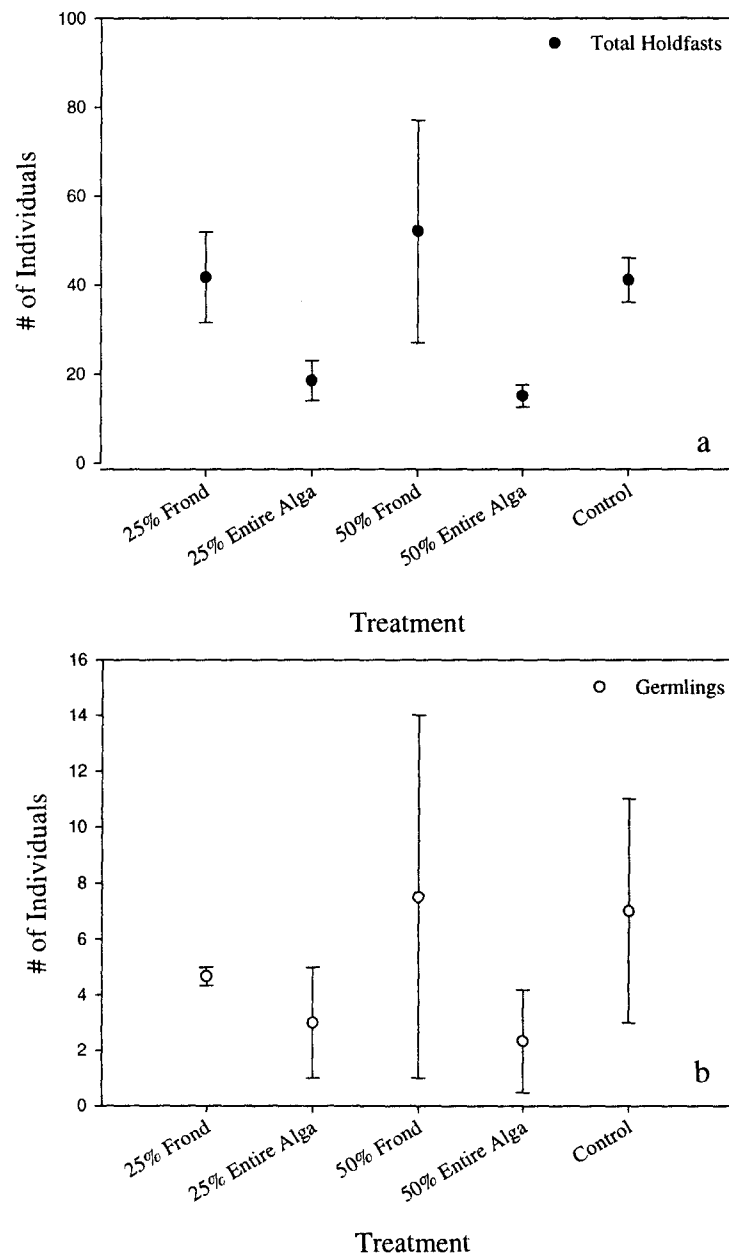


Figure 15: Recovery of *Laminaria* from South Cove after the Selective/ Method of Harvest Experiments. Data points show the mean (a) total and (b) germling holdfast density. Error bars show one standard error from the mean.

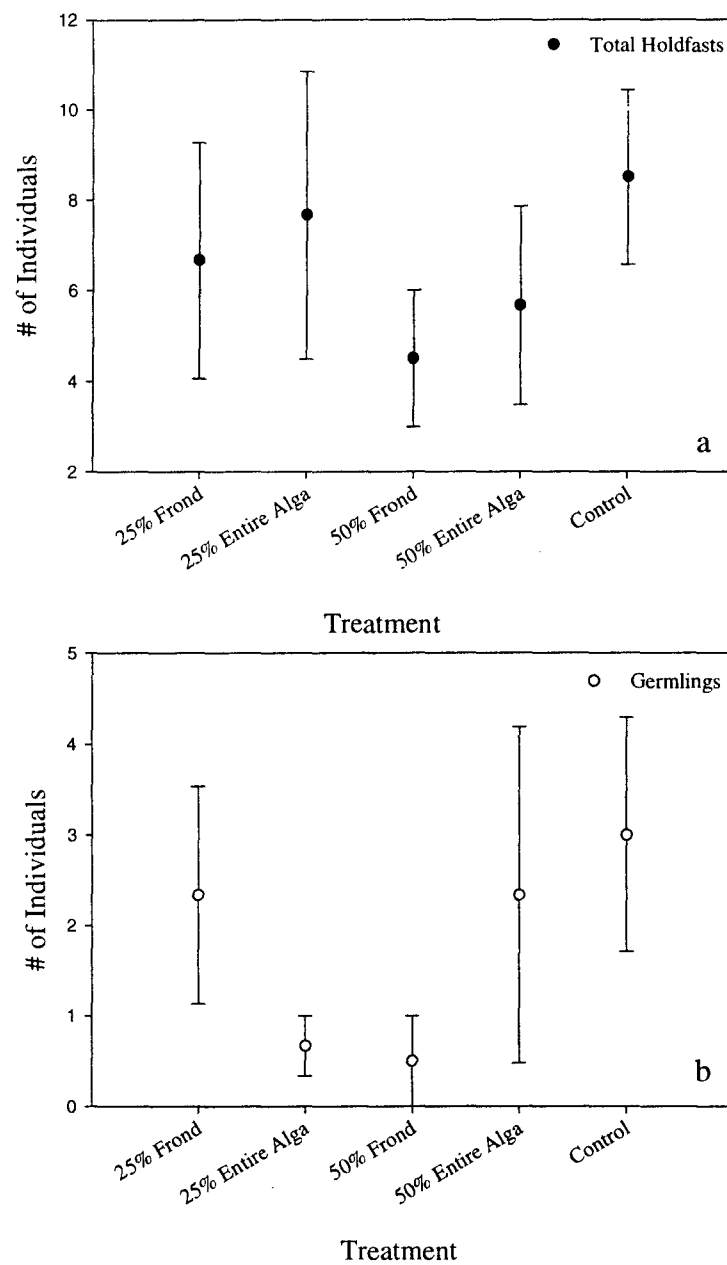


Figure 16: Recovery of *Fucus* from Lone Ranch Creek after the Selective/ Method of Harvest Experiments. Data points show the mean (a) total and (b) germling holdfast density. Error bars show one standard error from the mean.

Densities were lower in treatments of 25% entire alga and 50% frond removal but not significantly so.

Mastocarpus papillatus

None of the harvests had significant effects on percent cover of plots (Fig 17; Appendix A: Table 7). There was a trend of 25% removal having the highest second year cover, followed by 50% removal. Interestingly, the control treatment had the lowest second year cover.

Mazzaella splendens

There were significant treatment effects in the percent cover of *Mazzaella* plots one year after harvesting (Fig, 18; $p=0.005$; Appendix A: Table 7). Removing 50% of the algae present at the holdfast produced the lowest percent cover in 2003. *Post hoc* tests found significant differences between the 50% entire alga removal and all other treatments. The treatments of 25% and 50% frond removal both had mean percent covers not significantly different from control plots. Plots with 25% removal of the entire alga were not assessed in 2003 because of plot marker tag loss.

Discussion

For all species examined, the season of harvest had no effect on net growth. At the end of summer, the May-harvested treatments produced the same results as the June

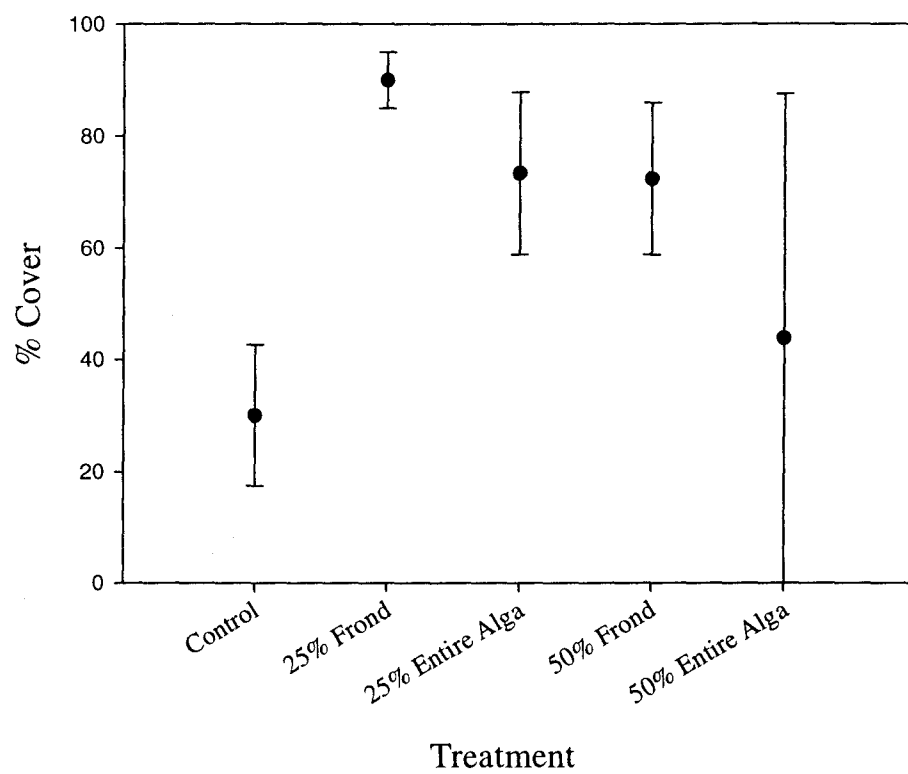


Figure 17: Recovery of *Mastocarpus* from Lone Ranch Creek after the Selective/ Method of Harvest Experiments. Data points show the mean percent plot cover. Error bars show one standard error from the mean.

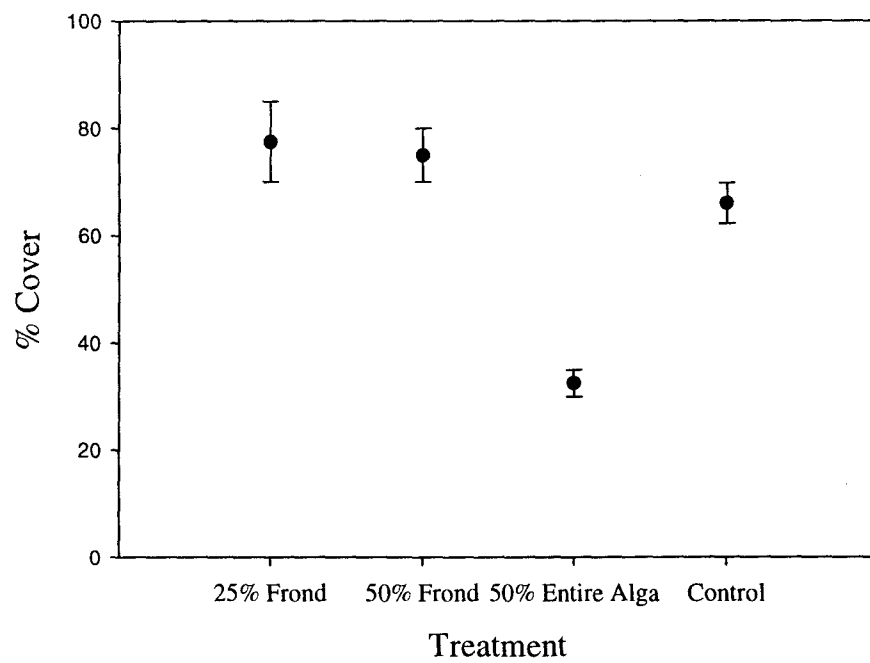


Figure 18: Recovery of *Mazzaella* from Hooskanaden Creek after the Selective/ Method of Harvest Experiments. Data points show the mean percent plot cover. Error bars show one standard error from the mean.

harvests. These comparisons lead to the conclusion that, in terms of net growth, harvesting in May or June had no effect on recovery within the same year that these species were harvested.

Alaria marginata

Alaria exhibits a typical laminarian life-history with an alteration of generations. Under short day conditions the macroscopic sporophyte stage releases zoospores which settle and grow into microscopic male or female gametophytes. The gametophytes are fertile and produce sporophytes throughout the summer (Lee 1999). Vegetative growth in the sporophyte occurs through an intercalary meristem between the stipe and the frond (Buggeln 1974; tom Dieck 1991). The sporophyte frond is collected by harvesters.

Harvesting *Alaria* as early as May and as late as August was unlikely to have significant effects on reproduction and recruitment. This is supported by the lack of significant differences between total and germling holdfast densities between treatment and control plots one year after treatments. Pfister (1992) found removal of the vegetative frond throughout the growing season significantly decreased the reproductive investment of *Alaria nana* yet, reproductive investment was not different between controls and plants with portions of the frond removed. My harvest times would allow for regeneration of fronds before the zoospores are shed in the fall. Additionally, I found the net growth of *Alaria* to increase following a harvest. The lengths of both May and June harvested plants, by August, were not significantly different from control lengths. The lack of apparent growth of the controls is likely due to breakage of the frond rather

than reaching a terminal length. Larger (e.g. uncut) blades were probably more vulnerable to breakage. The experimentally shortened plants are less subject to breakage from wave action and rock abrasion which can cause catastrophic wounds in larger plants (DeWreede *et al* 1992). Furthermore, the congener *Alaria esculenta* (L.) has been demonstrated to grow throughout the year (Buggelin 1974) with growth pulses between April and Late June (Buggelin 1977). Herbivory is not likely to contribute significantly to the shortening of the control plants because the high concentration of phenolics in growing *Alaria marginata* (Steinberg 1984; Duggins and Eckman 1997) probably results in little grazing. The results comparing the biomass of experimental and control plots suggest recovery within the growing season and a possibility for two harvest yields per year.

The slower net growth of plants at South Cove is likely due to less nutrient input. Upwelling along the Oregon coast is known to intensify south of Cape Blanco (Strub *et al* 1987). This would increase the nutrient levels at Hooskanaden Creek above those of South Cove. Microclimate variations can have significant impacts on local vegetation (Begon *et al* 1996).

Removal of 50% of fronds from plots in the selective/method of harvest experiments produced the highest recruitments, although the differences were not statistically significant. Removing just the frond spares the sporophylls allowing production of spores and increased reproduction. Furthermore, thinning adult fronds from the plots increased the light penetration to juveniles allowing heightened growth. The lower recruitment observed in plots where 50% of the algae present were removed at the

holdfast supports this argument. This treatment removed the sporophylls and therefore lowered spore potential. Dispersal distance in marine algae is thought to be relatively low (see Dayton 1973; Reed *et al* 1988) so these treatments are likely to have localized effects.

Laminaria setchellii

The life history of *Laminaria* is similar to that of *Alaria* except sporangia form on the sporophyte frond. Vegetative growth is via an intercalary meristem (tom Dieck 1991; Lee 1999). Again, the frond is collected by harvesters.

Net growth was slow in individuals following both May and June harvests. The significant differences in plot biomass between harvested plots and controls indicate that *Laminaria* was unable to recover during the same year it was harvested. This could be attributed to the timing of frond removal. Kain (1963) and Lüning (1969) found the growth of *Laminaria hyperborea* to be punctuated by two phases: the fastest growth occurring between January and June and a slow growth period between July and December. In this study, both spring and summer harvests occurred during the end of the period of fast growth, which could explain the minimal net growth observed in all treatments. Harvesting *Laminaria* earlier in the year during the period of rapid growth might ameliorate the effects seen in our May and June harvests.

Lüning (1969), however, showed that second year *L. hyperborea* sporophytes assimilate reserve materials from the previous year's frond. Late summer harvests of *Laminaria* could reduce growth in subsequent seasons due to the removal of the frond

containing this reserve material. Also, the lack of frond lengthening in our treatments could affect reproductive potential because the sori form on the frond. Days with 8 or less hours of light induce the formation of sori in *L. saccharina* (Lüning 1988). Earlier harvests may allow for greater frond lengthening and a possible increase in reproductive potential. Lüning *et al* (2000) found that frond removal can, however, prevent the formation of sporangia which could negate any benefits of earlier harvests.

Despite these possibilities for lowered reproductive potential, recovery in the subsequent year was evident by the lack of significant differences in total and germling holdfast densities between May harvest, June harvest, and control plots. This supports the conclusion that the tested times of harvest had no effect on the recovery of *Laminaria*.

Removing 25% of *Laminaria* present from plots resulted in the lowest total holdfast density in the subsequent year. There was, however, no effect on germling density. Species of *Laminaria* are able to produce large numbers of spores per plant (Kain 1975; Chapman 1984). This allows a population to persist through disturbance events such as harvesting (Chapman 1984) and ice scour (Heine 1989). The removal of more plants from plots may open more space for early settling germlings, allowing them to reach adult size in the following year. Chapman (1984) found high reproductive pulses for two species of Nova Scotia *Laminaria* in all months except July. Additionally, removal of fewer plants from the plots may be hindering the growth of juvenile sporophytes through shading. Juvenile sporophytes of *L. saccharina* off Long Island survived summer conditions only if they settled the previous autumn (Lee and Brinkhuis 1988). Late year thinning may facilitate an autumnal settlement event by freeing space

for new recruits. However, in this study germling densities were not significantly different between treatments.

Fucus gardneri

Fucus displays a different life-history than the previous two brown algal species. Gametes are produced by antheridia and oogonia that develop in conceptacles on the receptacles of the adult thallus. Therefore, no gametophyte stage exists separate from the parent frond. Conceptacles form under short day (8:16 hr LD) conditions (Lee 1999) and gametes are dropped near parent fronds to fertilize (Pearson and Brawley 1996). The zygote grows into the adult thallus with apical growth (Lee 1999). The adult thallus is harvested.

Following cutting *Fucus* failed to grow for the rest of the season. Cutting removes the apical meristems preventing further net growth of the alga. Adventitious growth was not observed. Harvesting removes the receptacles preventing conceptacle formation and therefore reproduction. Leaving the holdfasts of harvested plants still attached to the rock possibly limited the desiccation, thermal, and wave force stress on germlings (Speidel 2001). This allowed for recovery to occur in plots harvested during May. This is evident by the lack of significant differences between the biomasses of control plots and those harvested in May. Recovery, however, is relatively slow because the biomass of June harvest plots were significantly different from control plots. All plots were indistinguishable in total and germling holdfast density one year following treatment. *Fucus distichus* has been demonstrated to be reproductive throughout the year

and recruits through new settlement only (Ang 1991). Harvesting of large plants may have freed space for more germlings to settle. High densities of *F. distichus* germlings have been demonstrated reduce mortality (Ang and DeWreede 1992).

The lack of significant differences in total and germling holdfasts between the control and selective/method of harvest experimental plots were maybe due to the remaining adults protecting germlings from stressors. Speidel (2001) showed that removal of up to 80% of *Fucus* adults from plots recovered within one year, however, removal of 100% resulted in a significantly longer recovery period. A similar pattern was seen in *Fucus* populations disturbed by oil spills (van Tamelen *et al* 1997). *Fucus* recovery is relatively rapid if a few adults survive the disturbance event (Speidel 2001). The four experimental treatments in my study all left some adults still attached to the rock which could have facilitated the recruitment of the germlings. It is important to note, however, that reproduction can only occur in uncut plants. Harvesting at commercial scales would reduce the reproductive potential of the population resulting in lower recruitment and density. Kim and DeWreede (1996) compared *Fucus distichus* recovery between three patch sizes where all algae were removed and found the intermediate size of 10x10cm produced the highest percent cover after 20 months. Our plot sizes for *Fucus* were 20x20cm, suggesting a smaller harvest area may result in faster recovery.

Mastocarpus papillatus

The complex life-history of *Mastocarpus* begins with macroscopic male and female gametophytes (Lee 1999). The male releases spermatia to fuse with the carposonium to produce the second stage carposporophyte, which grows upon the female gametophyte. The carposporophyte releases carpospores that germinate into the tetrasporophyte stage. The tetrasporophyte of *Mastocarpus* forms a dark crust referred to as the “petrocelis” stage. This stage releases tetraspores that geminate into male and female gametophytes (Lee 1999). Alternatively, *Mastocarpus* can reproduce through an apogamous life-history where carpospores geminate into the erect form (Polanshek and West 1977). Vegetative growth is through apical cell divisions of filamentous axes (Lee 1999). Only the gametophyte stage is harvested.

Due to the removal of the apical meristems little net growth was observed in harvested *Mastocarpus*. Removal of gametophyte fronds would lead to lowered reproductive output because fewer spermatia would be formed. Also, the carposporophyte generation is removed along with female gametophytes. The negative effects on reproduction due to harvesting, however, may be mitigated by the tetrasporophyte stage. Harvesting would have no direct impact on tetraspore production which could replenish gametophyte stocks. Sussmann and DeWreede (2001) found annual variations in abundance of the tetrasporophyte stage with peaks in the summer and early autumn. This suggests a high tetraspore potential for *Mastocarpus* shortly after our harvests would have cleared space for new recruits. This conclusion is supported by the apparent recovery of *Mastocarpus* after both harvests. Lack of significant differences in the biomasses of control versus experimental plots suggest recovery within the harvest

year. Furthermore, the mean percent covers of all treatments were not significantly different one year after experimentation, suggesting recovery after one year's time.

Through natural breakage *Mastocarpus* may experience disturbances similar to harvesting. Large fronds of the congener *Mastocarpus stellatus* are subject to removal by drag forces during periods of high wave energy (Pratt and Johnson 2002). *Mastocarpus papillatus* does not increase the diameter of its stipe in proportion with frond size and, therefore, larger thalli are more vulnerable to breakage (Carrington 1990). By manually shortening the fronds, harvesting may lessen the consequences of drag forces during winter storms allowing the basal disc to survive into subsequent years.

The experiments comparing different removal amounts and methods also produced no significant differences in second year percent cover. This suggests recovery within one year of these harvests. Space may have been opened for new recruits by experimentally thinning plots allowing for the observed recovery.

Mazzaella splendens

The life-history of *Mazzaella* is similar to that of *Mastocarpus* described above. *Mazzaella* growth is also the same as described above. The two algae differ, however, in that the gametophyte and tetrasporophyte stages in *Mazzaella* are isomorphic and that an apogamous life-history is not known (Lee 1999). Both the gametophyte and tetrasporophyte stages of *Mazzaella* are collected by harvesters.

The lack of within-season net growth observed in harvested *Mazzaella* is attributed to the removal of the meristems. These harvests likely removed both

gametophytes (with associated carposporophytes) and tetrasporophytes. This has the potential to lower the population's reproductive potential significantly. However, the differences in biomass of June harvested and control plots were not significant suggesting recovery within the harvest season.

Mazzaella thalli typically senesce at the end of the autumn down to the basal disc which is responsible for holding space for the subsequent year's holdfast and initiating growth of the next year's blade (Hansen 1977). Our harvests were unlikely to have effects lasting through the winter because the holdfast was spared. This is supported by the lack of significant differences in the percent cover of experimental and controls plots one year after treatment. Scrosati (1999) reported on harvest recovery of the congener *M. parksii* (as *M. cornucopiae*) and showed complete recovery in early spring harvested plants when the holdfasts were spared and suggested a high sustainable yield when only thalli were cut. Harvesting at commercial scales may, however, lower the recovery ability of *Mazzaella* since the absence of neighboring plants following extended harvests would limit recruitment in cleared areas. Harvested individuals cannot contribute significantly to reproduction therefore, recruitment must be from neighboring plants.

Removal of *Mazzaella* at the holdfast resulted in significantly lower percent cover the following year. Loss of the perennial basal disc caused the alga to lose its space on the rock and allowed the invasion of other organisms (Hansen 1977). Both frond removal treatments were not significantly different from controls because the basal discs were spared.

Limitations and Conclusions

These experiments did not assess the effects of harvesting on the associated community. Pieces of macroalgae that break off of growing fronds enter the food web as detritus. Duggins and Eckman (1997) showed *Alaria* and *Laminaria* to be an important food source for invertebrates once the secondary metabolites had been leached from the frond. Harvesting would reduce this food source.

The findings in these experiments represent the first two years of a three year study. The results to date suggest these species can support sustainable harvesting. These data suggest that leaving the holdfast allows for the fastest recovery in most cases and recovery is evident after one year. The biomass of all experimental and control plots will be compared at the end of three years to fully assess recovery. Associated fauna will be collected during this time and compared between treatments. These results will provide data useful in drafting plans for the management of Oregon's algal resource.

BRIDGE I

The previous chapter examined the effects of different harvest times, amounts, and methods. All species reached initial density after most treatments one year following harvesting. Harvest time and amount had little effect on recovery. Sparing the holdfast allowed for faster recovery in most cases. These data suggested that the marine algae of Oregon can support a commercial industry. Chapter III uses the results from the harvest experiments to recommend a management strategy that would protect Oregon seaweed from overexploitation. I suggested harvest times, methods, and removal amounts to reduce harvest impacts on the recovery of the five species examined.

CHAPTER III

PROPOSED MANAGEMENT RECOMMENDATIONS FOR THE HARVEST OF FIVE MACROALGAL SPECIES ALONG THE OREGON COAST

Here I present suggestions recommendations for the harvest management of the five species discussed in the previous chapter. These suggestions are based on the data collected during the first two years of a three year study. Data collected from the third year may result in changed the following management strategies recommendations. In addition, these recommendations may be inappropriate during years with anomalous climate conditions. For example, the warm phase El Niño Southern Oscillations may reduce nutrient input leading to longer recovery periods for harvested algae. I will begin with general recommendations for the management of algal harvesting along the Oregon coast and then suggest species-specific management strategies (Table 1).

The macroalgae of Oregon can potentially support a commercial harvest. Strict management, however, will be required to prevent overexploitation. Prior to issuing of harvest permits, Oregon Parks and Recreation Department (OPRD) should survey the coast and delineate areas suitable for harvest. These areas should support an abundance of macroalgae. If they occur in state park boundaries, other criteria (e.g. preserving a

natural environment for park visitors) may be relevant but are not considered here. Algal spore dispersal distance are often relatively small (see Daton 1973; Reed *et al* 1988). Therefore, I recommend harvests to occur along straight transect lines parallel or perpendicular to shore through dense beds of target species. Based on the size of my experimental plots, I recommend these transects should be 50cm wide and 50 meters long with 100 meters between each harvest transect. Harvesting along transects would allow spore dispersal into the harvested areas from neighboring plants.

To finance the cost of enforcement, OPRD might consider selling permits. Applications for harvest should specify which species are to be harvested and where. The permittee would be required to report wet weights of all harvested species, take pictures of harvested areas before and after removal, and estimate percent of standing crop harvested. These data would help the state further manage the harvest of marine algae.

Alaria marginata

Alaria grows rapidly following harvesting. Data from harvest experiments suggest that two crops of *Alaria* can be produced during one growing season. The timing of the first harvest should be between April and May to allow plants to recover before a second harvest in August. My data suggests that *Alaria* can fully recover from two harvests within one year. *Alaria* should be harvested by cutting the frond at least six inches (\approx 12cm) above the stipe. This allows for the meristems and the sporophylls to be spared which facilitates recovery. The highest recruitment and plot densities were seen in

plots where the holdfasts and sporophylls were not removed. My experiments removed 68.6 kg (\approx 151 lbs) of *Alaria* wet weight from a study site and full recovery was seen within one year. James Jungwirth of Nature Spirit Herbs and Sea Vegetables, the sole current permittee, harvests 400 lbs of *Alaria* under an experimental commercial harvest permit with no apparent impact in subsequent years. My plot sizes and harvest amounts, however, are too small to suggest that any amount greater than what I took will have no detectable impact.

Laminaria setchellii

Net growth of *Laminaria* was slow following harvesting. *Laminaria* should be harvested only between March and May to allow for the intra-annual recovery of the harvested individuals. Harvest experiments showed that the method of removal had no measurable effect of removal method on recovery. The scale of my experiments, however, may have been too small to detect significant effects of holdfast removal. It is thereforeTo be cautious, I am recommending that fronds should be cut at least 6 inches (\approx 12cm) from the stipe. I removed 46.5 kg (\approx 102 lbs) of *Laminaria* wet weight from a site and full recovery was evident within one year. Jungwirth is allowed 400 lbs under his permit. My experiments found significantly higher plot density following recovery when larger amounts were50% of *Laminaria* were harvested in plots than when lesser amounts were harvested. This result suggests that larger amounts could be taken without affecting recovery. , hData are not available, however, to recommend an upper limit of harvest amount.

Fucus gardneri

Fucus failed to grow following harvesting since cutting removed the apical meristems, preventing further growth of harvested individuals. Furthermore, harvesting removed the reproductive structures of *Fucus*. Recovery, therefore, was dependent on neighboring individuals. In this study, removal method had no measured effect on *Fucus*. However, previous work has shown that recovery was significantly longer when all holdfasts were removed from a plot (Speidel 2002). Therefore, *Fucus* should be harvested by cutting the frond at least six inches ($\approx 12\text{cm}$) above the holdfast. My experiments found no significant differences in biomass between May harvest and control plots, but did find significant differences between June harvest and control plots. Therefore, I recommend *Fucus* be harvested only between April and May to facilitate intra-annual recovery. I removed 7.3 kg (≈ 16 lbs) wet weight of *Fucus* from a site without measured effects. Jungwirth is allowed 800 lbs of *Fucus* annually. *Fucus* is vulnerable to overexploitation because recovery is dependent on neighboring individuals repopulating harvested areas. I therefore, cannot safely recommend harvest amounts greater than those which I removed.

Mastocarpus papillatus

Harvesting of *Mastocarpus* removes the apical meristems preventing further growth within the harvest year. However, I observed full recovery one year after

harvests. Biomass comparisons between May harvest, June harvest, and control plots produced no significant differences. Therefore, I recommend *Mastocarpus* be harvested between May and August. Removal method had no measurable affect on *Mastocarpus* suggesting recovery can occur either by regrowth from spared holdfasts or settlement of new recruits. *Mastocarpus* can be harvested by cutting the frond or pulling off the holdfast. I removed 2.2 kg (\approx 4.8 lbs) wet weight of *Mastocarpus* from a site with no detectable effect. I found no significant differences in recovery between removal amounts suggesting greater amounts could be harvested without effect. , hHowever, more data are needed to set an upper harvest limit.

Mazzaella splendens

Harvesting removes the apical meristems of *Mazzaella* preventing further growth within the harvest year. Additionally, harvesting removes all life-history stages of *Mazzaella*. I found no significant differences in biomass between June harvest and control plots. This suggests *Mazzaella* can be harvested between June and August and recover intra- and inter-annually. The removal of *Mazzaella* holdfasts resulted in significantly lower percent cover one year after harvest. Therefore, I recommend *Mazzaella* should be cut at least 4 inches (\approx 8cm) above the holdfast. *Mazzaella* should not be harvested in such a way that the holdfast is removed. I was unable to test the effects of different harvest amounts for *Mazzaella* and therefore, cannot make recommendations as to harvest limits.

Table 1. Recommended Management Strategies for the Harvest of Five Macroalgal Species of Oregon.

Species	Harvest time	Harvest method	Harvest amount per transect
<i>Alaria marginata</i>	April to May August	Cut 6 inches above stipe	150 pounds/year
<i>Laminaria setchellii</i>	March to May	Cut 6 inches above stipe	100 pounds/year
<i>Fucus garneri</i>	April to May	Cut 6 inches above holdfast	15 pounds/year
<i>Mastocarpus papillatus</i>	May to August	Cut frond or pull holdfast	5 pounds/year
<i>Mazzaella splendens</i>	June to August	Cut/tear 4 inches above holdfast	No Data

BRIDGE II

The previous two chapters dealt with effects of seaweed harvest and possible management strategies. Chapter II examined the effects of seaweed harvest on the harvested species only. Potential impacts on the associated community were not assessed and . Accordingly, the management recommendations presented in Chapter III do not consider those possible impacts. Examination of associated communities is needed before any potential full effects from harvesting can be elucidated.

Chapter IV provides a first step in understanding the community dynamics of marine macrophytes. The following chapter gives a detailed analysis of the epiphytic diatom community upon *Mastocarpus papillatus* (C. Agardh) Kützing. Additionally, I examine temporal changes in this community structure over a growing season and examine the role of grazing by *Littorina keenae* in changing epiphytic community structure. These data will allow comparison of epiphytic communities to be used as an additional metric to assess recovery of *M. papillatus* after harvesting. The information is also valuable in itself. Epiphytic communities in estuaries have been well studied, but similar communities in the rocky intertidal are virtually unknown.

CHAPTER IV

ANALYSIS OF THE EPIPHYTIC DIATOM COMMUNITY UPON THE MACROALGA *Mastocarpus papillatus* (C. Agardh) Kützing

Introduction

Micro-organisms have often been used as metrics to assess various environmental factors. Fecal coliforms are common indicators of sewage contamination and bacterial diversity has been used to test restoration success (Milbrandt 2003). Epiphytic diatoms are used as biomonitors of water quality (Kelly *et al* 1998) and have been used to assess habitat fidelity (Winter and Duthie 2000), disturbance (Luttenton and Rada 1986), and paleolimnological conditions (Christie and Smol 1993). Diatoms are good bio-indicators because the silicified frustules are taxonomically distinct and easily preserved and variations in community composition track environmental conditions (Christie and Smol 1993). Epiphytes are ideal indicators of nutrient loading because they quickly respond via changes in their community structure. Experiments have shown that the epiphytic assemblage of *Zostera marina* L. changed following nutrient addition both in the laboratory (Coleman and Burkholder 1994) and *in situ* (Coleman and Burkholder 1995), making these epiphytes good indicators of eutrophication.

Epiphytic diatoms are also important components of estuarine communities because of their significant role in the food web. The primary production of algal epiphytes has been estimated at times to be greater than that of the substrate providing seagrasses (Morgan and Kitting 1984; Kitting *et al* 1984; Mazzella and Alberte 1986). Epiphytic diatoms also have high nutritional value and likely lack the phenolic compounds found in seagrasses that inhibit herbivory (Zimmerman *et al* 1979; Harrison 1982). Studies have shown epifaunal grazers derive more nutrition from algal epiphytes than seagrasses (Kitting *et al* 1984; Harrison 1982; Howard 1982). These properties make epiphytes important determinates in epifaunal abundances and assemblages (Hall and Bell 1988; Nelson 1997).

Like estuaries, the rocky intertidal is a dynamic and productive system, yet epiphytic communities have been less well studied. Macroalgae are the dominate vegetation of the intertidal zone, and they provide substrate for epiphytic colonizers.

Despite their importance, algal epiphytes in rocky bottom systems have been the subject of few ecological investigations. Belegatis *et al* (1999) examined the epiphytic community of *Cystoseira* species and Christie *et al* (1998) assessed epiphyte recolonization following kelp harvest. However, both these studies focused on macroepiphytes. Additionally, epifaunal abundance on marine macroalgae has been linked to epiphytic biomass (Hagerman 1966; Gunnill 1982; Johnson and Scheibling 1987). Yet, to date no studies have attempted to quantify and describe the microepiphytic community of intertidal macroalgae.

Given the use of epiphytic diatoms in assessing environmental factors (i.e., water quality, habitat fidelity, disturbance) and their importance in energy cycling (O'Quinn and Sullivan 1983), it is important to establish a community baseline in the rocky intertidal. This study identified and catalogued the epiphytic diatom community on the macroalga *Mastocarpus papillatus* (C. Agardh) Kützing throughout a growing season. These data may be useful in assessing recovery from disturbance events such as trampling, harvesting, or oil spills. Furthermore, this work provides a first crucial step in using these organisms as a nutrient indicator in open coastal areas.

Materials and Methods

Diatom communities were analyzed from dried samples of *Mastocarpus papillatus* (Rhodophyta) archived from a harvest study. Three monthly replicates were analyzed beginning in May 2002 and continuing through September 2002. All samples were collected from Lone Ranch Creek (42°05.98'N, 124°20.91'W, Fig. 19) in Samuel H. Boardman State Park, Oregon, USA from the same cove and tidal level. Collected *M. papillatus* were briefly rinsed in freshwater to remove all macrofauna and then dried in an oven set at 60°C for 14 days.

Initial comparisons of epiphyte abundance between rinsed samples (dipped in freshwater) and unrinsed samples were made. Aliquots from these samples were counted using a hemocytometer. Comparisons were analyzed by a student's T-test. No significant difference was found in epiphytic abundance between rinsed and unrinsed

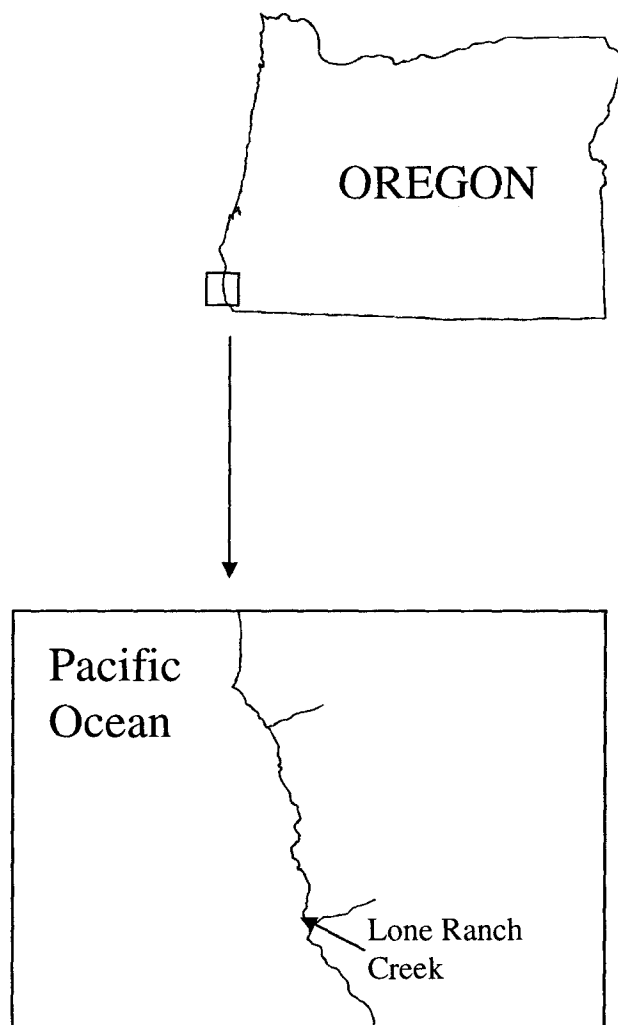


Figure 19: Location of Lone Ranch Creek. All samples of *Mastocarpus papillatus* were collected at this site.

samples ($t= 3.18$, $p<0.468$). Rinsing *Mastocarpus* in freshwater had no effect on epiphytic abundance.

Dry weight of *Mastocarpus papillatus* was correlated with surface area so surface area estimations could be made from archived samples. Samples for analysis were collected on 6th July, 2003. I assumed that this correlation would not differ between months and years. Surface area was measured using the program OPTIMUS (Optimus Corporation) and correlated with known sample weights. Measured surface area was doubled to account for both sides of the frond. Surface area was natural log transformed and correlated with dry weight. There was a strong correlation between the natural log of surface area and the dry weight of *Mastocarpus* ($r^2=0.881$, $n=108$, $p< 0.0001$, Fig. 20). Algal dry weight is a good predictor of surface area.

The bumpy surface of *Mastocarpus* was not scraped to remove algae. Rather, three 0.5g replicate samples of *Mastocarpus* from each month were chemically digested by submergence in concentrated KMnO_4 for 14hrs. Equal portions of 18M HCl was added to the solution and gently warmed at 75°C in a sand bath for 4hrs. Samples were washed six times by centrifuging at 15,000 rpms for 20 minutes or until the solution pH was neutral and diluted with distilled water to 40mL. One milliliter aliquots from each replicate were analyzed. Ten slides with 100 μL each per sample were mounted in NAPHRAX. Transects were counted across the cover slip of each slide. Fifty valves were identified and counted per slide so that each replicate was rarefied to 500 individuals. Diatoms were identified according to Hustedt (1962), Hendey (1964), Ricard (1987), Round (1990), and Hartley *et al* (1996). The area of transects and the

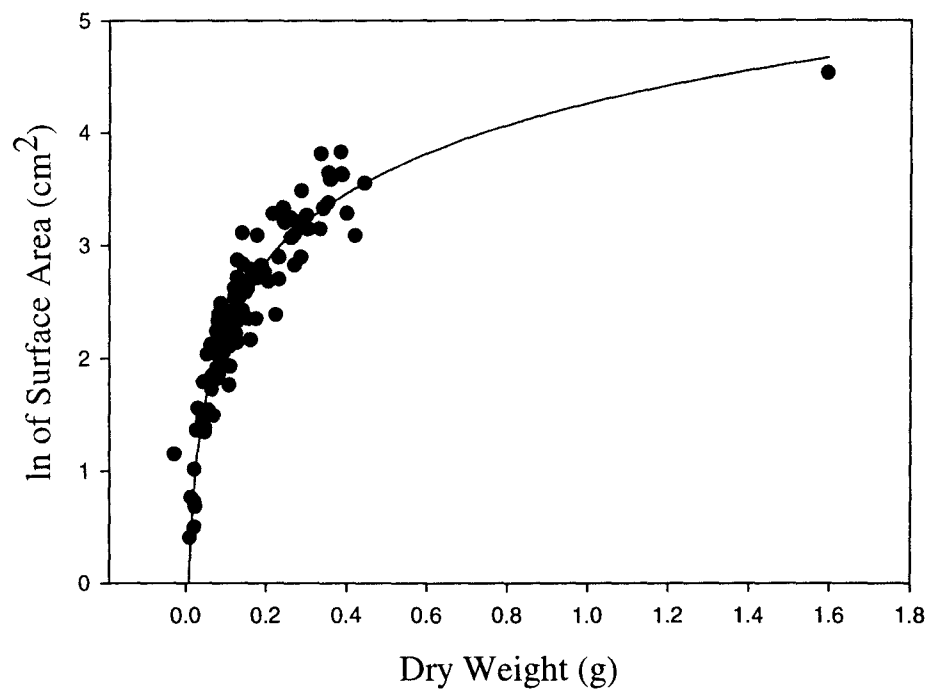


Figure 20: Correlation between the ln of Surface Area and the Dry Weight of *Mastocarpus papillatus* ($r= 0.881$, $n=108$, $p<0.0001$).

volume on each slide was used to calculate diatom abundance per mm² on the host alga. The total number of all araphid and centric species were divided by two and either the p or r-value was counted for raphid species to avoid over estimation.

Changes in epiphytic abundance were analyzed with a one-way ANOVA with different months or days as treatments. A Bonferroni *post-hoc* test was performed on all significant results. A non-parametric Kruskal-Wallis test was used if the assumptions necessary for an ANOVA were violated.

Mastocarpus blades were sampled intensely between 15 July, and 18 July, 2003. Three replicates were collected each day for analysis. All samples were collected from the site described above and treated in the same manner. Analysis was the same as described above. This was done to ensure that any patterns seen over a monthly scale were not just an artifact of the day samples were collected.

Changes in epiphytic diversity were measured with the Shannon-Weiner index.

$$H = -\sum_{i=1}^i (P_i * \ln P_i)$$

where P_i represents the proportion of the i^{th} species in the sample. Differences in epiphytic diversity were measured using an ANOVA with month or day as the treatment factor. Changes in epiphytic communities were measured by creating a similarity index using the Bray-Curtis coefficient where y_{ij} represents the i th row (species) and j th column (species abundance) in the generated data matrix (Clarke and Warwick 2001). Non-

$$S_{jk} = 100 \left\{ 1 - \frac{\sum_{i=1}^p |y_{ij} - y_{ik}|}{\sum_{i=1}^p (y_{ij} + y_{ik})} \right\}$$

metric Multi Dimensional Scaling (MDS) plots and cluster diagrams were made from 4th root transformed similarity matrices. One-way ANOSIMs were used to test for differences in epiphytic communities across different months and different days. All univariate analyses were performed using the statistical software package Statistica 6.0 (Statsoft). Multivariate statistics analyzed with the statistic package PRIMER E (Clarke and Gorley 2001).

Littorina keenae removed from samples collected between 15 and 18 July 2003 were analyzed for ingested diatoms. Snails were placed in MgCl₂ and all soft body tissue was removed and chemically digested as described above. Littorine gut contents were qualitatively sampled and mounted in NAPHRAX. Diatom valves were counted as described above and compared to the ambient epiphytic community using the same multivariate statistical methods.

Results

A total of 38 diatom taxa were identified from *Mastocarpus* fronds (Appendix B, Table 8). *Cocconeis scutellum* was the most abundant species in all samples, however, its abundance increased over the growing season. The abundance of *C. scutellum* (Fig. 21) was lowest in May with a mean of 232.6 (± 27.8 S.E.) per rarified sample, and increased to its highest value of 380.3 (± 14.3 S.E.) in July.

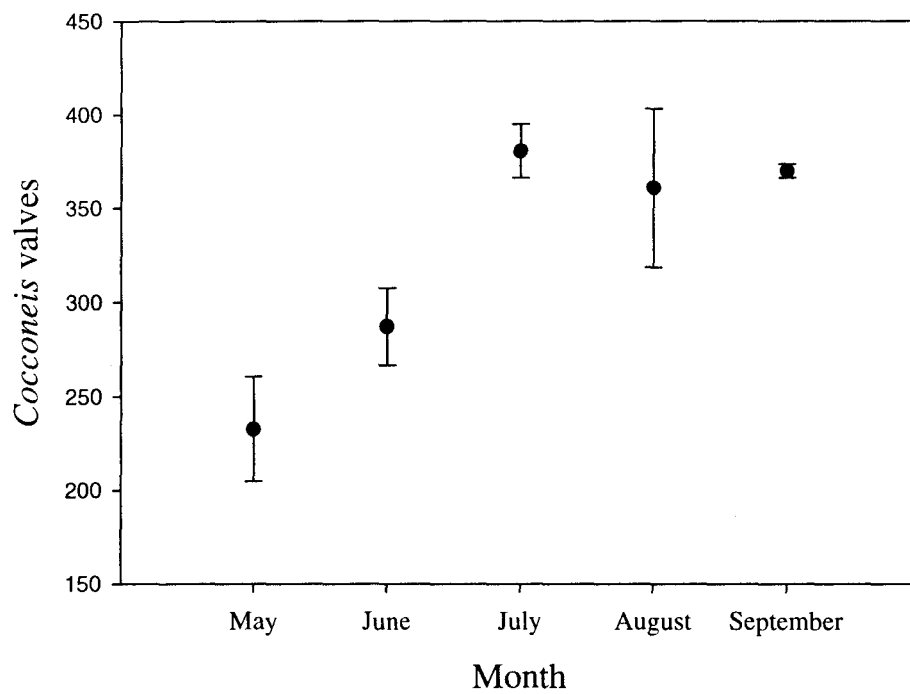


Figure 21: Mean Numbers of *Cocconeis scutellum* Valves Counted per Sample. Error bars show one standard error from the mean.

Abundance differed significantly during the 2002 growing season ($\chi^2=12.32$, $p=0.015$, Fig. 22a). Abundance was the lowest in May with 79.5 cells per mm^2 (± 20.3 S.E.) and peaked in July with 3361.2 cells per mm^2 (± 87.9 S.E.). Abundance declined slightly during August and September. Shannon-Weiner diversity (H') also differed significantly ($F=9.889$, $p<0.0017$, Fig. 22b). Diversity peaked in May with a mean $H'=1.907 \pm 0.14$ S.E. and reached a low in July ($H'=.9688 \pm 0.14$ S.E.). Post-hoc analyses revealed significant differences between May diversity and July, August, and September diversity. The four day intensive sampling period yielded no significant differences in epiphytic abundance and diversity ($F=0.433$, $p=0.735$, Fig. 23a and $F=1.35$, $p=0.325$, Fig. 23b, respectively).

The MDS plot and cluster diagram showed that samples from both May and June grouped closely (Figs. 24a and 24b). July, August, and September samples yielded no distinct grouping in the MDS. The ANOSIM comparing epiphytic communities across months produced a global R of 0.370 ($p=0.006$), suggesting distinction between monthly communities. Pair-wise testing found a strong distinction between the epiphytes of May and July ($R=0.889$). This was further supported by the May and June replicates grouping closely and independently. The May community was also distinct from August ($R=0.741$). Other pair-wise tests failed to produce significant differences between communities sampled during a month. There was little distinction between communities sampled on consecutive days ($R=0.275$, $p=0.019$, Fig. 25a).

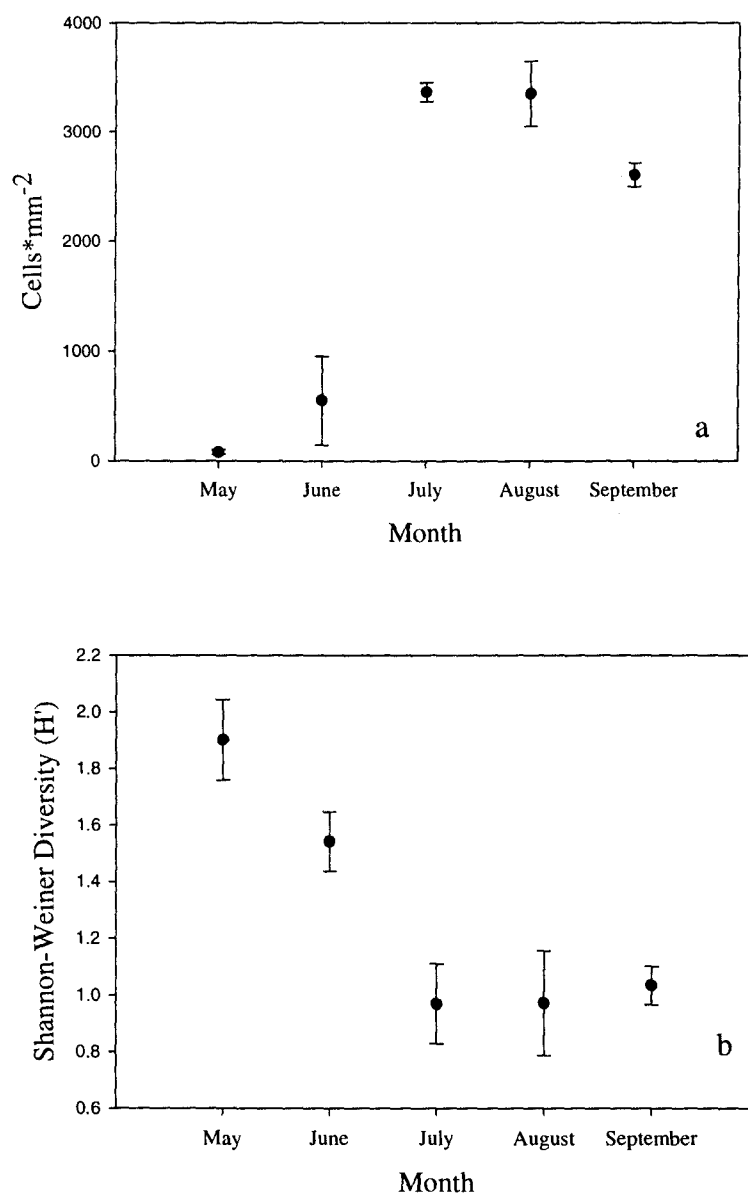


Figure 22: Epiphytic Diatom Patterns over the 2022 Growing Season. Mean epiphyte (a) abundance and (b) diversity is shown with data points. Error bars show one standard error from the mean.

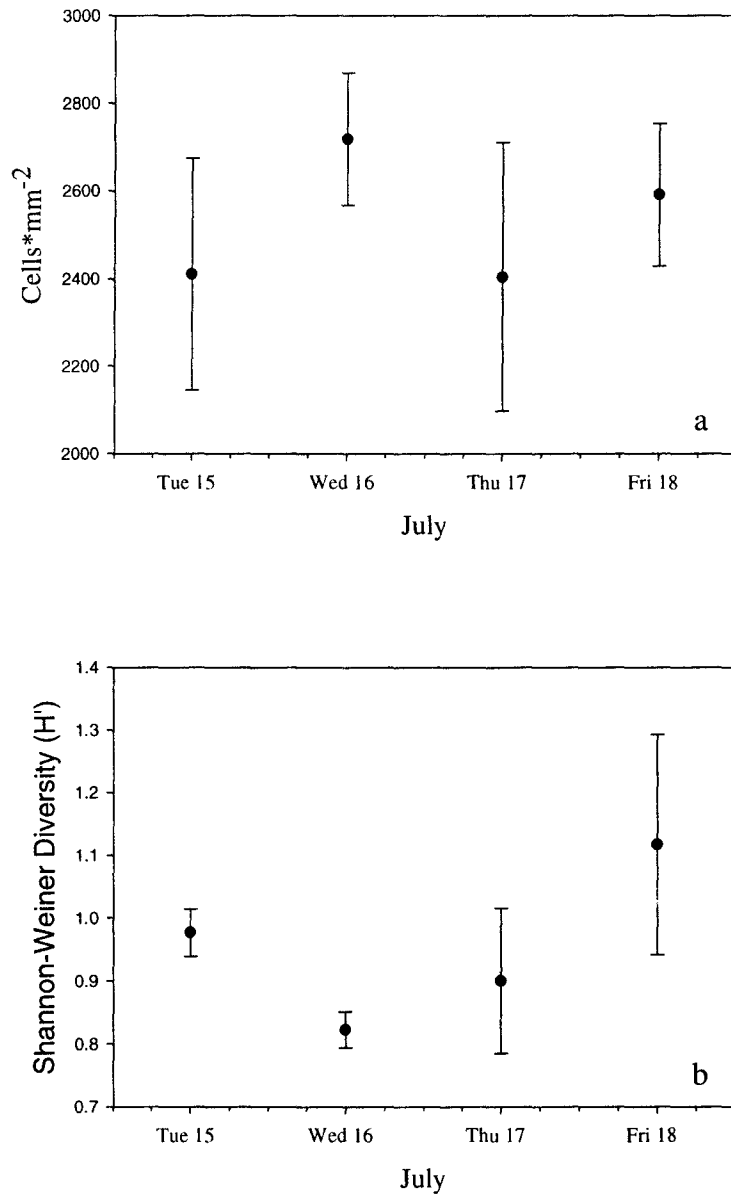


Figure 23: Epiphytic Diatom Patterns over Four Consecutive Days in 2003. Mean epiphyte (a) abundance and (b) diversity is shown with data points. Error bars show one standard error from the mean.

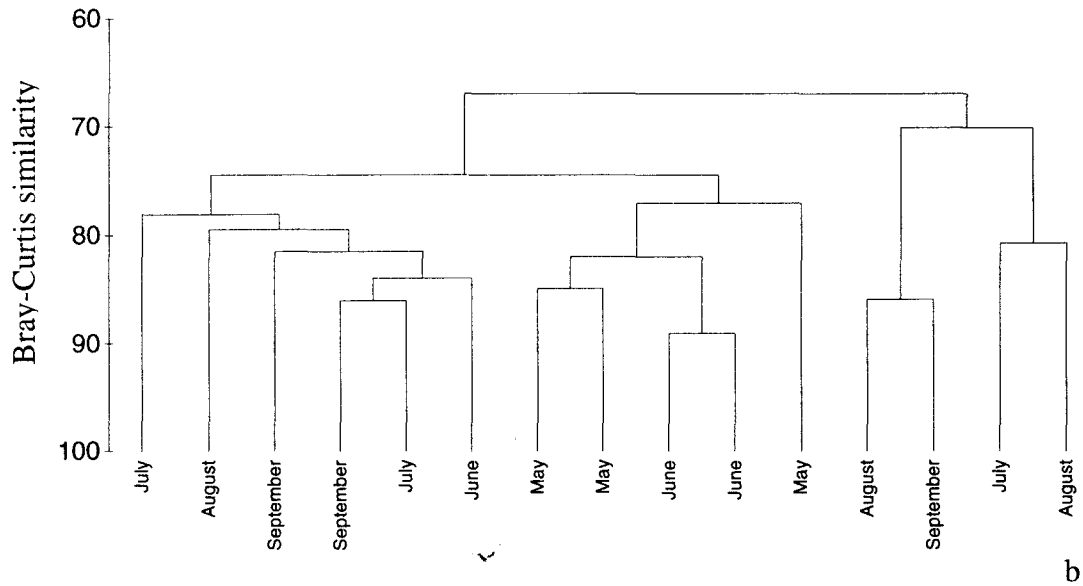
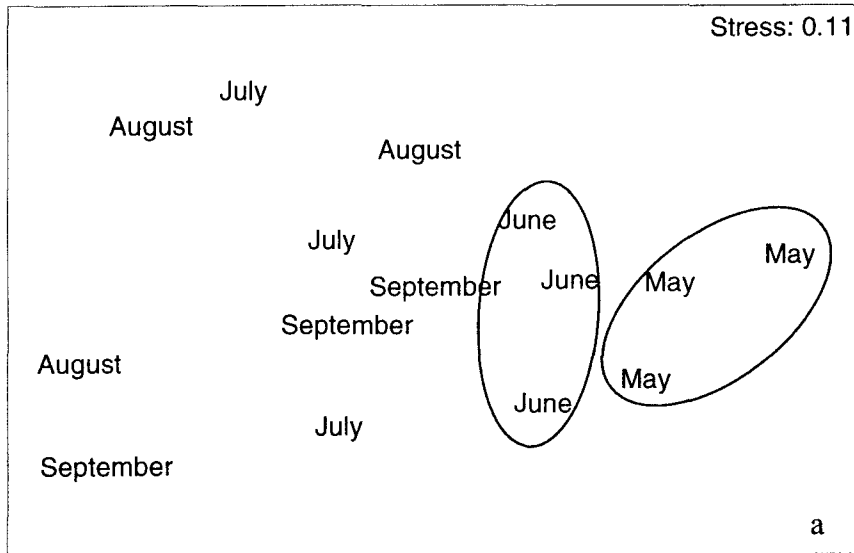


Figure 24: Epiphytic Community Patterns in 2002. Communities are shown with (a) MDS plot and (b) cluster diagram. Both figures are based on Bray-Curtis similarity matrices from 4th root transformed data.

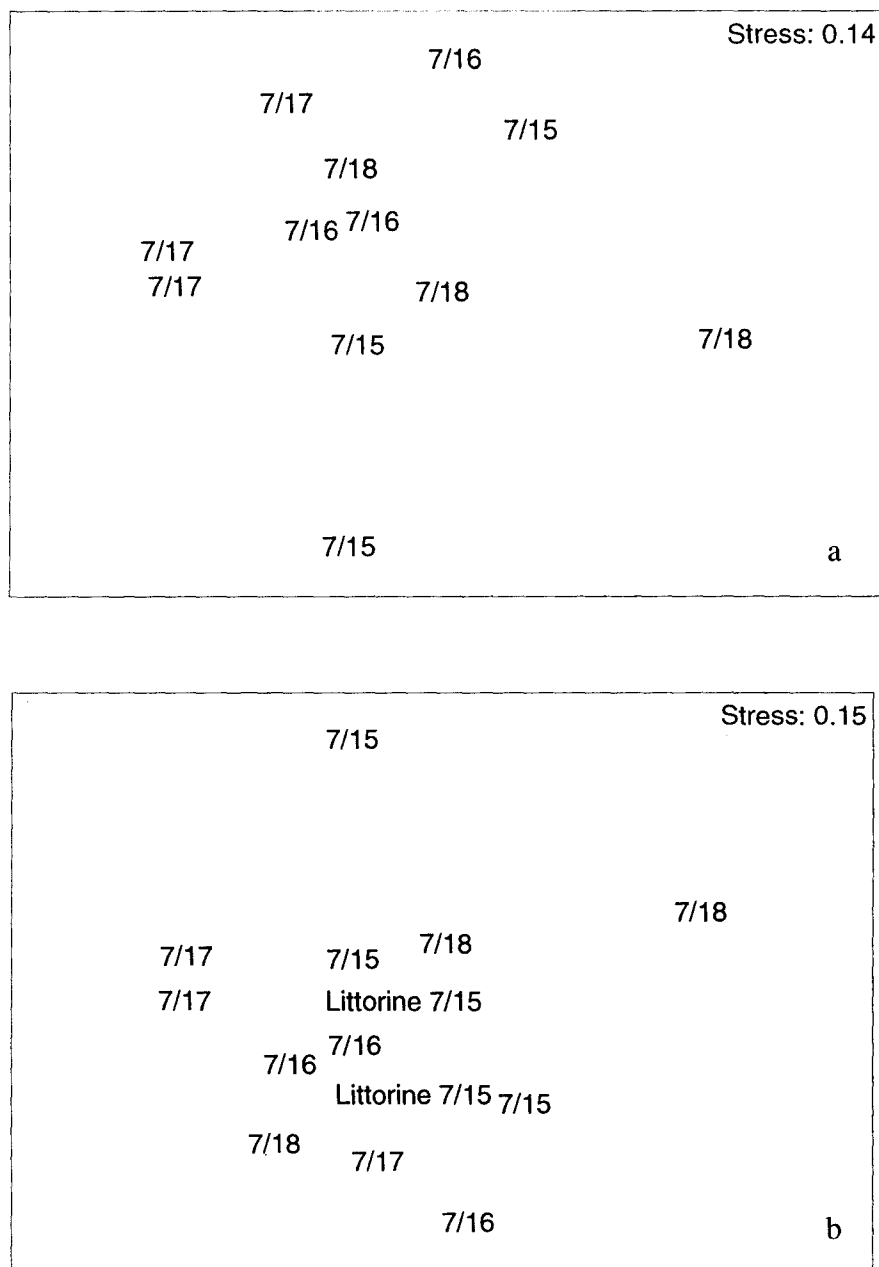


Figure 25: MDS Plots of the Epiphytic Communities from 2003. Communities are from (a) four consecutive days in 2003 and (b) with littorine gut diatom community superimposed.

The analysis of littorine gut diatoms showed no evidence of selective feeding. The gut diatom community grouped closely with the ambient epiphytic diatom community from the same sampling day (Fig. 25b).

Discussion

The epiphytic community of *Mastocarpus* changed over the growing season between May and September. The changes in *Mastocarpus* epiphytes were directional in the early portion of the season with distinct May and June communities. However, distinct monthly communities broke down beginning in July. That is, the community distinctions broke down when abundance increased and diversity decreased. The decrease in diversity was attributed to the dominance of *Cocconeis scutellum*, which comprised nearly eighty percent of valves identified in the July, August, and September samples. This dominance would, in turn, increase the index of similarity between samples and obscure distinctions between monthly communities.

Seasonal succession has been demonstrated in planktonic diatom communities (Sancetta 1989; McQuoid and Hobson 1995; Hobson and McQuoid 1997; Tilstone *et al* 2000; Rousseau *et al* 2002). A host of biotic and abiotic factors have been attributed to drive these successional processes such as silica availability (Rousseau *et al* 2002), diatom resting stages (McQuoid and Hobson 1995), and nutrient availability (Kamykowski and Zentara 1985). These patterns have been observed in many places

around the globe and can be relatively predictable. Changes in attached diatom communities have received less attention. Amspoker and McIntire (1978) reported on the distribution of intertidal diatoms in the Yaquina estuary, Oregon and found sediment size and salinity to be determinates in species composition, explaining community differences between sites. Salinity and sediment size are not responsible for the epiphytic patterns observed upon *Mastocarpus* at Lone Ranch Creek. There is minimal freshwater input so salinity is unlikely to change and the substrate was constant between samples. Epiphytic diatoms communities in the Yaquina estuary were also found to be strongly determined by desiccation as well as biotic factors such as host-epiphyte interactions (McIntire and Overton 1971). Desiccation stress should vary little between sampling dates because between the spring and fall equinox all extreme tides occur during the daylight and all samples were taken from the same tidal height. Interactions with *Mastocarpus* could possibly be an important factor structuring the epiphytic community. However, since the fronds displayed little net growth between May and September, possible interactions should not vary between sampling dates. Any possible interactions are likely minor because the quality (size, thickness, stipe strength) of *Mastocarpus* remained unchanged between May when the epiphyte load is low and September when there was high epiphytic abundance. A seasonal pattern is likely to exist in this system because the basal disc of *Mastocarpus* is perennial, but the frond is annual and, therefore, only available for colonization during the growing season.

With abiotic factors such as salinity, dessication, and substrate unlikely to be strong determinates in shaping these communities, the question remains: what forces the

observed changes? Grazers have been demonstrated to be important in altering the trajectories of algal succession in freshwater streams (Steinman *et al* 1989); benthic algal biomass decreased in streams subjected to herbivory. Furthermore, herbivory was responsible for slowing the natural succession of these communities. Similar results have been reported in intertidal diatoms from the Oregon coast where littorines and limpets reduced benthic diatom biomass significantly during the summer but not in the winter (Castenholz 1961). Experimental enclosures showed that littorines were able to clear diatom films and keep areas nearly denuded of benthic microalgae (Castenholz 1961). Diatoms are known to be a principle constituent of littorine diets (Castenholz 1961; Davies and Beckwith 1999; Worm and Sommer 2000). Thus, herbivory may be a strong determinate in the observed patterns of *Mastocarpus* epiphytes. My gut content results confirmed that *Littorina keenae* does feed on benthic diatoms. The results suggested, however, that they feed indiscriminately as evidenced by the lack of distinction between the epiphytic and gut diatom communities from the same day. The patterns observed by Steinman *et al* (1989) and Castenholz (1961) differed from mine in that the abundance of the *Mastocarpus* epiphytic community increased in the presence of herbivory. Herbivore density was not measured during the sampling days so community changes cannot be attributed solely to herbivore density. Exclusion experiments where littorines and other herbivores are kept from *Mastocarpus* fronds would accurately test the hypothesis that metazoan herbivory is shaping this epiphytic community. This would not eliminate the possibility that micrograzers are exerting pressure and driving community change.

Admiraal (1977) found grazing by ciliates were responsible for the change in species composition of benthic diatoms in a Wadden Sea mudflat.

Steinman *et al* (1989) found that a species of *Cocconeis* became the most abundant benthic species following increased herbivore density. The genus *Cocconeis* is a common epiphytic species with a global distribution (Hendey 1964). De Stefano *et al* (2000) found *Cocconeis* to be the dominate epiphytic genus upon *Posidonia oceanica* (L.) Delile in the Mediterranean Sea. *Cocconeis* was also the dominate genus in North Brittany mudflats during the winter, but was less dominate during the summer (Riaux-Gobin 1991). Conversely, in this study *C. scuttelum* was common in all monthly samples of *Mastocarpus*, but reached its highest abundance in July. Therefore, it is reasonable to assume that *C. scuttelum* is a successful competitor in this system. It may be more efficient in occupying space, acquiring nutrients and light, and surviving adverse conditions. Hudon and Bourget (1983) reported on the low light tolerance of the genus *Cocconeis*, and *C. placentula* is typically considered to be a shade specific species (Tuji 2000). Dense periphyton mats have been shown to induce physiological stress on individuals deeper in the mat through nutrient attenuation (Meulemans and Roos 1985; Hudon *et al* 1987).

Stevenson *et al* (1991) hypothesized that succession in a Kentucky stream was driven by late succession species reducing available nutrients to a level where early succession species can no longer survive, and then out competing them. This may be the most likely explanation for the increase in abundance of *C. scuttelum* upon *Mastocarpus* between May and August. Nutrients are usually high in May when *C. scuttelum* is

present but in lower numbers. *C. scutellum* may reduce the nutrient pool to levels where other species can no longer persist during periods between local upwelling events. The Oregon coast experiences intermittent periods between strong north winds and calm conditions (Huyer 1976). The north winds drive upwelling, which increases the nutrient pool (Mann and Lazier 1996). These nutrients are typically depleted by phytoplankton during the downwelling that occurs between upwelling events. This intermittent nutrient input may allow *C. scutellum* to gain a competitive advantage and dominate in the periphyton. This hypothesis, however, remains untested. Microcosm experiments with mixed species and various nutrient regimes could be performed to assess this possibility.

The forces shaping the community dynamics of *Mastocarpus* epiphytes and for the mid summer increase in *C. scutellum* remains unclear. However, the pattern of increasing biomass and decreasing diversity is not unique to this system. Diversity often decreases with increasing latitude and altitude. Communities at intermediate latitudes are dominated by fewer species well suited to prevailing conditions. Succession generally follows a path from a low diversity of early colonizers to a stable community with high relative diversity. However, climatic variations may lead to a climax community with lower diversity (Begon *et al* 1996).

CHAPTER V

CONCLUDING SUMMARY

There were two objectives of this thesis: (1) to explore possible impacts of commercial seaweed harvest in Oregon and to recommend strategies to manage the resource, and (2) describe the epiphytic diatom community of *Mastocarpus papillatus*. Data from these experiments were needed to prevent the overexploitation of Oregon's wild algae stocks. This work provides a first step in developing a sustainable commercial seaweed harvest industry in Oregon.

The goals of the experiments from Chapter II were to compare algal recovery following harvesting during different seasons, harvesting different amounts, and different harvest methods. The data suggested that all five species should be harvested in the spring. Only *Alaria marginata* supported a second late seasonal harvest. My experiments found no measurable effect of different harvest amounts, and, with the exception of *M. papillatus*, recovery increased when the holdfast was not removed. The results from these experiments suggested that Oregon's seaweed can support a sustainable commercial harvest if managed correctly as outlined in Chapter III.

The experiments from in Chapter IV catalogued the epiphytic diatom community upon *M. papillatus* and chronicled community changes over a growing season. A distinct pattern was seen starting with relatively high epiphytic epiphyte diversity and low

abundance early in the season shifting to relatively low diversity and high abundance in the mid to late summer. Similar patterns were not seen when communities were compared over four consecutive days. These patterns are were attributed to the mid season dominance of the diatom species *Cocconeis scutellum*. Comparisons of gut contents from the dominant epiphyte grazer *Littorina keenae* to ambient epiphyte communities eliminated herbivory as one possible process controlling the dominance of *C. scutellum*. *C. scutellum* may out out-compete other epiphytes leading to its dominance in this system.

APPENDIX A
STATISTICAL TABLES FROM CHAPTER II

Table 2. Man-Whitney U Tests Comparing Mean Lengths of Harvested and Unharvested Algae in August 2002.

Alaria setchellii

Hooskanaden Creek

	n	U	p
May Harvest vs. Control	5	34.0000	0.6203
June Harvest vs. Control	5	26.0000	0.5217

South Cove

	n	U	p
June Harvest vs. Control	10	24.0000	0.000364

Laminaria setchellii

Hooskanaden Creek

	n	U	p
May Harvest vs. Control	4	0.00	0.0017
June Harvest vs. Control	4	0.00	0.0055

South Cove

	n	U	p
May Harvest vs. Control	7	25.00	0.0080
June Harvest vs. Control	22	1.00	0.0000

Table 2. *continued.**Fucus gardneri*

	n	U	p
May Harvest vs. Control	4	0.00	0.0021
June Harvest vs. Control	4	0.00	0.0018

Mastocarpus papillatus

	n	U	p
May Harvest vs. Control	5	0.00	0.0045
June Harvest vs. Control	4	0.00	0.0014

Mazzaella splendens

	n	U	p
June Harvest vs. Control	5	2.00	0.0001

Table 3. ANOVA Source Tables Comparing Biomass of Season of Harvest Plots in 2002.

Alaria marginata

Hooskanaden Creek

Source	d.f.	MS	F	p
Harvest Month	2	23076.1	0.58527	0.5910
Error	5	39428.0		

South Cove

Source	d.f.	MS	F	p
Harvest Month	1	4760	0.23717	0.646857
Error	5	20071.6		

Laminaria setchellii

Hooskanaden Creek

Source	d.f.	MS	F	p
Harvest Month	2	1263.2	23.069	0.0008
Error	7	54.757		

South Cove

Source	d.f.	MS	F	p
Harvest Month	2	9943.9	3.81364	0.076
Error	7	2607.5		

Table 3. *continued.**Fucus gardneri*

Source	d.f.	MS	F	p
Harvest Month	2	663196	7.4247	0.0186
Error	7	89323		

Mastocarpus papillatus

Source	d.f.	MS	F	p
Harvest Month	2	39.817	0.22539	0.8047
Error	6	176.656		

Mazzaella splendens

Source	d.f.	MS	F	p
Harvest Month	1	34.706	0.97537	0.3687
Error	5	35.582		

Table 4. ANOVA Source Tables for Total and Germling Holdfast Density of Season of Harvest Plots in 2003.

Alaria marginata

Hooskanaden Creek

Total Holdfasts

Source	d.f.	MS	F	p
Harvest Month	3	301.026	0.438671	0.7309
Error	9	686.222		

Germling Holdfasts

Source	d.f.	MS	F	p
Harvest Month	3	210.906	0.267269	0.8474
Error	9	789.117		

South Cove

Total Holdfasts

Source	d.f.	MS	F	p
Harvest Month	2	192.952	0.786457	0.4844
Error	9	245.344		

Germling Holdfasts

Source	d.f.	MS	F	p
Harvest Month	2	43.369	0.629623	0.5547
Error	9	68.881		

Table 4. *continued.**Laminaria setchellii*

Hooskanaden Creek

Total Holdfasts

Source	d.f.	MS	F	p
Harvest Month	3	24.587	0.5783	0.6424
Error	10	42.517		

Germling Holdfasts

Source	d.f.	MS	F	p
Harvest Month	3	15.1111	0.66084	0.5947
Error	10	22.8667		

South Cove

Total Holdfasts

Source	d.f.	MS	F	p
Harvest Month	3	172.91	1.7440	0.2449
Error	7	99.14		

Germling Holdfasts

Source	d.f.	MS	F	p
Harvest Month	3	51.1111	0.87548	0.4980
Error	7	58.3810		

Table 4. *continued.**Fucus gardneri*

Total Holdfasts

Source	d.f.	MS	F	p
Harvest Month	3	31.504	0.41870	0.7435
Error	10	75.242		

Germling Holdfasts

Source	d.f.	MS	F	p
Harvest Month	3	2.5159	0.29368	0.8291
Error	10	8.5667		

Mastocarpus papillatus

Source	d.f.	MS	F	p
Harvest Month	3	1498.58	2.19404	0.1766
Error	7	683.02		

Mazzaella splendens

Source	d.f.	MS	F	p
Harvest Month	2	635.35	4.7616	0.06955
Error	5	133.43		

Table 5. Factorial ANOVA Source Tables for Total and Germling Holdfast Density of Selective/Method of Harvest Plots in 2003.

Alaria marginata

Hooskanaden Creek

Total Holdfasts

Source	d.f.	MS	F	p
Removal Method	1	13.762	0.09355	0.7660
Removal Amount	2	133.962	0.91068	0.4332
Method*Amount	2	534.115	3.63097	0.0652
Error	10	147.100		

Germling Holdfasts

Source	d.f.	MS	F	p
Removal Method	1	0.21066	0.05191	0.8243
Removal Amount	2	2.90917	0.71694	0.5117
Method*Amount	2	20.4228	5.03299	0.0307
Error	10	4.05779		

South Cove

Total Holdfasts

Source	d.f.	MS	F	p
Removal Method	1	26.694	0.10040	0.7573
Removal Amount	2	78.935	0.29689	0.7489
Method*Amount	2	123.432	0.46426	0.6404
Error	11	265.871		

Table 5. *continued.*

Germling Holdfasts

Source	d.f.	MS	F	p
Removal Method	1	0.1111	0.001732	0.9676
Removal Amount	2	13.7225	0.213856	0.8107
Method*Amount	2	107.5191	1.675622	0.2316
Error	11	64.1667		

Laminaria setchellii

Hooskanaden Creek

Germling Holdfasts

Source	d.f.	MS	F	p
Removal Method	1	12.9643	0.32752	0.5798
Removal Amount	2	24.1295	0.60959	0.5626
Method*Amount	2	10.3449	0.26134	0.7751
Error	10	39.5833		

Fucus gardneri

Total Holdfasts

Source	d.f.	MS	F	p
Removal Method	1	1.3444	0.07401	0.7917
Removal Amount	2	13.2365	0.72861	0.5090
Method*Amount	2	9.4032	0.51760	0.6127
Error	9	3.83333		

Table 5. *continued.*

Germling Holdfasts

Source	d.f	MS	F	p
Removal Method	1	5.87778	1.53333	0.2469
Removal Amount	2	3.45721	0.90188	0.4395
Method*Amount	2	9.60135	2.50470	0.1365
Error	9	3.83333		

Table 6. Kruskal-Wallis Test Results from Selective/Method of Harvest Plots of *Laminaria setchellii* at Hooskanaden Creek. Results are for total holdfast density only.

Source	d.f.	χ^2	p
Removal Method	1	0.2539683	0.6143
Removal Amount	2	7.8666667	0.0196

Table 7. ANOVA Source Tables for Plot Density of Selective/Method of Harvest Plots in 2003.

Laminaria setchellii

South Cove

Total Holdfasts

Source	d.f.	MS	F	p
Treatment	4	616.77	2.15960	0.1760
Error	7	285.60		

Germling Holdfasts

Source	d.f.	MS	F	p
Treatment	4	12.2083	0.586	0.6834
Error	7	20.8333		

Mastocarpus papillatus

Source	d.f.	MS	F	p
Treatment	4	1694.09	2.08647	0.1652
Error	9	811.94		

Mazzaella splendens

Source	d.f.	MS	F	p
Treatment	3	865.30	16.5766	0.0050
Error	5	52.20		

APPENDIX B
SUMMARY OF EPIPHYTIC DIATOM SPECIES ABUNDANCE OVER THE 2002
GROWING SEASON

Table 8. Summary of the Mean Relative Abundance of *Mastocarpus* Diatom Epiphytes Collected and Counted During the 2002 growing season. Estimations of relative abundance are indicated as follows: X = absent (0%), R = rare (<1%), C = common (1-10%), F = frequent (10-50%), and D = dominant (>50%).

Taxon	Sample Month				
	May	June	July	August	September
<i>Achnanthes brevipes</i> Agardh	X	X	X	X	R
<i>Achnanthes groenlandica</i> Cleve	R	R	R	X	R
<i>Achnanthes</i> spp.1	X	R	R	R	R
<i>Amphora exigua</i> Gregory	R	X	X	X	X
<i>Berkeleya rutilans</i> (Trentepohl ex Roth) Grunow	X	R	X	X	X
<i>Berkeley</i> spp.1	X	X	X	X	R
<i>Cocconeis californica</i> Grunow	F	F	F	F	F
<i>Cocconeis clandestine</i> A. Schmidt	R	C	R	R	R
<i>Cocconeis costada</i> Gregory	C	C	R	R	R
<i>Cocconeis scuttelum</i> Ehrenberg	F	D	D	D	D

Table 8. *continued.*

Taxon	Sample Month				
	May	June	July	August	September
<i>Cocconeis speciosa</i> Gregory	C	R	X	R	R
<i>Cuneolus skvortzowii</i> (Nikolaev) Medlin	R	R	R	R	R
<i>Fragilaria striatula</i> Lyngbye	X	R	R	R	X
<i>Gomphoseptatum aesuarii</i> (Cleve) Medlin	C	R	C	C	C
<i>Licmophora</i> spp. 1	R	R	X	X	R
<i>Navicula directa</i> (Wm. Smith) Ralfs in Pritchard	C	R	X	R	X
<i>Navicula distans</i> (Wm. Smith) Schmidt	C	C	R	R	R
<i>Navicula</i> spp. 1	X	X	X	R	X
<i>Navicula</i> spp. 2	R	R	R	R	R
<i>Navicula</i> spp. 3	X	R	R	R	R
<i>Navicula</i> spp. 4	X	R	X	X	X

Table 8. *continued.*

Taxon	Sample Month				
	May	June	July	August	September
<i>Navicula</i> spp. 5	R	R	R	R	R
<i>Navicula</i> spp. 6	R	R	R	X	R
<i>Navicula</i> spp. 7	X	X	R	X	X
<i>Nitzschia frustulum</i> (Kützinger) Grunow in Cleve et Grunow	R	R	R	R	R
<i>Opephora marina</i> (Gregory) Petit	C	C	R	C	C
<i>Opephora pacifica</i> (Grunow) Petit	C	C	C	C	R
<i>Parlibellus delognei</i> (Van Huerck) Medlin	R	R	R	X	R
<i>Pseudogomphonema kamtschaticum</i> (Grunow) Medlin	C	C	R	R	R
<i>Skeletonema costata</i> (Greville) Cleve	R	X	X	X	X
<i>Thalassionema nitzschioides</i> (Grunow) Grunow ex Hustedt	C	C	C	R	R

Table 8. *continued.*

Taxon	Sample Month					
	May	June	July	August	September	
<i>Thalassiosira</i> spp. 1	R	R	X	X	X	
<i>Thalassiosira</i> spp. 2	R	X	X	X	X	
Unknown 1	R	X	R	X	R	
Unknown 2	R	X	X	X	X	
Unknown 3	X	X	R	R	X	

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