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Jill C. Fegley

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**ECOLOGICAL IMPLICATIONS OF ROCKWEED,
ASCOPHYLLUM NODOSUM (L.) LE JOLIS, HARVESTING**

By

Jill C. Fegley

B.S. The Richard Stockton College of New Jersey, 1989

A THESIS

Submitted in Partial Fulfillment of the

Requirements for the Degree of

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(in Ecology and Environmental Science)

The Graduate School

The University of Maine

May, 2001

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Thesis Advisor: Dr. Robert L. Vadas

An Abstract of the Thesis Presented
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Harvesting of natural resources usually entails substantial removal of the target species. Where such species are dominant members of natural communities, their removal can have important consequences for their own regeneration as well as for the species assemblages associated with them. Rockweed is an ecologically and commercially important intertidal alga in the North Atlantic, and is increasingly being harvested in Maine. The effects of harvesting on regrowth are well known but little is known about its effects on the species that use this alga as habitat. This research focused on the ecological implications of *A. nodosum* harvesting on the associated community.

Three different harvesting regimes (uncut/control; cut at 18 cm; and cut at 36 cm) were imposed on four separate sites in mid-coast Maine, USA. Post-harvest changes in community structure were followed for two years (July 1997 to June 1999).

Removal of the seaweed canopy resulted in a loss of habitat and a decrease in several associated species. Significant effects were detected in individual species analyses and in community-level analyses. The intensity of the disturbance was an

important factor in the rate of recovery. Although numerous species within the community experienced short-term effects (1-2 years), few effects persisted through time. This suggests that a single harvest event can cause short-term changes to the community structure but that the community is resilient to this type of disturbance.

Considerable differences were found in the overall community structure. Species composition and relative abundances varied within and among the four sites. The apparent homogeneity of the *Ascophyllum* beds does not necessarily mean that the associated communities are similar. The spatial heterogeneity associated with the *Ascophyllum* community structure made it difficult to detect overall harvesting effects.

Ascophyllum population and morphological characteristics were affected by the harvest. The number of medium-sized shoots increased by 108% in the harvested plots. The number of branches at 18 cm and the number of apical dichotomies also increased in harvested areas. At the end of the experiment, control plants were found to be significantly longer (–32%) than the plants in the cut plots indicating a lack of complete recovery.

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Chapter 1

Introduction

Ascophyllum nodosum (L.) Le Jolis is a dominant, intertidal, brown alga on North Atlantic shores, where it occurs in both open coastal and sheltered estuarine habitats (Baardseth, 1970). Commonly known as "knotted wrack", it is one of the most abundant intertidal algae found on the coast of Maine where it dominates the mid-to-lower littoral zone in most estuaries and bays (Vadas et al., 1976; Keser et al., 1981; Topinka et al., 1981; Vadas and Wright, 1986). Availability of solid substrata, resistance to grazing, tolerance to temperature and salinity fluctuation, and intolerance to water motion are thought to be responsible for its patterns of abundance in the North Atlantic Ocean (Baardseth, 1970; Vadas et al., 1978; Chock and Mathieson, 1979; Stromgren, 1983; Vadas et al., 1990).

Individual plants can reach two meters in length on sheltered shores, but do not attain that size on more exposed shores (MacFarlane, 1952; Vadas and Ring, 1968; Vadas and Wright, 1986). Within a single site, exposure to wave action may result in great variation in growth, morphology and pigmentation over very short distances (Cousens, 1982). Main axes of the thallus are compressed and often dichotomously branched. All except the oldest parts of the thalli bear numerous, short, secondary lateral branches. At intervals along the axes, prominent air bladders are present to provide buoyancy to support the thallus while submerged. The formation of annual air bladders along the thallus provides a means for aging plants (Cousens, 1985). *Ascophyllum* has a relatively long life span (–10-12 years), compared to the two- to three-year life span of other

perennial fucoid algae (Keser et al., **1981**). Maximum age recorded for *Ascophyllum* plants in sheltered locations on the coast of Maine is 22 years (Fegley, personal observation).

The primary growing region of *Ascophyllum* is at the tips of the branches (apical meristem) where new cells are created by cell division (Moss, **1970**). The growing season in Maine is from April to November. Average annual growth rates in this region are approximately **8-11** cm per year (Vadas et al., **1976; 1978**).

Ascophyllum nodosum is dioecious. During the winter, in response to short photoperiod, small receptacles attached by short ~~stalks~~ form along the length of the plant (Terry and Moss, **1980**). The reproductive season starts with a considerable uptake of water by the receptacles, followed by the release of gametes in April or May, and ends with the shedding of the fruiting bodies. In Maine, the reproductive period of *Ascophyllum* follows a latitudinal gradient from west to east that is correlated with increasing water temperatures (Bacon and Vadas, **1991**). By mid-June all of the receptacles have dehisced and the plant's energy is primarily devoted to growth. Despite the large amount of energy devoted to reproduction (40-50% of the biomass in April is in reproductive structures), few zygotes grow and survive beyond one year, due in part to the high degree of mortality from wave action on exposed shores (Vadas et al., **1990**) and littorinid grazing on sheltered shores (Miller and Vadas, **1984**).

Easy access to large quantities of *Ascophyllum* has led to the commercial exploitation of this species in many countries where it is used for alginates, organic fertilizers and fodder. The largest industrial harvests of *Ascophyllum* are found in Western Norway, Britain, Ireland, Iceland, Northern France and Eastern Canada

(Baardseth, 1970). Although *Ascophyllum* has been harvested commercially in these areas for decades, only recently have similar large-scale harvests begun in the U.S.A., especially in Maine. Despite the absence of harvests in the past, biomass values in the Gulf of Maine are as high as the most productive Canadian and European shores (Keser et al., 1981; Cousens, 1984; Sharp, 1987).

The ecological effects of seaweed harvesting are not straightforward and depend on a number of factors, including the size of the clearance, the intensity of removal, the harvesting technique, the season of harvest, and the vulnerability of the species or habitat to perturbation (Sharp and Pringle, 1990; Schiel and Nelson, 1990). Although populations of *Ascophyllum* have been harvested for decades, little information exists on the impact of harvesting on the associated intertidal communities.

Seaweed canopies have long been identified as playing important community structuring roles by modifying the physical and biological conditions in the habitats where they dominate (Dayton, 1975; Menge, 1978; Eckman et al., 1989; Bertness et al., 1999). Structurally complex seaweeds, such as *Ascophyllum*, not only provide a secondary substratum for organisms to colonize but they also provide important habitats and refuges for a wide range of marine organisms (Duggins et al., 1990; Sebens, 1991). The structural complexity also alters the physical environment, thereby influencing the abundance and distribution of associated species (Bertness, 1999). Emergent algal or seagrass structure alters the quality and quantity of light reaching the substratum (Lobban and Harrison, 1994), increases sedimentation (Duggins et al., 1990), and changes the fluid dynamics near the seafloor, reducing local water flow and thus the transport of resources and propagules within the community (Jackson and Winant, 1983; Bodkin, 1988;

Eckman and Duggins, 1991 ; Irlandi and Peterson, 1991 ; Sebens, 1991). Removal of these habitats, or reduction of structural complexity within a habitat, can have important ecological consequences for the associated flora and fauna. This dissertation examines the ecological implications of harvesting *Ascophyllum nodosum* on the associated community.

Chapter 2

Short-term effects of *Ascophyllum nodosum* harvesting on the intertidal community

2.1. Abstract

Ascophyllum nodosum (rockweed) is an ecologically and commercially important intertidal alga in the North Atlantic and is increasingly being harvested in the Gulf of Maine. The effects of harvesting on regrowth have been studied but little is known about harvesting effects on the associated species that use this alga as habitat. Here, I test the effects of three harvest treatments (unharvested/control and harvested at 18 cm and 36 cm from the holdfast) at four intertidal sites in mid-coast Maine, USA. A single harvest (disturbance) event was imposed upon each site in June 1997. The short-term effects (< 1 year) of the various treatments on the associated macroscopic floral and faunal (non-fish) assemblages were examined to assess possible changes in community structure (e.g., species abundances and diversity).

Ten of the most common species were significantly affected by the harvesting of *Ascophyllum nodosum*. There were significant decreases in the percent cover of several understory algal species including *Fucus vesiculosus*, *Hildenbrandia rubra* and *Phymatolithon lenormundii*. Abundances of *Carcinus maenas*, *Dynamenapumila*, *Halichondria* sp., and *Littorina obtusata* were also negatively affected by the reduction in the canopy. *Nucella lapillus* abundance, however, increased in the plots that were intensively harvested. A change in the density of *Spirorbis spirorbis* was also observed but the direction depended on the intensity of the canopy removal. While abundances of

many organisms remained stable following the harvest, the intensity of the disturbance was an important factor in the recovery rate of those species that were affected. In conclusion, both the target species and the associated community are resilient to single perturbations at a moderate (– 36-cm cut) harvesting intensity.

Keywords: *Ascophyllum nodosum*; epifauna; habitat; invertebrates; macroalgal harvesting; rocky intertidal

22. Introduction

Ascophyllum nodosum is a dominant intertidal brown alga on the North Atlantic shores of Europe and North America, where it occurs in both open coastal and sheltered estuarine habitats (Baardseth, 1970). Commonly known as “knotted wrack”, it is one of the most abundant intertidal algae found on the coast of Maine where it dominates the mid-to-lower littoral zone in most estuaries and bays (Vadas et al., 1976; Keser et al., 1981; Topinka et al., 1981; Vadas and Wright, 1986). The existence of concentrated stands of *Ascophyllum* has encouraged harvesting in many countries where it is used for alginates, organic fertilizers and fodder (Baardseth, 1970). The largest industrial harvests of *Ascophyllum* are in Western Norway, Britain, Ireland, Northern France, Iceland and Eastern Canada (Baardseth, 1970). Biomass values in the Gulf of Maine (Keser et al., 1981) are as high as the most productive Canadian and European shores (Cousens, 1984; Sharp, 1987) where the alga is extensively exploited.

The Gulf of Maine is extensive (ca 3000 miles), and preliminary calculations suggest that the total standing crop could exceed one million wet metric tons (Keser et

al., **1981**). Sustained annual yields could easily be **30** to 40% of this value based on the biomass estimates of Topinka et al. (**1981**), the harvest-growth studies of Keser et al. (**1981**), and the productivity estimates of Vadas and Wright (**1986**). Although *Ascophyllum* is abundant along the Maine coast, in the past, it was harvested only in moderate quantities in the southern portion of the state. A recent increase in demand for the production of seaweed meal as a supplement to animal fodder **has** caused an increase in harvesting throughout the Gulf of Maine (Pers. comm., G. Hood, **2001**; Source Inc., Brunswick, Maine).

In marine systems, macrophytes that extend into the water column have a profound influence on coexisting plants and animals by providing physical structure to an otherwise structurally homogeneous environment (Irlandi and Peterson, **1991**). The emergent structure provides habitat for epibiota, influences fish orientation, alters the behavior of predators, increases shelter and changes fluid dynamics near the seafloor (Jackson and Winant, **1983**; Bodkin, **1988**; Eckman and Duggins, **1991**; Irlandi and Peterson, **1991**). Macroalgal canopies also reduce local water flow, light intensities and microalgal cover, and increase sedimentation (Duggins et al., **1990**). *Ascophyllum* not only provides habitat for species in the water column but its large size, branching morphology and perennial nature combine to provide a moist shelter for many marine organisms that otherwise could not survive the rigors of the intertidal habitat when exposed (Mathieson et al., **1976**; Hillson, **1977**).

By cropping marine plants, a layer of physical habitat is removed and with it the associated epibiota (Pringle and Sharp, **1980**). The ecological impact of macrophyte harvesting on the associated assemblages is related to the frequency and intensity of

exploitation, the harvesting technique and the vulnerability of the species or habitat to perturbation (Sharp and Pringle, 1990; Vasquez, 1995). Some potential negative effects of harvesting include loss of colonization space for other resources that initiate succession, loss or reduction of understory habitat, reduction of populations of fish or invertebrates and the removal of detrital carbon from the near-shore ecosystem (Foster and Barilotti, 1990; Vasquez, 1995; Lavery et al., 1999). Macrophyte harvesting also has been shown to lead to habitat (structural) changes in the short term (< 1 year) and changes in species composition and trophic structure in the longer term (> 1 year) (Sharp and Pringle, 1990; Serafy et al., 1994).

Numerous studies have assessed effects of harvesting on target species and determined limits for maintaining sustainable yields (Baardseth, 1970; Pringle and Sharp, 1980; Keser et al., 1981; Ang et al., 1996; Lazo and Chapman, 1996). Relatively few studies, however, have assessed the ecological impact of harvesting on the suite of organisms using rockweed as habitat.

Boaden and Dring (1980) examined an *Ascophyllum nodosum* bed in Northern Ireland 2.5 years after it was severely harvested (95% biomass removal). They found that *Mytilus* densities were lower but limpet (*Patella vulgata*) densities were higher. The cryptic and emergent fauna, including sponges and barnacles, was impoverished compared to that in an adjacent, unharvested area. The green crab, *Carcinus maenas*, was unaffected. Although this study was comprehensive regarding the types of species sampled, the lack of temporal and spatial replication limited the generalization of these results.

Harvesting of natural resources usually entails substantial removal of the target species. Where such species are dominant or important members of natural communities, their removal or loss may have important consequences for their own regeneration as well as for the species assemblages associated with them. This paper presents results of field manipulations at four locations in Maine that tested the general hypothesis that alterations of furoid canopy height (and hence its surface area) affects the abundance and composition of the associated faunal and floral community.

2.3. Materials and Methods:

2.3.1. Study sites

Four *Ascophyllum nodosum* beds with similar standing crops were selected in the mid-coast region of Maine (Fig. 2.1). All four sites were moderately sheltered, had a slope 15° or less, and supported a dense, continuous cover of *Ascophyllum* (>70% cover). Although an attempt was made to standardize sites by visually selecting stands of similar biomass, differences in standing crop between sites could not be avoided. Mean standing crop was approximately 9 kg/m², but individual sites ranged from 7 to 12 kg/m². Mean tidal amplitude of this region is 3.1 m and the mean tidal level is 1.7 m. Substrate at three of the sites (Castine - 44°27'8"N; 68°47'29"W, Blue Hill Falls - 44°22'21"N; 68°33'9"W and Lamoine Beach - 44°27'18"N; 68°16'34"W) consisted mainly of small to medium-sized granite rocks interspersed with sand and pebbles. Ledge was occasionally present. The substrate at the remaining site, Rackliff Island (43°59'28"N; 69°9'6"W), consisted of large bedrock outcroppings embedded in muddy substrate.

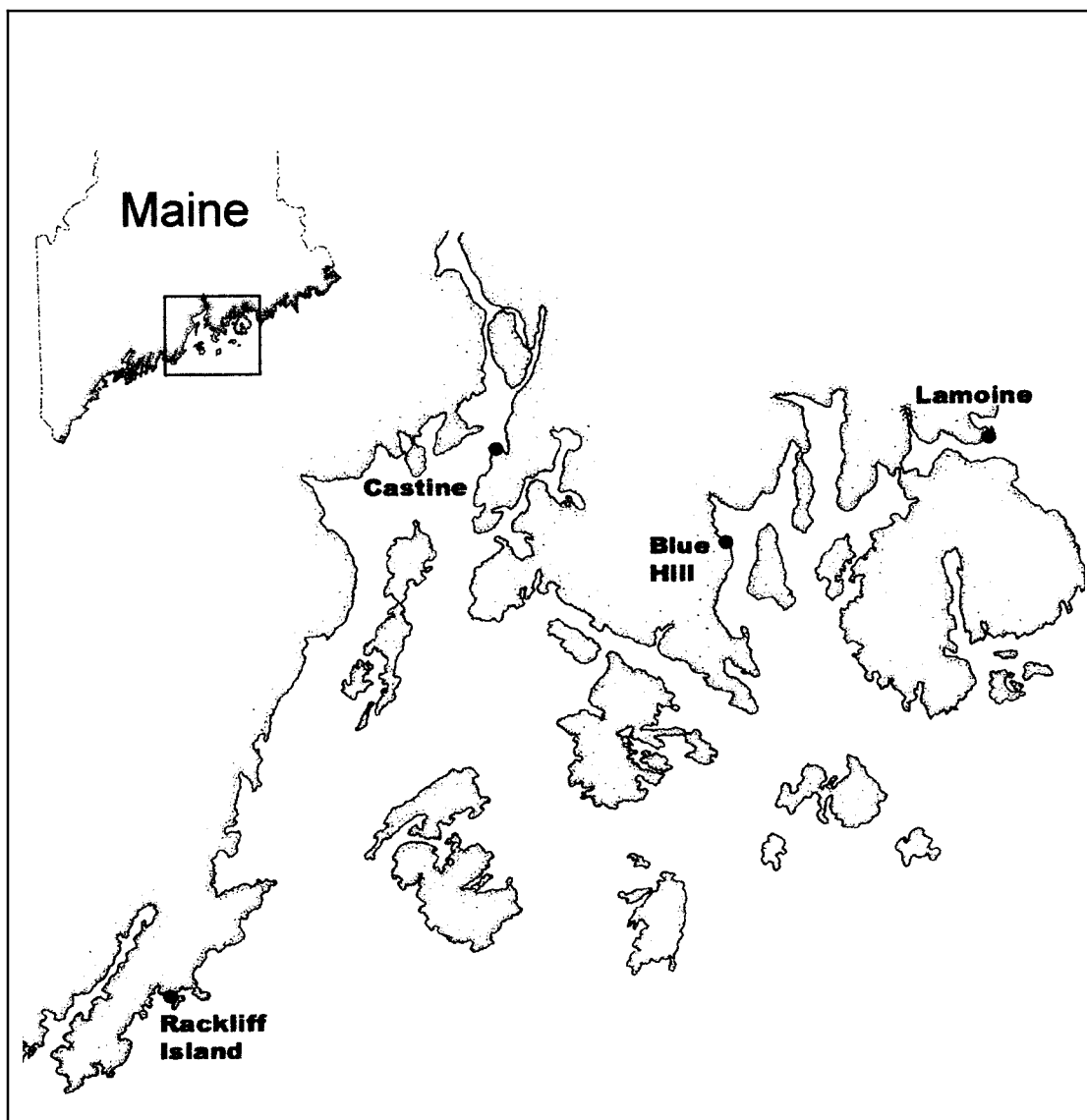


Figure 2.1. Location of experimental sites along the mid-coast region of Maine, USA.

2.3.2. Experimental design and sampling methods

The experimental design included four sites; each consisting of nine permanently marked 5 m x 5 m plots placed at mean low water. Each plot was a minimum of 5 meters from an adjacent plot to assure treatment independence. Three different treatments were imposed on the plots: (1) *Ascophyllum* uncut (control), (2) *Ascophyllum* cut 36 cm above the holdfast (36-cm cut), and (3) *Ascophyllum* cut 18 cm above holdfast (18-cm cut). At each site, three plots were randomly assigned to each of the three treatments while assuring that the treatments were adequately interspersed (Hurlbert, 1984).

The experimental cutting heights were selected based on information gathered from the Nova Scotian fishery. In the late 1970's mechanical harvesters cut at a mean stump height of 35.2 +/- 0.6 cm (Sharp, 1981) and thus a treatment height of 36 cm effectively mimics a mechanical harvester's cut. The cutting height of 18 cm was based on the Canadian Atlantic Coast Marine Plant Regulations, which requires that at least 12.5 cm above the holdfast be left intact. Hand harvesting of *Ascophyllum* in Nova Scotia has been found to leave a mean stump height of 23.8 +/- 12.9 cm which is, on average, higher than required by law (Sharp, 1981). The experimental cutting height of 18 cm therefore represents an intense hand-harvesting strategy.

Harvesting was done at all four sites in June of 1997 using hand shears. The seaweed was shaken vigorously to minimize the amount of epifauna removed from a plot, and then discarded on the shore.

To sample both macroscopic flora and fauna (epiphytic, sessile and sedentary) a grid system was overlaid on each plot during low tide. Approximately every five to six weeks through the year (June 1997 - June 1998) three new sampling locations within the

grid were randomly selected without replacement. These locations were overlaid by **25** cm x **25** cm quadrats and species abundance (if mobile) and percent cover (if sessile) of organisms were enumerated. Percent cover for sessile species was selected as the measurement of abundance because it was non-destructive and rapid (Harlin et al., **1996**). In cases where sampling included multi-layered macrophyte canopies, overstory species were moved aside and additional percentages were taken to measure stratification (Seapy and Littler, **1982**). Mean abundance and mean percent cover per plot per time period ($n = 3$) was used in the statistical analyses to avoid pseudoreplication (Hurlbert, **1984**). Thus twelve replicate samples per treatment (**3** per site x **4** sites) were taken every five to six weeks throughout the year.

Surface water temperature was measured at each site at the time of sampling (during low tide). Water temperature was measured with a mercury-column thermometer at approximately **30** cm depth in water 75 cm deep. At the same time, salinity samples were collected for analysis in the laboratory. A density hydrometer was used to determine salinity (correcting for temperature) to **0.1** parts per thousand (ppt).

2.3.3. Statistical analyses

Faunal and flora assemblages (described by abundance and percent cover) from the different treatments were compared using an analysis of similarities (ANOSIM), a non-parametric analogue to a multivariate analysis of variance (MANOVA). This statistical method required neither the assumption of multivariate normality nor homogeneity of the covariance structure (Clarke, **1993**). To determine how close the abundance levels compared between any pair of samples, Bray-Curtis similarity

coefficients were computed (Clarke, 1993). These coefficients are defined such that 100% represents total similarity between samples and 0% complete dissimilarity. ANOSIM assigned ranks to the coefficients and then used a permutation test to compare ranked similarities between and within treatment groups (Clarke and Warwick, 1994). The permutation test involved randomly reassigning the treatment labels, recalculating the test statistic, and repeating the process a large number of times to build a null distribution. ANOSIM calculated the significance level by comparing the observed value of the test statistic to its permutation distribution. Individual ANOSIM tests involved 5000 simulations using the PRIMER (Plymouth Routines In Multivariate Ecological Research) package from Plymouth Marine Laboratory, England (Clarke and Warwick, 1994).

To emphasize the distribution of less common species in the analysis, the PRIMER manual suggested transforming raw counts using the 4th root ($x^{0.25}$). ANOSIMs were performed on one-year post-harvest data with all time periods combined. The program SIMPER was used to analyze the similarity matrix used in ANOSIM to identify the months making the largest contribution to between-treatment differences (Clarke, 1993). The significance level for all global tests was set at 0.05 while for *post-hoc* comparisons the level was Bonferroni-adjusted to 0.017 to account for the three possible pair-wise contrasts. Only those species whose mean percent coverage was greater than 0.1% or whose mean numerical abundance was greater than one (1) were included in the analyses. Figures showing parametric means and standard errors were provided to elucidate some of the observed differences but do not necessarily reflect the multi-dimensional nature of the ANOSIM results.

2.4. Results

Highest mean surface water temperatures were reached during August and September and the lowest in January (Fig. 2.2). Highest salinities occurred in late fall, and lowest were found in early spring (Fig. 2.3). The greater variability in salinity at Castine reflects the site's more estuarine nature due to its proximity to the Penobscot River.

2.4.1. Algal species

Of the 16 algal and one fungal taxa found in the experimental plots during the first year following harvest, only seven were present in sufficient quantities (mean values $> 0.1\%$) to warrant statistical analyses (Table 2.1). ANOSIM comparisons for dominant algal species pooled over all time periods indicate *Ascophyllum* harvesting significantly affects the percent cover of several associated algal species (Table 2.2). Significant harvesting effects were found in *Ascophyllum nodosum* (the harvested species, $P = 0.0001$), *Fucus vesiculosus* (another furoid alga, $P = 0.002$), *Hildenbrandia rubra* (a red, fleshy, epilithic crust, $P = 0.003$) and *Phymatolithon lenormandii* (a red, crustose coralline alga, $P = 0.033$; Table 2.2).

Ascophyllum nodosum, the harvested species, showed significant treatment effects (Table 2.2). The highest mean percent cover was found in the control plots (83.6% \pm 1.6 S.E.), followed by the 36-cm cut plots (69.3% \pm 1.9 S.E.), and then the 18-cm cut plots (47.8% \pm 2.0 S.E.; Fig. 2.4a). All treatments were significantly different from each other ($P = 0.0001$) with July, August, and September contributing the most to treatment differences based on an analysis of the similarity matrix (Table 2.2; Fig. 2.5a).

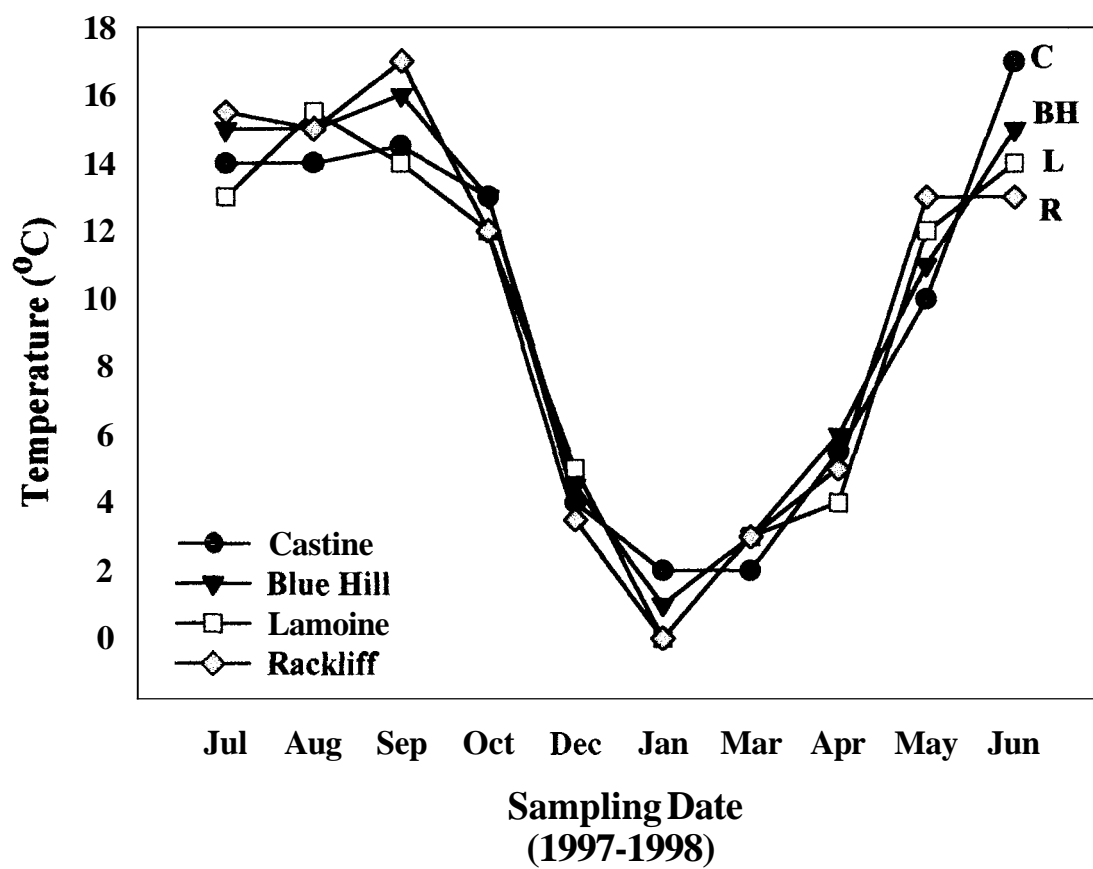


Figure 2.2. Monthly water temperatures (°C) measured at low tide at the study sites, July 1997 - June 1998.

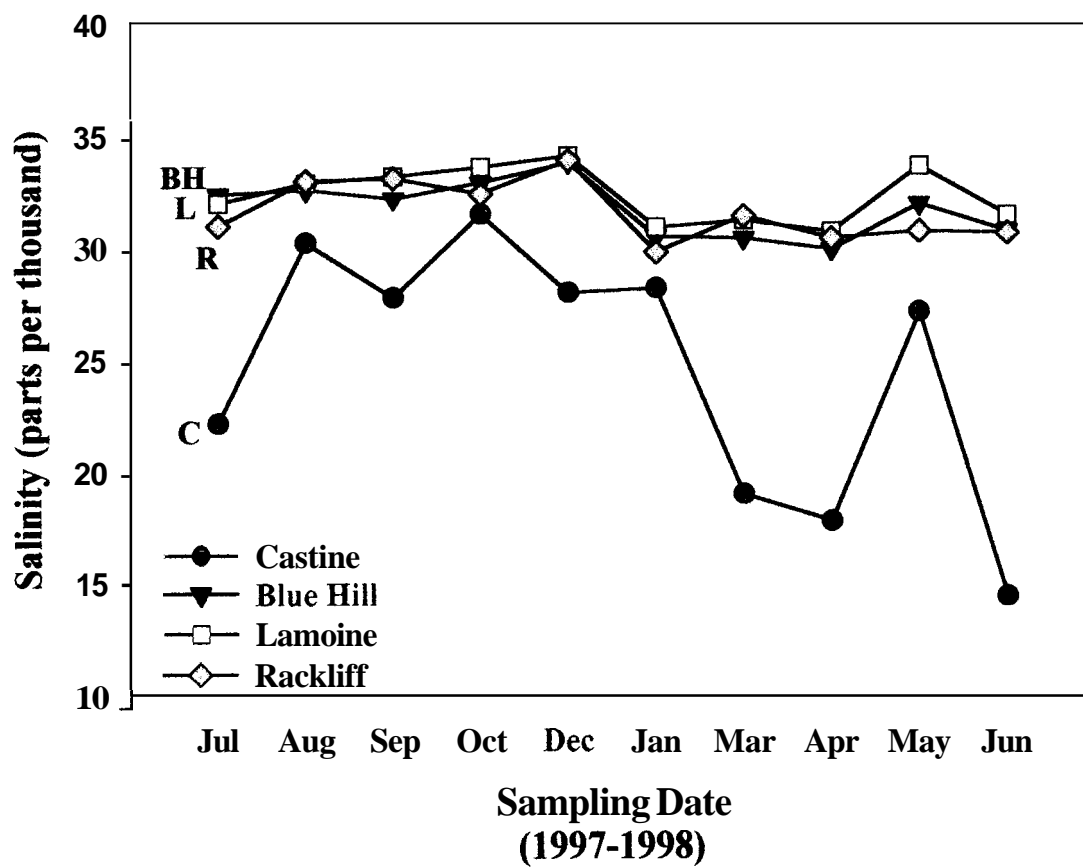


Figure 2.3. Monthly salinity measurements (ppt.) taken at low tide at the study sites, July 1997- June 1998.

Table 2.1. Taxonomic list of algal and fungal species recorded in the experimental plots during the period one-year post-harvest. * indicates those species that were found in sufficient quantities to allow statistical analyses.

Aleal species

PHAEOPHYCEAE

Ascophyllum nodosum *
Elachista fucicola
Fucus vesiculosus *
Petaloniafascia
Pilayella littoralis *
Ralfsia sp.
Scytosiphon lomentaria

FLORIDEOPHYCEAE

Chondrus crispus *
Clathromorphum sp.
Devaleraea ramentacea
Hildenbrandia rubra *
Phymatoiithon sp. *
Polysiphonia lanosa

ULVOPHYCEAE

Monostroma grevillei
Rhizoclonia tortuosum
Ulothrix sp.

Fungal species

ASCOMYCOTINA

Verrucaria sp. *

Table 2.2. Results of ANOSIM tests examining one-year post-harvest differences in the percent coverage of algal species. *Post-hoc* comparisons appear below each main factor. * P-values indicate significance (global α levels = 0.05; *post-hoc* comparison α levels = 0.017). (n = 40 per treatment for all species except *Pilayella* where n = 12 per treatment)

Algal Species	Global ANOSIM, 'Treatment' effect	Main months contributing to treatment differences
<i>Ascophyllum nodosum</i>	P = 0.0001 *	Aug, Sep, Jul
Control vs. 36cm	P = 0.0001 *	
Control vs. 18cm	P = 0.0001 *	
36cm vs. 18cm	P = 0.0001 *	
<i>Chondrus crispus</i>	P = 0.294	
<i>Fucus vesiculosus</i>	P = 0.002 *	May, Jan, Dec, Jun
Control vs. 36cm	P = 0.061	
Control vs. 18cm	P = 0.001 *	
36cm vs. 18cm	P = 0.041	
<i>Hildenbrandiu rubra</i>	P = 0.003 *	Aug, Sep, Jul
Control vs. 36cm	P = 0.052	
Control vs. 18cm	P = 0.004 *	
36cm vs. 18cm	P = 0.028	
<i>Phymutolithon lenormandii</i>	P = 0.033 *	Aug, Sep, Jul, Oct
Control vs. 36cm	P = 0.035	
Control vs. 18cm	P = 0.038	
36cm vs. 18cm	P = 0.293	
<i>Pilayella littoralis</i>	P = 0.480	
<i>Verrucaria</i> SDD.	P = 0.228	

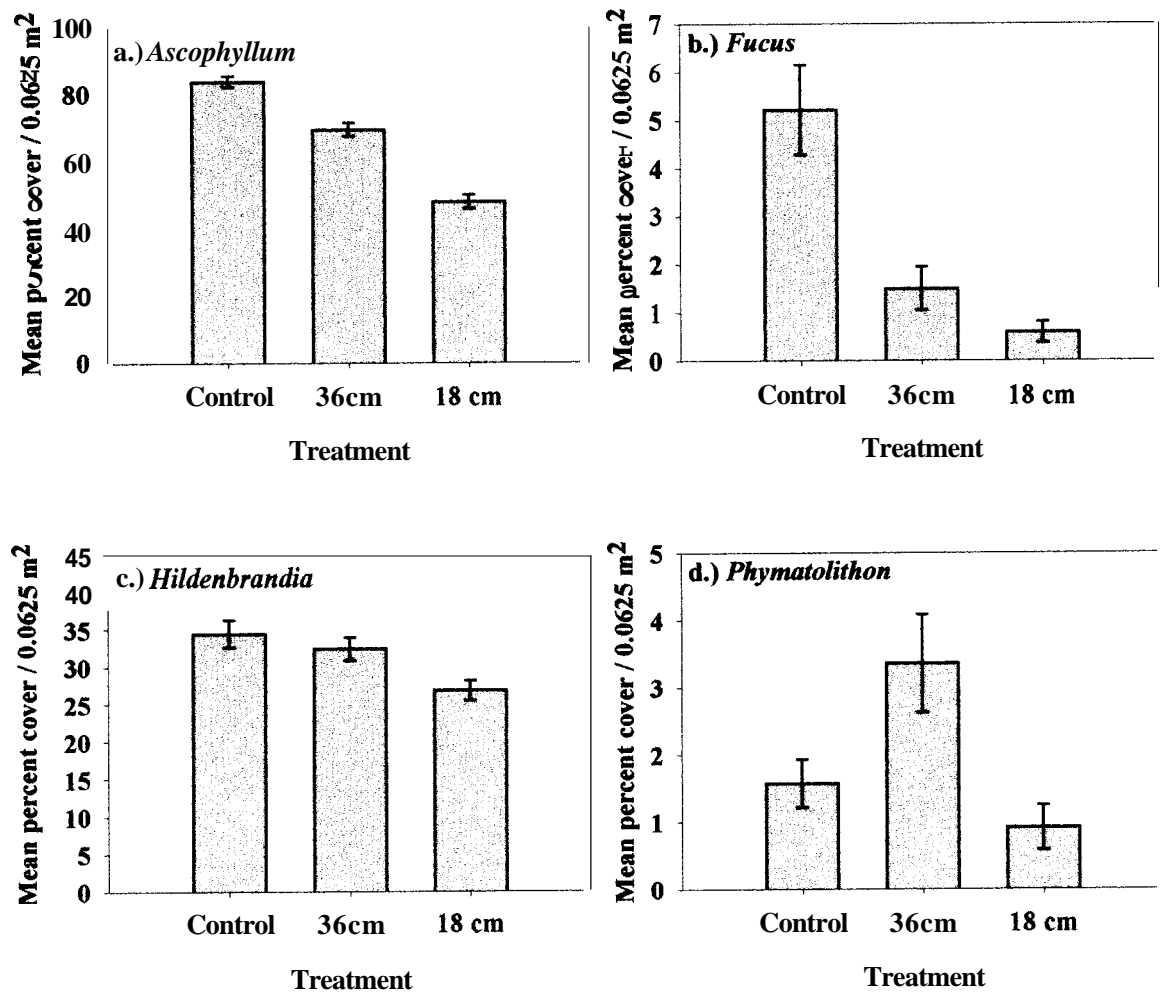


Figure 24. Mean treatment effects of significant algal species (based on global ANOSIM results) averaged over the one-year post-harvest time period. Mean values per site per time period are used as replicates. Error bars represent +/- S.E. (n = 40 per treatment except *Pilayella* where n = 12 per treatment)

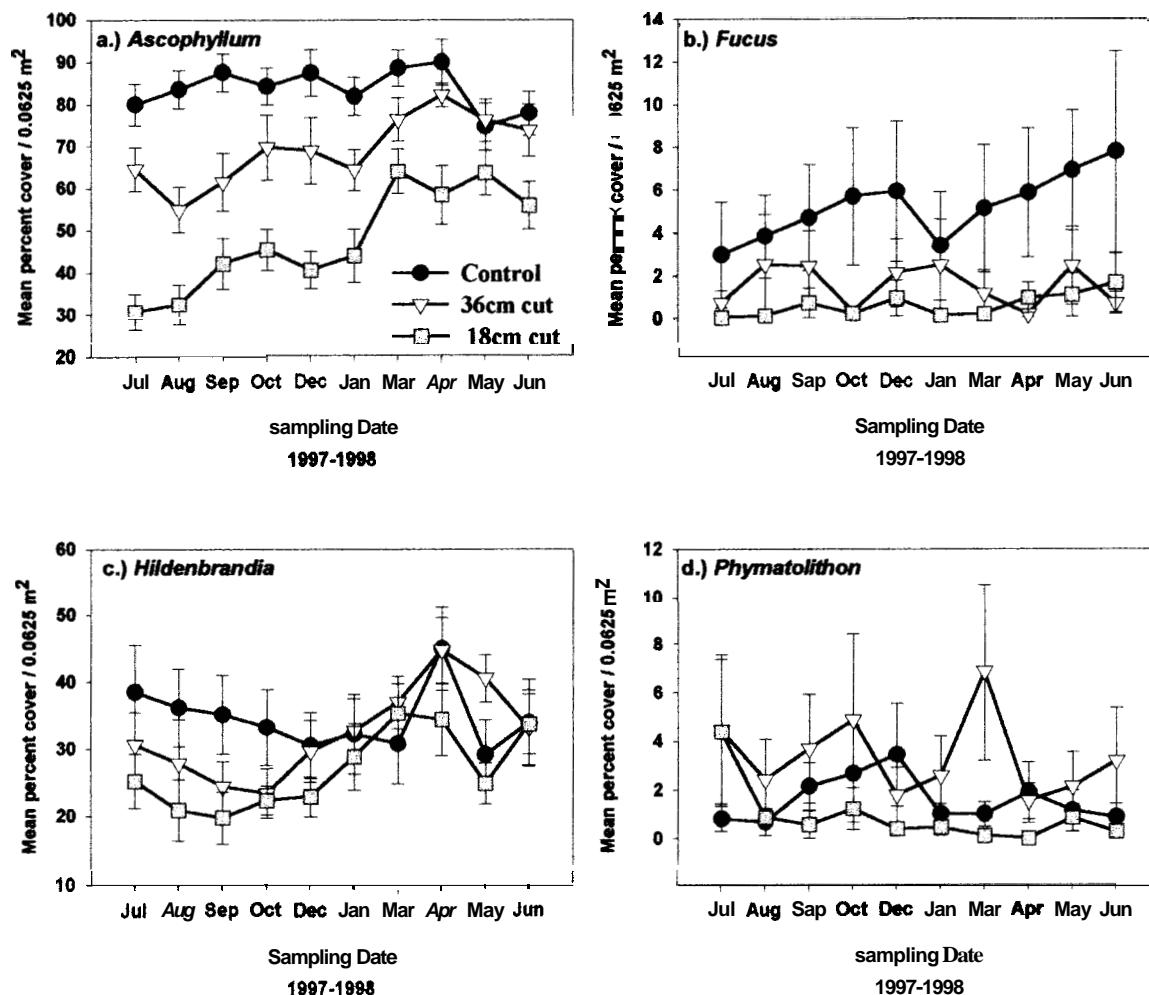


Figure 2.5. Seasonal changes in mean treatment levels of significant algal species (based on global ANOSIM results). Standard errors ranged from 5% to 94% of the mean. The key for the treatments is in the upper left panel. (n = 4 sites x 3 reps/site = 12/treatment/time)

By March of 1998, the plants had regenerated until there was no difference in percent cover of the control plots and those cut at 36 cm (Fig. 2.5a).

Fucus vesiculosus showed an overall treatment effect ($P = 0.002$; Table 2.2). There was a significant difference in the mean percent cover of *Fucus* when comparing control plots with 18-cm cut plots ($P = 0.001$; Figs. 2.4b & 2.5b). Analysis of the similarity matrix shows December, January, May and June as the months making the largest contribution to between-group differences (Table 2.2, Fig. 2.5b). The coverage of *Fucus* in the control plots appeared to increase through time. In the harvested plots, however, the cover remained depressed throughout the year.

ANOSIM results also indicate that the red crust, *Hildenbrandia rubra*, was significantly affected by removal of the canopy (Table 2.2; Fig. 2.4c). The control plots had 7% more ($P = 0.004$) *Hildenbrandia* coverage in the understory than the plots cut 18 cm above the holdfast (Figs. 2.4c & 2.5c). The reduction in the mean percent cover occurred during the first three months following harvest (Fig. 2.5).

Phymutolithon lenormandii, another crustose red algal species, was also affected significantly by the removal of *Ascophyllum* ($P = 0.033$; Table 2.2). When the data are pooled over the one-year post-harvest time period, an overall treatment effect is detected (Figs. 2.4d & 2.5d). *Post-hoc* comparisons, however, failed to detect significant differences between treatments at the adjusted alpha level.

2.4.2. Invertebrate species

During the year following the treatment initiation, 33 different species of invertebrates were found in the experimental plots (Table 2.3). Of the 33 species, 10 were regularly found and were analyzed for treatment differences. ANOSIM results

Table 23. Taxonomic list of invertebrate species recorded in the experimental plots during the period one-year post-harvest. * indicates those species that were found in sufficient quantities to allow statistical analyses.

Invertebrate species

PORIFERA	MOLLUSCA	ANNELIDA
<i>Hulichondriu</i> spp. *	<i>Aeolidiu papillosa</i>	<i>Lepidonotus squamatus</i>
	<i>Anomiu simplex</i>	<i>Spirorbis spirorbis</i> *
CNIDARIA	<i>Colus stimpsoni</i>	
<i>Diudumene lineata</i>	<i>Crepidula fornicutu</i>	ARTHROPODA
<i>Dynamena pumila</i> *	<i>Dendronotus frondosus</i>	<i>Balanus balanus</i>
<i>Metridium senile</i>	<i>Flabellina (Coryphellu)</i>	<i>Curcinus maenas</i> *
<i>Urticiniufelina</i>	<i>Lacuna vinctu</i>	<i>Pandalus borealis</i>
	<i>Littorinu littoreu</i> *	<i>Semibalanus balanoides</i>
PLATYHELMINTHES	<i>Littorinu obtusata</i> *	
<i>Notopluna utomuta</i>	<i>Modiolus modiolus</i>	ECHINODERMATA
	<i>Mytilus edulis</i> *	<i>Asterius rubens</i>
ECTOPROCTA	<i>Nucella lapillus</i> *	<i>Strongylocentrotus</i>
<i>Alcyonidium</i> spp.	<i>Onchidoris bilamellata</i>	<i>droebuchiensis</i>
<i>Flustrellidra hispida</i>	<i>Onchidoris muricata</i>	
<i>Electru pilosa</i>	<i>Tectura testudinalis</i> *	
	<i>Urosalpinx cinereu</i>	

revealed that harvesting significantly affected six of the 10 common invertebrates that use *Ascomyllum* as a habitat. Significant differences were found in *Curcinus maenas*, ($P = 0.0001$), *Dynamena pumila* ($P = 0.002$), *Halichondria* spp. ($P = 0.013$), *Littorina obtusata* ($P = 0.0001$), *Nucella lapillus* ($P = 0.040$) and *Spirorbis spirorbis* ($P = 0.0001$) (Table 2.4, Fig. 2.6).

Green crabs, *Carcinus maenas* (ranging in size from 0.5 - **9.5** cm in carapace width), were more abundant in the control plots than in the cut plots ($P = 0.001$ - 36 cm; $P = 0.0001$ - 18 cm; Table 2.4, Figs. 2.6a & 2.7a). There was no difference in abundance between the two harvested plots ($P = 0.051$). The largest differences in abundance occurred immediately following the June harvest during the months of July, August and September (Table 2.4). Green crabs were absent from all control and experimental plots during the winter and those months were excluded from the analyses.

The population of *Dynamena* was significantly higher on control plants than on plants in the 18-cm treatment (Table 2.4; Fig. 2.6). The main months contributing to this difference were July, June and May (Table 2.4; Figs. 2.6b & 2.7b). Although percent cover in the 36-cm treatment was reduced it was not statistically different from the control due to the Bonferroni adjusted alpha level.

ANOSIM comparisons also detected a significant treatment effect for *Halichondria* (Table 2.4). Seasonal variation in abundance within the different treatments tends to mask the overall effect (Fig. 2.7c). When all data are pooled for the one-year post-harvest period a distinct pattern emerges showing reduced abundance of the sponge in the 18-cm cut plots compared to control plots ($P = 0.012$; Fig. 2.6c).

Table 2.4. Results of ANOSIM tests examining one-year post-harvest differences in the numerical abundances (if mobile) or percent coverage (if sessile) of invertebrate species. *Post-hoc* comparisons appear below each main factor. * P-values indicate significance (global α levels = 0.05; *post-hoc* comparison α levels = 0.017). (n = 40 per treatment for all species except *Carcinus* where n = 32 per treatment and *Halichondria* where n = 36 per treatment)

Invertebrate Species	Global ANOSIM, 'Treatment' effect	Main months contributing to treatment differences
<i>Carcinus maenas</i>	P = 0.0001 *	Aug, Sep, Jul
Control vs. 36cm	P = 0.001 *	
Control vs. 18cm	P = 0.0001 *	
36cm vs. 18cm	P = 0.051	
<i>Dynamenapumila</i>	P = 0.002 *	Jul, Jun, May
Control vs. 36cm	P = 0.022	
Control vs. 18cm	P = 0.0001 *	
36cm vs. 18cm	P = 0.163	
<i>Halichondria</i> spp.	P = 0.013 *	Apr, Jan, Mar
Control vs. 36cm	P = 0.201	
Control vs. 18cm	P = 0.012 *	
36cm vs. 18cm	P = 0.051	
<i>Littorina littorea</i>	P = 0.210	
<i>Littorina obtusata</i>	P = 0.0001 *	Jul, Jan, Oct
Control vs. 36cm	P = 0.477	
Control vs. 18cm	P = 0.001 *	
36cm vs. 18cm	P = 0.0001 *	
<i>Nucella lapillus</i>	P = 0.040 *	Sep, Jul, Oct
Control vs. 36cm	P = 0.261	
Control vs. 18cm	P = 0.164	
36cm vs. 18cm	P = 0.013 *	
<i>Mytilus edulis</i>	P = 0.186	
<i>Mytilus</i> recruits	P = 0.884	
<i>Semibalanus balanoides</i>	P = 0.177	
<i>Spirorbis spirorbis</i>	P = 0.0001 *	Jul, Aug, Apr
Control vs. 36cm	P = 0.002 *	
Control vs. 18cm	P = 0.0001 *	
36cm vs. 18cm	P = 0.002 *	
<i>Tectura testudinalis</i>	P = 0.540	

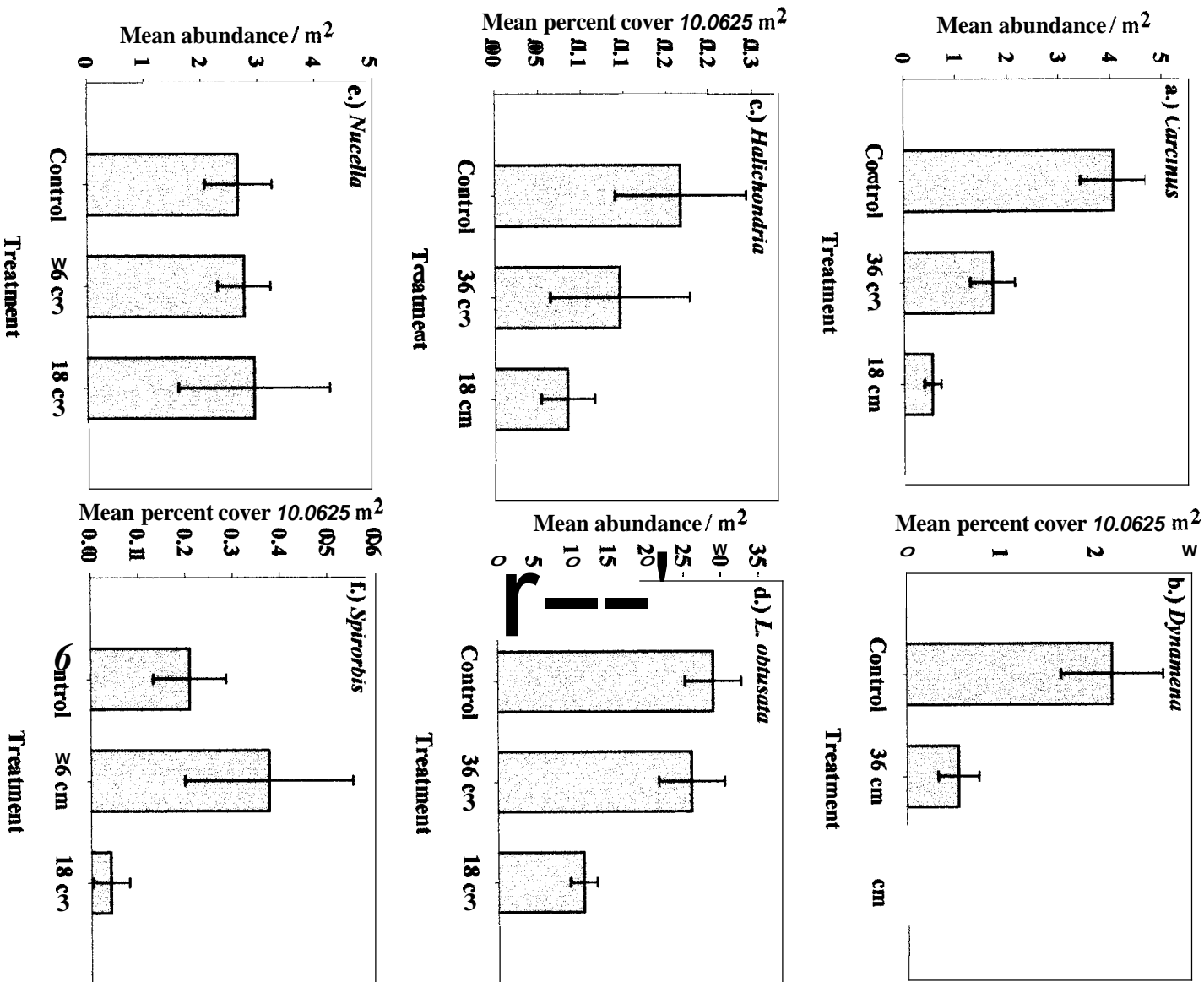


Figure 2.6. Mean treatment effects of significant invertebrate species (based on global ANOSIM results) averaged over the one-year post-harvest time period. Mean values per site per time period are used as replicates. Error bars represent \pm S.E. (n = 40 per treatment except *Carcinus* where n = 32 per treatment and *Halichondria* where n = 36 per treatment)

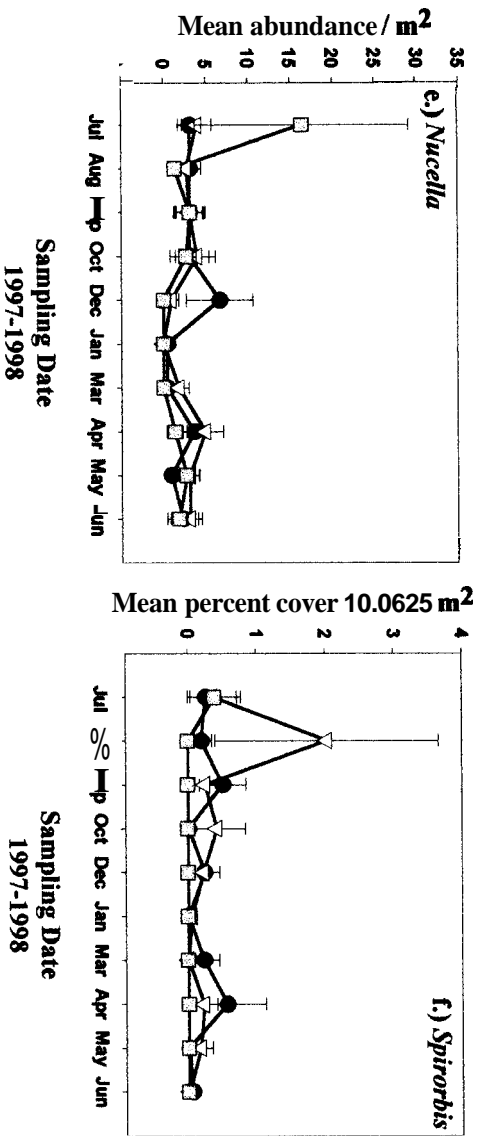
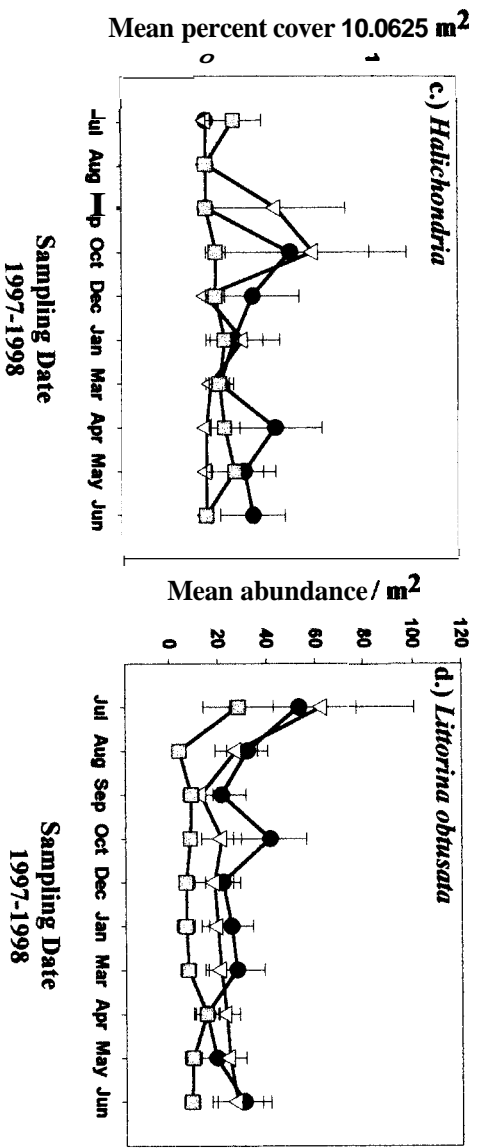
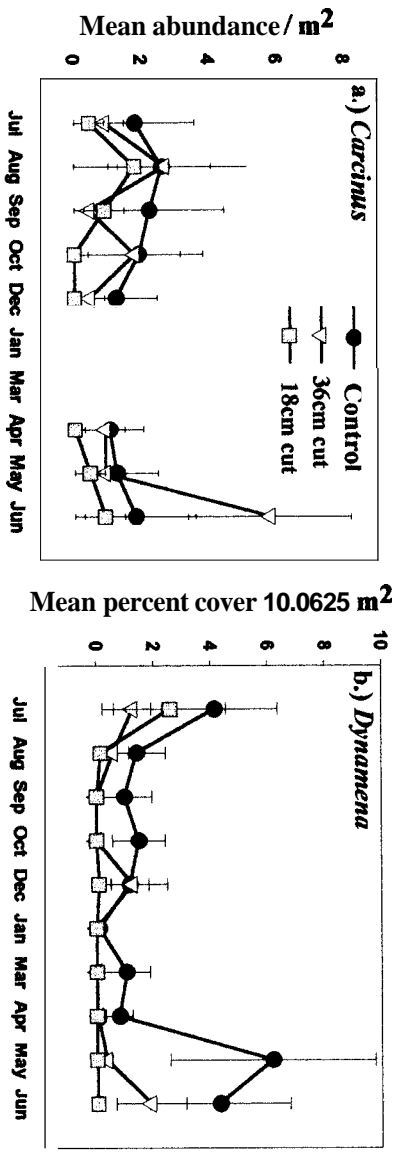


Figure 2.7. Seasonal changes in mean treatment levels of significant invertebrate species (based on global ANOSIM results). Standard errors ranges from 24% to 100% of the mean. The key for the treatments is in the upper left panel. (n = 4 sites x 3 reps/site = 12/treatment/time)

Two mollusks, *L. obtusata* and *Nucella*, were also affected significantly by the canopy removal (Table 2.4). There was no difference in abundance of *L. obtusata*, the smooth periwinkle, when comparing control plots to those cut at 36 cm ($P = 0.477$; Fig. 2.6d). Both the control and the 36-cm treatments, however, had significantly higher periwinkle densities than the 18-cm cut plots ($P = 0.001$ and $P = 0.0001$, respectively). The main months contributing to these differences were July, October and January (Fig. 2.7d). Unlike most of the other species that were affected by the harvesting, *Nucella* densities increased ($P = 0.040$) when the plants were cut (Table 2.4; Fig. 2.7e). This effect, however, was short-lived. ANOSIM results indicate that there was no difference in the number of *Nucella* when comparing the control densities to the densities in the 36-cm cut plots. There was also no difference in densities between the controls and the 18-cm treatments (Table 2.4). A significant difference was detected when comparing *Nucella* densities in the 36-cm cut plots with those in the 18-cm cut plots ($P = 0.013$). Examination of the mean treatment effect collapsed over the one-year post-harvest time period (Fig. 2.6e) failed to show a distinct treatment pattern due to the multidimensional nature of the data.

Spirorbis spirorbis, a tube-dwelling polychaete, was also affected by rockweed harvesting ($P = 0.0001$). All treatments were significantly different from one another (Table 2.4). Densities of *Spirorbis* were highest in the 36-cm cut plots followed by the control plots and then the 18-cm cut plots (Fig. 2.6f). July, August and April were the main months contributing to treatment differences (Table 2.4; Fig. 2.7f).

25. Discussion

2.5.1. Algal species

A single harvesting event had the immediate effect of reducing macrophyte biomass and density of associated macroscopic flora and fauna. This decline was not surprising given that the primary aim of harvesting is to remove biomass, which also removes anything attached to it or residing within the canopy. During the first year following harvest, the mean percent cover of all treatment regimes was significantly different from one another for *Ascophyllum*. These data do not allow me to determine the precise time-scale of habitat recovery, however, it is clear that by the end of the first year the plants cut 36 cm from the holdfast had regrown so that there was no apparent difference in the mean percent cover compared to control plots. Recovery of the percent cover of the plants is not indicative of biomass recovery (Vadas and Wright, 1986; Chapter 6).

Following the June 1997 harvest, there was an immediate decline in the percent cover of several understory algal species including *Hiidenbrandia*, *Phymatolithothamnion*, and *Fucus*. *Hiidenbrandia* and *Phymatolithothamnion* are both crustose algal species found in the intertidal zone under boulders, in rock crevices, in tide pools, as well as under thick canopies of macroalgae (Lewis, 1964). *Fucus*, on the other hand, is normally an intertidal canopy-forming species. In sheltered areas, the rocky intertidal is dominated by large *Ascophyllum* plants (1-2 meters in height) which outcompete shorter *Fucus* plants (25-50 cm) (Keser et al., 1981).

In general, seaweeds that live under the canopy are adapted to lower light levels and reduced levels of desiccation (Lobban and Harrison, 1994). The thickness of the

rockweed canopy not only reduces the amount of light to the understory but also prevents the understory from drying out (Johnson and Scheibling, 1987). During low tide the algal fronds provides some thermal buffering: temperatures within the mat are up to 3.0 °C cooler in the summer and up to 2.0 °C warmer in the winter than air temperatures (Hruby and Norton, 1979; Johnson and Scheibling, 1987). The protection that the canopy offers allows both algal and invertebrate species to extend their range from the subtidal into the intertidal zone. Removal of the canopy exposes the understory assemblage to an immediate increase in light and desiccation stress. The magnitude of the increased physical stress on the understory is related to the intensity of the removal as well as the seasonality of the removal.

Understory algae are characteristically adapted to the chronic lack of light, and thus are less competitive at higher light levels (Dring, 1987; Luning, 1990). When exposed to intense light, understory algae are easily damaged particularly by short wavelengths, which causes photo-reduction of pigments and depression of photosynthesis (Round, 1981). Immediately following the harvest there ~~was~~ a significant increase in the percent cover of *Phymatolithon* in both of the cut treatments. Within a month, however, 75% of the *Phymatolithon* in the 18cm-cut plots had been bleached, presumably due to high irradiance (Schiel and Taylor, 1999). The percent cover of live *Phymatolithon* in these plots remained depressed throughout the year. Growth of calcified species in low light intensities tends to reduce calcification and the algae are then more susceptible to damage from bleaching when transferred to high light intensities (Round, 1981; Schiel and Taylor, 1999). In a similar study examining the removal of a furoid (*Fucus serratus*) canopy, Jenkins et al. (1999) also found when the understory was exposed to sunlight,

bleaching of understory algae resulted, particularly in calcareous forms. In our study, *Hildenbrandia* also experienced a significant decrease in percent cover in the plots cut 18 cm from the holdfast.

Although there have been no studies to date examining the effects of high irradiance on understory furoid plants, fucoids, in general, are highly resistant to changes in light levels (Chapman, **1995**). Fucoids can survive long periods in the dark and, conversely, they have protection mechanisms against damage from high light levels (Chapman, **1995**). Therefore, it is unlikely that the decline in the understory *Fucus* population was due to a dramatic increase in the light level immediately following the opening of the canopy. Several studies have shown that high levels of irradiation inhibit the growth of lower shore furoid species, however, the bulk of observations indicate that desiccation and overheating are be more critical components of aerial emersion than high irradiation (Stromgren, **1977**). The fact that the overstory was removed during mid-summer, when desiccation stress was highest may have been a contributing factor in the decline of the understory *Fucus* plants. In addition, many of the *Fucus* plants (particularly at Rackliff Island) grew epiphytically on *Ascophyllum* and thus their immediate decline may simply reflect a loss due to by-catch removal. Interestingly, in control populations the abundance of *Fucus* increased over the course of the year.

2.5.2. Invertebrate species

In control plots *Carcinus maenas* exhibited a regular annual cycle, with a peak in autumn followed by a decrease in numbers in winter, which is related to seasonal temperature patterns (Attrill and Thomas, **1996**). Immediately following the June

harvest, there was a significant reduction in the density of green crabs in the cut plots. Intertidal macrophytes have been shown to provide shelter for crab species from gull predation (*Larus argentatus* and *L. marinus*) during emersion (Lubchenco, 1978; Bertness, 1999). The loss of habitat complexity caused by the removal of the overstory may have made the sites less suitable as a refuge (Schneider and Mann, 1991; Edgar et al., 1994; Lavery et al., 1999; Leonard, 1999). Alternatively, a reduction in the green crab's food source in the harvested plots (e.g., an indirect effect) could also have contributed to the observed pattern of abundance. Both harvesting regimes negatively affected the green crab population in the short-term. In a study conducted in Northern Ireland, Boaden and Dring (1980) examined the effects of *Ascophyllum* harvesting at one site 2.5 years after the canopy was removed. No significant difference in *Carcinus* frequency or density was found (Boaden and Dring, 1980). This study suggests, however, that green crab populations are affected by a reduction in the canopy but that the population is resilient and reestablishes itself within a year. This recovery is most likely due to an increase in the habitat structure from the regeneration of the harvested species leading to an immigration of *Carcinus* from adjacent areas.

Dynamena is a colonial, epiphytic, hydroid. It is commonly found in the subtidal but can also be found in moist areas of the intertidal (Lewis, 1964). In the subtidal, *Dynamena* is frequently found on the upper surfaces of *Laminaria*; however, in the upper part of the sublittoral zone it is found only on laminarian stipes (Lewis, 1964). In the intertidal zone, *Dynamena* is restricted to the lower portion of plants. Farther up shore, these hydroid colonies tend to recruit lower on the plant stipes, apparently to avoid increased risk of desiccation. On *Ascophyllum*, *Dynamena* attaches only to interior

branches on the lower third of the plant. This position reduces the risk of desiccation during emersion because the plants lie flat and only the distal canopy is subjected to aerial stress. Harvesting negatively affects this species in two ways. First, it reduces the amount of substrate available for attachment. Second, it potentially increases the amount of light and heat reaching the lower portion of the plants. Removal of the canopy presumably increases desiccation stress causing a decline in the percent cover.

Dynamena shows a seasonal abundance pattern in Maine with **high** numbers in spring and summer and **a** decline in the fall when the abundance of its primary predator, the nudibranch *Flabellina verrucosa rufibranchialis*, increases (Lewis, **1964**).

Halichondria, an encrusting sponge, generally avoids desiccation by living in moist areas either under rock overhangs or in crevices in the lower littoral zone under dense macroalgal canopies (Lewis, **1964**). Our study showed an overall decline in the percent cover of this encrusting sponge. This reduction was highly correlated with the intensity of harvest. Boaden and Dring (**1980**) also found a significant decrease in the percent cover of *Halichondria* on the underside of boulders from **8.9%** in the control area to 0.2% in the cut areas. Removal of a large portion of the canopy likely resulted in an increase in desiccation stress, which led to a reduction in percent cover.

L. obtusata is largely restricted to the fronds of *Ascophyllum* and *Fucus vesiculosus*, where it attaches and feeds on the microalgal covering (Lewis, **1964**). This close association is reflected in the reduction in densities corresponding to the reduction in plant structure. *Ascophyllum* plants harvested at **36** cm had twice as many branches as those cut **18** cm from the holdfast. Since many lateral branches remained in the 36-cm cut plots, the density of snails remained high. The foliose portion of the plants in the **18-**

cm cut plots was practically denuded and had few remaining branches for the snails to graze.

There was a dramatic increase in *Nucella* densities in the 18-cm cut plots immediately following the canopy removal. This increase coincided with a significant decrease in the number of green crabs inhabiting the harvested plots. On rocky shores green crabs are *Nucella*'s major predator (Hughes and Elner, 1979), it is possible that the sudden reduction in predator densities caused an increase (4x) in the number of prey species using that space (Menge, 1976; Kitching, 1986). The increase in *Nucella* densities could also be attributed to a decrease in whiplash effect from the substantial removal of *Ascophyllum* fronds within the 18-cm cut plots. The sudden increase in *Nucella* densities in the 18-cm cut plots in early July was short-lived. By August, snail densities in all treatments were back to baseline levels. The reduction in snail densities could be due to *Nucella*'s inability to resist excessive desiccation or a reduction in its primary food sources (*Mytilus* and *Semibalanus*) (Kitching, 1986).

There was no immediate effect of harvesting on *Spirorbis*, but by the second month, the populations in the 18-cm cut plots had almost disappeared. There was a significant increase in density in the 36-cm cut plots. The reduction in numbers in the 18-cm cut plots may be due, in part, to an increase in light intensity causing an increase in desiccation. Duggins et al. (1990) found that spirorbid polychaetes are less abundant in areas of high light. It is unclear whether this is due to differential mortality or larval settlement patterns. Although spirorbids have an operculum, it may not be effective against high desiccation stress. In addition, in areas with less canopy coverage the spirorbids may also be more visually exposed to predators, which could contribute to

decreased abundances. *Spirorbis* abundance remained low in the 18-cm cut plots the entire year. The increase in abundance in the 36-cm cut plots suggests that the decrease in canopy at that particular harvest intensity had a positive effect on settlement and early survival and may have been caused by changes in sedimentation. Duggins et al. (1990) found that increased spirorbid abundance was related to decreased sedimentation rates. Apparently, the effect did not persist, because a month later the spirorbid densities in the 36-cm cut plots returned to baseline levels.

Many of the differences observed in species abundances among treatments could have resulted from **direct** or indirect effects (Wootton, 1993; Menge, 1995; Menge, 1997). However, the design utilized in this study does not all me to clearly identify which of these alternate mechanisms were relatively more importance in each instance.

2.6 Conclusion

Although many studies have shown that macroalgal harvesting significantly decreases the abundance and diversity of flora and fauna (Boaden and Dring, 1980; Pringle and Sharp, 1980; Pringle and Mathieson, 1987; Vasquez, 1995), this paper specifically documents the short-term ecological effects associated with harvesting *Ascophyllum*. Despite the fact that numerous species within the community experienced short-term effects, few effects persisted through time. Many important members of the intertidal community did not experience significant (detectable) changes in their population levels following the perturbation (*Chondrus*, *Pilayella*, *Verrucaria*, *L. littorea*, *Mytilus* and *Semibalanus*) (Tables 2.2 & 2.3). This suggests that a single harvest event can cause short-term changes to the community structure but that the community is

resilient to this **type** of disturbance on this (25 m²) spatial scale and at this time of year. However, this level of disturbance at larger spatial scales could have greater and more long-lasting effects.

Previous studies have shown that the effect of a disturbance, whether man-made or natural, on the community of organisms involved are most severe where natural disturbance is least prevalent (Watling and Norse, 1998). Where natural disturbances are high, the communities of organisms are resilient to habitat alterations. Natural physical disturbances to intertidal assemblages include sedimentation, sand and ice scouring, impact and abrasion by large water-borne objects and stresses associated with wave energy (Sousa, 1985). The **high** natural disturbance regime associated with intertidal zones may be the underlying reason why this habitat is resilient to perturbation due to harvesting. It remains to be seen how this community will react to an increase in the frequency and intensity of the harvesting disturbance.

In the Gulf of Maine, *Ascophyllum* is the most important intertidal alga, economically and ecologically, and we need to fully understand its ecology and its habitat value before the species becomes overexploited and the habitat degraded. It is clear that habitat structure, provided by the dominant plant, has an important influence on the functional value of the habitat for resident plants and animals. Baseline studies of the ecological impact of different exploitation strategies are needed to understand biological dynamics before the species is harmed significantly. The results of this work will be useful for management decisions regarding the sustainable harvest and conservation of this habitat.

Chapter 3

Ecology of *Ascophyllum* harvesting: effects on the associated algal species

3.1. Abstract

Ascophyllum nodosum is the dominant plant cover and habitat **type** on sheltered shores in the North Atlantic. It has long been identified as playing an important community-structuring role by modifying the physical and biological conditions in the areas where it occurs. Commercial harvesting of this species has not only the potential to disrupt the integrity of the alga but also to alter the associated seaweed assemblages. Here, I test the effects of three harvest treatments (unharvested/control and harvested at 18 cm and 36 cm from the holdfast) on the associated understory algae at four separate sites in mid-coast Maine, USA. A single harvest disturbance was imposed upon replicate areas within each site in June 1997. A three-factor, repeated-measures MANOVA was used to analyze effects of harvesting treatment on percent cover of understory algal species.

Ascophyllum nodosum (the harvested, canopy species), *Fucus vesiculosus* (another brown alga), *Hildenbrandia rubra* (a red, fleshy, epilithic crust) and *Phymatolithon lenormandii* (a red, crustose coralline alga) were all significantly affected by the canopy removal. The mean percent cover of *A. nodosum* was reduced significantly following the experimental harvest but returned to baseline values within nine months. The cover of *Fucus* also decreased in cut plots. Also, there was a reduction in the mean percent cover of *Hildenbrandia* at **three** of the four experimental sites (Castine, Blue Hill and Lamoine) that was correlated with the intensity of harvest. At the

fourth site (Rackliff Island), however, the mean coverage of *Hildenbrandia* increased in the 36-cm cut plots compared to controls, suggesting that *Hildenbrandia* may be light-limited under natural conditions depending on site characteristics. Similarly, *Phymatolithon* may also be light-limited under natural conditions. At sites where *Phymatolithon* was abundant, removal of some of the canopy (36-cm cut) resulted in an increase in the percent cover, whereas an 18-cm cut resulted in death of plants. No treatment effects were detected at sites with a low baseline percent coverage of *Phymatolithon*. In conclusion, the response of understory algal species to harvesting was species- and site-specific.

Key words: algal canopies; *Ascophyllum nodosum*; community ecology; habitat; macroalgal harvesting; rocky intertidal; understory.

3.2. Introduction

Ascophyllum nodosum is a dominant, intertidal, brown alga species on Atlantic shores in the northern latitudes. It ranges in geographic distribution from the White Sea to Northern Portugal in the eastern Atlantic and from Baffin Island to Northern New Jersey in the western Atlantic (Baardseth, 1970). This species is most abundant and productive in areas with large tidal ranges and in areas not exposed to heavy surf (Cousens, 1985). The Gulf of Maine and Bay of Fundy provide protection from extreme wave exposure and offer large tidal ranges which produce large, homogeneous stands of *Ascophyllum* that extend from the upper intertidal to the sublittoral fringe. Macroalgal

growth in this region is impressive and rivals that of some of the most productive intertidal systems in the world (Mathieson et al., 1991).

Ascophyllum nodosum accounts for 80 to 90% of the plant cover on sheltered shores in estuaries and produces dry-weight standing crops of 5 to 6 kg/m² (Keser et al., 1981). Substrate coverage and biomass estimates for more exposed shores are considerably lower (50 to 70% and 3 to 4 kg/m², respectively) (Keser et al., 1981). With increasing shelter from wave exposure, frond lengths and plant biomass increase and the distribution of biomass is concentrated at greater heights above the substrate (Cousens, 1986).

The existence of concentrated stands of *Ascophyllum* has encouraged harvesting in many countries where it is used for alginates, organic fertilizers, and fodder (Baardseth, 1970). Harvestable quantities around the Western Atlantic are found in the center of its distribution, namely eastern Maine and Canada. The ecological effects of harvesting attached algae are not straightforward but depend on a number of factors including the size of clearance, the intensity of removal, the harvesting technique, the season of harvest, and the vulnerability of the species or habitat to perturbation (Sharp and Pringle, 1990; Schiel and Nelson, 1990). Harvesting has a similar effect on the resource as that produced by physical and biological disturbances (*sensu* Sousa, 1984; Underwood, 1989). Both remove, totally or partially, the dominant populations and modify the distribution and abundance of associated species (Cancino and Santelices, 1981; Foster and Barilotti, 1990; Vasquez and Santelices, 1990; Vasquez, 1995). Although populations of *Ascophyllum* have been commercially harvested for decades,

little information exists on the impact of harvesting on associated intertidal seaweed communities.

Substrate or habitat space is a well-recognized limiting factor for sessile organisms in marine ecosystems. *Ascophyllum* serves as a host substratum for numerous macro- and microalgae, invertebrates, and other microorganisms (Johnson and Scheibling, 1987; Jarvis and Seed, 1996). Removal of the *Ascophyllum* canopy, however, does more than reduce available substrate for colonization. It also changes the microclimate in the understory of the fronds thereby potentially affecting species that cannot withstand increased light, temperature, or desiccation (e.g., some red algae) (Luning, 1990; Lobban and Harrison, 1994; Bertness et al., 1999). A reduction in the number of fronds and the opening of stipe space may alter flow patterns and increase current velocities in the understory, similar to the effects that cutting has on flow velocities in seagrass beds (Fonseca et al., 1982; Jackson and Winant, 1983; Irlandi and Peterson, 1991). The underlying surface topography may also have a more pronounced effect on both flow and sedimentation rates following the canopy removal. Irradiance levels and desiccation stress also increase proportionally with canopy removal (Hruby and Norton, 1979; Johnson and Scheibling, 1987; Vasquez and Santelices, 1990). Changes in sedimentation patterns are also possible, especially in areas of reduced flow and wave action. Sedimentation rates will likely decrease with the absence or reduction of fronds, but scour by sediments may increase because of the increased flow in the understory. Each broad process represents a mechanism whereby habitat structure, provided by the dominant plant, has an important indirect influence on the functional value of the habitat for understory algal species (Irlandi & Peterson, 1991).

Despite the vital role of macroalgal habitats on coastal ecosystems little is known about the consequences of harvesting these habitats on the associated species. The aim of the present study was to investigate the effects over two years of various macroalgal harvesting regimes on the associated understory algal community.

3.3. Materials and Methods

3.3.1. Study sites

Four *Ascophyllum nodosum* beds with similar standing crops were selected in the mid-coast region of Maine (Fig. 3.1). All four sites were moderately sheltered, had a slope 15° or less, and supported a dense, continuous cover of *Ascophyllum* (>70% cover). Although an attempt was made to standardize sites by visually selecting stands of similar biomass, differences in standing crop between sites could not be avoided. Mean standing crop was approximately 9 kg/m², but individual sites ranged from 7 to 12 kg/m². Mean tidal amplitude of this region is 3.1 m and the mean tidal level is 1.7 m. Substrate at three of the sites (Castine - 44°27'8"N; 68°47'29"W, Blue Hill Falls - 44°22'21"N; 68°33'9"W and Lamoine Beach - 44°27'18"N; 68°16'34"W) consisted mainly of small to medium-sized rocks interspersed with sand and pebbles. Ledge was occasionally present. The substrate at the remaining site, Rackliff Island (43°59'28"N; 69°9'6"W), consisted of large bedrock outcroppings embedded in muddy substrate.

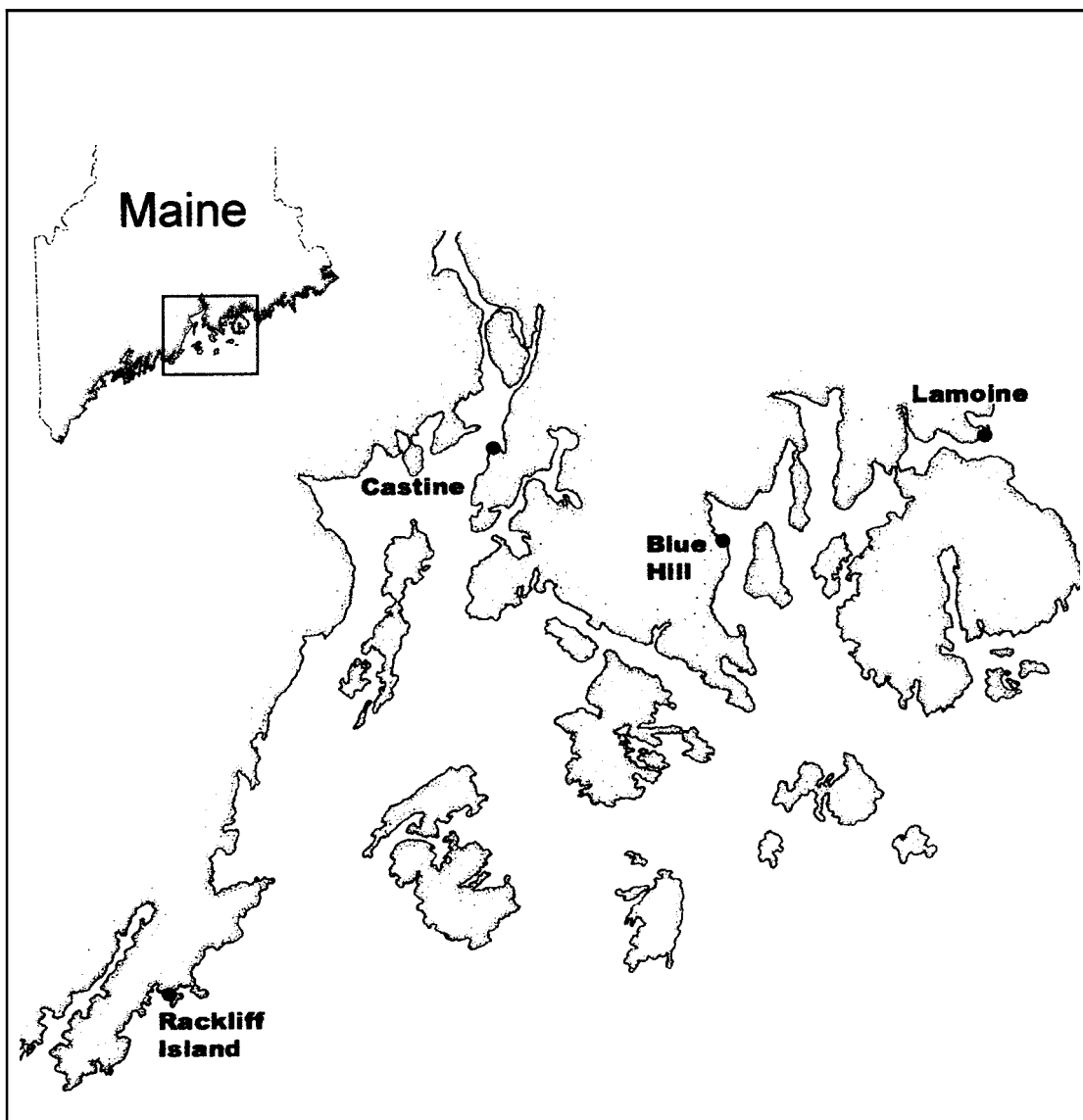


Figure 3.1. Location of experimental sites along the mid-coast region of Maine, USA.

3.3.2. Experimental design and sampling methods

The experimental design included four sites (described above) each consisting of nine permanently marked 5 m x 5 m plots placed at mean low water. Each plot was a minimum of 5 meters from ~~an~~ adjacent plot to assure treatment independence. Three different treatments were imposed on the plots: (1) *Ascophyllum* uncut (control), (2) *Ascophyllum* cut 36 cm above the holdfast (36 cm cut), and (3) *Ascophyllum* cut 18 cm above holdfast (18 cm cut). At each site, three plots were randomly assigned to each of the three treatments while assuring that the treatments were adequately interspersed (Hurlbert, 1984). Harvesting was done at all four sites in June of 1997 using hand shears.

To sample both upright and crustose macroscopic flora, a grid system was overlaid on each plot during low tide. Approximately every five to six weeks throughout the two-year study, three new sampling locations within the grid were randomly selected without replacement. These locations were overlaid by 25 cm x 25 cm quadrats, and the percent cover of organisms was enumerated. Percent cover was selected as the measurement of abundance because it was non-destructive and rapid (Harlin et al., 1996). In cases where sampling included multi-layered macrophyte canopies, overstory species were moved aside and additional percentages were taken to measure stratification (Seapy and Littler, 1982). Mean percent cover per plot per time period ($n = 3$) was used in the statistical analyses to avoid pseudoreplication (Hurlbert, 1984). Thus twelve replicate samples per treatment (3 per site x 4 sites) were taken every five to six weeks throughout the two-year study yielding 18 sampling periods.

Surface water temperature was measured at each site at the time of sampling (during low tide). Water temperature was measured ~~with~~ a mercury-column thermometer

at approximately 30 cm depth in water **75** cm deep. At the same time, salinity samples were collected for analysis in the laboratory. A density hydrometer was used to determine salinity (correcting for temperature) to **0.1** parts per thousand (ppt).

3.3.3. Statistical analyses

A three-factor, repeated-measures multivariate analysis of variance (MANOVA), with replicate time periods as the repeated unit, was used to analyze the effect of harvesting treatment on the percent cover of algal species (Winer et al., **1991**). Treatment and time were considered fixed factors because the treatment levels were the same at all sites and sites were sampled on a fixed time schedule (every 5-6 weeks for 2 years). Sites were treated **as** a random factor because then the results of the study could be generalized to the population of all such *Ascophyllum* sites (Winer et al., **1991**; Underwood, **1997**). This full model allows one to examine treatment, time and site, as well as their interactions, on percent cover. Several pre-planned, orthogonal comparisons of treatment means were used to test *apriori* hypotheses (Winer et al., **1991**). Two mutually orthogonal, single-degree-of-freedom contrasts were constructed to test (1) whether percent cover is affected by the mean of the harvesting treatments (Control vs. Cut), and (2) whether the two cut treatments (36-cm cut vs. 18-cm cut) differed. Statistica (Release **5.1**, StatSoft) and SAS (Mainframe Version **6.1**) software were used for all analyses.

Because sites are random and, therefore, irrelevant to the overall question of treatment effects, a reduced, two-factor repeated-measures MANOVA model excluding sites was also examined. The reduced model allows us to analyze how much difference

there is among the experimental treatments, over and above the intrinsic Qfference associated with sites.

The multivariate, repeated-measures approach was employed because the assumptions of the univariate, repeated-measures model could not be met (in particular, sphericity). Observations closer in time will almost inevitably correlate more highly than those separated further in time (Maxwell and Delaney, 1990). The multivariate approach does not require the assumption of homogeneity but does require multivariate normality. Despite a reduction in model assumptions, the data generated in this study failed to achieve multivariate normality due to the large number of zeros present. Most of the species had skewed data distributions, which could not be fixed with transformations. Comparative tests on means are remarkably insensitive to general non-normality of the parent population, in particular skewness (Geary, 1947; Gayen, 1950; Box, 1953; Jensen, 1982). As long as the skewness of the data is in the same direction across all treatments, the general skewness tends to cancel out (Box, 1953). With respect to the data in this study, skewness was similar across all treatment levels and thus cancels out when conducting comparative tests on the means. The significance level for all apriori comparisons was set at 0.05 while for *post-hoc* comparisons the level **was** Bonferroni-adjusted according to the number of contrasts. Only those species whose mean percent coverage was greater than 0.1% were included in the analyses. For clarity of presentation, on graphs showing temporal changes standard errors have been plotted only on figures where $n \geq 9$. On all other figures the range of standard errors is provided.

3.4. Results

The highest mean surface water temperatures were reached during August and September and the lowest in January (Fig. 3.2). The highest salinities occurred in late fall, the lowest were found in early spring (Fig. 3.3). The greater variability in salinity at Castine reflects the site's more estuarine nature due to its proximity to the Penobscot River.

Of the 18 algal and one fungal taxa found in the experimental plots during the two-year, post-harvest sampling period, only seven were in sufficient quantities to warrant statistical analyses (Table 3.1). MANOVA comparisons for dominant algal species indicate *Ascophyllum* harvesting significantly affects the percent cover of several associated species (Table 3.2).

3.4.1. Full MANOVA model

Harvesting significantly affected the mean percent cover of *Ascophyllum nodosum*, *Fucus vesiculosus*, *Hildenbrandia rubra* and *Phymatolithon lenormandii*. According to the three-factor, repeated-measures MANOVA model, the mean percent cover of both *A. nodosum* and *F. vesiculosus* decreased following the experimental harvest. The mean cover of *Hildenbrandia* also decreased in the cut plots at three of the four sites (Castine, Blue Hill and Rackliff). At Lamoine, however, the percent cover increased in the 36-cm cut plots. *Phymatolithon* coverage also increased in the 36-cm cut plots.

Ascophyllum nodosum, the harvested species, had significant 'Treatment', 'Time' and 'Treatment x Time' effects ($P = 0.0040$, $P = 0.0000$, and $P = 0.0000$, respectively;

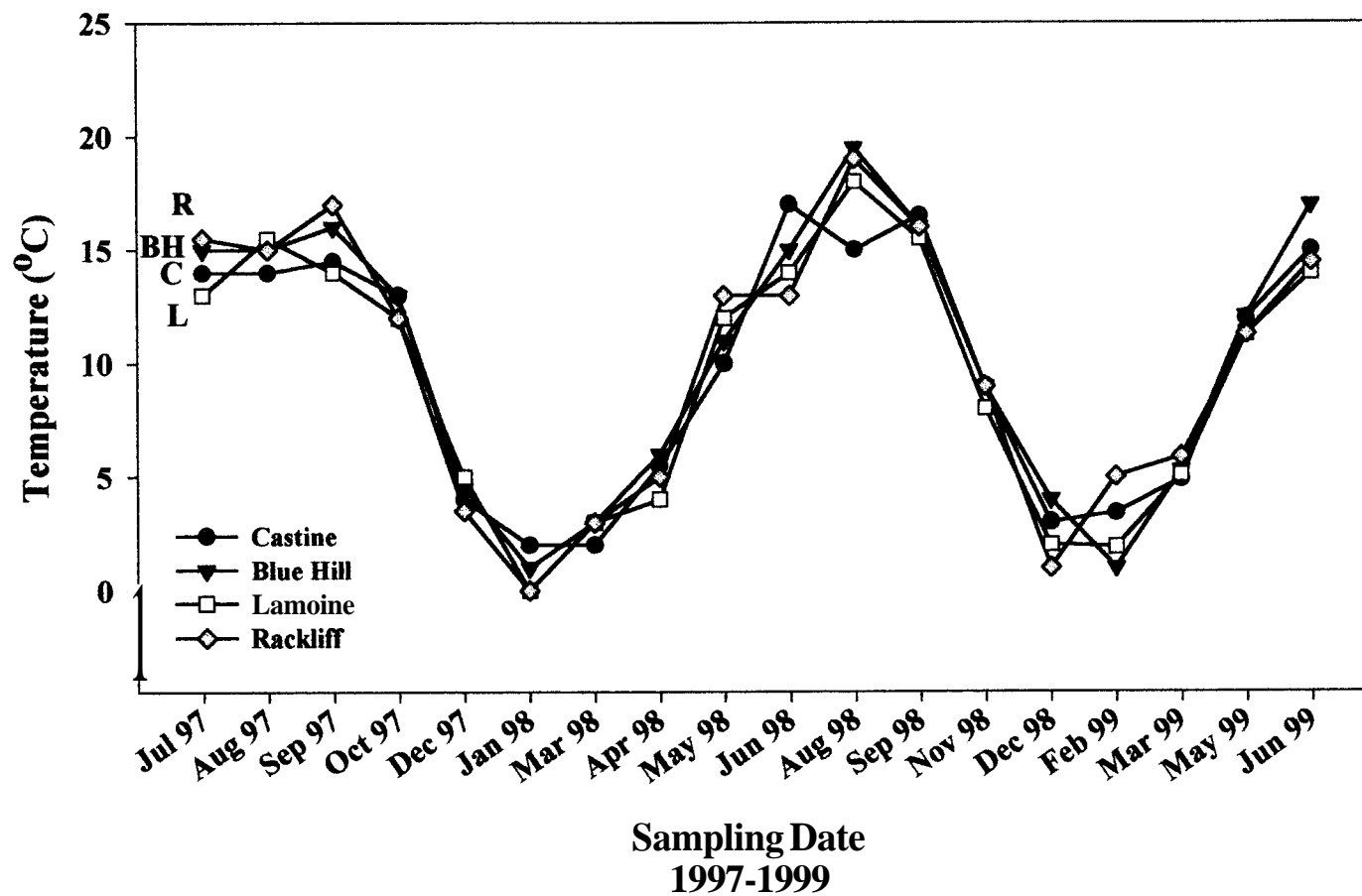


Figure 32. Monthly water temperatures (°C) measured at low tide at the study sites, July 1997 - June 1999.

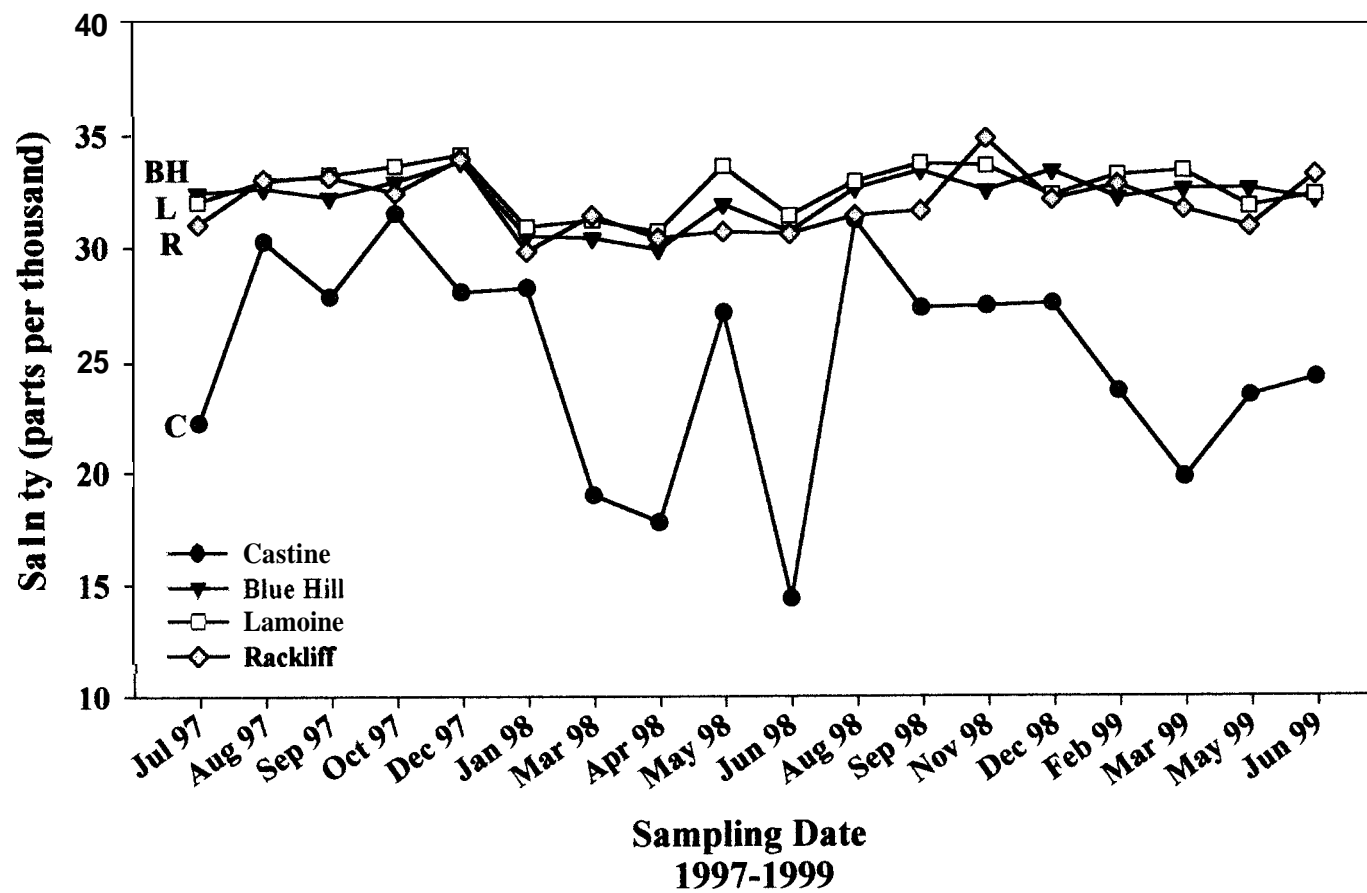


Figure 33, Monthly salinity measurements (ppt.) taken at low tide at the study sites, July 1997 - June 1999.

Table 3.1. Taxonomic list of algal and fungal species recorded in the experimental plots during the two years following harvest. * indicates those species that were found in sufficient quantities to allow statistical analyses.

Algal Species		
PHAEOPHYCEAE	FLORIDEOPHYCEAE	ULVOPHYCEAE
<i>Ascophyllum nodosum</i> *	<i>Chondrus crispus</i> *	<i>Monostroma grevillei</i>
<i>Elachista fucicola</i>	<i>Clathromorphum</i> sp.	<i>Rhizoclonia tortuosum</i>
<i>Fucus vesiculosus</i> *	<i>Devaleraea ramentacea</i>	<i>Ulothrix</i> sp.
<i>Petaloniafascia</i>	<i>Hildenbrandia rubra</i> *	
<i>Pilayella littoralis</i> *	<i>Mastocarpus stellatus</i>	
<i>Ralfsia</i> sp.	<i>Phymatolithon</i> sp. *	
<i>Scytosiphon lomentaria</i>	<i>Polysiphonia lanosa</i>	
	<i>Porphyra</i> sp.	
Fungal Species		
ASCOMYCOTINA		
<i>Vewucaria</i> spp. *		

Table **32**. Results of a repeated-measures MANOVA examining the influence of harvesting treatment on the percent cover of intertidal algal species. (A) Three-factor, mixed effects model ('Sites' are random). (B) Two-factor, fixed effects model. A priori orthogonal contrasts appear below the treatment main effect. Significant effects are in bold ($\alpha = 0.05$; $n = 3$).

^a The analysis for *Pilayella* only included time periods when it was present (March, April, May 1998 and March, May, June 1999).

(A) MANOVA TABLE		<i>Ascophyllum</i>	<i>Chondrus</i>	<i>Fucus</i>	<i>Hildenbrandia</i>	<i>Phymatolithon</i>	<i>Pilayella</i> ^a	<i>Verrucaria</i>
	df	Pr>F	Pr>F	Pr>F	Pr>F	Pr>F	Pr>F	Pr>F
Between-subject effects								
Treatment	2	0.0040	0.5954	0.2985	0.2209	0.3577	0.2065	0.8533
Control vs. cut	1	0.0049	0.9735	0.1364	0.2172	0.8251	0.3692	0.9036
36cm vs. 18cm	1	0.0110	0.3285	0.8865	0.2206	0.1724	0.1234	0.5979
Site	3	0.1823	0.0255	0.0001	0.0000	0.0042	0.0617	0.0001
Treatment x Site	6	0.1037	0.8115	0.0002	0.0467	0.1780	0.3391	0.3094
Error	24							
Within-subject effects								
Time	17	0.0000	0.3366	0.4208	0.0015	0.4510	0.0884	0.1286
Time x Treatment	34	0.0000	0.0873	0.4328	0.1747	0.4828	0.2893	0.5134
Time x Site	51	0.3084	0.4212	0.0001	0.2958	0.0001	0.0450	0.0147
Time x Treatment x Site	102	0.4621	0.0730	0.0001	0.9626	0.0001	0.54%	0.0680
Error	408							
TOTAL	647							

(B) MANOVA TABLE		<i>Ascophyllum</i>	<i>Chondrus</i>	<i>Fucus</i>	<i>Hildenbrandia</i>	<i>Phymatolithon</i>	<i>Pilayella</i> ^a	<i>Verrucaria</i>
	df	Pr>F	Pr>F	Pr>F	Pr>F	Pr>F	Pr>F	Pr>F
Between-subject effects								
Treatment	2	0.0001	0.7886	0.1273	0.3345	0.2851	0.1412	0.9123
Control vs. cut	1	0.0001	0.9822	0.0446	0.2930	0.8133	0.3384	0.9249
36cm vs. 18cm	1	0.0001	0.4942	0.8576	0.2970	0.1197	0.0822	0.6784
Error	33							
Within-subject effects								
Time	17	0.0000	0.0824	0.7455	0.0008	0.2135	0.0034	0.4708
Time x Treatment	34	0.0187	0.4935	0.2228	0.0827	0.6534	0.1847	0.6638
Time x Control vs. cut	17	0.0020	0.3456	0.1043	0.2379	0.3323	0.2027	0.4598
Time x 36cm vs. 18cm	17	0.0700	0.4775	0.5157	0.0497	0.8739	0.2737	0.6904
Error	561							
TOTAL	647							

Table 3.2a). Where interactions are present and significant, main factors cannot be fully evaluated (Winer et al., 1991). Examination of the 'Treatment x Time' interaction (Fig. 3.4) shows initially the highest mean percent cover in the control plots, followed by the 36-cm cut plots and then the 18-cm cut plots. Through time, plants regenerated until there was no statistical difference in percent cover between the control plots and those harvested (Table 3.3). Although not detectable statistically, examination of Figure 3.4 shows that except for 1 or 2 spurious points, treatment effects in the 18-cm cut plots persisted through the end of the study.

The percent cover of *Chondrus crispus*, a perennial red macroalga, was unaffected by the harvesting treatments (Table 3.2a). 'Site' effects, however, were detected indicating that the overall percent cover of this species is site-dependent (Fig. 3.5). Lamoine had a higher mean percent cover of *Chondrus* than any of the other sites. This analysis indicates that understory algal communities within an *Ascophyllum* bed can vary from site-to-site (Table 3.2a; Fig. 3.5).

Fucus vesiculosus showed significant 'Site', 'Treatment x Site', 'Time x Site', and 'Treatment x Site x Time' effects (Table 3.2a). Although 'Site' effects cannot be fully evaluated because of the significant interaction terms, an examination of the overall pattern of this species at the different 'random' locations reveals that only one location (Rackliff Island) had *Fucus* in any amount (Fig. 3.5). This fact alone could cause the significant interaction effects detected in the analysis. A closer inspection of the data shows a 'Treatment x Time' interaction at Rackliff Island (Fig. 3.6). A two-way MANOVA ('Treatment x Time') conducted on the Rackliff Island data revealed a significant 'Treatment' effect ($P = 0.0194$). Tukey's post-hoc comparison tests failed to

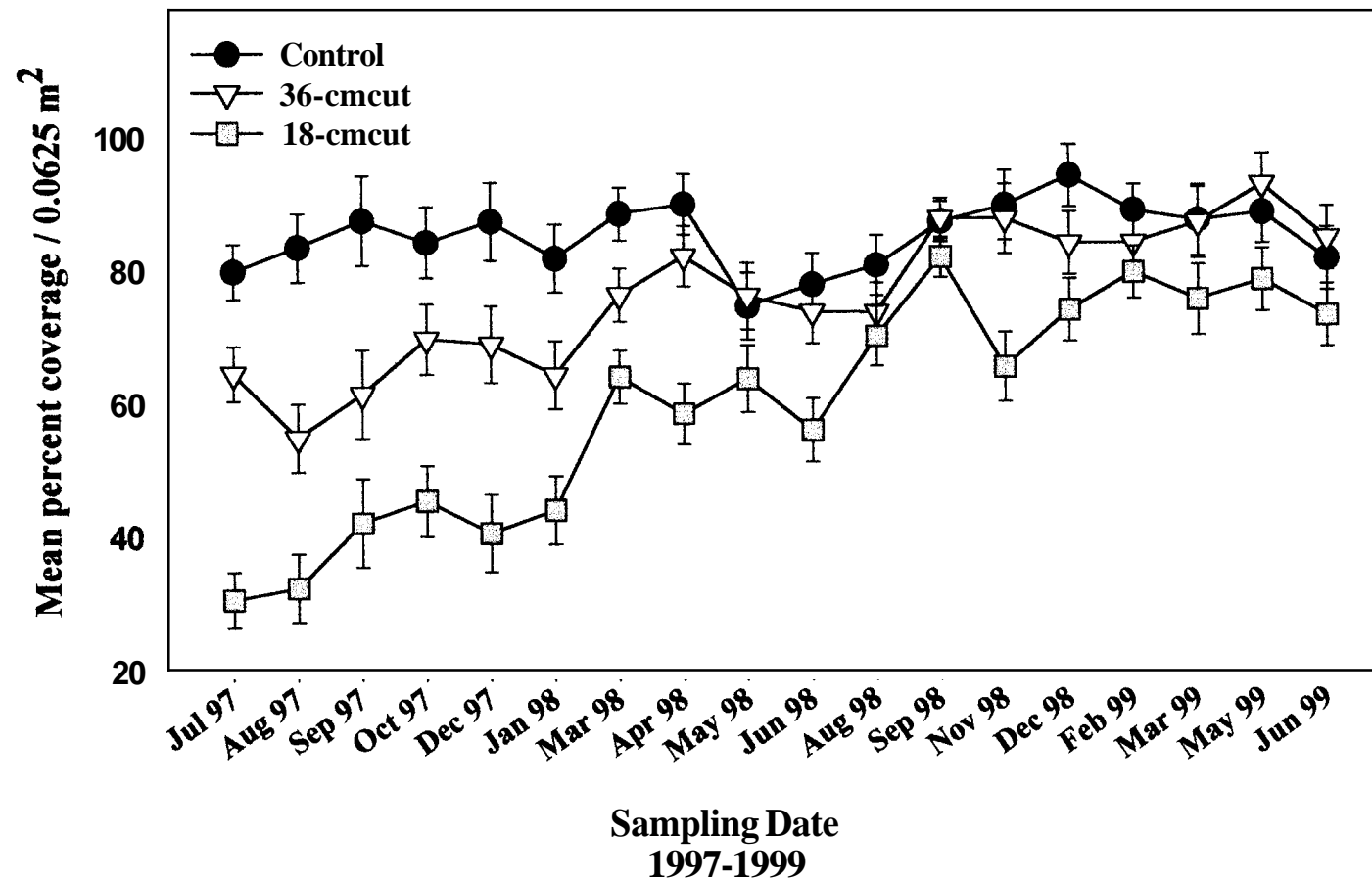


Figure 3.4. Temporal changes in the percent coverage of *Ascophyllum nodosum* at various treatment levels. Values represent means \pm S.E. ($n = 4$ sites \times 3 reps/site = 12/treatment/time).

Table 33. **Ryan-Einot-Gabriel-Walsh** Multiple Range Test (REGWQ grouping) indicating significant ‘Treatment x Time’ interactions for *Ascophyllum nodosum*. Common underlines in the REGWQ groupings denote lack of statistical Qfference between the treatments.

SAMPLING DATE	REGWQ GROUPING	SIGNIFICANCE
July, 1997	<u>C > 36cm > 18cm</u>	*
August, 1997	<u>C > 36cm > 18cm</u>	*
September, 1997	<u>C > 36cm > 18cm</u>	*
October, 1997	<u>C > 36cm > 18cm</u>	*
December, 1997	<u>C > 36cm > 18cm</u>	*
January, 1998	<u>C > 36cm > 18cm</u>	*
March, 1998	<u>C > 36cm > 18cm</u>	NS
April, 1998	<u>C > 36cm > 18cm</u>	NS
May, 1998	<u>36cm > C > 18cm</u>	NS
June, 1998	<u>C > 36cm > 18cm</u>	NS
August, 1998	<u>C > 36cm > 18cm</u>	*
September, 1998	<u>36cm > C > 18cm</u>	NS
November, 1998	<u>C > 36cm > 18cm</u>	NS
December, 1998	<u>C > 36cm > 18cm</u>	*
February, 1999	<u>C > 36cm > 18cm</u>	NS
March, 1999	<u>C > 36cm > 18cm</u>	NS
May, 1999	<u>36cm > C > 18cm</u>	NS
June, 1999	<u>36cm > C > 18cm</u>	NS

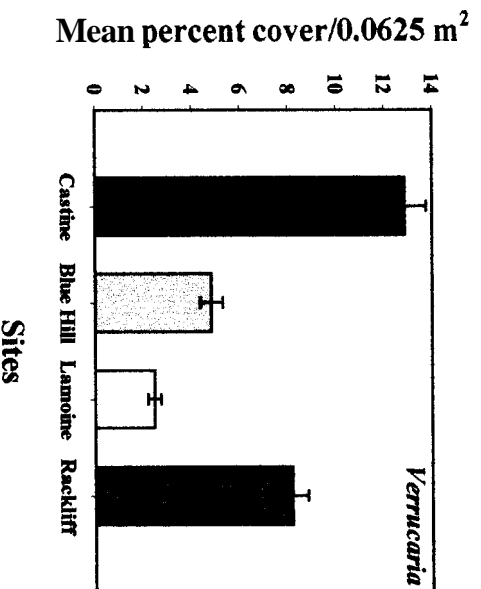
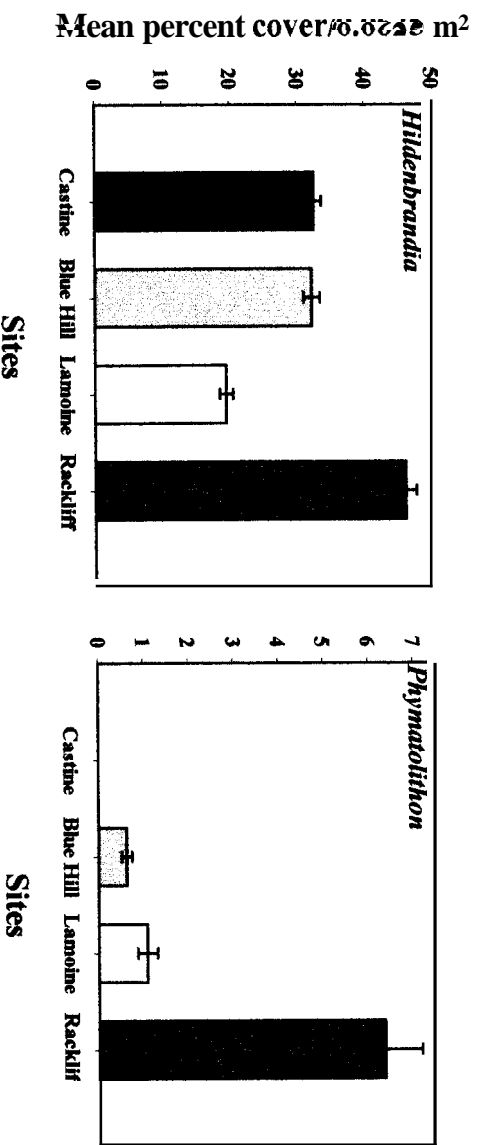
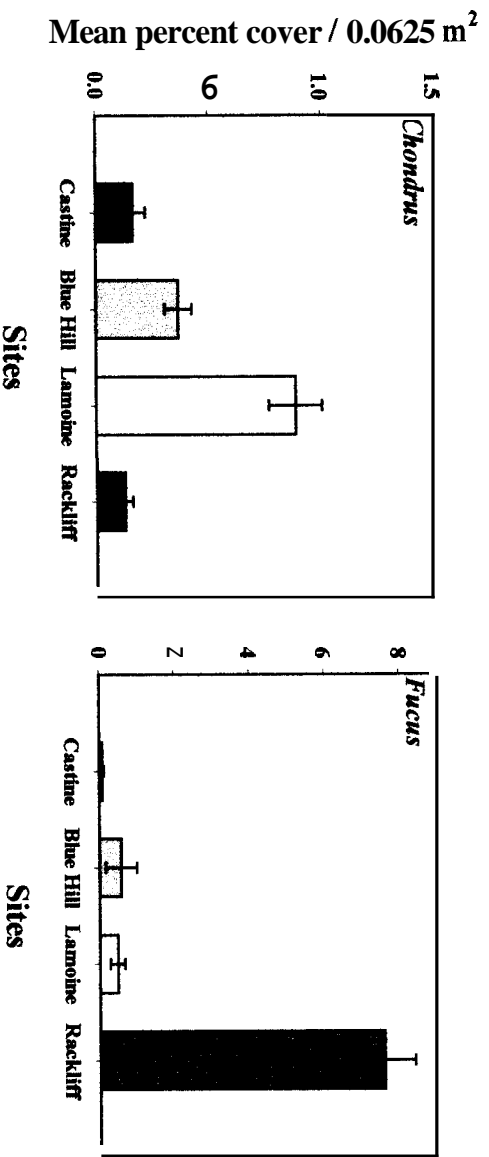


Figure 3.5. Mean percent cover / 0.0625 m² of different algal species at four experimental sites along the coast of Maine. Values represent means \pm S.E. (n = 9 plots/site x 18 time periods = 162/site).

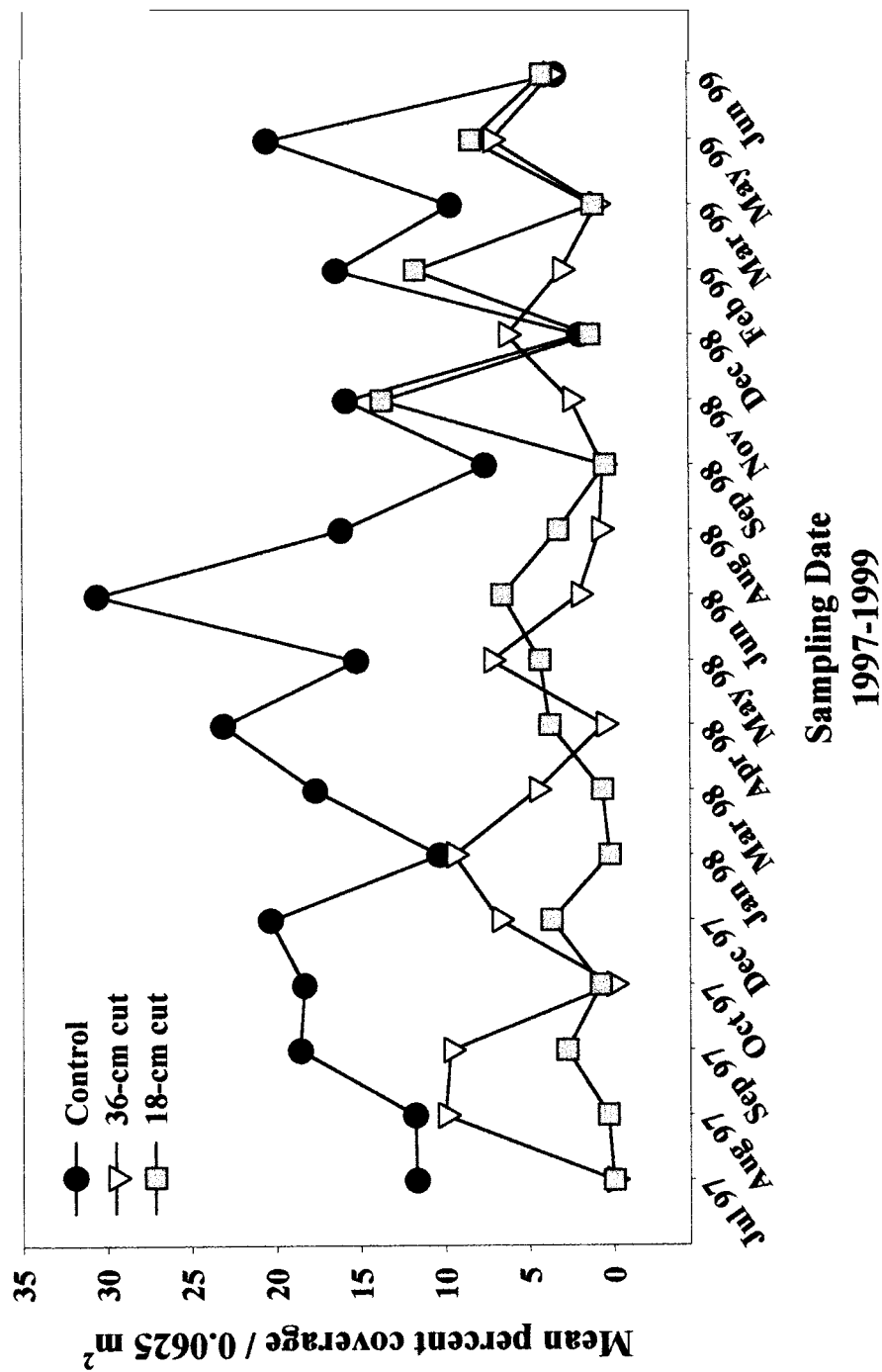


Figure 3.6. Temporal changes in the percent coverage of *Fucus vesiculosus* at various treatment levels at Rackliff Island, Maine. Standard errors are omitted for clarity but ranged from 7% to 97% of the mean. (n = 3/treatment/time).

detect significant differences (C vs. 36 - $P = 0.0325$; C vs. 18 - $P = 0.0277$) between treatments at the Bonferroni-adjusted alpha level ($\alpha = 0.017$ for three comparisons). The failure to detect treatment and temporal differences can be attributed to large fluctuations in the means due to high natural variability and low treatment replication ($n = 3$) at individual sites.

Hildenbrandia rubra was also significantly affected by the removal of the canopy species. 'Site', 'Treatment x Site' and 'Time' effects were all detected (Table 3.2a). **An** examination of the 'Treatment x Site' interaction showed that plants at Castine, Blue Hill and Rackliff reacted the similarly to the different treatment levels even though there were differences in the magnitude of their responses (Fig. 3.7). At these sites, *Hildenbrandiu* ~~was~~ most abundant in the control plots with a decrease in its percent cover correlated to the intensity of harvest. The 'Treatment x Site' interaction is significant because plants at Lamoine responded differently under the same treatment regimes (Table 3.2a). At Lamoine, the 36-cm cut plots had the highest percent cover of *Hildenbrandiu* followed by the 18-cm cut plots and the control plots (Fig. 3.7). **Post-hoc** tests failed to detect individual treatment differences at Lamoine.

Phymatolithon lenormandii, a crustose alga species, was not present at all in Castine, found only in small quantities at Blue Hill and Lamoine but ~~was~~ relatively abundant at Rackliff Island (Table 3.2a; Fig. 3.5). Plotting the changes in mean percent cover by treatment over time at each site demonstrates the three-way interaction detected by the MANOVA (Fig. 3.8). No discernible pattern by treatment emerges from the Blue Hill or Lamoine graphs. Data from Rackliff Island shows an increase in the mean percent cover of *Phymutolithon* in the 36-cm cut plots compared to the controls (Fig. 3.8). A

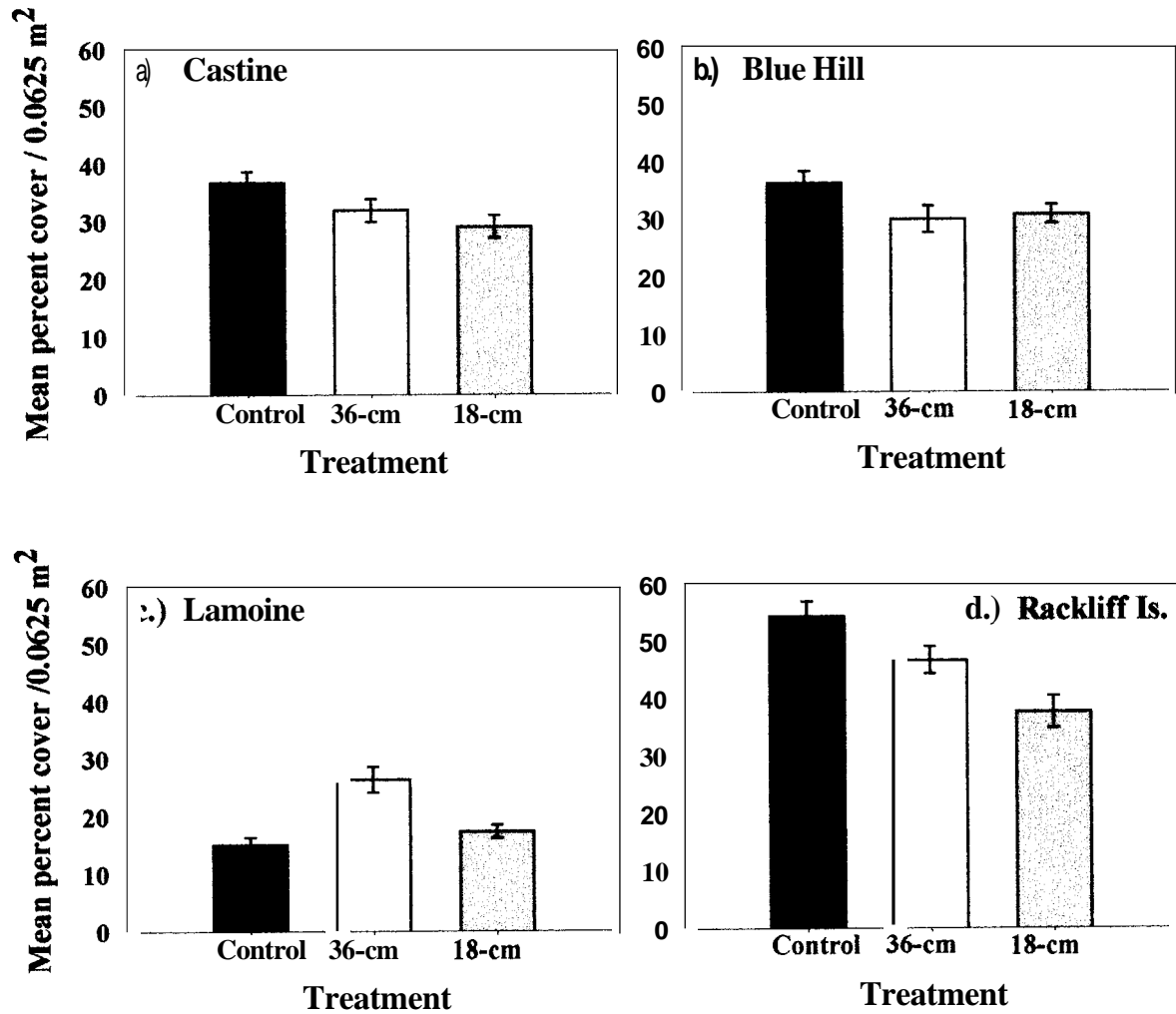
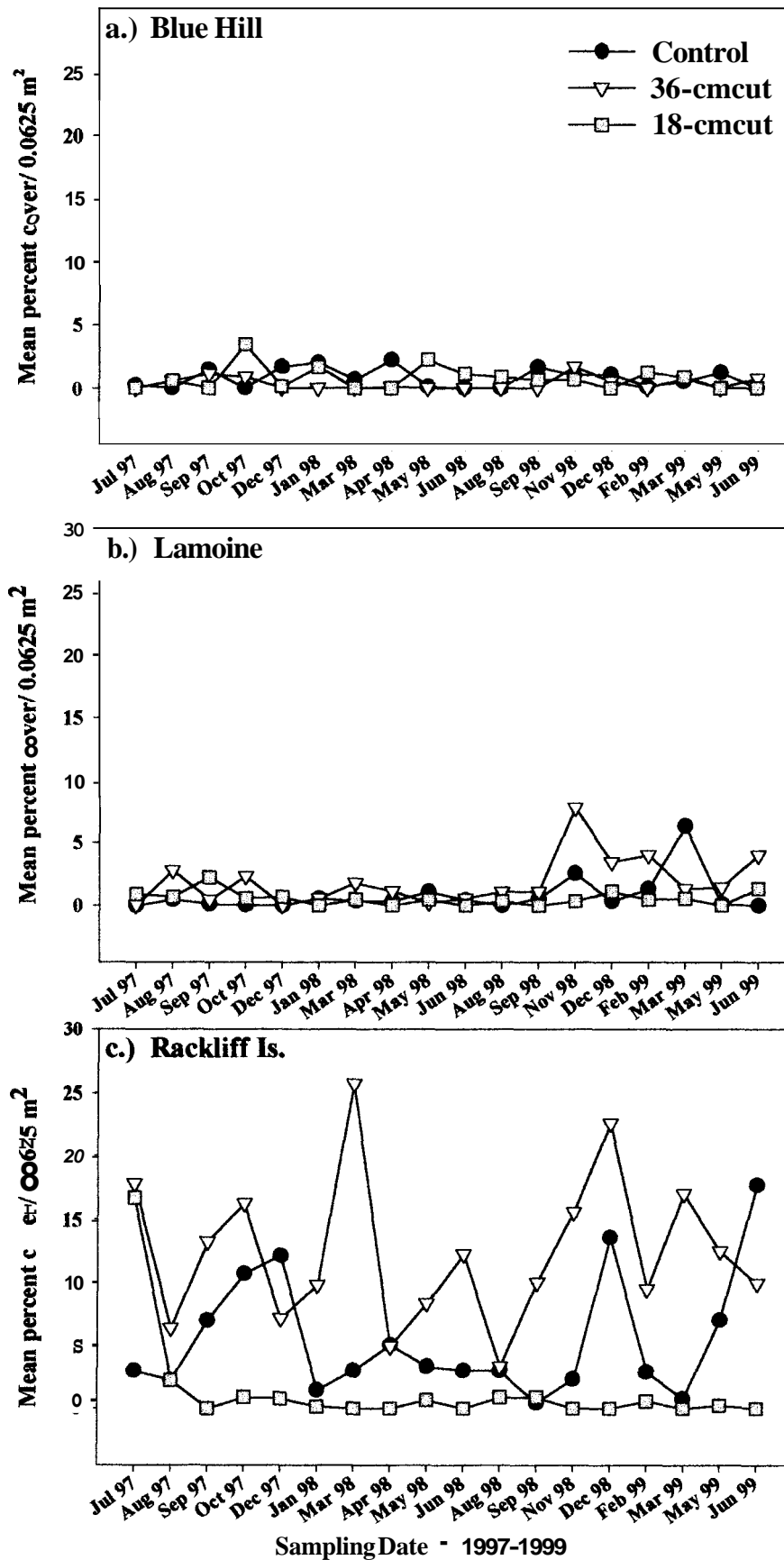


Figure 3.7. The effects of harvesting treatment level on *Hildenbrandia rubra* at different sites in Maine. Values represent means \pm S.E. ($n = 3$ reps/site \times 18 time periods = 54/treatment/site).

Figure 3.8. The effect of differing levels of *Ascophyllum* removal on *Phymatolithon lenormandii* for two years following an experimental harvest at three different sites along the coast of Maine. Standard errors are omitted for clarity but ranged from 25% to 100% of the mean. (n = 3/treatment/time period)



two-way MANOVA ('Treatment x Time') conducted on the Rackliff Island data did not detect any significant effects due to the high variability associated with the response variables (e.g., the intermediate cut - 36-cm). Within a month following harvest, the percent cover in the 18-cm cut plots dropped to near-zero levels and remained depressed for the entire two-year experiment.

The filamentous brown alga, *Pilayella littoralis* was not affected by either harvesting treatment (Table 3.2a). *Pilayella* is a seasonal epiphyte present mainly in spring and is generally quite abundant. Ten months after the harvest, *Pilayella* recruited into the *Ascophyllum* beds and settled onto plants regardless of treatment. In the spring of 1998 the highest abundances at Blue Hill and Rackliff Island were reached in April whereas the highest abundances at Castine and Lamoine occurred in May (Fig. 3.9). In 1999, the highest percent cover of *Pilayella* occurred during April for all of the sites except Blue Hill where it was absent. The temporal and spatial patterns of abundance were detected by the MANOVA analysis in the form of a significant 'Time x Site' effect (Table 3.2a).

The percent cover of *Verrucaria*, a green lichen, was not influenced by the removal of the canopy species. 'Site' and 'Site x Time' effects were, however, detected. Examination of the 'Site x Time' effect reveals that Castine had the highest percent cover followed by Rackliff, then Blue Hill and Lamoine (Fig. 3.10). The abundance of *Verrucaria* was highly variable from sampling period to sampling period at Castine due to spatial heterogeneity but relatively stable at both Blue Hill and Lamoine. In November of 1998 the percent cover at Rackliff Island increased, causing the 'Site x Time' interaction effect (Table 3.2a).

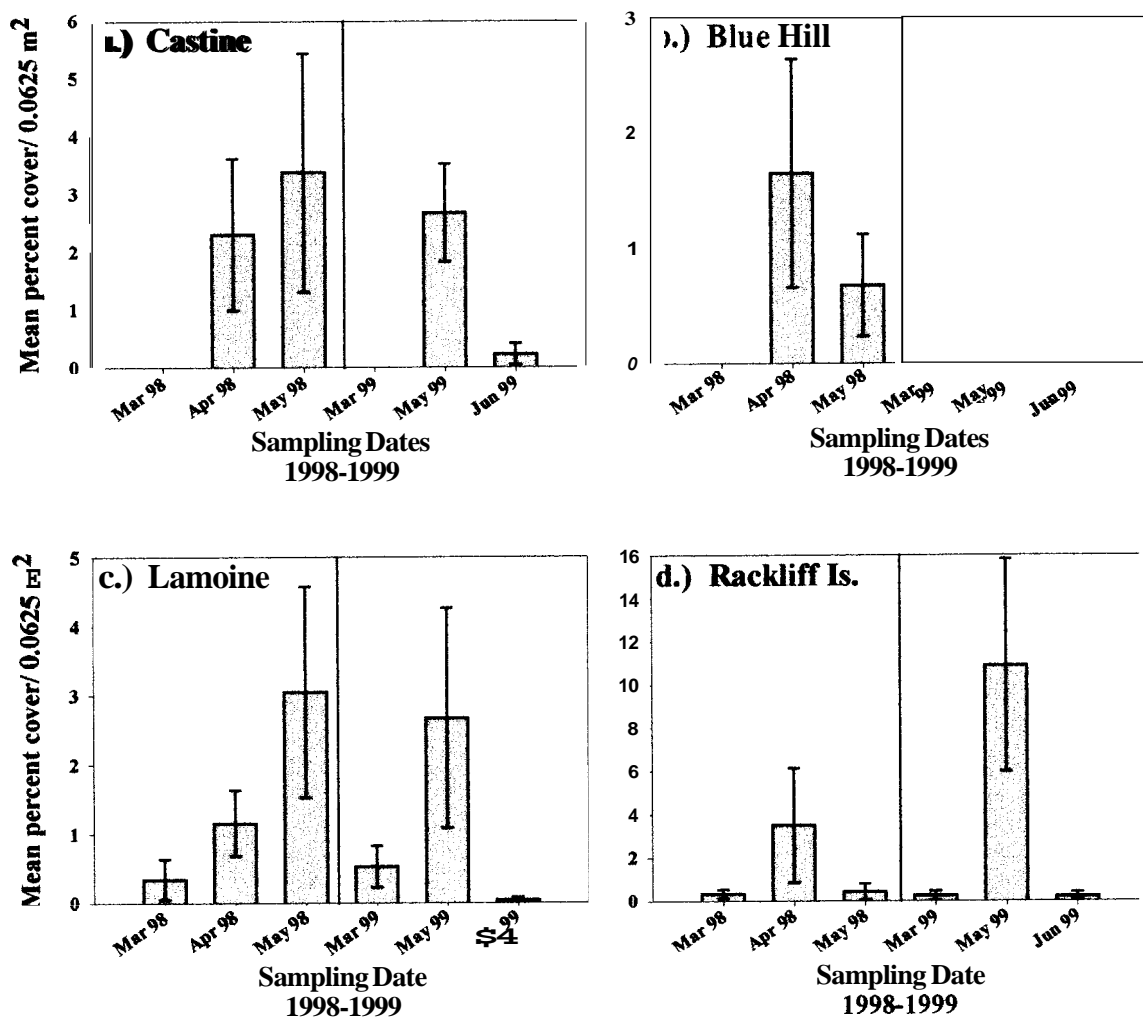


Figure 3.9. Mean percent cover / 0.0625 m² of *Pilayella littoralis* through time at the four experimental sites. Values represent means \pm S.E. ($n = 3$ treatments \times 3 reps/site = 9/site/time). *Pilayella* was only present during March, April and May of 1998 and March, May and June of 1999. The vertical line through each plot separates the two years.

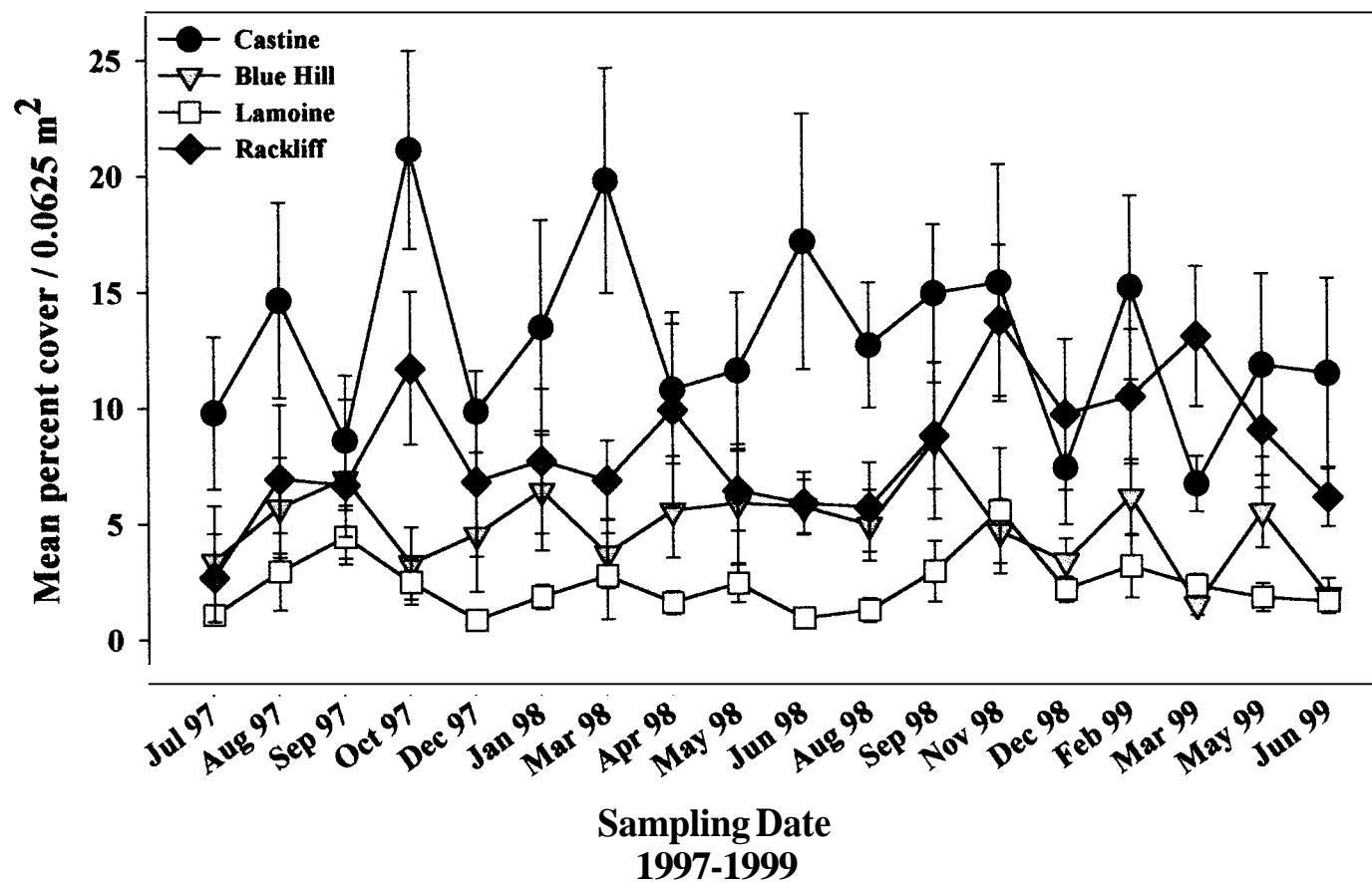


Figure 3.10. Percent cover / 0.0625 m² of *Verrucaria* sp. through time at the four experimental sites. Values represent means \pm S.E. (n = 9 plots/site/time).

3.4.2. Reduced **MANOVA** model

The reduced, repeated-measures **MANOVA** model was conducted to analyze the relative difference among experimental treatments, over and above the intrinsic difference associated with sites. The two **MANOVA** models (full and reduced) are presented separately to reduce confusion. The reduced model, which excluded sites, also detected significant treatment effects (Table 3.2b).

Treatment effects were detected for *Ascophyllum nodosum*, *Fucus vesiculosus* and *Hildenbrandia rubra*. Similar to the full **MANOVA** model, the reduced model detected a 'Treatment x Time' interaction for the harvested species. *A priori* contrasts were conducted on the within-subjects effects which revealed a significant 'Time x Control vs. Cut' effect ($P = 0.002$). The mean percent cover of *Ascophyllum* was significantly higher in the control plots when compared to the mean of the cut plots for the first eight months following the harvest. Although the coverage in the control plots remained consistently higher (Fig. 3.4), after March 1998 no statistical difference could be detected between the control and the mean of the harvested plots (Table 3.3).

An overall treatment effect was detected for *Fucus vesiculosus* ($P = 0.0446$; Table 3.2b). When collapsed over all sites and time periods, the percent cover of the control plants was significantly higher than the mean value of the cut plants (Figure 3.11).

The analysis for *Hildenbrandia rubra* showed a temporal effect as well as a 'Time x 36cm vs. 18cm' effect. Despite there not being a significant overall 'Time x Treatment' effect, the powerful *a priori* contrasts detected a temporal effect between the two cut treatments. The percent cover of *Hildenbrandia* in the 36-cm cut plots was consistently higher than the percent cover in the 18-cm cut plots for the first year (Fig. 3.12). During

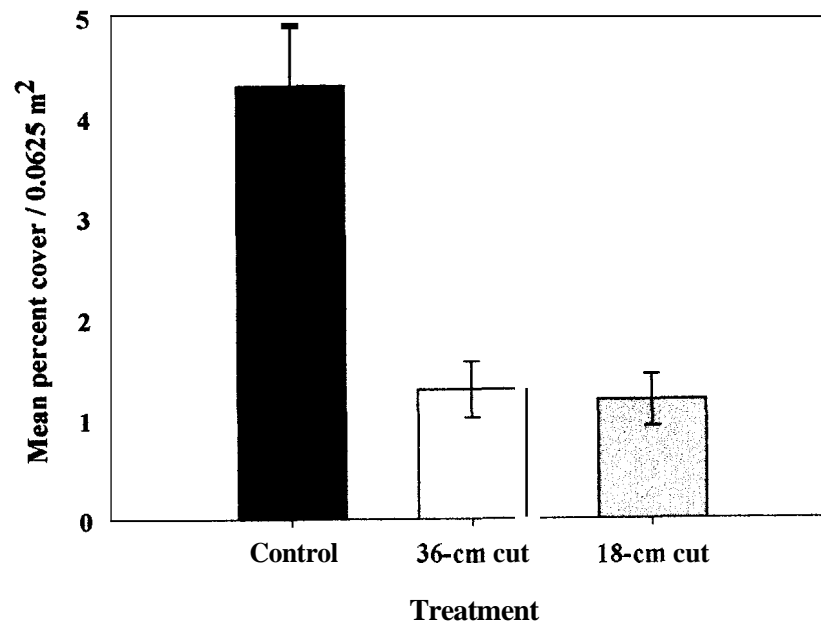


Figure 3.11. Mean treatment effects for *Fucus vesiculosus* averaged over the two-year post-harvest time period. Error bars represent \pm S.E. ($n = 4$ sites \times 3 reps/site \times 18 time periods = 216 per treatment)

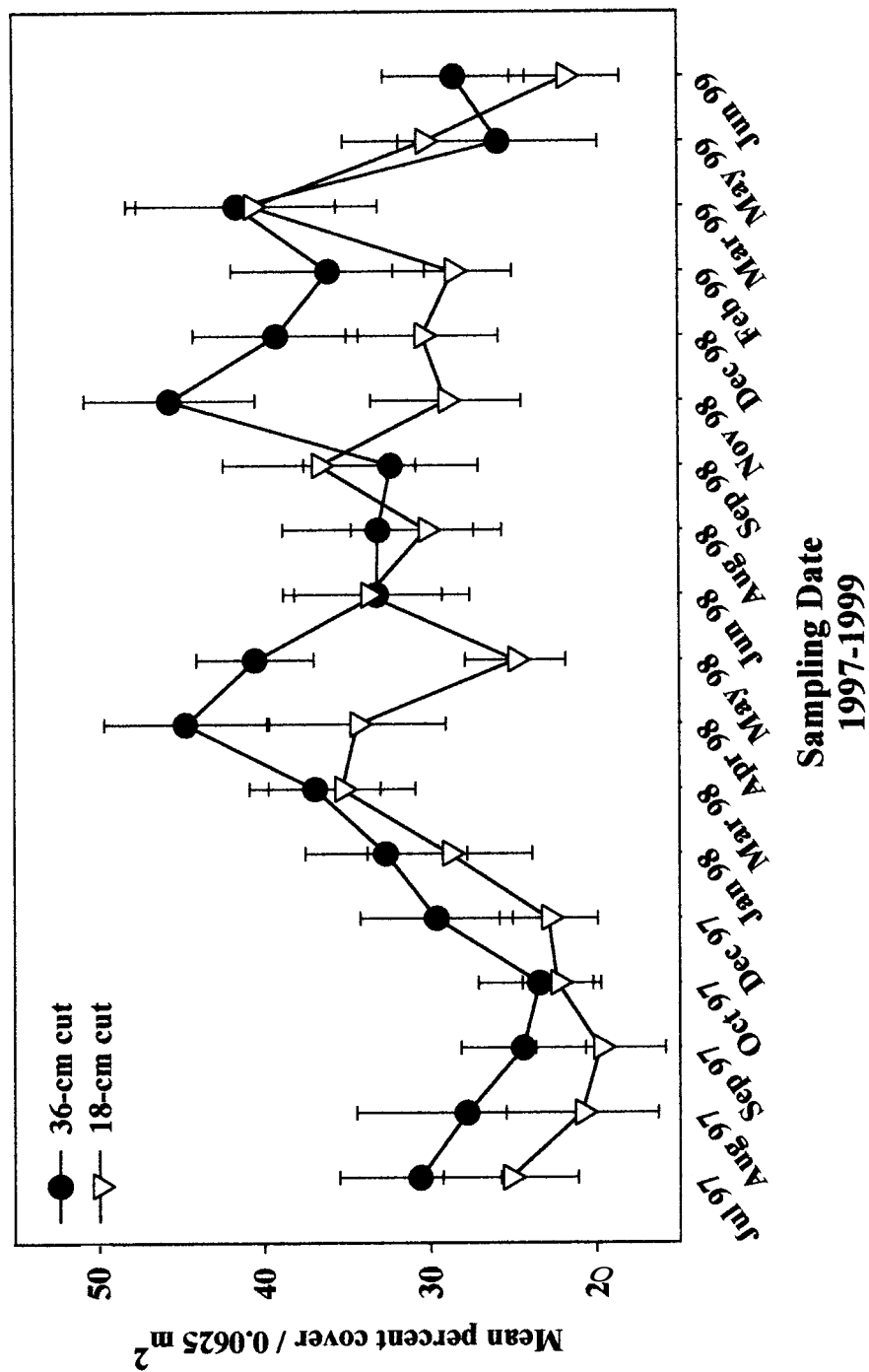


Figure 3.12. Mean percent cover \pm S.E. of *Hildenbrandia rubra* in the harvested plots.
(n = 4 sites x 3 reps/site = 12/time/trt)

the second year, the percent cover in the 18-cm cut plots increased to about the same level as the 36-cm treatment.

The reduced model detected no significant effects for *Chondrus crispus*, *Phymatolithon lenormandii* and *Verrucaria* spp. A significant temporal effect was detected for *Pilayella*, which is indicative of the species seasonality.

3.5. Discussion

3.5.1. Canopy species

Removal of the canopy species in any ecosystem can have dramatic effects on the underlying plants. Because canopy species succeed in competitively dominating the light resource, their removal is often followed by the disappearance or reduction of obligate understory species and by blooms of fugitive species (Dayton, 1975). In stressful environments, such as the rocky intertidal, algal canopies modify the habitat by ameliorating the harsh physical conditions for understory species. Removal of the canopy exposes the understory assemblage to an immediate increase in light and desiccation. The magnitude of the increased physical stress on the obligate understory algae is related to the intensity of the removal as well as the seasonality of the removal.

When the intertidal zone is inundated by the tide, the high density of *Ascophyllum* plants along with the highly branched morphology of fronds create a low-light understory environment where only shade-tolerant species can survive. As the water retreats, the fronds of the *Ascophyllum* canopy lie over the rock surface, providing a layer of protection to the understory species during emersion. The plant material buffers the understory algae from light and desiccation. Bertness et al. (1999) found that maximum

daily rock temperatures were 5-10°C lower and evaporative water loss was an order of magnitude less under an *Ascophyllum* canopy than in adjacent areas where the canopy had been removed. Removal of the algal canopy results in increased physical stresses to obligate understory species. Other algal species, however, are capable of surviving the rigors of tidal emersion without the presence of the canopy (e.g., they are not obligate understory species). For these species, removal of the canopy may release the plants from competition and they may grow faster and survive better.

The mean percent cover of the canopy species, *Ascophyllum nodosum*, was reduced significantly following the experimental harvest. This reduction in coverage was not surprising since the plants were cut at set heights (36-cm and 18-cm). Within nine months the harvested plants had regenerated to a point where no statistical difference in the percent coverage could be detected between the treatments. The recovery in percent cover, however, is not necessarily indicative of biomass or habitat recovery (Vadas and Wright, 1986; Chapter 6). For at least a nine-month period following the harvest, the understory algae were exposed to increased levels of physical stress due to the reduction in canopy coverage.

3.5.2. Understory algal species

After the experimental harvest, the percent cover of *Fucus vesiculosus* at Rackliff Island was significantly lower in both of the cut plots compared to the control plots. This condition persisted for about **14** months. *Fucus* is normally a canopy-forming species but in sheltered areas the larger *Ascophyllum* plants (1-2 meters in height) outcompete the shorter *Fucus* plants (25-50 cm) (Keser et al., 1981). Following the removal of the

canopy, one would have anticipated an increase in the percent cover of *Fucus* due to a competitive release. However, in this study the *Fucus* population decreased. Fucoids are highly resistant to changes in light levels: they can survive long periods in the dark and, conversely, they have protection mechanisms against damage from high light levels (Chapman, 1995). Therefore, it is unlikely that the dramatic increase in the light level due to an opening in the canopy caused a decline in this understory population. In fucoids, desiccation and overheating have been found to be more critical components of aerial emersion than high irradiation (Stromgren, 1977). The fact that the canopy was removed during mid-summer, when desiccation stress was highest may have been a contributing factor in the decline in *Fucus*. *Fucus* plants at Rackliff Island were also frequently found growing epiphytically on *Ascophyllum* plants. These fucoids were likely removed during the harvest.

Mean percent cover of *Hildenbrandia rubra* was reduced at three of the four experimental sites and was correlated to the intensity of harvest. At Castine, Blue Hill, and Rackliff, the more canopy that was removed, the lower the percent cover of *Hildenbrandia*. At Lamoine, however, the percent cover increased in the 36-cm cut plots compared to the controls. This suggests that *Hildenbrandia* may be light-limited under natural conditions at Lamoine. Removal of part of the canopy in the 36-cm cut plots had a positive effect on *Hildenbrandia* growth. This effect was not the same in the 18-cm cut plots, where *Hildenbrandia* may have been receiving too much light to show an increase in percent cover. The *Ascophyllum* canopy at Lamoine was much shorter and bushier than that found elsewhere. The shorter, bushier plants may have reduced the understory light levels to below that needed for growth. When compared to the other experimental

sites, Lamoine had a lower overall percent cover of *Hildenbrandia* in the control plots, which may be indicative of light-limiting conditions. The observed increase in *Hildenbrandia* in the 36-cm cut plots at Lamoine is not likely due to an herbivore effect because snail densities remained stable regardless of treatment level (Chapter 4).

Like *Hildenbrandia*, *Phymatolithon lenormandii* may have also been light-limited under natural conditions. Removal of some of the canopy (36-cm cut) resulted in an increase in the mean percent cover, whereas cutting *Ascophyllum* plants to 18cm lulled most plants. Other studies have shown that calcareous species, such as *Phymatolithon*, reduce calcification in low light intensities which makes them more susceptible to damage from bleaching when transferred to high light intensities (Round, 1981). Schiel and Taylor (1999) experimentally removed an intertidal fucoid canopy in New Zealand, which led to a reduction in the percent cover of understory corallines presumably due to bleaching and die-off following the total canopy removal. Jenkins et al. (1999) also observed the bleaching of understory calcareous and crustose species following a total canopy (*Fucus serratus*) removal in the intertidal. *Phymatolithon* appears to be an "obligate understory" species (*sensu* Dayton, 1975) in the intertidal zone because of the complete die-off in the intensely harvested plots.

3.5.3. Spatial effects

Sites were considered a random factor at the onset of the experiment so that the results of the study could be generalized to the population of all such *Ascophyllum* dominated communities. I was interested in the effects of rockweed harvesting over and above the intrinsic differences associated with sites. In five of seven algal species

examined, the baseline percent cover of the species varied by site. This indicates that the overall algal assemblages associated with *Ascophyllum* beds are not uniform but site-specific. Although I cannot focus specifically on site effects because of the difficulty of attributing differences to specific causes, it should be noted that the effects of *Ascophyllum* harvesting are site-specific and dependent on the community of organisms in each rockweed bed. Not only does the species composition differ between sites, but the ecological impacts of harvesting appear to have site-specific components.

3.6. Conclusion

The ecological importance of seaweeds as habitats and habitat modifiers often parallels their value as potential resources (Santelices and Griffiths, 1994). In general, the species most sought after for exploitation tend to be those that grow to an exceptionally large size or those that form dense monocultures. Frequently, the most economically valuable seaweeds are those same species that are ecologically most important.

In the Gulf of Maine, *Ascophyllum* is the most important intertidal alga economically and ecologically because of its wide-spread abundance. It is clear that habitat structure, provided by the dominant plant, has an important influence on the functional value of the habitat for resident plants. The algal canopy plays a crucial ecological role in ameliorating thermal and desiccation stresses to the understory. In some instances partial canopy removal actually stimulated the growth of understory algae (e.g., *Phymutolithon* and *Hildenbrandia*). In areas that were intensively harvested (cut at 18-cm) the understory algae either experienced a reduction in the percent cover or completely died from the increased physical stress associated with canopy removal. The

experimental studies **of** *A. nodosum* have revealed several ecological effects of harvesting that should be considered when managing wild stocks **of** this species. Removal of any part **of** the canopy will result in increased physical stresses to the understory algal assemblage and will likely change the structure of most underlying species in the community over the short-term.

Chapter 4

Ecology of *Ascophyllum* harvesting: effects on the associated invertebrate assemblage

4.1. Abstract

Despite the vital role of macroalgal habitats in coastal ecosystems little is known about the long-term consequences of decreased habitat complexity (caused by commercial harvesting) on the associated invertebrate communities. To test the hypothesis that a reduction in the macroalgal canopies and hence a reduction in structural complexity will lead to a subsequent reduction in the associated invertebrates, I imposed three different harvesting treatments (unharvested/control and harvested at **18** cm and 36 cm from the holdfast) at four separate sites of beds dominated by *Ascophyllum nodosum* in mid-coast Maine, USA, and followed the changes in invertebrate community structure for two years.

A three-factor, repeated-measures MANOVA was used to analyze the effects of harvesting treatment on both sessile and mobile invertebrate species. Removal of the algal canopy significantly affected both positively and negatively the numerical abundances of green crabs (*Carcinus maenas*), common periwinkles (*Littorina Eittorea*), blue mussels (*Mytilus edulis*), and limpets (*Tectura testudinalis*). Harvesting also affected several understory, sessile invertebrates such as *Dynamena pumila* (a colonial hydroid), *M. edulis* recruits (blue mussel spat), and *Semibalanus balanoides* (barnacles).

Following the single experimental harvest, there was a significant decline in the abundance of green crabs in both cut treatments. Within a year, however, the population

had reestablished itself, presumably due to an increase in the habitat structure from the regeneration of the canopy. These findings suggest that the density of green crabs is positively correlated to the percent cover of the algal canopy. In the spring of both years following the experiment, the mean abundance of *L. littorea* in cut plots was higher than in control plots. The increased snail abundance in the cut plots may be due to an increase in ephemeral algae, the preferred food for littorines. *Dynamena* experienced significant treatment effects at high population levels, yet at lower densities the effect of canopy removal was equivocal. Considerable differences were found in the species abundances at the four experimental sites. Apparent homogeneity of the structuring species, in this case *Ascophyllum*, does not necessarily mean that the associated communities are similar. With the *Ascophyllum* communities being *so* different from site to site, impacts of regional or coast-wide harvesting will be difficult to assess.

Key words: *Ascophyllum nodosum*; community ecology; habitat; invertebrates; macroalgal harvesting; rocky intertidal; structural complexity; understory.

4.2 Introduction

Macroalgal canopies form an important part of intertidal and shallow subtidal marine communities worldwide. Their upright growth form adds a three-dimensional structural component to an otherwise two-dimensional benthic environment. The habitat structure provided by the macroalgal canopies can be defined **as** consisting of two components: (1) habitat heterogeneity, or patchiness of habitat types across a landscape, and (2) habitat complexity, the physical or architectural component of the structure

(McCoy and Bell, **1991**). Thus, a complex landscape may consist of several habitat types, each with its own degree of physical structure. This paper focuses on the effects of decreased habitat complexity or structure on an associated invertebrate community in a homogeneous, intertidal seaweed habitat.

Marine algal canopies have long been identified as playing important community-structuring roles by modifying the physical and biological conditions in the habitats in which they dominate (Dayton, **1975**; Menge, **1978**; Eckman et al., **1989**; Bertness et al., **1999**). Increased structural complexity within a habitat is considered a contributing factor to increased species diversity because of increased niche availability (Hicks, **1980**; Sebens, **1991**; Gee and Warwick, **1994**; Jarvis and Seed, **1996**). Structurally complex seaweeds not only provide a secondary substratum for organisms to colonize but they also provide important habitats and refuges for a wide range of marine organisms (Duggins et al., **1990**; Sebens, **1991**). The added structural complexity also alters the physical environment, thereby influencing the abundance and distribution of associated species (Bertness, **1999**). The emergent structure alters the quality and quantity of light reaching the substratum (Lobban and Harrison, **1994**), increases sedimentation (Duggins et al., **1990**), and changes the fluid dynamics near the seafloor by reducing local water flow and thus the transport of resources and propagules within the community (Jackson and Winant, **1983**; Bodkin, **1988**; Eckman and Duggins, **1991**; Irlandi and Peterson, **1991**; Sebens, **1991**).

Intertidal seaweeds possess additional habitat-modifying characteristics. When the intertidal habitat is exposed, the fronds of the macroalgal canopy lie horizontally upon the substrate and provide a moist, understory environment for organisms beneath it.

Reduction in habitat complexity can have significant effects on the understory microclimatic conditions such as light level, desiccation stress, and temperature.

In this paper I examine the effects of decreased habitat complexity in an intertidal seaweed bed on the associated invertebrate community. *Ascophyllum nodosum* is a dominant, intertidal, brown alga in the North Atlantic and has been commercially harvested for decades. Little information exists on the impact of harvesting with regard to changes in the structural complexity of the habitat and how these changes affect the associated community. Here we test the general hypothesis that a reduction in the *Ascophyllum* canopy, and, hence a reduction in structural complexity, will lead to a subsequent reduction in the associated invertebrates. By selecting homogeneous (> 70% mean cover) stands of *Ascophyllum*, the study is not confounded with large between-site heterogeneity but is able to directly assess the impact of reduced structural complexity (caused by harvesting) on the abundance and diversity of associated fauna.

4.3. Materials and Methods

4.3.1. Study sites

Four *Ascophyllum nodosum* beds with similar standing crops were selected in the mid-coast region of Maine (Fig. 4.1). All four sites were moderately sheltered, had a slope 15° or less, and supported a dense, continuous cover of *Ascophyllum* (>70% cover). Although an attempt was made to standardize sites by visually selecting stands of similar biomass, differences in standing crop between sites could not be avoided. Mean standing crop was approximately 9 kg/m², but individual sites ranged from 7 to 12 kg/m². Mean tidal amplitude of this region is 3.1 m and the mean tidal level is 1.7 m. Substrate at three

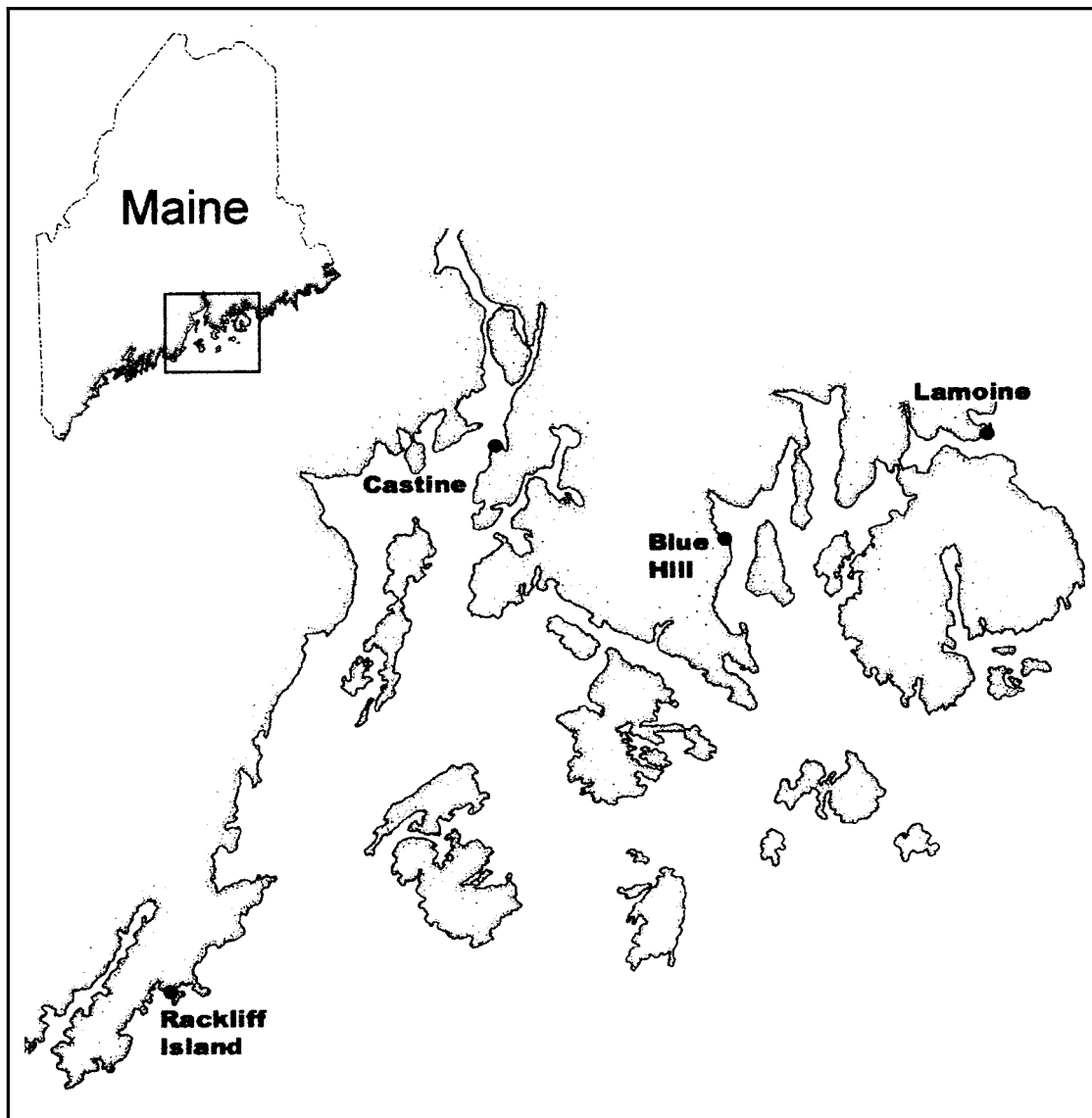


Figure 4.1. Location of experimental sites along the mid-coast region of Maine, USA.

of the sites (Castine - **44°27'8"N; 68°47'29"W**, Blue Hill Falls - **44°22'21 "N; 68°33'9"W** and Lamoine Beach - **44°27'18"N; 68°16'34"W**) consisted mainly of small to medium-sized rocks interspersed with sand and pebbles. Ledge was occasionally present. The substrate at the remaining site, Rackliff Island (**43°59'28"N; 69°9'6"W**), consisted of large bedrock outcroppings embedded in muddy substrate.

4.3.2. Experimental design and sampling methods

The experimental design included four sites (described above) each consisting of nine permanently marked **5 m x 5 m** plots placed at mean low water. Each plot was a minimum of 5 meters from an adjacent plot to assure treatment independence. Three different treatments were imposed on the plots: (1) *Ascophyllum* uncut (control), (2) *Ascophyllum* cut **36 cm** above the holdfast (36-cm cut), and (3) *Ascophyllum* cut **18 cm** above holdfast (18-cm cut). At each site, three plots were randomly assigned to each of the three treatments while assuring that the treatments were adequately interspersed (Hurlbert, **1984**).

Harvesting was done at all four sites in June of **1997** using hand shears. The seaweed was shaken vigorously to minimize the amount of epifauna removed from the plot, and then discarded on the shore.

To sample epiphytic, sessile and sedentary macroscopic fauna, a grid system was overlaid on each plot during low tide. Approximately every five to six weeks throughout the two-year study, three new sampling locations within the grid were randomly selected without replacement. These locations were overlaid by **25 cm x 25 cm** quadrats, and species abundance (if mobile) and percent cover (if sessile) of organisms was

enumerated. Percent cover for sessile species was selected as the measurement of abundance because it was the only non-destructive method available for measuring sessile and colonial organisms in the field and it was rapid to obtain (Harlin et al., 1996). The mean percent cover/abundance per plot per time period ($n = 3$) was used in the statistical analyses to avoid pseudoreplication (Hurlbert, 1984). Thus twelve replicate samples per treatment (3 per site x 4 sites) were taken every five to six weeks throughout the two-year study yielding 18 sampling periods.

The abundance of blue mussels, *Mytilus edulis*, was quantified using two different measures. Individuals greater than 5 mm in size were numerically counted in each quadrat. Mussel recruits (< 5 mm), however, were measured by percent cover because the number of individuals within a quadrat was too great to count.

Surface water temperature was measured at each site at the time of sampling (during low tide). Water temperature was measured with a mercury-column thermometer at approximately 30 cm depth in water 75 cm deep. At the same time, salinity samples were collected for analysis in the laboratory. A density hydrometer was used to determine salinity (correcting for temperature) to 0.1 parts per thousand (ppt).

4.3.3. Statistical analysis

A three-factor, repeated-measures multivariate analysis of variance (MANOVA), with replicate time periods as the repeated unit, was used to analyze the effect of harvesting treatment on either the numerical abundance (if mobile) or percent cover (if sessile) of invertebrate species (Winer et al., 1991). Treatment and time were considered fixed factors because the treatment levels were the same at all sites and sites were

sampled on a fixed time schedule (every 5-6 weeks for 2 years). Sites were treated **as** a random factor because there were no *a priori* reasons for selecting those specific sites which allows the results to be generalized to all such populations of *Ascophyllum* beds (Winer et al, 1991; Underwood, 1997). This full model allows us to examine treatment, time and site, **as** well as their interactions on the abundance or percent cover of the different invertebrates. Several pre-planned comparisons of treatment means were used to test *a priori* hypotheses (Winer et al., 1991). Two mutually orthogonal, single-degree-of-freedom contrasts were constructed to test (1) whether percent cover/numerical abundance is affected by the mean of the harvesting treatments (Control vs. Cut), and (2) whether the two cut treatments (36-cm cut vs. 18-cm cut) differed. The multivariate analyses only included those time periods when the species was present in one of the experimental plots. Dates that contained all zeros were excluded from the analyses. Statistica (Release 5.1, StatSoft) and SAS (Mainframe Version 6.1) software were used for all analyses.

Because sites are random and, therefore, irrelevant to the overall question of treatment effects, a reduced, repeated-measures MANOVA model excluding sites was also examined. The reduced model allows us to analyze differences among experimental treatments, over and above the intrinsic difference associated with sites.

The multivariate, repeated-measures approach was employed because the assumptions of the univariate, repeated-measures model could not be met (in particular, sphericity). Observations closer in time will almost inevitably correlate more highly than those separated further in time (Maxwell and Delaney, 1990). The multivariate approach does not require the assumption of homogeneity but does require multivariate normality.

Despite a reduction in model assumptions, the data generated in this study failed to achieve multivariate normality due to the large number of zeros present. Most of the species had skewed data distributions, which could not be fixed with transformations. Comparative tests on means are remarkably insensitive to general non-normality of the parent population, in particular skewness (Geary, **1947**; Gayen, **1950**; Box, **1953**; Jensen, **1982**). As long as the skewness of the data is in the same direction across all treatments, the general skewness tends to cancel out (Box, **1953**). With respect to the data in this study, skewness was similar across all treatment levels and thus cancels out when conducting comparative tests on the means. The significance level for all *apriori* comparisons was set at **0.05** while for *post-hoc* comparisons the level was Bonferroni-adjusted according to the number of contrasts. *A posteriori* comparisons examining spatial and temporal differences were conducted using either Ryan-Einot-Gabriel- Welsh (REGW) Multiple Range tests or Tukey's honestly-significant-difference(hsd) test, both of which control the Type 1 error rates (Winer et al., **1991**; Underwood, **1997**). Only those species whose mean percent coverage was greater than **0.1%** or whose numerical abundance was greater than one (1) were included in the analyses. For clarity of presentation, on graphs showing temporal changes standard errors have been plotted only on figures where $n \geq 9$. In cases where $n = 3$ individual site effects through time are being examined and will likely have **high** variation. On these figures the range of standard errors is provided.

4.4. Results

The highest mean surface water temperatures were reached during August and September and the lowest in **January** (Fig. 4.2). The highest salinities occurred in late fall, the lowest were found in early spring (Fig. 4.3). The greater variability in salinity at Castine reflects the site's more estuarine nature due to its proximity to the Penobscot River.

Of the 39 invertebrate taxa found in the experimental plots during the two-year, post-harvest sampling period, only 10 were in sufficient quantities to warrant statistical analyses (Table 4.1). MANOVA comparisons for dominant invertebrate species indicate *Ascophyllum* harvesting significantly affects the abundance of several associated species (Tables 4.2 & 4.3).

4.4.1. Full MANOVA model

Removal of the algal canopy significantly affected the numerical abundances of green crabs (*Carcinus maenas*), common periwinkles (*Littorina littorea*), blue mussels (*Mytilus edulis*), and limpets (*Tectura testudinalis*) (Table 4.2a). Harvesting also affected several understory, sessile invertebrates such as *Dynamena pumila* (a colonial hydroid), *Mytilus edulis* recruits (blue mussel spat), and *Semibalanus balanoides* (barnacles) (Table 4.3a).

The analysis for *Carcinus maenas* demonstrated significant 'Treatment', 'Site', 'Time', and 'Treatment x Site' effects (Table 4.2a). Main factors cannot be fully evaluated in situations where significant interactions are present (Winer et al., 1991). The 'Treatment x Site' interaction, however, reveals no difference in the number of green

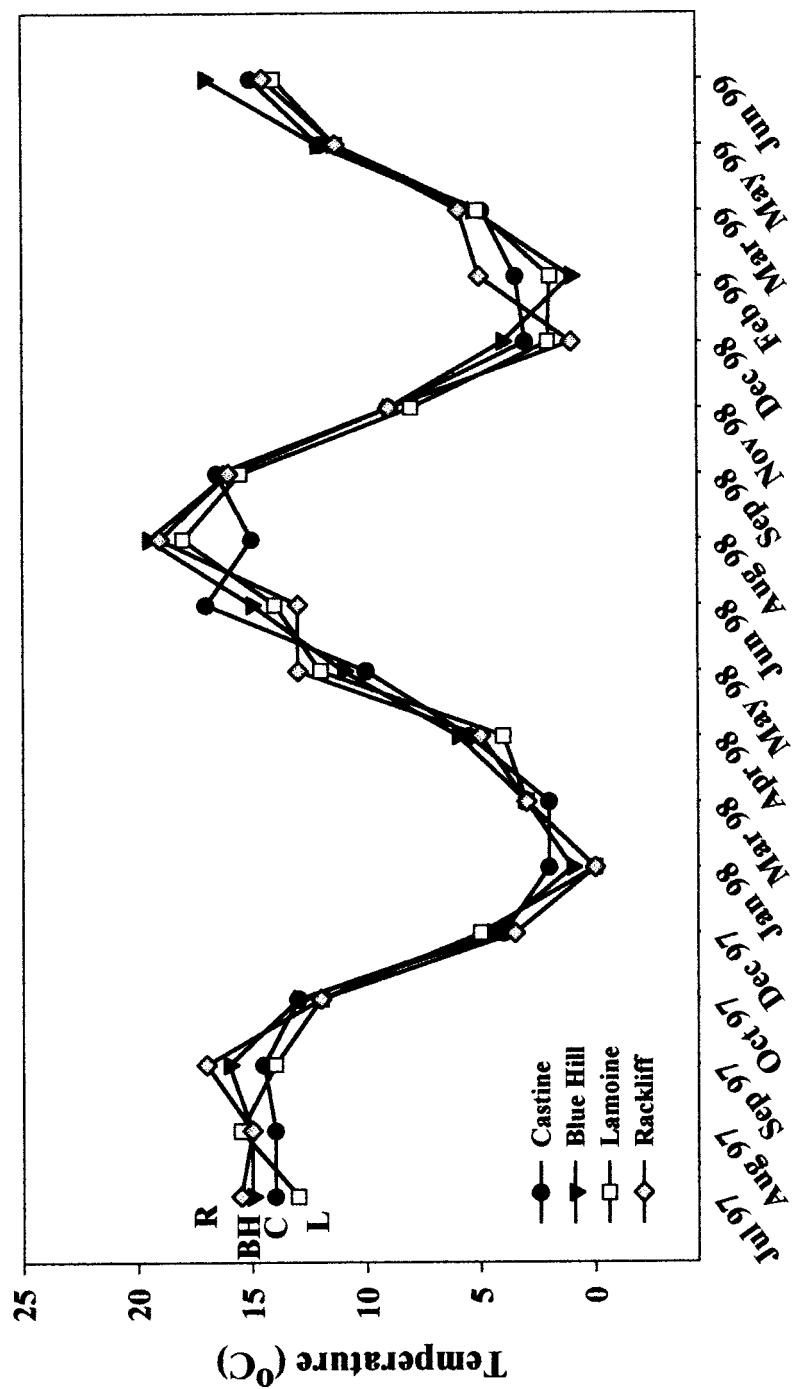


Figure 4.2. Monthly water temperatures (°C) measured at low tide at the study sites, July 1997 - June 1999.

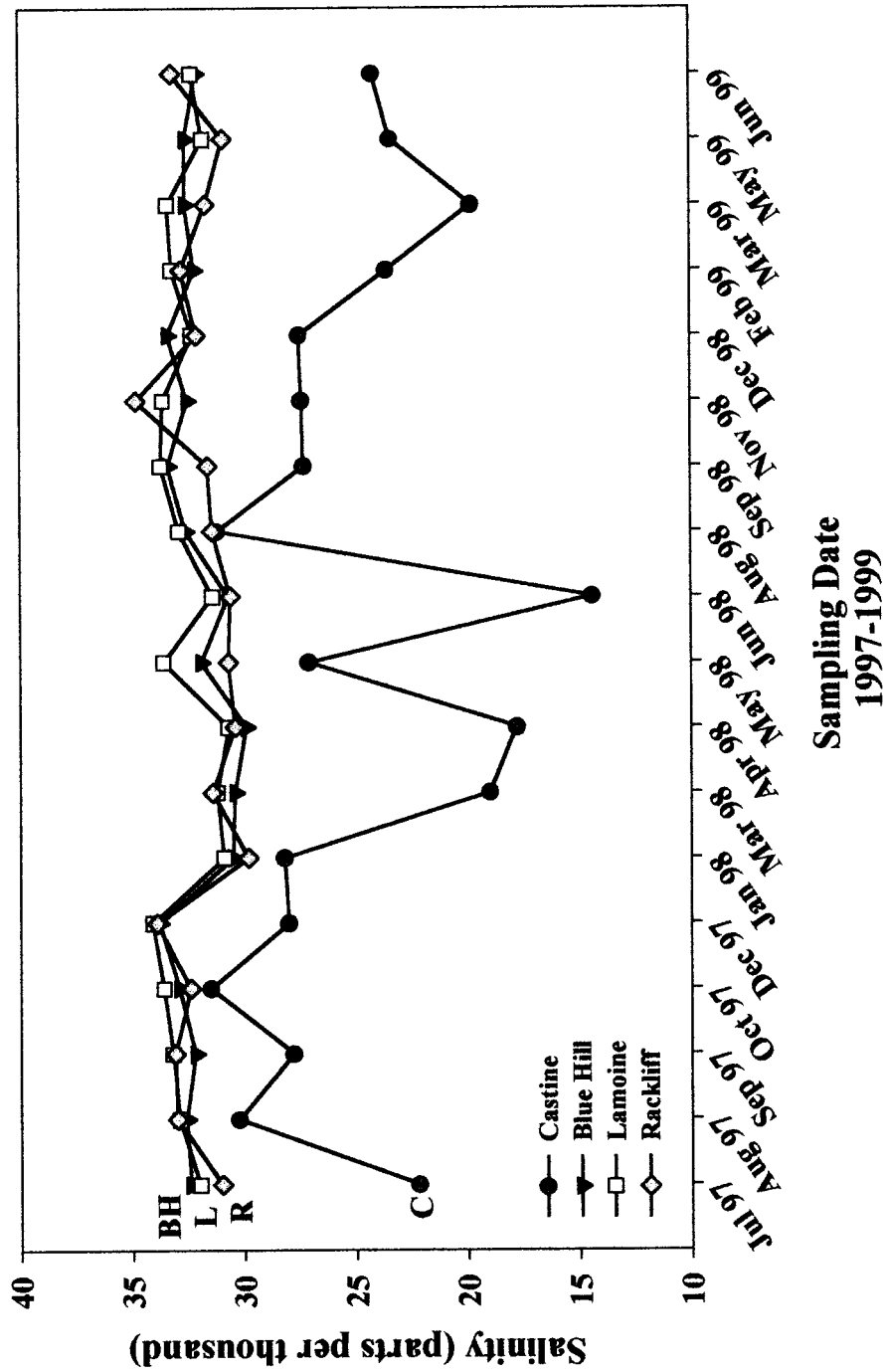


Figure 4.3. Monthly salinity measurements (ppt.) taken at low tide at the study sites, July 1997 - June 1999.

Table 4.1. Taxonomic list of invertebrate species recorded in the experimental plots during the two years following harvest. * indicates those species that were found in sufficient quantities to allow statistical analyses.

Invertebrate species	Invertebrate species
PORIFERA	MOLLUSCA
<i>Hulichondriu</i> sp. *	<i>Aeolidiu papillosa</i>
<i>Halisarca</i> sp.	<i>Anomiu simplex</i>
CNIDARIA	<i>Colus stimpsoni</i>
<i>Cerianthus borealis</i>	<i>Crepidula fornicatu</i>
<i>Clava multicornis</i>	<i>Lacuna vinctu</i>
<i>Diudumene lineata</i>	<i>Littorinu littorea</i> *
<i>Dynamena pumila</i> *	<i>Littorinu obtusata</i> *
<i>Metridium senile</i>	<i>Modiolus modiolus</i>
<i>Urticiniufelina</i>	<i>Mytilus edulis</i> *
CTENOPHORA	<i>Nucella lapillus</i> *
<i>Beroe cucumis</i>	<i>Onchidoris bilamellata</i>
PLATYHELMINTHES	<i>Onchidoris muricata</i>
<i>Notoplana atomata</i>	<i>Tectura testudinulis</i> *
ECTOPROCTA	<i>Urosalpinx cinereu</i>
<i>Alcyonidium</i> sp.	<i>Dendronotus frondosus</i>
<i>Flustrellidra hispida</i>	<i>Flabellina (Coryphellu) sp.</i>
<i>Electru pilosa</i>	<i>Hiatella urtica</i>
ARTHROPODA	ANNELIDA
<i>Balanus balanus</i>	<i>Lepidonotus squamatus</i>
<i>Carcinus maenas</i> *	<i>Spirorbis spirorbis</i> *
<i>Pandalus borealis</i>	ECHINODERMATA
<i>Semibalanus balanoides</i> *	<i>Asterius rubens</i>
CHORDATA	<i>Strongylocentrotus droebachiensis</i>
<i>Molgula</i> sp.	

Table **4.2**. Results of a repeated-measures MANOVA examining the influence of harvesting treatment on the numerical abundance of intertidal invertebrates. (A) Three-factor, mixed effects model ('Sites' are random). (B) Two-factor, fixed effects model. A *priori* orthogonal contrasts appear below the treatment main effect. Significant effects are in bold ($\alpha = 0.05$; $n = 3$).

^a The analysis for *Carcinus* only included time periods when it was present. The months January, March and December of 1998 and February of 1999 were excluded from the analysis ('Time' $df = 13$).

(A) MANOVA TABLE		<i>Carcinus</i> ^a	<i>L. littorea</i>	<i>L. obtusata</i>	<i>Mytilus</i>	<i>Nucella</i>	<i>Tectura</i>
	df	Pr>F	Pr>F	Pr>F	Pr>F	Pr>F	Pr>F
Between-subject effects							
Treatment	2	0.0701	0.6720	0.2101	0.6521	0.7280	0.5115
Control vs. cut	1	0.0291	0.6065	0.3173	0.6814	0.6397	0.2902
36cm vs. 18cm	1	0.5424	0.4845	0.1393	0.4247	0.5377	0.7053
Site	3	0.0005	0.0001	0.0001	0.0001	0.0235	0.0001
Treatment x Site	6	0.0323	0.3214	0.1121	0.1293	0.7961	0.9980
Error	24						
Within-subject effects							
Time	17	0.0047	0.2464	0.6890	0.3875	0.1586	0.0162
Time x Treatment	34	0.6015	0.0247	0.0724	0.4647	0.6557	0.6279
Time x Site	51	0.1168	0.0292	0.0004	0.0001	0.0733	0.0001
Time x Treatment x Site	102	0.3054	0.3323	0.4387	0.0001	0.1854	0.0001
Error	408						
TOTAL	647						

(B) MANOVA TABLE		<i>Carcinus</i> ^a	<i>L. littorea</i>	<i>L. obtusata</i>	<i>Mytilus</i>	<i>Nucella</i>	<i>Tectura</i>
	df	Pr>F	Pr>F	Pr>F	Pr>F	Pr>F	Pr>F
Between-subject effects							
Treatment	2	0.0062	0.8954	0.4037	0.6909	0.8646	0.9834
Control vs. cut	1	0.0020	0.7831	0.4668	0.6999	0.7468	0.8636
36cm vs. 18cm	1	0.4517	0.7060	0.2583	0.4453	0.6688	0.9531
Error	33						
Within-subject effects							
Time	17	0.0001	0.1309	0.1313	0.0509	0.1273	0.2639
Time x Treatment	34	0.3574	0.0658	0.3323	0.8870	0.3768	0.4420
Time x Control vs. cut	17	0.1044	0.0421	0.4581	0.9031	0.2354	0.9333
Time x 36cm vs. 18cm	17	0.8470	0.3380	0.3073	0.6659	0.6362	0.1033
Error	561						
TOTAL	647						

Table **4.3**. Results of a repeated-measures MANOVA examining the influence of harvesting treatment on the percent cover of intertidal invertebrates. (A) Three-factor, mixed effects model ('Sites' are random). (B) Two-factor, fixed effects model. Apriori orthogonal contrasts appear below the treatment main effect. Significant effects are in bold ($\alpha = 0.05$; $n = 3$).

^a The analysis for *Hulichondria* did not include the month of August 1997 because the species was not recorded in any of the experimental plots ('Time' $df = 16$).

^b The analysis for *Mytilus* recruits only included time periods when the species was present. The months of July 1997, December 1998, and February and June of 1999 were excluded from the analysis ('Time' $df = 13$). Within-subject p-values are based on univariate tests since the **data** matrices were nearly singular and could not be inverted.

^c Within-subject p-values are based on univariate tests since the data matrices were nearly singular and could not be inverted.

(A) MANOVA TABLE		<i>Dynamena</i>	<i>Halichondria</i> ^{a,c}	<i>Mytilus</i> recruits ^b	<i>Semibalanus</i>	<i>Spirorbis</i> ^c
	df	Pr>F	Pr>F	Pr>F	Pr>F	Pr>F
Between-subject effects						
Treatment	2	0.3451	0.8883	0.4297	0.9112	0.2609
Control vs. cut	1	0.1629	0.6439	0.3971	0.7109	0.8285
36cm vs. 18cm	1	0.8797	0.9459	0.3307	0.8521	0.1175
Site	3	0.0106	0.0079	0.0001	0.0011	0.0603
Treatment x Site	6	0.0126	0.9782	0.0081	0.0307	0.8186
Error	24					
Within-subject effects						
Time	17	0.0644	0.5978	0.4686	0.4749	0.1431
Time x Treatment	34	0.1306	0.6894	0.4858	0.5433	0.1463
Time x Site	51	0.0001	0.6724	0.0001	0.0001	0.2244
Time x Treatment x Site	102	0.0001	0.2617	0.0002	0.0001	0.8112
Error	408					
TOTAL	647					

(B) MANOVA TABLE		<i>Dynamena</i>	<i>Halichondria</i> ^{a,c}	<i>Mytilus</i> recruits ^b	<i>Semibalanus</i>	<i>Spirorbis</i> ^c
	df	Pr>F	Pr>F	Pr>F	Pr>F	Pr>F
Between-subject effects						
Treatment	2	0.0976	0.9818	0.6463	0.8695	0.4779
Control vs. cut	1	0.0330	0.8505	0.5435	0.6386	0.8808
36cm vs. 18cm	1	0.8266	0.9781	0.4811	0.8139	0.1313
Error	33					
Within-subject effects						
Time	17	0.4450	0.4668	0.2262	0.0870	0.4762
Time x Treatment	34	0.4630	0.4810	0.4992	0.3645	0.5015
Time x Control vs. cut	17	0.2791	0.5060	0.3992	0.3079	0.2938
Time x 36cm vs. 18cm	17	0.6987	0.4297	0.5776	0.4354	0.7161
Error	561					
TOTAL	647					

crabs in the ~~three~~ different harvesting treatments at Castine, Blue Hill and Lamoine (based on Tukey's *post-hoc* comparison tests), where overall crab densities were low (Figs. 4.4 and 4.5). At higher baseline densities (e.g., Rackliff Island), harvesting negatively affected crab abundance. The reduction in abundance was correlated with the intensity of the removal (Fig. 4.4). *Carcinus* also exhibited temporal effects indicative of seasonal population fluctuations (Fig. 4.6). Green crabs were absent from all control and experimental plots during the winter so those months were excluded from the analyses, which are based on 14 rather than 18 sampling dates. Green crabs ranged in size from 0.5 - 9.5 cm in carapace width.

The abundance of common periwinkles varied spatially and interacted temporally with both treatment and site (Table 4.2a; Figs. 4.5 and 4.7). Irregardless of treatment effects, the *L. littorea* population was highest at Blue Hill and lowest at Rackliff Island. Significant differences between sites were detected at all time periods using Ryan-Einot-Gabriel-Welsch (REGW) Multiple Range tests (α level < 0.05; Fig. 4.7). Although a significant 'Time x Treatment' effect was detected by the MANOVA, no discernible pattern is present (Fig. 4.8). For a significant 'Time x Treatment' effect to be detected, all that is needed is for the level of treatment response to vary with time in an inconsistent manner.

Littorina obtusata also varied spatially and interacted temporally with sites but was unaffected by the canopy removal (Table 4.2a; Figs. 4.5 and 4.9). The mean abundance of *L. obtusata* was five times higher at Rackliff Island compared to the other sites. Immediately following the harvest the overall abundance at Rackliff Island was quite high (Fig. 4.9). One month later the population declined significantly and remained

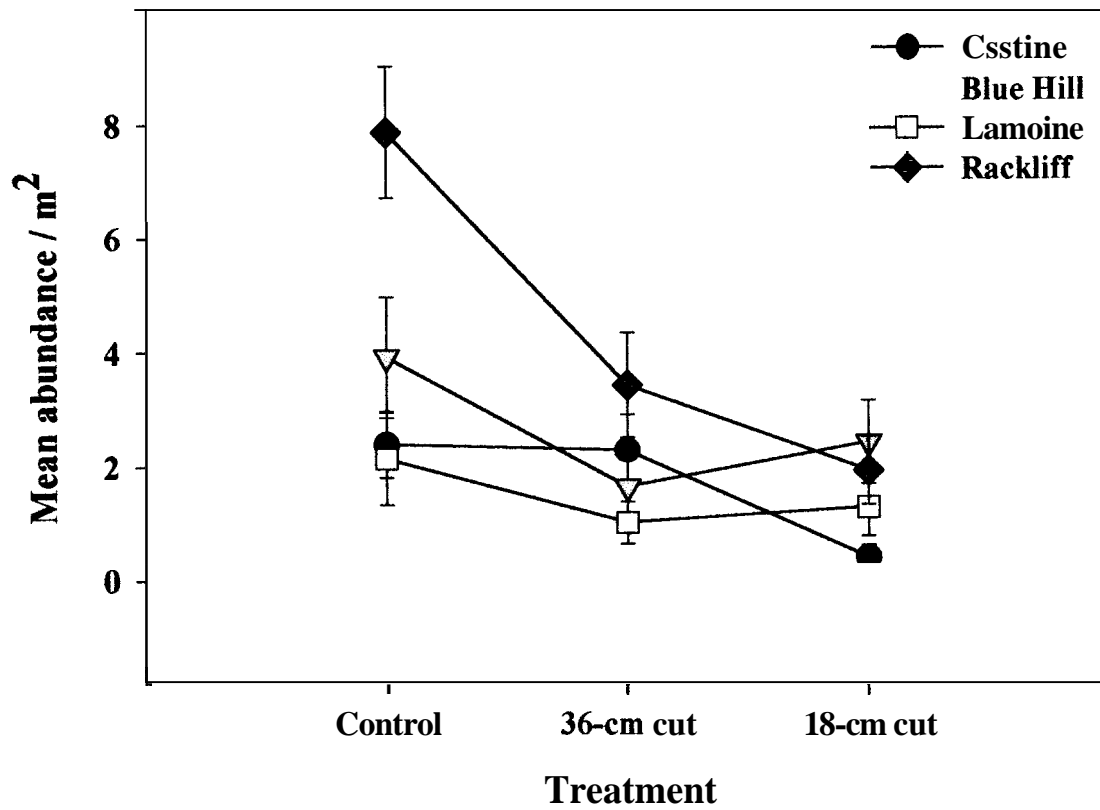


Figure 4.4. The effects of harvesting treatment level on *Carcinus maenas* at different sites in Maine. Values represent means \pm S.E. (n = 3 reps/time/site x 14 time periods = 42/treatment/site).

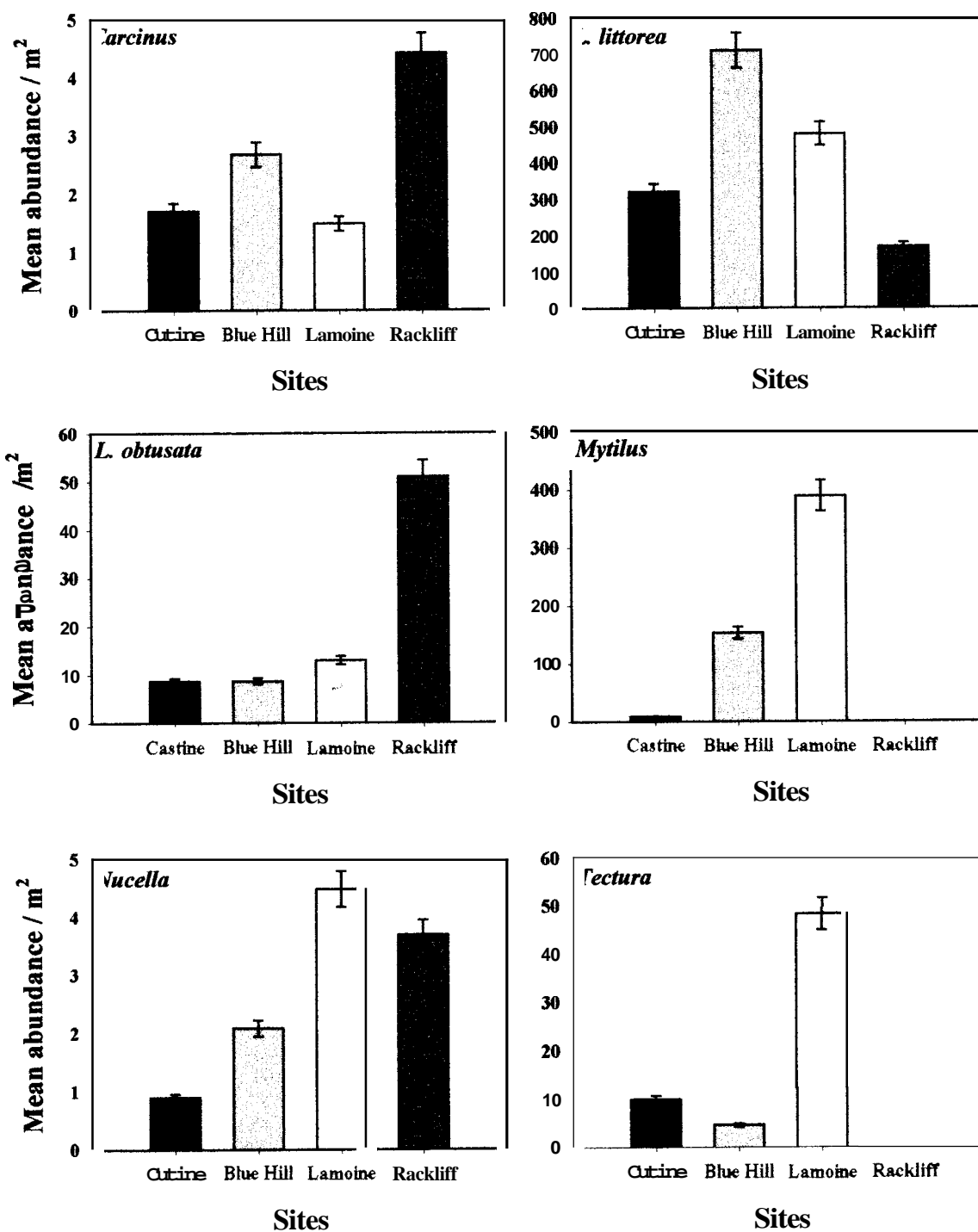


Figure 4.5. Mean abundance / m^2 of different invertebrate species at four experimental sites along the coast of Maine. Values represent means \pm S.E. (n = 9 plots/site x 18 time periods = 162/site except for *Carcinus* where n = 9 plots/site x 14 time periods = 126/site).

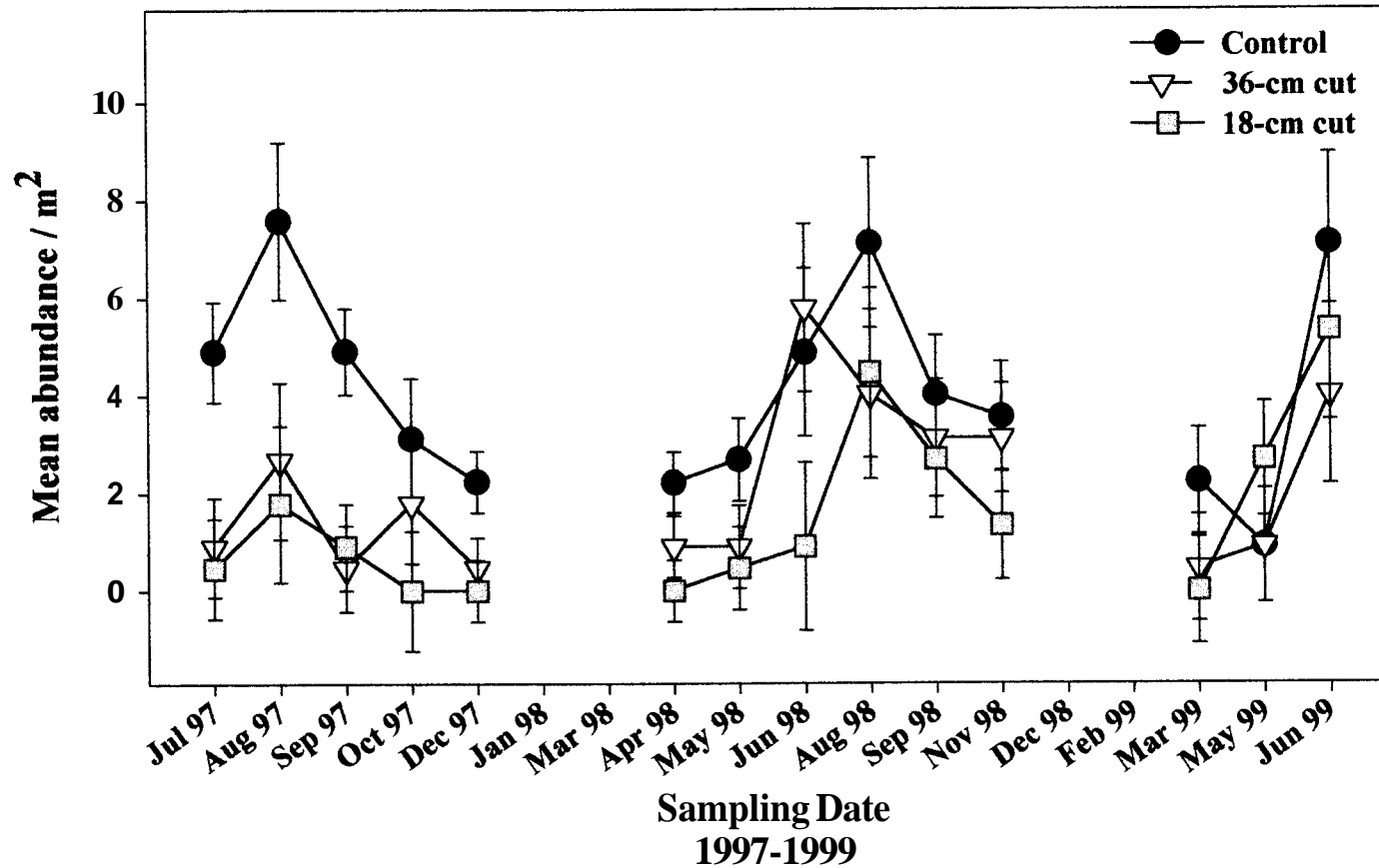


Figure 4.6. Temporal changes in the numerical abundance of *Carcinus maenas* at various treatment levels. Values represent means \pm S.E. ($n = 4$ sites \times 3 reps/site/time = 12/treatment/time). Jan 98, Mar 98, Dec 98 and Feb 99 were excluded from the analyses because the species was not present in any experimental plot ('Time' df = 13). MANOVA revealed there was no 'Time \times Treatment' interaction ($P = 0.6015$).

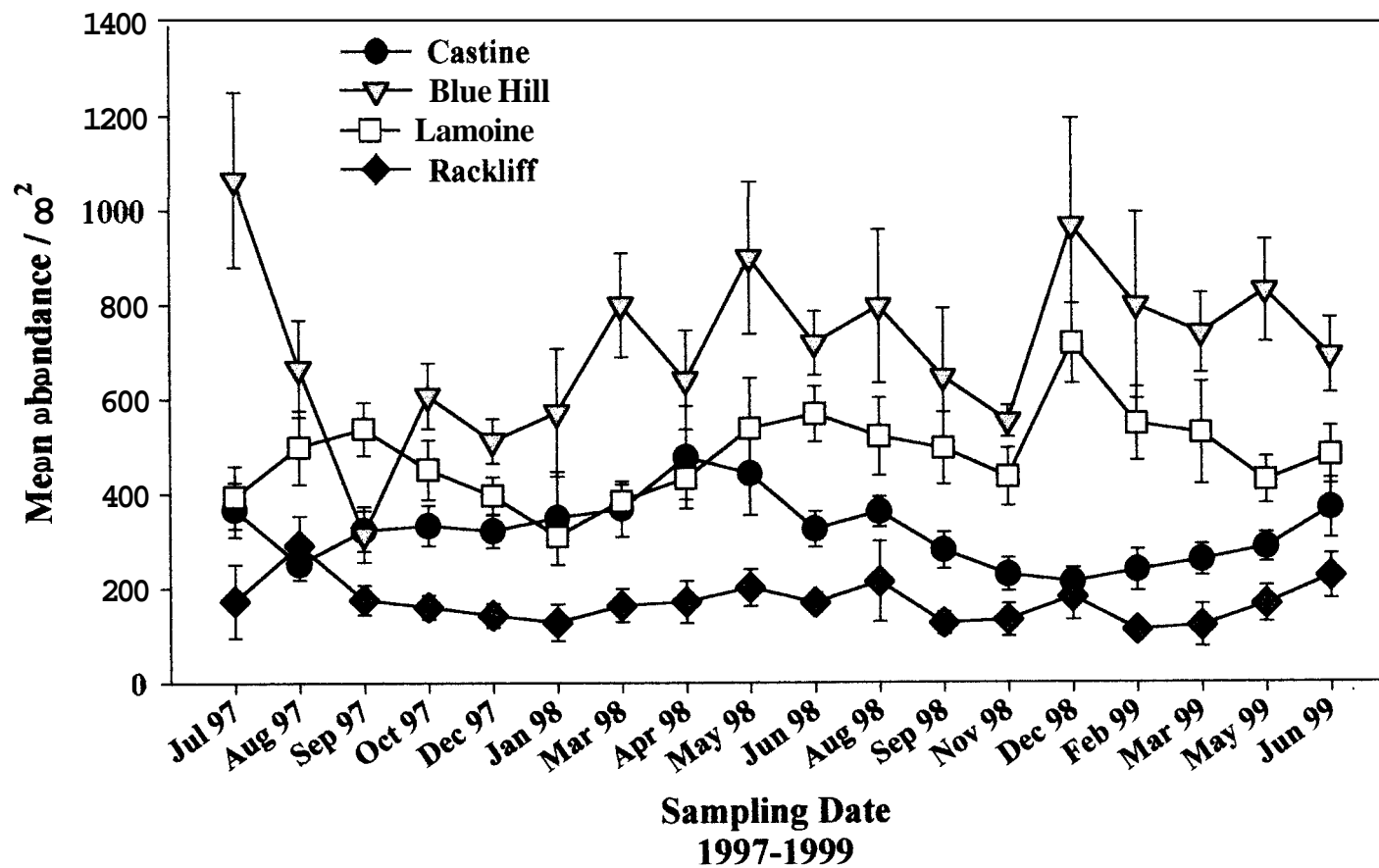


Figure 47. Temporal changes in the mean abundance \pm S.E. of *Littorina littorea* at the **four** experimental sites. Data are collapsed over treatment. (n = 9 plots/site/time period)

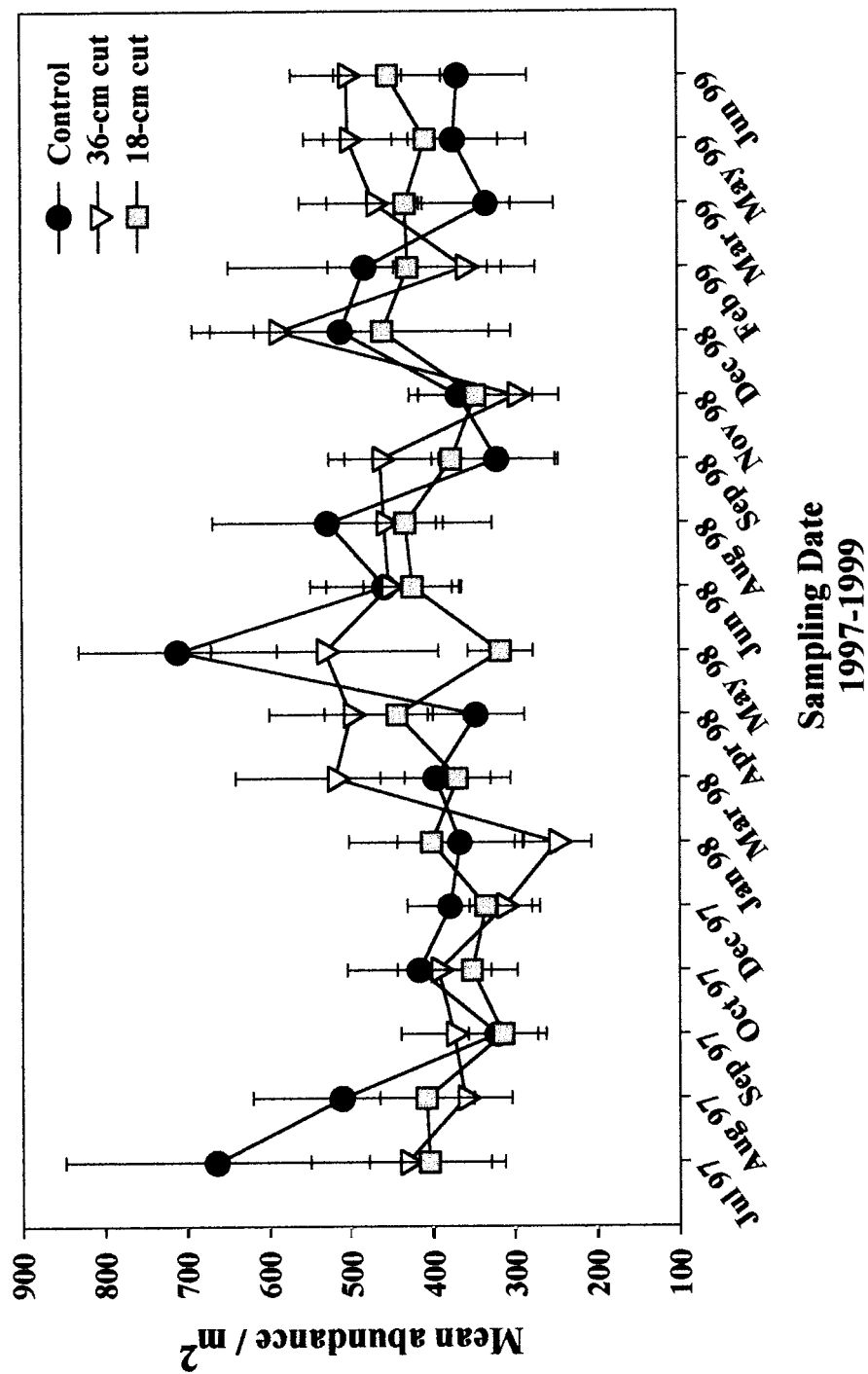


Figure 4.8. Temporal changes in the numerical abundance of *Littorina littorea* at various treatment levels. Values represent means \pm S.E. (n = 4 sites x 3 reps/site = 12/treatment/time)

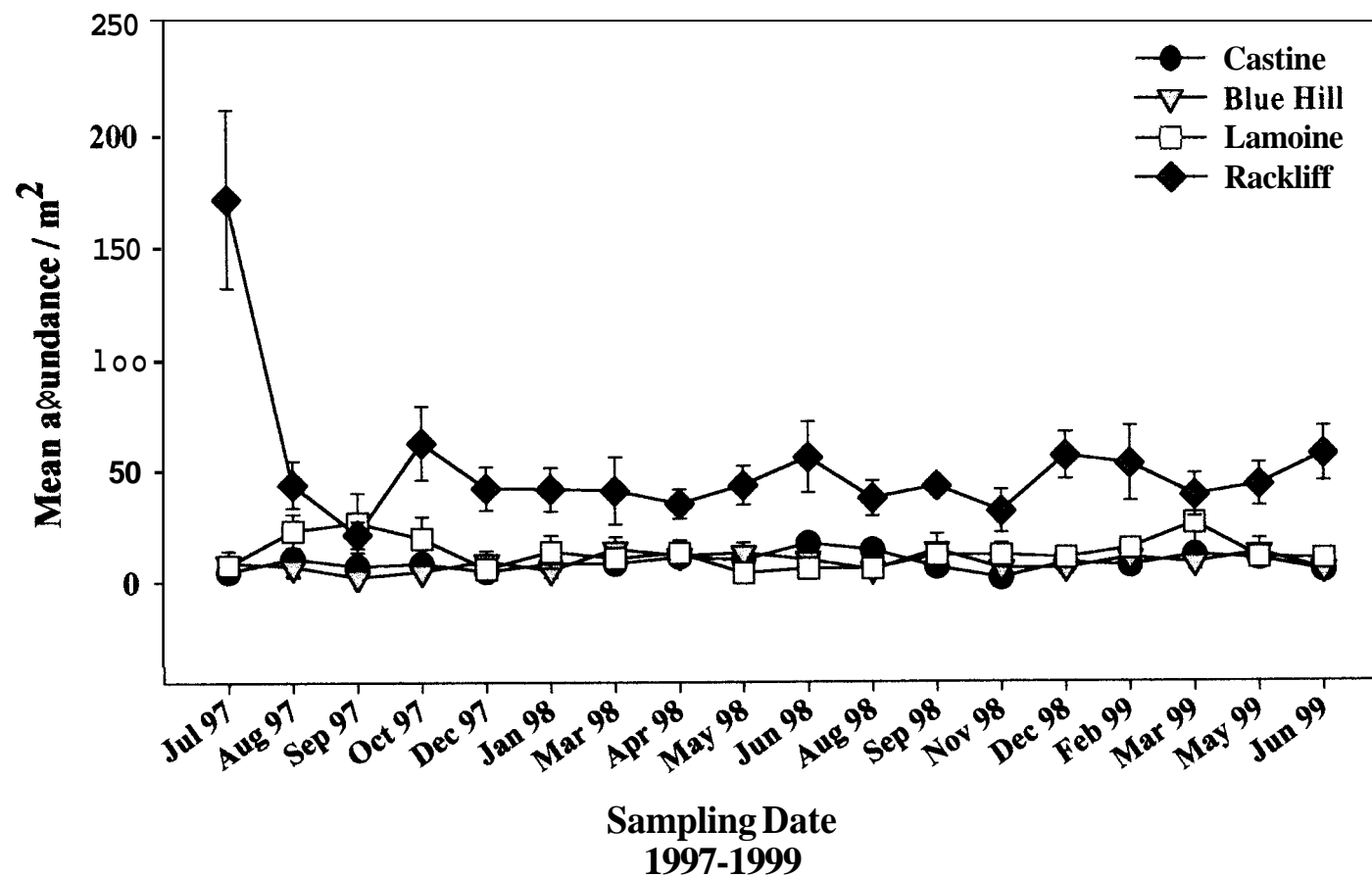


Figure 4.9. Mean abundance \pm S.E. per m^2 of *Littorina obtusata* through time at the four experimental sites. Data are collapsed over treatment. (n = 9 plots/site/time)

depressed for the rest of the experiment. The population decline at Rackliff Island caused the significant 'Time x Site' effect detected by the MANOVA analysis.

Overall *Mytilus* abundance was high at Lamoine, moderate at Blue Hill, very low at Castine, and zero at Rackliff Island (Fig. 4.5). The analysis for the blue mussel, *Mytilus edulis*, showed significant 'Site', 'Time x Site' and 'Time x Treatment x Site' effects (Table 4.2a). Although I cannot fully evaluate the lower-order effects ('Site' and 'Time x Site'), an examination of them helps elucidate the three-way interaction. The 'Time x Site' graph shows a very low abundance of *Mytilus* (> 5mm in size) at Lamoine until November 1998 when the mussel population increased significantly due to a successful recruitment event (Fig. 4.10). The moderate-sized mussel population at Blue Hill remained at a stable level throughout the entire two-year study. The 'Time x Treatment x Site' interaction, therefore, must have been due to the Lamoine population. Inspection of the 'Time x Treatment' interaction at Lamoine reveals the highest abundance of mussels in the 18-cm cut plots, followed by the controls and then the 36-cm cut plots (Fig. 4.11).

Nucella lapillus, an intertidal whelk, exhibited spatial variation in its abundance (Table 4.2a). Highest densities were found at Lamoine, followed by Rackliff, Blue Hill, and Castine (Fig. 4.5). No other significant effects were detected for this species.

Mean abundance of the Atlantic limpet, *Tectura testudinalis*, varied spatially and temporally (Table 4.2a). Lamoine had the highest limpet density, followed by Castine, then Blue Hill (Fig. 4.5 and 4.12). The mean abundance at both Lamoine and Castine peaked during May 1998. Examination of the 'Time x Treatment' effects at Castine and

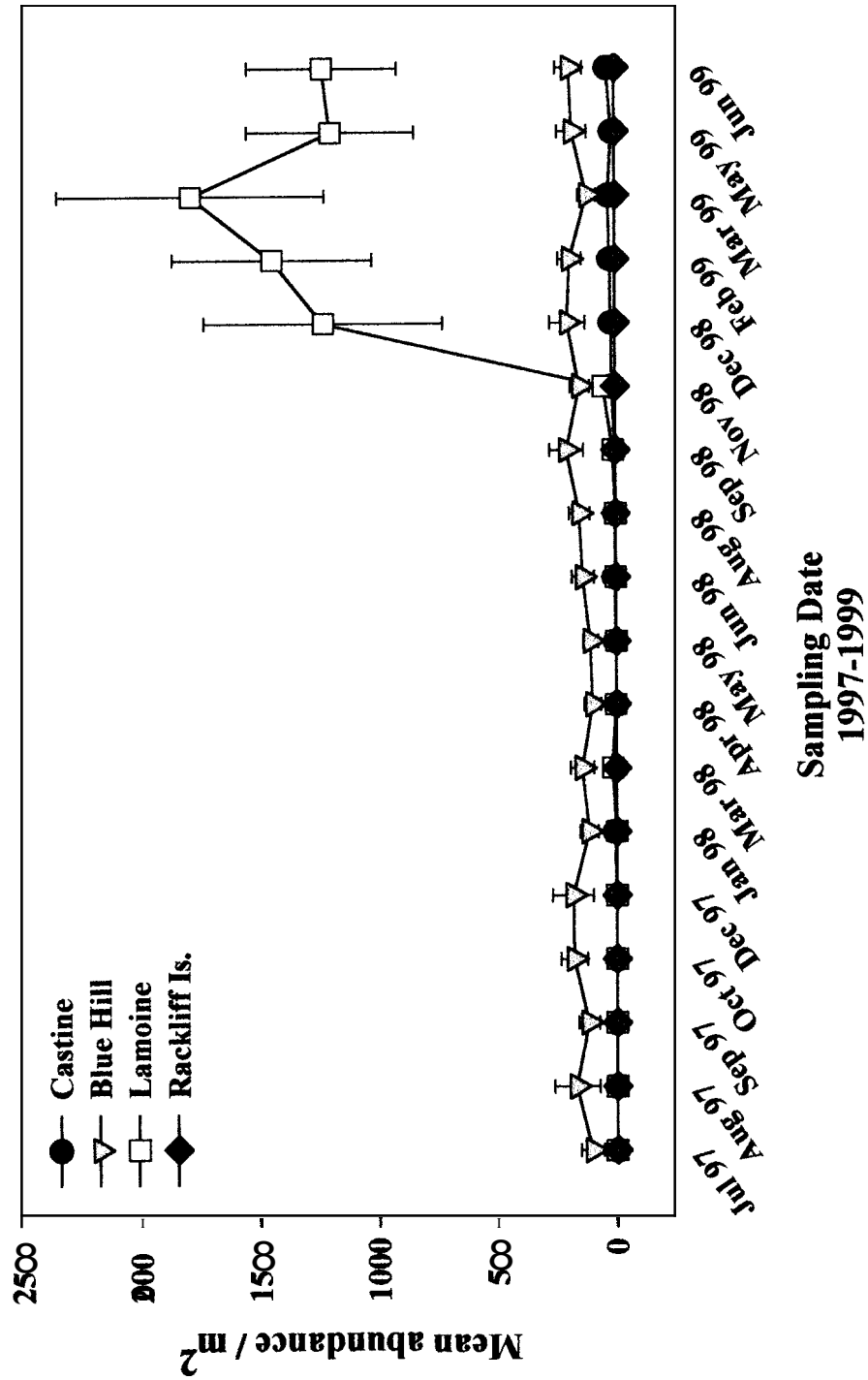


Figure 4.10 Mean abundance \pm S.E. per m² of *Mytilus edulis* through time at the four experimental sites. Data are collapsed over treatment. (n = 9 plots/site/time)

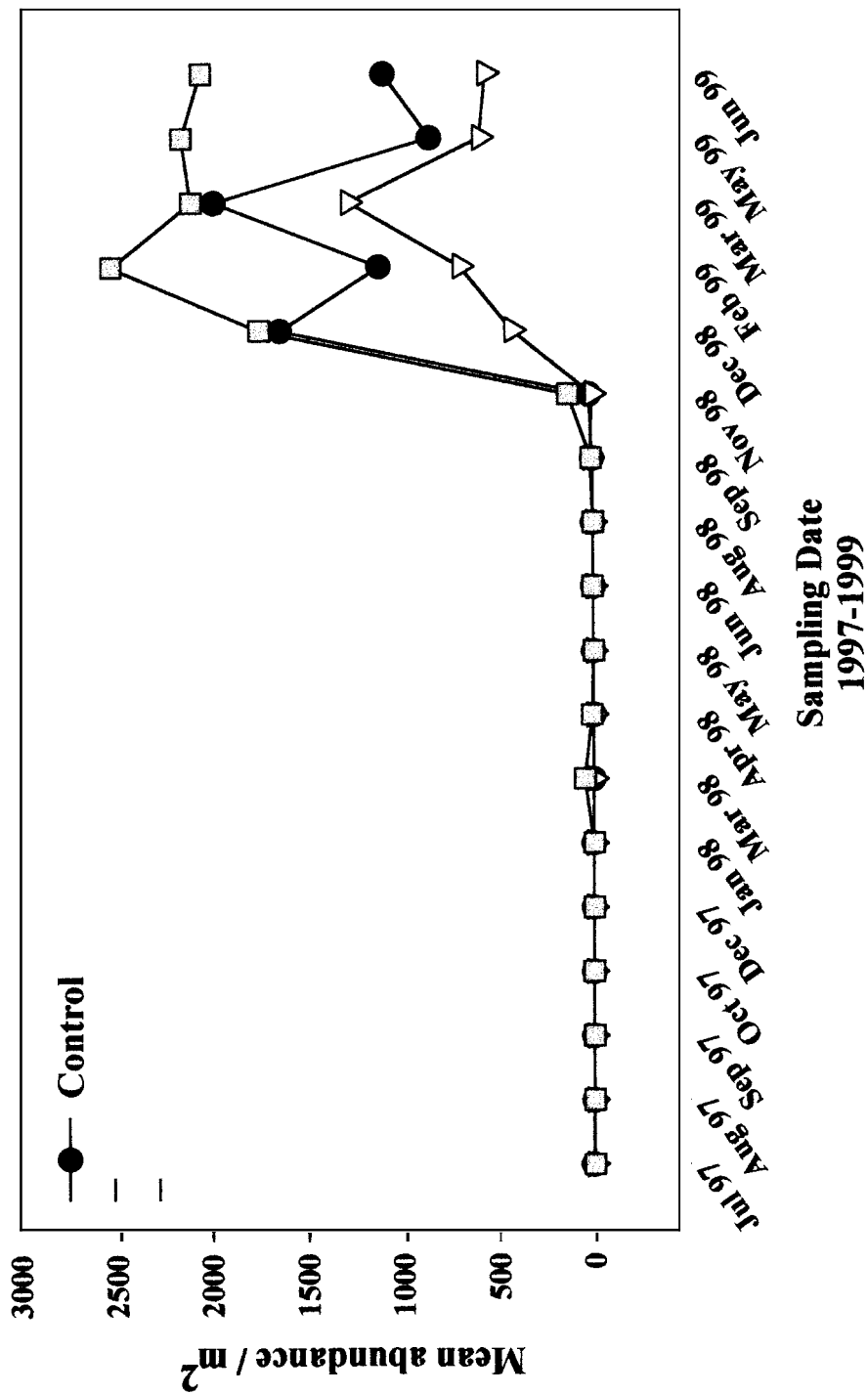


Figure 4.11. Temporal changes in the numerical abundance of *Mytilus edulis* (> 5 mm in size) at various treatment levels at Lamoine. Values represent means. Standard errors are omitted for clarity but ranged from 24% to 100% of the mean. (n = 3 treatment/time)

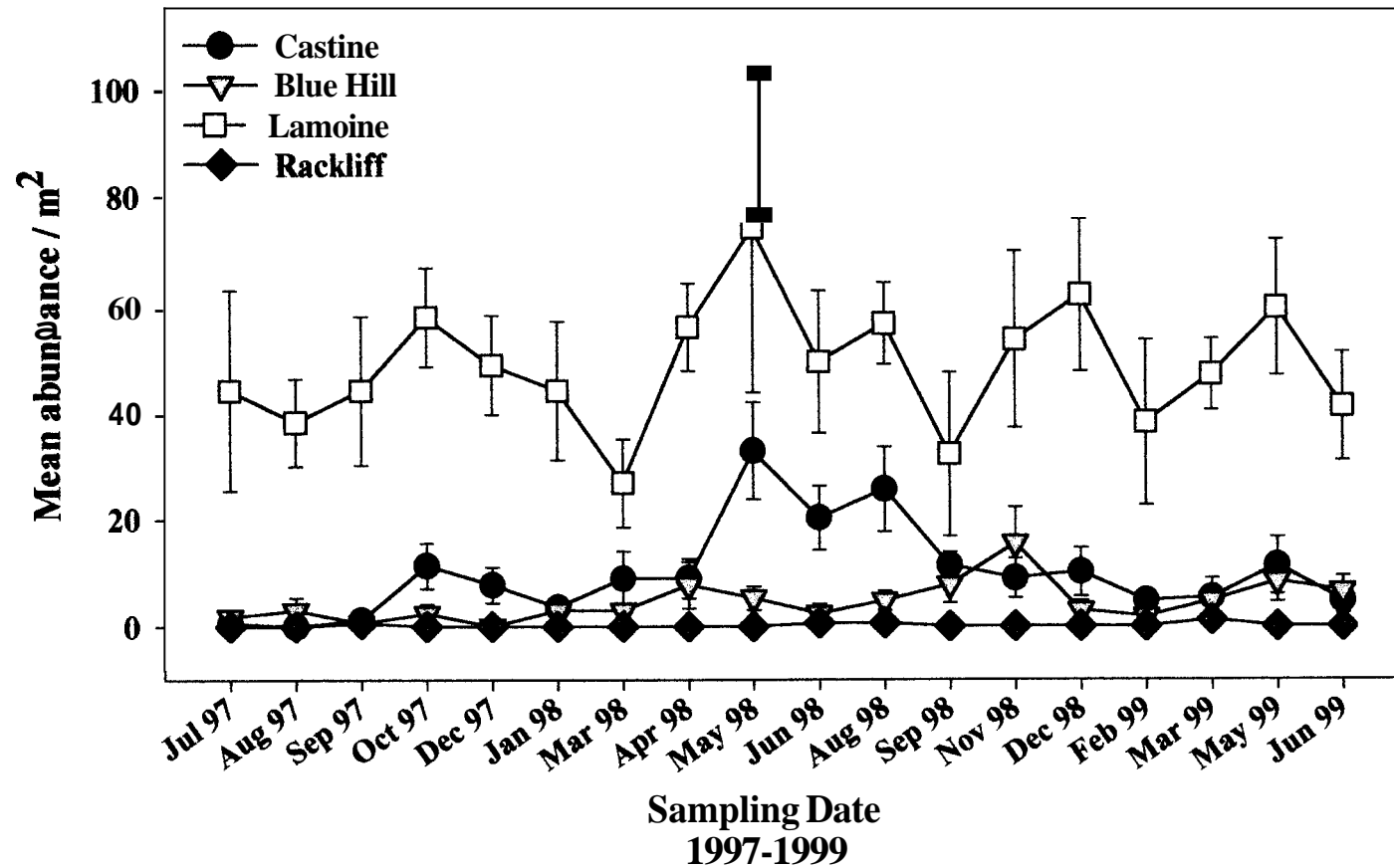


Figure 4.12. Temporal changes in the mean abundance of *Tectura testudinalis* at the four experimental sites. Data are collapsed over treatment. (n = 9 plots/site/time period)

Lamoine revealed no discernible pattern (Fig. 4.13). The large fluctuation associated with the means was due to natural variability and low replication at individual sites.

Sessile, understory invertebrates were also affected by the harvesting treatments (Table 4.3a). The MANOVA detected significant 'Site', 'Treatment \times Site', 'Time \times Site', and 'Time \times Treatment \times Site' effects for the colonial hydroid, *Dynamena pumila*. The percent cover of *Dynamena* was highest at Rackliff Island, followed by Lamoine and Castine (Fig. 4.14). This species was not present at the Blue Hill site. When present at high densities, these colonial hydroids experienced a significant treatment effect ('Treatment \times Site' effect; $P = 0.0126$) (Fig. 4.15). At Rackliff Island, the percent cover in the control plots was significantly higher than the percent cover in either of the treatments. At low densities this species appears unaffected by the canopy removal (Fig. 4.15). This species also exhibits considerable temporal variability (Figure 4.16). In general, the highest quantities occur in summer when the colony reproduces and the lowest in mid-winter when the population dies off due to low temperatures. The significant three-way interaction ('Time \times Treatment \times Site') was due to Rackliff Island where the percent cover in the control plots was consistently higher than the percent cover in either of the treatments even though the magnitude varied seasonally (Fig. 4.17).

Halichondria, a bread-crumble sponge, was found at only two of the four experimental sites (Lamoine and Blue Hill) as evidenced by the detection of significant 'Site' effects (Table 4.3a; Fig. 4.14). Significant 'Treatment' and 'Time' effects were not detected. The MANOVA analysis for this species only included 17 time periods ('Time' $df = 16$) because the species was not recorded in any of the experimental plots during the month of August 1997; thus this month was excluded.

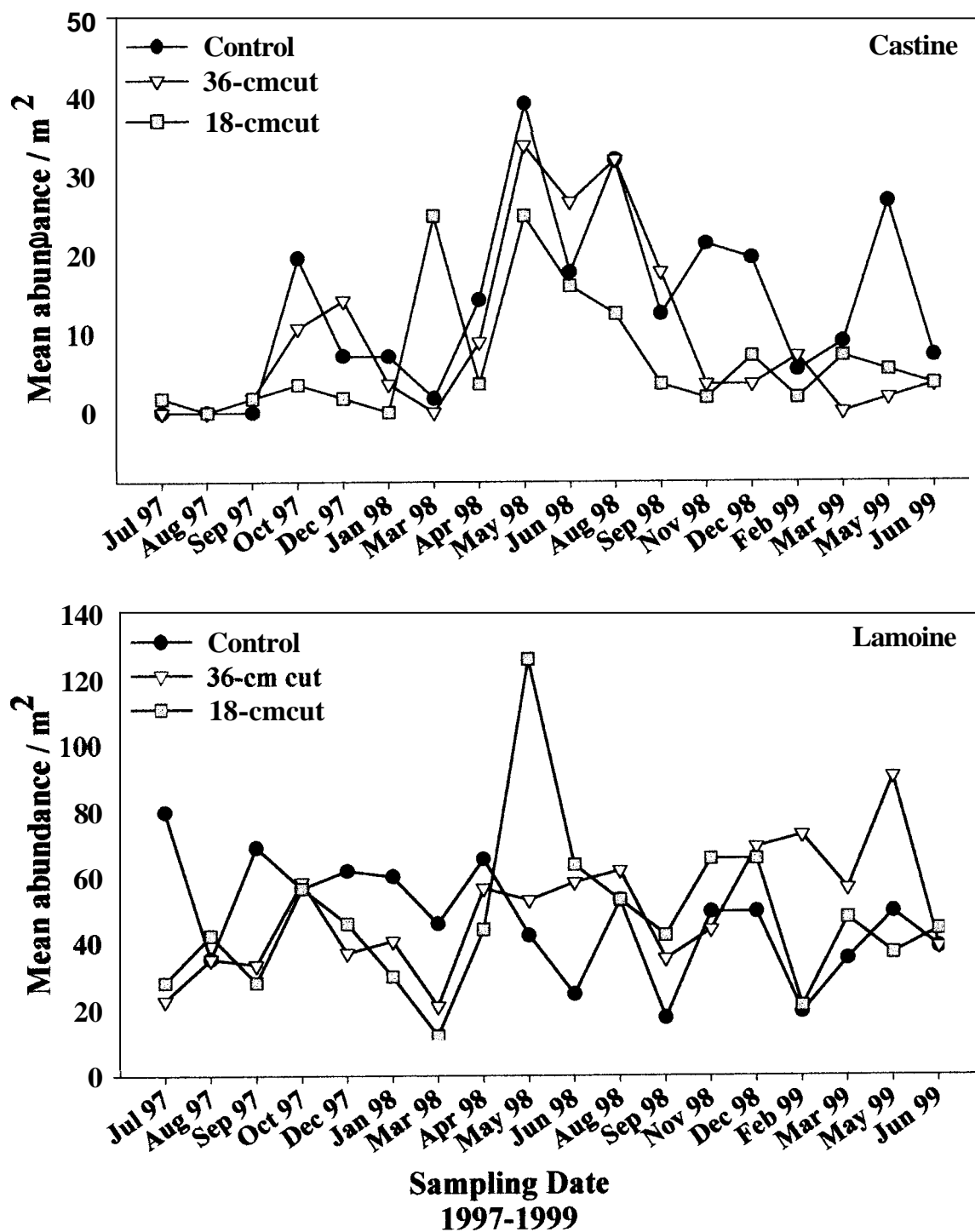


Figure 4.13. 'Time x Treatment' effects at Castine and Lamoine for *Tectura testudinalis*. Standard errors are omitted for clarity but ranged from 7% to 100% of the mean. (n = 3/treatment/time period).

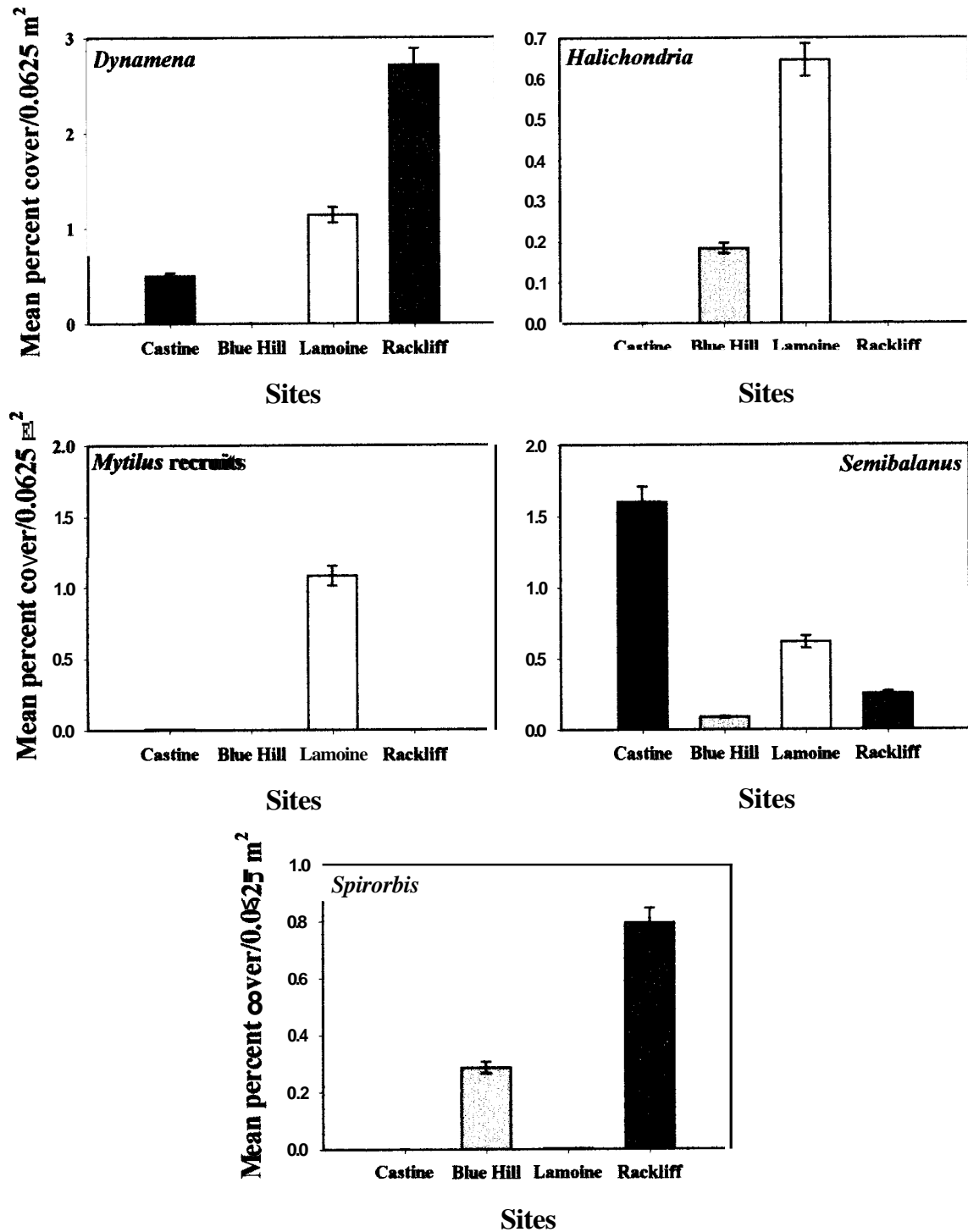


Figure 4.14. Mean percent cover/0.0625 m² of different invertebrate species at four experimental sites along the coast of Maine. Values represent means \pm S.E. (n = 9 plots/site \times 18 time periods = 162/site; except *Halichondria* where n = 9 plots/site \times 17 time periods = 153/site; and *Mytilus* recruits where n = 9 plots/site \times 14 time periods = 126/site).

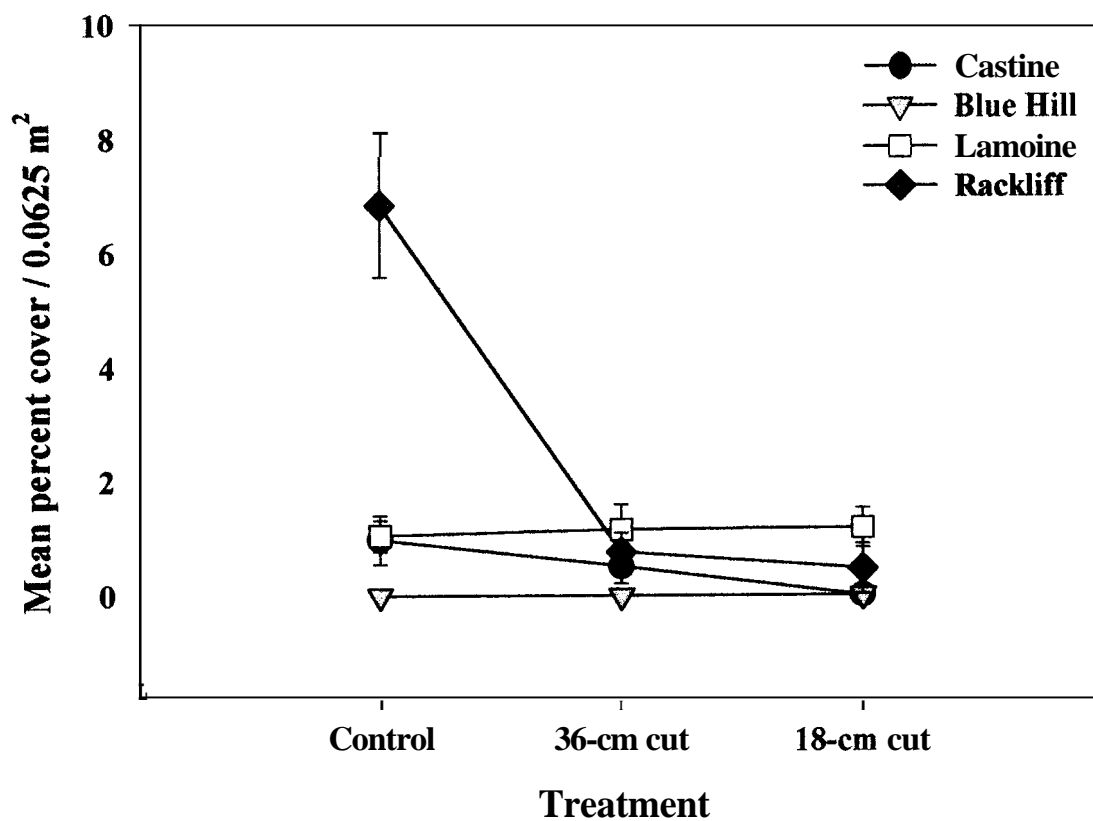


Figure 4.15. The effects of harvesting treatment level on *Dynamena pumila* at different sites in Maine. Values represent means \pm S.E. ($n = 3$ reps/site \times 18 time periods = 54/treatment/site).

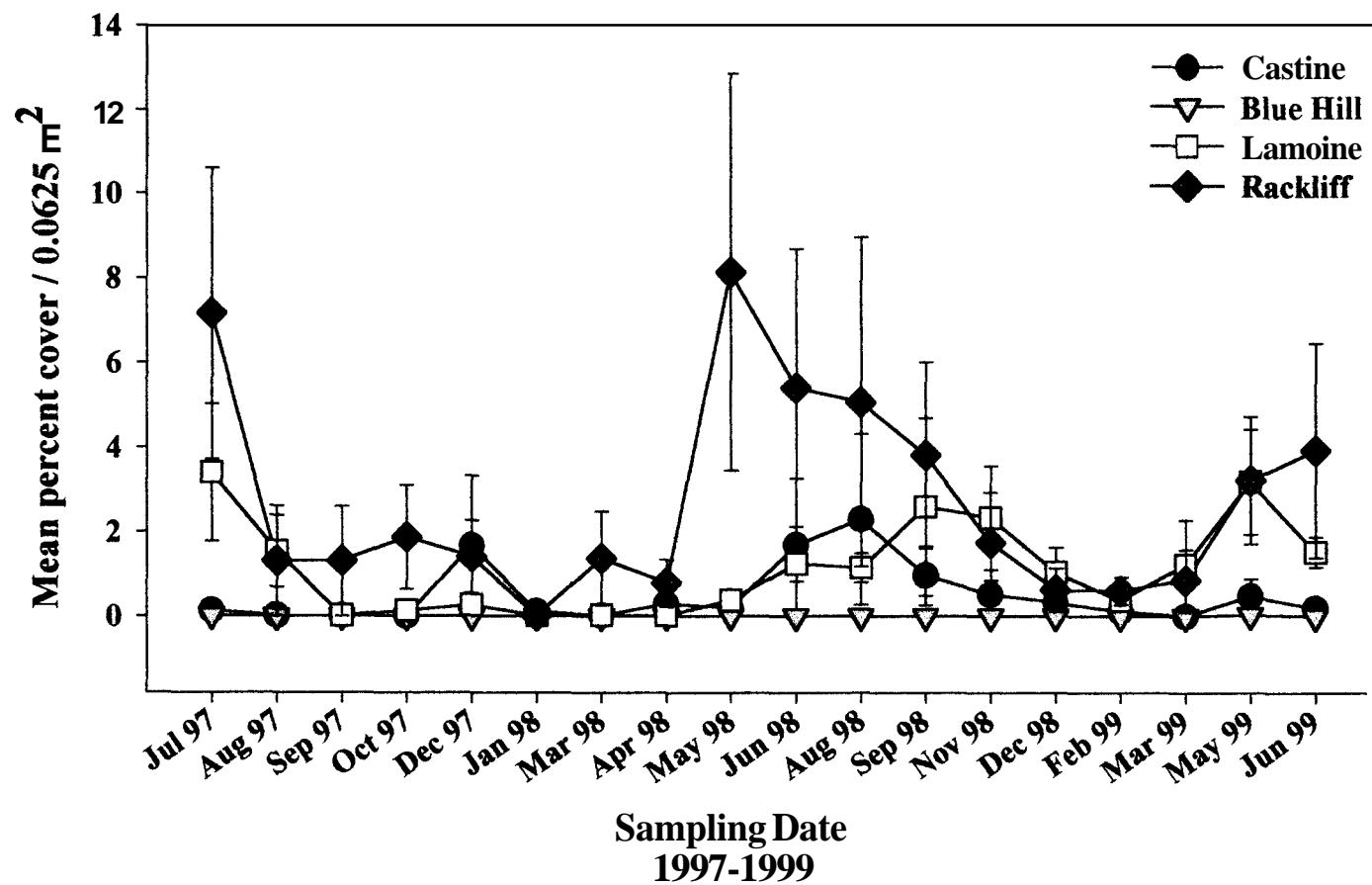


Figure 4.16. Temporal changes in the mean percent cover/0.0625 m² of *Dynamena pumila* at the four experimental sites. Data are collapsed over treatment. (n = 9 plots/site/time period).

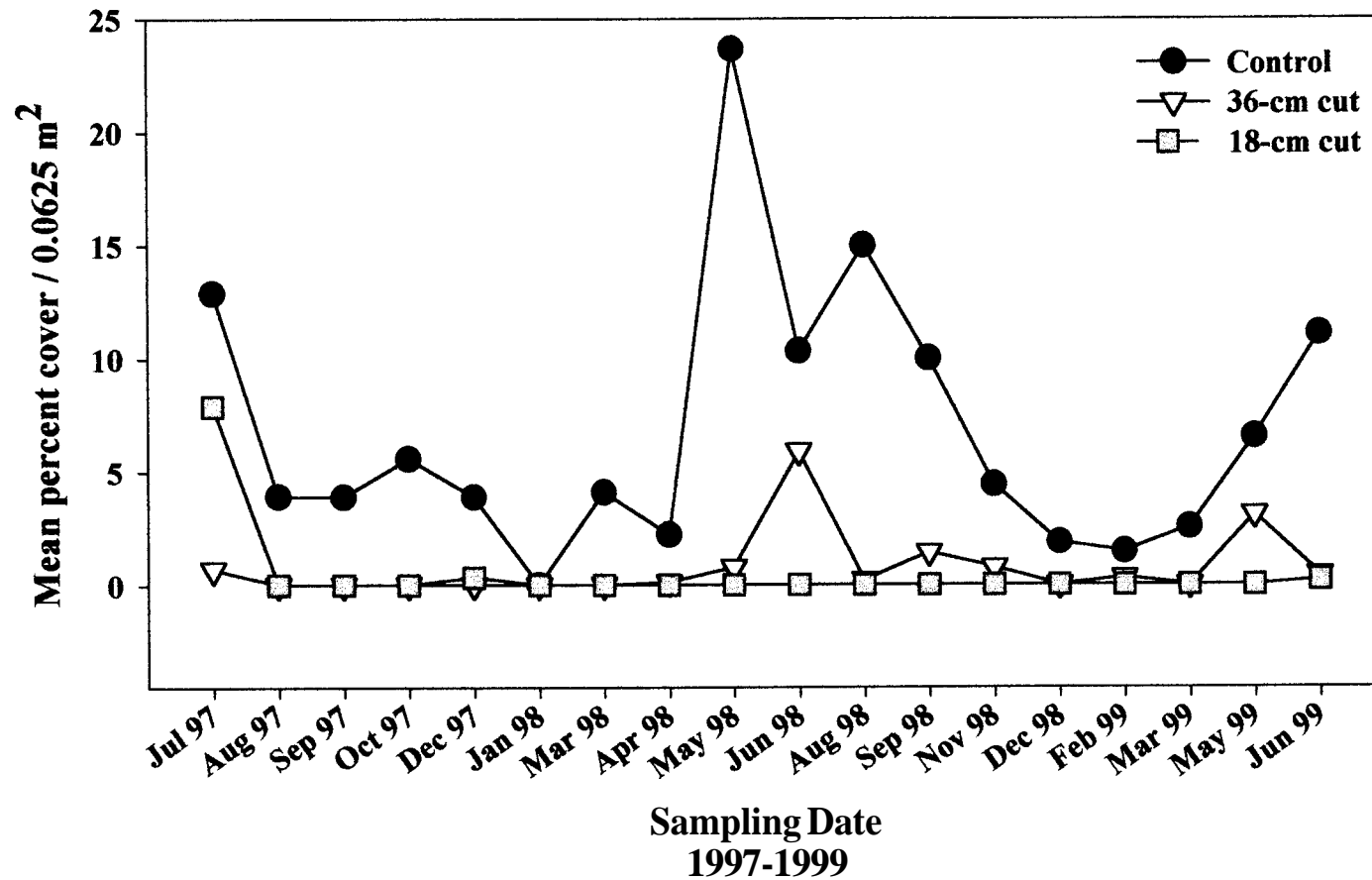


Figure 4.17. Temporal changes in the percent cover of *Dynamena pumila* at various treatment levels at Rackliff Island. Values represent means. Standard errors are omitted for clarity but ranged from 39% to 100% of the mean. (n = 3/treatment/time)

The MANOVA detected several significant effects for *Mytilus edulis* recruits (< 5 mm in size). Normally 'Site' effects cannot be evaluated because higher order interactions are significant. In this case, however, the only site where *Mytilus* recruits were present was Lamoine, so all higher-order interactions automatically detected a 'Site' interaction effect (Fig. 4.14). A two-way MANOVA ('Treatment x Time') on the Lamoine data did not detect an overall 'Treatment' effect but did detect a significant 'Time' ($P = 0.0019$) and 'Time x Treatment' effect ($P = 0.0238$). In the fall of each year, Lamoine experienced a significant increase in the number of *Mytilus* recruits (Fig. 4.18). In 1997, the increase in recruits occurred in the control plots but their appearance was short-lived. In 1998, *Mytilus* recruits were found in all experimental plots, with the 18-cm cut plots experiencing the highest densities. Months when *Mytilus* recruits were absent from all plots (July 1997, December 1998, February 1999 and June 1999) were excluded from the analysis. This resulted in a total of 14 time periods ('Time' $df = 13$) that were included in the MANOVA.

The abundance of *Semibalanus balanoides*, the common barnacle, varied spatially and was also influenced by several interacting effects (Table 4.3a). Barnacle populations were most abundant at Castine and Lamoine (Fig. 4.14). Variation in the abundance through time was most noticeable where baseline abundances were highest (Fig. 4.19). At Castine, significant increases in the mean percent cover were detected in the fall of 1997, and the spring and fall of 1998. The only other significant change in barnacle abundance occurred at Lamoine in the fall of 1998. A closer examination of these two sites revealed significant 'Treatment x Time' interactions (Fig. 4.20). In Castine, during the fall of 1997, a significant increase in percent cover occurred in the 36-

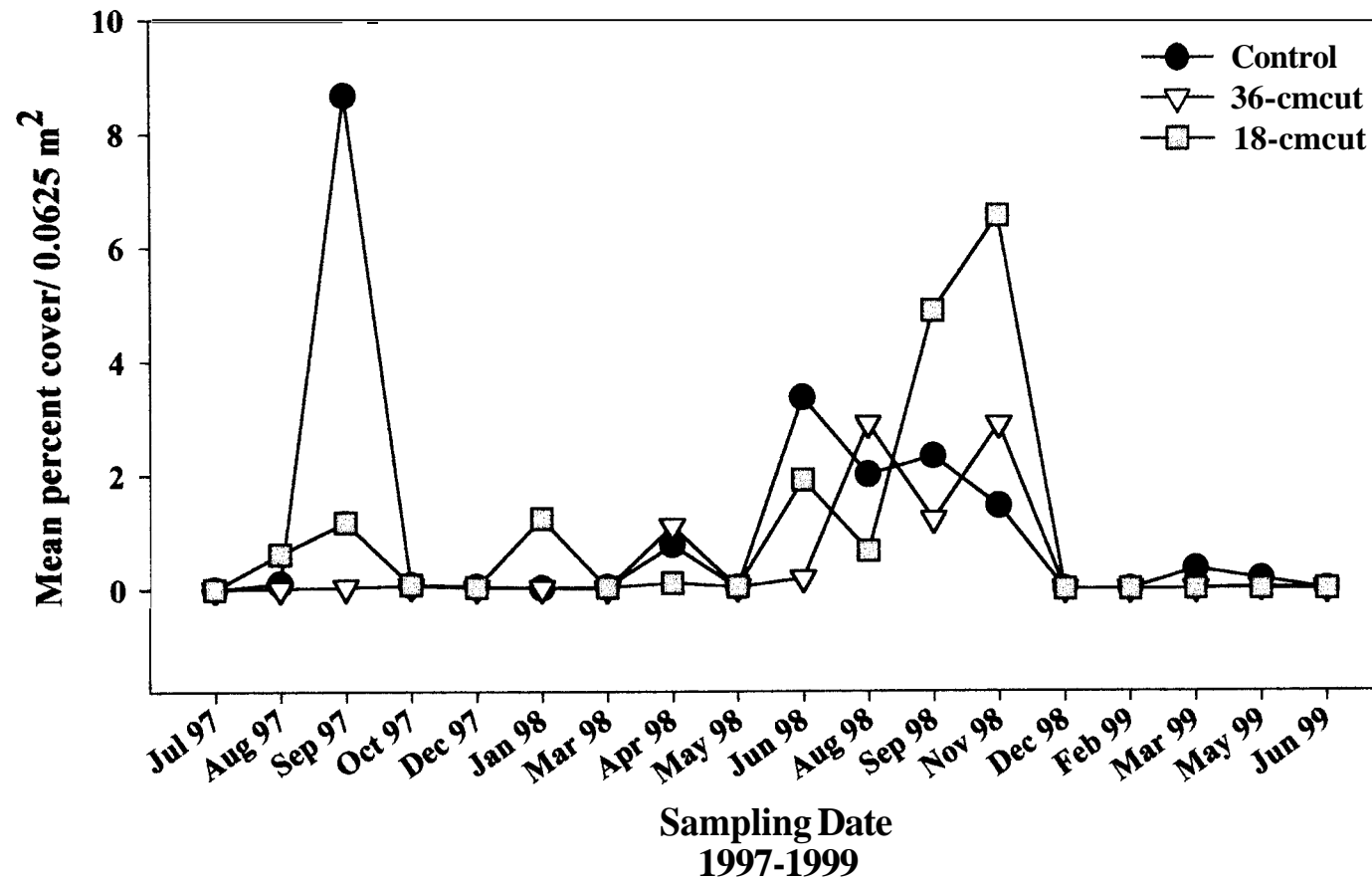


Figure 4.18. 'Time x Treatment' effects at Lamoine for *Mytilus edulis* recruits (< 5 mm in size). Standard errors are omitted for clarity but ranged from 12% to 100% of the mean. (n = 3/treatment/time)

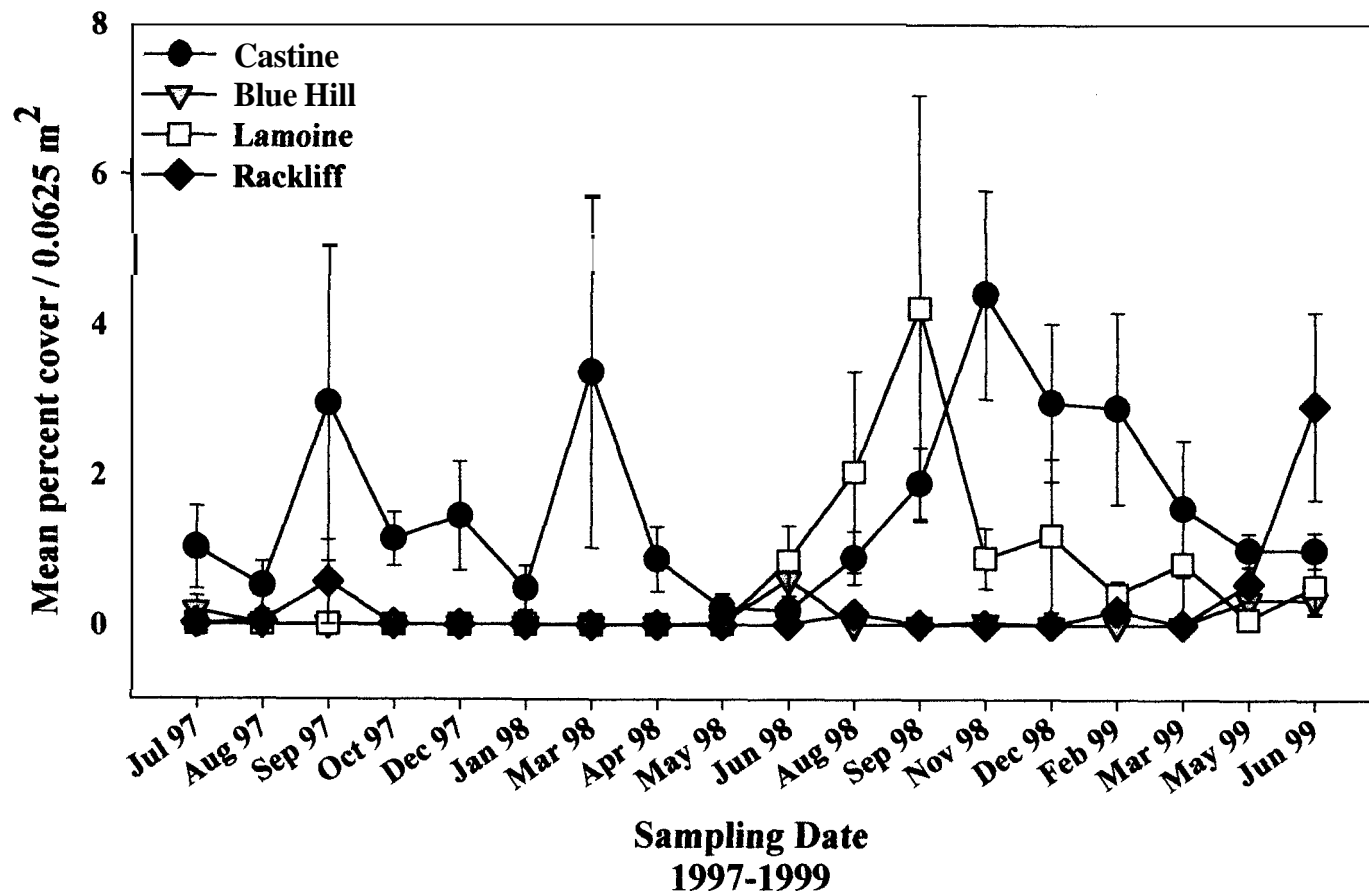


Figure 4.19. Temporal changes in the mean percent cover \pm S.E. per 0.0625 m² of *Semibalanus balanoides* at the four experimental sites. Data are collapsed over treatment. (n = 9 plots/site/time)

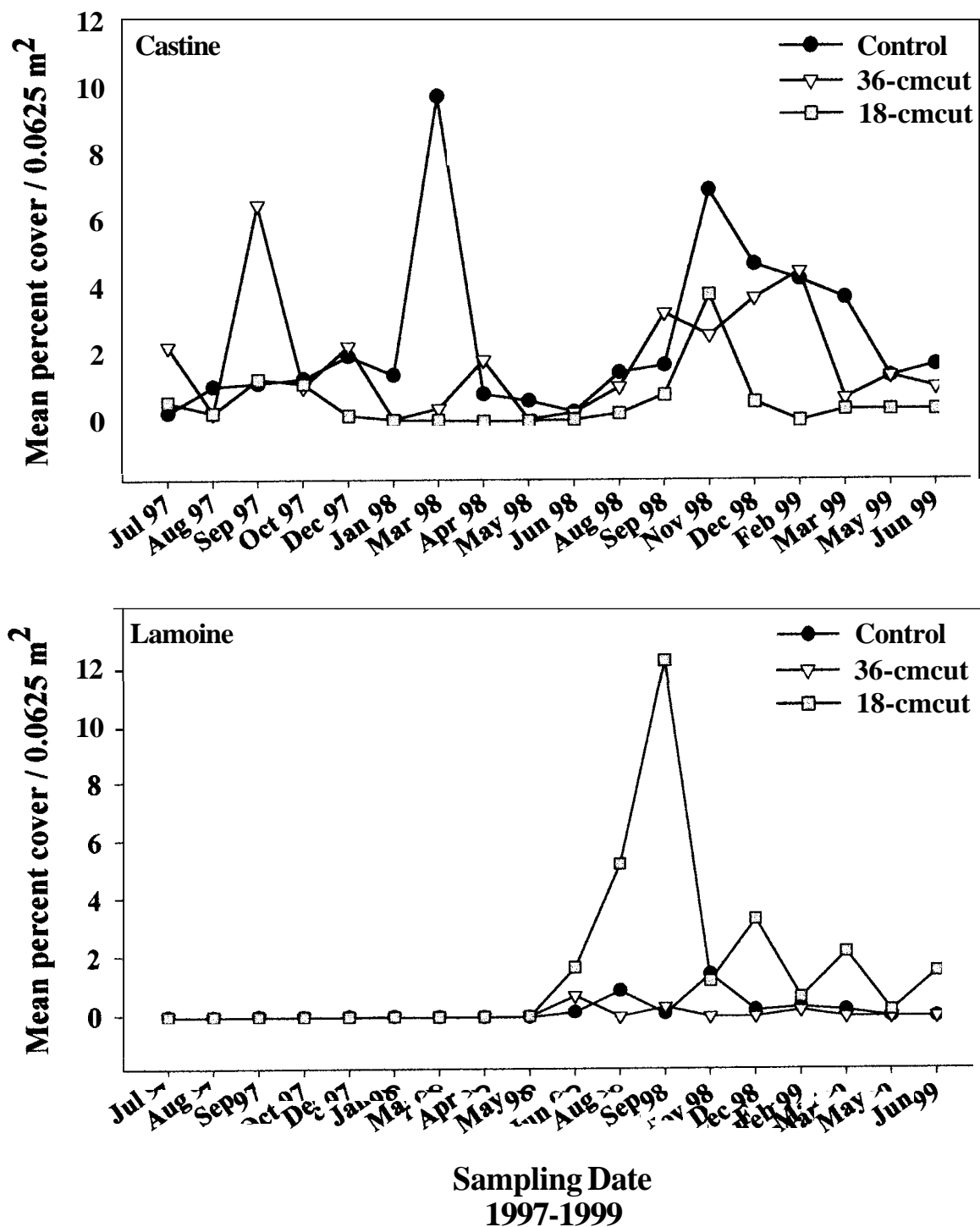


Figure 4.20. 'Time x Treatment' effects at Castine and Lamoine for *Semibalanus balanoides*. Standard errors are omitted for clarity but ranged from 14% to 100% of the mean. (n = 3/treatment/time)

cm cut plots. The spring and fall 1998 increase in barnacle abundance, however, occurred in the control plots. The pattern at Lamoine was quite different with a peak in barnacle abundance occurring in the 18-cm cut plots. The overall effects of harvesting at the different sites were either insignificant (e.g., Blue Hill and Rackliff) or unique to each site (e.g., Castine and Lamoine) (Fig. 4.21).

The full MANOVA did not detect any significant differences in *Spirorbis spirorbis* abundance across 'Treatments', 'Sites', and 'Time' (Table 4.3a). Although *Spirorbis* was only present at two sites, the abundances were low and the variance was high, so significant 'Site' effects were not detected ($P = 0.0603$).

4.4.2. Reduced MANOVA model

The reduced, repeated measures MANOVA model, which excluded sites, also detected significant treatment effects though not as many as the full model (Tables 4.2b and 4.3b). This reduced model allows us to analyze differences among experimental treatments, over and above the intrinsic difference associated with sites.

A significant overall 'Treatment' effect was detected for *Carcinus*, as was a significant *a priori*, orthogonal contrast (Table 4.2b; Fig. 4.22). The abundance of green crabs in the control plots was significantly higher than the abundance in the cut plots. A *priori* contrasts also detected a significant 'Time x Control vs. Cut' effect for *Littorina littorea* (Table 4.2b). In the spring of 1998 (March – April) and 1999 (March – June) the abundance of *L. littorea* was higher in the cut plots than in the controls (Fig. 4.23). During the rest of the year, however, the abundance was higher in the control plots when

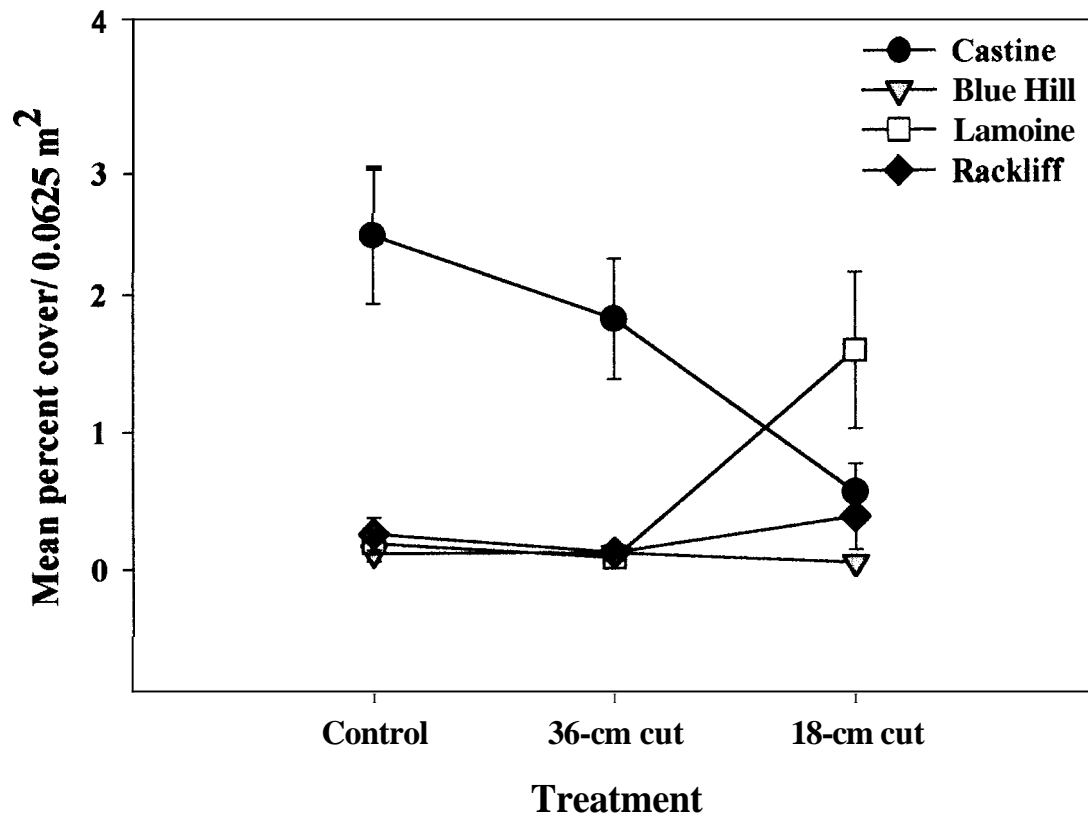


Figure 4.21. The effects of harvesting treatment level on *Semibalanus balanoides* at different sites in Maine. Values represent means \pm S.E. (n = 3 reps/site x 18 time periods = 54/treatment/site).

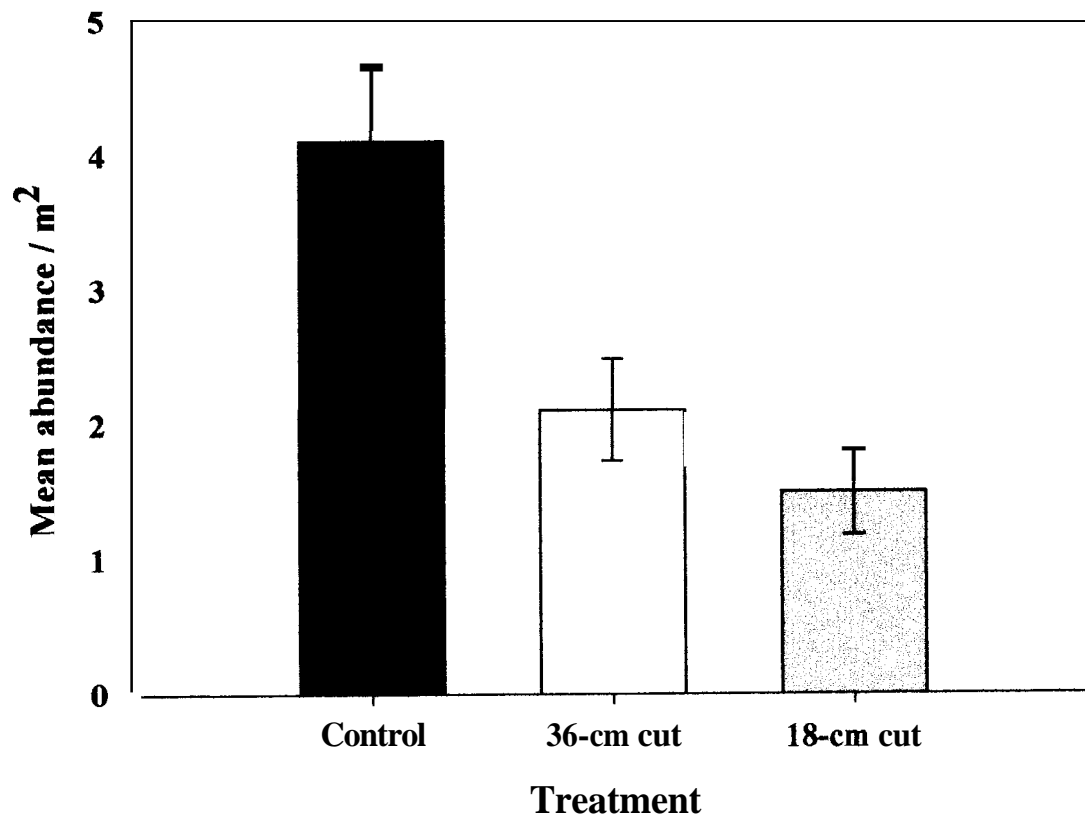


Figure 4.22. Mean treatment effects for *Carcinus maenas* averaged over the two-year post-harvest time period. Error bars represent +/- S.E. (n = 4 sites x 3 reps/site x 14 time periods = 168/treatment)

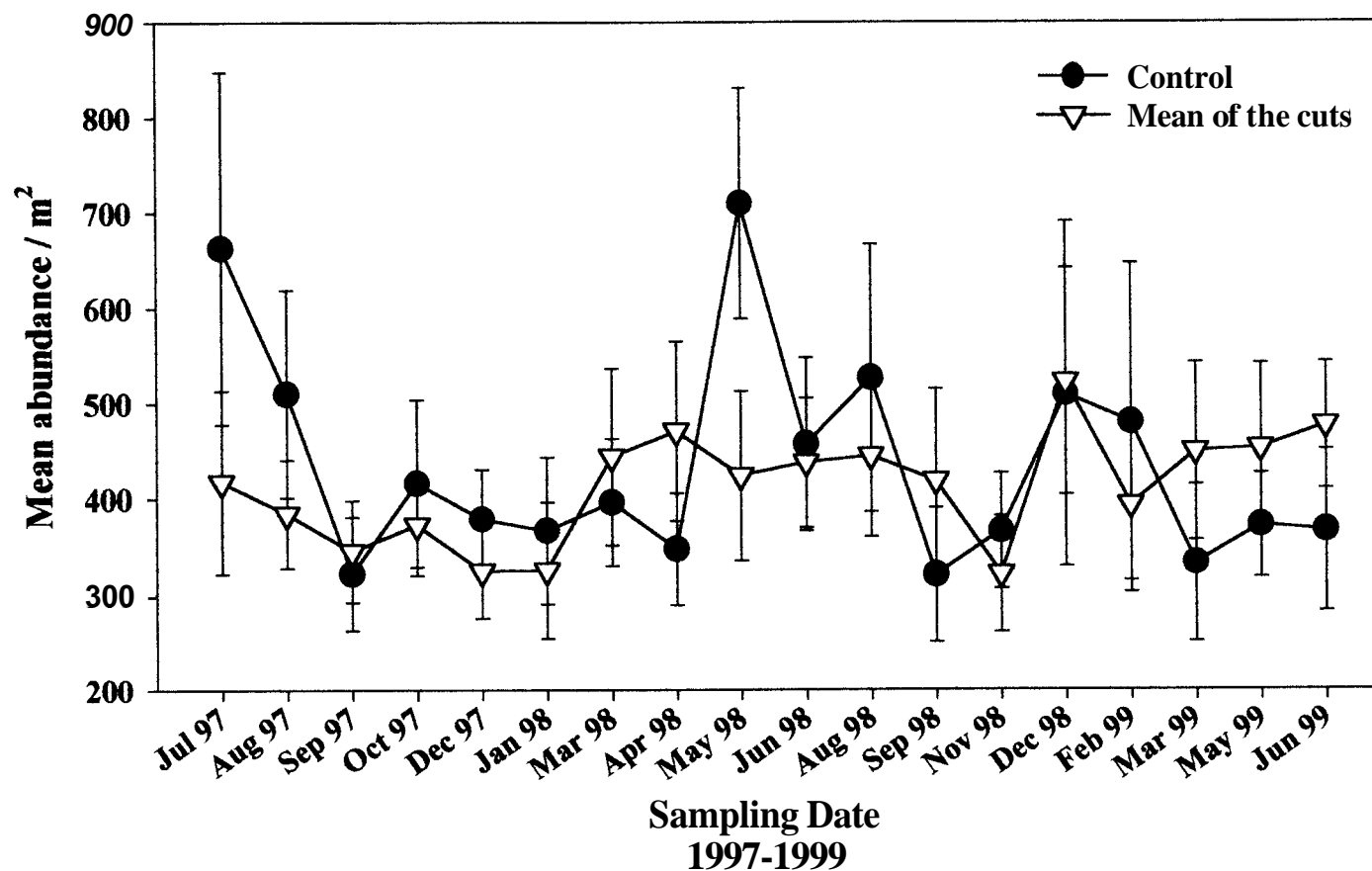


Figure 4.23. Temporal changes in the numerical abundance of *Littorina littorea* per m². Shown are the mean abundances in the control plots and the 'pooled' mean abundance (both treatments combined) for the harvested plots. (n = 4 sites x 3 reps/site = 12/time period for the controls; and n = 4 sites x 3 reps/site x 2 treatments = 24/time period for the 'cut' mean abundance).

compared to the ~~mean~~ of the cut plots. *Dynamena* also exhibited a significant ‘Treatment’ effect. The ‘Treatment’ effect, however, was detected only by the powerful *a priori*, orthogonal contrasts. The mean percent cover of *Dynamena* in the control plots was significantly higher than the mean percent cover in the harvested plots (Fig. 4.24).

4.5. Discussion

These results show that in moderately sheltered, rocky intertidal habitats, reduction in the algal canopy, and hence loss of habitat complexity, can affect the survival and abundance of several associated invertebrate organisms. The nature of the affect **was** dependent on the relative abundance of the species, which varied both temporally and spatially. In addition, the intensity of harvest also influenced the outcome.

Following the experimental harvest, there was a significant decline in the abundance of green crabs, *Carcinus maenas*, in both cut treatments (Fig. 4.4). Closer examination of the data reveals that at higher natural population levels, reduction of the algal canopy has a much greater impact on the species than at lower densities. Previous studies have shown that intertidal macrophytes provide shelter for crab species from gull predation (*Larus argentatus* and *L. marinus*) during emersion (Lubchenco, 1978; Bertness, 1999). The loss of habitat complexity caused by the removal of the overstory may have made the sites less suitable as a refuge (Schneider and Mann, 1991; Edgar et al., 1994; Lavery et al., 1999; Leonard, 1999). The green crab population, however, reestablished itself within a year, presumably due to an increase in the habitat structure from the regeneration of the canopy (Fig. 4.6). This study suggests that green crab

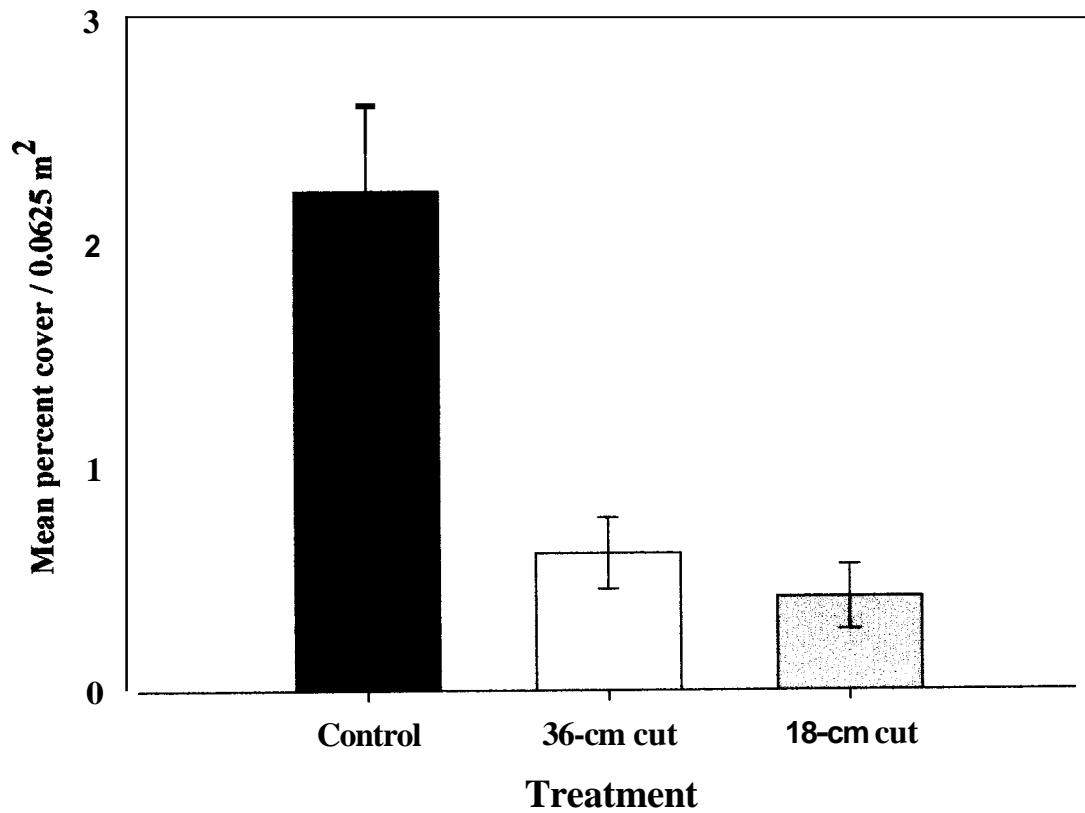


Figure 4.24. Mean treatment effect for *Dynamena pumila* averaged over the two-year post-harvest time period. Error bars represent +/- S.E. (n = 3 reps/site x 4 sites x 18 time periods = 216/treatment)

density is positively correlated with the percent cover of the algal canopy. Lubchenco (1978) found a similar correlation in tidepools.

The effect due to harvesting rockweed on *L. littorea* abundance varied through time. In the spring (March and April) of both years following the experiment the mean abundance of snails in the cut plots was higher than the mean abundance in the control plots (Fig. 4.23). During the rest of the year, *L. littorea* densities were either higher or no different than in the cut plots. During the colder months this species migrates into deeper waters (Vadas, 1992; Pollock, 1998). In early spring (about mid-April), the *L. littorea* population shifts from the lower intertidal region to the mid-intertidal zone (Bertness et al., 1983). The appearance of higher densities in the cut plots in the early spring may be due in part to seasonal migrational patterns. The snails may have preferentially moved through the cut habitats because of reduced whiplash effects by the shortened canopy. Bertness et al. (1999) has shown that the abundance of small littorines is negatively correlated to the amount of canopy, presumably due to whiplash.

Increased snail abundance in the cut plots may also be due to an increase in ephemeral algae, the preferred food for littorines (Lubchenco, 1978; Watson and Norton, 1985). Removal of the *Ascophyllum* canopy led to an increase in certain species of ephemeral algae in the cut plots, including *Monostroma grevillei* and *Scytosiphon lomentaria* (Fegley, unpublished data). These algal species were only found in the 18-cm cut plots and are both considered a preferred food source for littorines (Lubchenco, 1978). The snails may have moved into the harvested plots to graze on preferred food sources. The annual pattern of recruitment of opportunistic algae in the intertidal zone and the subsequent vertical movements and aggregations of *L. littorea* on these species

is well documented and suggests that these migrations are searches for food (Vadas, 1992).

Release from predatory pressure by the green crab may also have contributed to the increased *L. littorea* abundance in the cut plots. Since *Carcinus* is known to prey on small gastropods, the low densities of green crabs in the cut plots during this time period may have also played a role (Elner and Raffaelli, 1980; Elner, 1981).

Temporal patterns of blue mussel abundance were detected at Lamoine where an adjoining mussel bed exists. In the fall of each year, mussel larvae were found in the *Ascophyllum* bed where they settled on all available substrate, including the fronds of *Ascophyllum* plants. In 1997 the larvae did not persist due to post-settlement mortality. In 1998, however, the mussel spat survived and recruited into the adult population. Settling mussel spat frequently inundate algal beds located near adult mussel populations (Bertness, 1999). In a space-limited environment, such as the rocky intertidal, algal fronds offer additional attachment substrate for settling larvae. Use of algae as a settlement surface probably minimizes competition with adult mussels while providing the larvae shelter from physical stresses and predators (Bertness, 1999). After doubling in size, the juvenile mussels generally migrate into association with the adults (Bayne, 1964).

Lamoine not only experienced a temporal increase in the *Mytilus* population, but the magnitude of the increase in the plots was related to the harvesting intensity. The highest densities of *Mytilus* (both recruits and juveniles) were found in the 18-cm cut plots. This may simply reflect an increase in the availability of suitable settlement substrate (e.g., understory rock surface). Reduction of the canopy increases the available

understory substrata but may also reduce the whiplash effect thereby allowing higher densities of settlers. Increased flow rates in the 18-cm cut plots may also have contributed to the preferential settlement of mussels in these areas. The juvenile (< 5 mm) abundance pattern associated with the treatments may reflect an ecological balance between substrate availability (via understory space or algal fronds) and increased flow versus the negative effects associated with algal whiplash (e.g., dislodgement). It should be noted that in this experiment mussel spat did not settle on the *Ascophyllum* fronds in plots that had been harvested but only on rocky substratum (personal observation). Mussel settlement was, however, very abundant on the control plants. Lack of mussel settlement on the plants in the cut plots may reflect the release of secondary polyphenolic metabolites as a wounding response to the harvesting. *Ascophyllum* is known to elicit a “wounding” or defensive response when injured or cut by increasing the production of phlorotannins (Toth and Pavia, 2000). Increased levels of secondary metabolites have been shown to decrease the palatability of the seaweeds to periwinkles (Toth and Pavia, 2000). A similar response to the increased levels of defensive chemicals may have also deterred the settling spat.

Although *Dynamena* is a sessile organism, the effects of harvesting on this species are similar to that observed for *Carcinus*. At relatively high population levels (e.g., Rackliff Island) the effect of the canopy removal is highly significant, yet at lower densities the removal is equivocal (Figs. 4.15 and 4.17). The abundance of this species varies seasonally, with a peak in spring followed by a gradual decline to near-zero levels in the winter. *Dynamena* is typically found in the subtidal but can expand its distribution into the intertidal by settling in moist, protected habitats. As one moves from subtidal to

intertidal, the colonies recruit lower onto the plant stipes presumably to avoid increased risk of desiccation (Lewis, 1964). In the intertidal zone, *Dynamena* is only present on interior branches on the lower third of *Ascophyllum* plants (< 50 cm from the holdfast). This position reduces the risk of desiccation during emersion because the plants lie flat and only the distal canopy is subjected to aerial stress. Intense levels of harvesting negatively affect this invertebrate in two ways. First, harvesting potentially reduces the amount of substrate available for attachment. Second, it increases the amount of light and heat reaching the lower portion of the plants. Removal of the canopy likely increases desiccation stress, which kills the individual zooids causing an overall decline in the percent cover of the colony.

Significant 'Time x Treatment x Site' effects were detected for both *Tectura* and *Semibalanus*. Both species exhibited high spatial variability, with Lamoine having the highest densities of *Tectura* (Fig. 4.5) and Castine having the highest percent cover of *Semibalanus* (Fig. 4.14). Treatment effects were detected for both species at sites that contained high baseline abundances.

In May of 1998 the abundance of *Tectura* at Lamoine was significantly greater in the 18-cm cut plots when compared to the other treatments (Fig. 4.13). Examination of all other 'Time x Treatment x Site' interactions revealed no discernible pattern in treatment effect. During the May 1998 sampling period the 18-cm cut plots had the highest density of small-sized (< 7 mm) *Tectura* of the three treatments (Fegley, unpublished data). Interestingly, the highest percent cover of *Clathromorphum circumscriptum* was also found in the 18-cm cut plots during this time period (Fegley, unpublished data). Since *Tectura* is considered a feeding specialist that preferentially

settles and feeds on *Cluthromorphum*, its abundance pattern may be related to this phenomenon (Steneck, 1982). The high abundance in the 18-cm cut plots, however, was short-lived. *Tectura*, especially juveniles, generally seek refuge in the intertidal under dense algal canopies (Raffaelli and Hawkins, 1996). The protection afforded by the 18-cm cut plants may not have been sufficient to deter the increased desiccation stress caused by summer conditions.

The barnacle population at Castine and Lamoine experienced contrasting treatment effects (Fig. 4.2 1). Overall, the *Semibalanus* population appeared to be negatively affected by the canopy removal at Castine, whereas at Lamoine a positive effect occurred. At Castine the density of barnacles was higher in the control plots with population reductions correlated to the amount of canopy removal. In a similar harvesting study, Boaden and Dring (1980) found a decrease in the mean number of barnacles (*Balanus*) per boulder in cut areas and attributed the decrease to the reduction of *Ascophyllum*.

The increase in the barnacle population at Lamoine is likely the result of a late spring settlement event. Removal of the canopy freed understory substrate allowing the settlement of *Semibalanus* cyprids. Prior to the canopy removal, barnacles were excluded from this site probably due to the dense *Ascophyllum* canopy and lack of suitable settlement substrata. Post-settlement mortality was high and could be related to a variety of factors. Barnacles will settle on free substrates throughout the intertidal region but persist only in small patches between *Ascophyllum* holdfasts (Grant, 1977). Post-settlement survival is not very successful under the rockweed canopy due to the whiplash

effect of the algal fronds which dislodges a large proportion of the settling barnacles (Grant, 1977; Raffaelli and Hawkins, 1996).

Sites were considered a random factor at the onset of the experiment so that the results of the study could be generalized to similar sites with populations of *Ascophyllum*. The high spatial heterogeneity associated with the invertebrate populations was an unanticipated result. Although there was no interest in individual site effects *per se*, the fact that the analysis detected site effects for every species (except *Spirorbis*, $P = 0.060$) cannot be ignored. The apparent homogeneity of the structuring species, in this case *Ascophyllum*, does not necessarily mean that the associated communities are similar. With the *Ascophyllum* communities being so different from site to site, regional or coast-wide harvesting impacts will be difficult to assess. Only *Carcinus*, *L. littorea*, and *Dynamena* experienced harvesting effects, over and above the intrinsic differences associated with sites. The other treatment effects detected at specific sites should not be ignored because they could have overwhelming ecological importance to that particular community structure.

4.6. Conclusion

Biotic structures, such as seaweeds, play an important, habitat-modifying role in structuring natural communities, and their importance cannot be regarded. Removal of these habitats or reduction of structural complexity within a habitat can have important ecological consequences to the invertebrate fauna. The rocky intertidal zone is highly spatially structured and animal abundance and community structure are inextricably linked to this structure.

Ascophyllum serves as an important habitat for a large variety of invertebrates that use seaweed as exclusive habitat, nursery ground, refuge from waves, desiccation or predation, or shelter for reproductive adults. Numerous algae and sessile invertebrates also rely on *Ascophyllum* as a substrate. Following the single experimental harvest, there was a significant decline in the abundance of green crabs in both cut treatments. Within a year, however, the population had reestablished itself, presumably due to an increase in the habitat structure from the regeneration of the canopy. These findings suggest that the density of green crabs is positively correlated to the percent cover of the algal canopy. In the spring of both years following the experiment, the mean abundance of *L. littorea* in cut plots was higher than in control plots. The increased snail abundance in the cut plots may be due to an increase in ephemeral algae, the preferred food for littorines.

Dynamena experienced significant treatment effects at **high** population levels, yet at lower densities the effect of canopy removal was equivocal. Considerable differences were found in the species abundances at the four experimental sites. Apparent homogeneity of the structuring species, in this case *Ascophyllum*, does not necessarily mean that the associated communities are similar. With the *Ascophyllum* communities being *so* different from site to site, impacts of regional or coast-wide harvesting will be difficult to assess. Careless harvesting of this resource is likely to adversely affect not only the productivity of seaweed populations but also the diversity of the invertebrates and algae associated with it.

Chapter 5

Comparisons of species richness and community assemblages in harvested and unharvested *Ascophyllum* beds in mid-coast Maine

5.1. Abstract

Disturbance to structuring species has been well studied, but the resultant effects on organisms found within these habitats, including mobile species, are less well documented. Information is needed on the patterns and processes by which these associated populations recover following a disturbance. *Ascophyllum nodosum* (rockweed) is an ecologically and commercially important intertidal alga in the North Atlantic, and is increasingly being harvested in the Gulf of Maine. Harvesting is an anthropogenic disturbance that drastically reduces the structural complexity available to the associated assemblage. To test the effects of harvesting disturbance on the associated community, we imposed three different harvesting treatments (harvested at 18 cm and 36 cm from the holdfast and an unharvested/control) at four separate *Ascophyllum nodosum* beds in mid-coast Maine, USA, and followed the changes in community structure for two years. This paper specifically documents community-level responses to harvesting rockweed at various exploitation levels.

Removal of the seaweed canopy resulted in a loss of habitat, which caused a decrease in the number of species utilizing the affected areas. This reduction in species richness corresponded to the intensity of the disturbance. Not surprisingly, the recovery of species richness was correlated to the regeneration of the canopy. The diversity of species within *Ascophyllum* beds also varied temporally and spatially. Overall species

richness increased in summer and decreased in winter. Although all four experimental sites were located within **110 km** of each other, the number and variety of species present at each site varied widely.

The effects of *Ascophyllum* harvesting on the overall community structure were equivocal. Whether or not treatment effects were detected depended on the weight given to species abundance measures in the analyses. The subjectivity with which community data is analyzed makes it difficult to draw irrefutable conclusions about changes to community structure due to harvesting. 'Site' differences were detected in 68 out of 72 analyses of similarities (ANOSIM) indicating that community structure differs according to site-specific attributes. The apparent structural homogeneity of the *Ascophyllum* beds does not necessarily mean that the associated communities are similar. The difficulty in detecting treatment differences can be attributed to the **high** spatial heterogeneity of the associated organisms and the low replication of treatment variables.

Keywords: ANOSIM; *Ascophyllum nodosum*; community; disturbance; habitat; macroalgal harvesting; rocky intertidal; species richness

5.2. Introduction

Disturbance has been recognized as an important structuring force in intertidal marine communities for several decades (Dayton, **1971**; Grant, **1977**; Lubchenco and Menge, **1978**; Suchanek, **1978**; Paine and Levin, **1981**; Sousa, **1984**; Dethier, **1984**; Wetthey, **1985**; Chapman and Johnson, **1990**; Vadas et al., **1990**, Vadas, **1992**). Communities that are widely distributed over large, geographical regions, however,

generally show high resilience to both natural and anthropogenic disturbances (*sensu* Holling, **1973**). Examination of rocky shores shows an overall constancy in species composition and relative abundance, despite small-scale patterns of spatial heterogeneity (Menge and Branch, **2001**). It has been suggested that because intertidal species are constantly subjected to formidable physical stresses (e.g., wave action, desiccation, freezing, prolonged exposure to air) that resident organisms are able to adapt to resist such natural perturbations (Connell and Sousa, **1983**; Branch et al., **1987**). Thus when disturbed, rocky intertidal communities tend to return to a very similar condition, suggesting that these communities have some form of "adjustment stability" (Connell and Sousa, **1983**).

Most studies of disturbance in marine systems examine the effects of disturbance on assemblages of organisms that are either sessile or sedentary (Sousa, **2001**). This emphasis undoubtedly reflects the relative ease with which the impact of disturbance can be observed, compared to studies involving mobile species. Disturbance studies on hard substrata often focus on the larger, structure- and habitat-forming sessile species that represent the bulk of the biomass or cover -- organisms such as mussels, corals, macrophytes, and seagrasses (Sousa, **2001**). These "structural" species (*sensu* Huston, **1994**) provide food or habitat for associated assemblages, including mobile organisms (Sebens, **1991**; Rangeley and Kramer, **1995**; Seed, **1996**; Jarvis and Seed, **1996**; Bertness, **1999**). Thus, disturbance effects on "structural" species are likely to permeate throughout the entire community of organisms (Sousa, **2001**). Rarely are disturbance studies comprehensive in nature, examining both mobile and sessile organisms concurrently (Sousa, **2001**).

Ascophyllum nodosum (rockweed) is a dominant, intertidal, brown alga on North Atlantic shores. Its geographical distribution is from the White Sea to Northern Portugal in the eastern Atlantic and from Baffin Island to northern New Jersey in the western Atlantic (Baardseth, 1970). *Ascophyllum* has long been identified as playing an important community structuring role by modifying the physical and biological conditions in the habitats where it occurs (Baardseth, 1970; Menge, 1978; Hruby and Norton, 1979; Boaden and Dring, 1980; Bertness et al., 1999). The *Ascophyllum* community can be characterized by several associated algal and invertebrate species that have similar distributional patterns (e.g., *Fucus vesiculosus*, *Hildenbrandia rubra*, *Littorina littorea*, *L. obtusata*, *Carcinus maenas*, *Nucella lapillus*). The broad geographical distribution of *Ascophyllum*, combined with its structural role makes it an ideal species to test the hypothesis that communities such as these are resilient to varying intensities of disturbance.

The existence of concentrated stands of *Ascophyllum* has encouraged harvesting in many countries where it is used for alginates, organic fertilizers and fodder (Baardseth, 1970). The ecological effects of harvesting attached algae are not straightforward, but depend on a number of factors including the size of clearance, the intensity of removal, the harvesting technique, the season of harvest, and the vulnerability of the species or habitat to perturbation (Sharp and Pringle, 1990; Schiel and Nelson, 1990). The effects of *Ascophyllum nodosum* harvesting on the community of associated species has not been extensively studied (Boaden and Dring, 1980). Anthropogenic disturbances, such as harvesting, often occur over larger spatial scales than natural disturbances and are usually more severe, frequent and chronic in their impact (Sousa, 2001).

Although ecologists are interested in the effects of disturbance on individual species within a community, it is often of interest to determine community-level responses following a disturbance. Ecologists have developed a variety of numeric measures and qualitative descriptors to assess changes in community structure. Species diversity is a characteristic unique to the community level of organization. Diversity combines two distinct aspects of the species composition of communities: (1) the number of species present; and (2) the evenness of their abundance (Cox, 1996). Thus diversity can be measured by recording the number of species present (species richness), by describing their relative abundances (evenness), or by using a measure that combines the two components (Magurran, 1988). In this study, species-richness measures and analysis of similarities (ANOSIM) were used to determine whether the *Ascophyllum* communities in mid-coast Maine were resilient to various levels of disturbance by harvesting.

5.3. Materials and Methods

5.3.1. Study sites

Four *Ascophyllum nodosum* beds with similar standing crops were selected in the mid-coast region of Maine (Fig. 5.1). All four sites were moderately sheltered, had a slope 15° or less, and supported a dense, continuous cover of *Ascophyllum* (>70% cover). Although an attempt was made to standardize sites by visually selecting stands of similar biomass, differences in standing crop between sites could not be avoided. Mean standing crop was approximately 9 kg/m², but individual sites ranged from 7 to 12 kg/m². Mean tidal amplitude of this region is 3.1 m and the mean tidal level is 1.7 m. Substrate at three of the sites (Castine - 44°27'8"N; 68°47'29"W, Blue Hill Falls - 44°22'21"N; 68°33'9"W

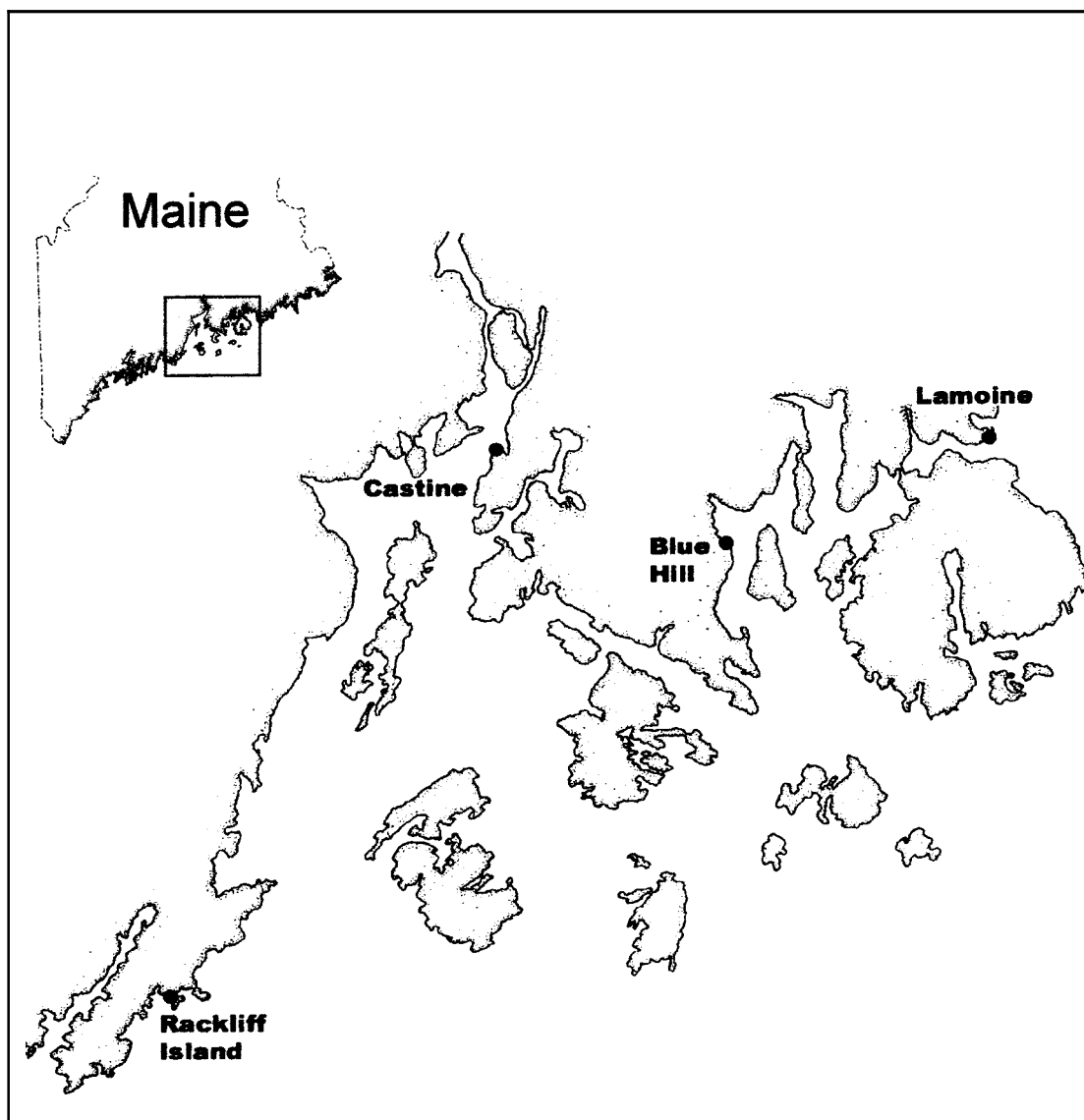


Figure 5.1. Location of experimental sites along the mid-coast region of Maine, USA.

and Lamoine Beach - 44°27' 18"N; 68°16'34"W) consisted mainly of small to medium-sized rocks interspersed with sand and pebbles. Ledge was occasionally present. The substrate at the remaining site, Rackliff Island (43°59'28"N; 69°9'6"W), consisted of large bedrock outcroppings embedded in muddy substrate.

5.3.2. Experimental design and sampling methods

The experimental design included four sites (described above) each consisting of nine permanently marked 5 m x 5 m plots placed at mean low water. Each plot was a minimum of 5 meters from an adjacent plot to assure treatment independence. Three different treatments were imposed on the plots: (1) *Ascophyllum* uncut (control), (2) *Ascophyllum* cut 36 cm above the holdfast (36-cm cut), and (3) *Ascophyllum* cut 18 cm above the holdfast (18-cm cut). At each site, three plots were randomly assigned to each of the three treatments while assuring that the treatments were adequately interspersed (Hurlbert, 1984).

Harvesting was done at all four sites in June of 1997 using hand shears. The seaweed was shaken vigorously to minimize the amount of epifauna removed from a plot, and then discarded on the shore.

To sample both macroscopic flora and fauna (epiphytic, sessile and sedentary) a grid system was overlaid on each plot during low tide. Approximately every five to six weeks throughout the two-year study, three new sampling locations within the grid were randomly selected. These locations were overlaid by 25 cm x 25 cm quadrats and species abundance (if mobile) and percent cover (if sessile) of organisms were enumerated. Percent cover for sessile species was selected as the measurement of abundance because

it was the only non-destructive method available for measuring sessile and colonial organisms in the field and it was rapid (Harlin et al., 1996). In cases where sampling included multi-layered macrophyte canopies, overstory species were moved aside and additional percentages were taken to measure stratification (Seapy and Littler, 1982). Sessile understory algal and invertebrate species were enumerated using percent cover. The mean abundance and mean percent cover per plot per time period ($n = 3$) were used in the statistical analyses to avoid pseudoreplication (Hurlbert, 1984). Thus twelve replicate samples per treatment (3 per site x 4 sites) were taken every five to six weeks throughout the two-year study yielding 18 sampling periods. Species richness, calculated as the total number of species present in each plot at each time period, was recorded as a measure of ecological diversity.

Surface water temperature was measured at each site at the time of sampling (during low tide). Water temperature was measured with a mercury column thermometer at approximately 30 cm depth in water 75 cm deep. At the same time, salinity samples were collected for analysis in the laboratory. A density hydrometer was used to determine salinity (correcting for temperature) to 0.1 parts per thousand (ppt).

5.3.3. Statistical analyses

A three-factor, repeated-measures multivariate analysis of variance (**MANOVA**), with replicate time periods as the repeated unit, was used to analyze the effect of harvesting treatment on species richness (Winer et al., 1991). Treatment and time were considered fixed factors because the treatment levels were the same at all sites and sites were sampled on a fixed time schedule (every 5-6 weeks for 2 years). Sites were treated

as a random factor because there were no *apriori* reasons for selecting those specific sites which allows the results to be generalized to all such populations of *Ascophyllum* beds (Winer et al, 1991; Underwood, 1997). This full model allows us to examine treatment, time and site, as well as their interactions on species richness. Several pre-planned comparisons of treatment means were used to test *apriori* hypotheses (Winer et al., 1991). Two mutually orthogonal, single-degree-of-freedom contrasts were constructed to test (1) whether species richness is affected by the mean of the harvesting treatments (Control vs. Cut), and (2) whether the two cut treatments differed in the number of species (36-cm cut vs. 18-cm cut). The significance level for all *apriori* comparisons was set at 0.05 while for *post-hoc* comparisons the level was Bonferroni-adjusted based on the number of contrasts. The assumption of multivariate normality was met. Statistica (Release 5.1, StatSoft) and SAS (Mainframe Version 6.1) software were used for all analyses.

Faunal and flora assemblages (described by abundance and percent cover) from the different treatments were compared using an analysis of similarities (ANOSIM), a non-parametric analogue to a multivariate analysis of variance (MANOVA) (Clarke, 1993). This statistical method required neither the assumption of multivariate normality nor homogeneity of the covariance structure (Clarke, 1993). To determine how close the abundance levels compared between any pair of samples, Bray-Curtis similarity coefficients were computed. Bray-Curtis coefficients are defined such that 100% represents total similarity between samples and 0% complete dissimilarity. ANOSIM assigned ranks to the coefficients and then used a permutation test to compare ranked similarities between and within treatment groups (Clarke and Warwick, 1994). The

permutation test involved randomly reassigning the treatment labels, recalculating the test statistic (R), and repeating the process a large number of times to build a null distribution. **ANOSIM** then calculated the significance level by comparing the observed value of the test statistic to its permutation distribution. The test statistic (R) ranges from -1 to 1 but usually falls between 0 and 1 (Clarke and Warwick, **1994**). R is approximately zero if the null hypothesis is true, so that similarities between and within sites will be the same on average (Clarke and Warwick, **1994**). R equals one only if all replicates within treatments are more similar to each other than any replicates from different treatments (Clarke and Warwick, **1994**). The R statistic itself is a useful comparative measure of the degree of separation of treatments, though the main interest usually centers on whether it is significantly different than zero (Clarke and Warwick, **1994**). Individual **ANOSIM** tests involved **5000** simulations using the PRIMER (Plymouth Routines In Multivariate Ecological Research) package from Plymouth Marine Laboratory, England (Clarke and Warwick, **1994**).

Analyses were run on two different community data sets since different abundance measures were used to quantify different groups of organisms. In analyzing community data it is important to be consistent in the abundance measure used and not to mix, for example, numerical-abundance with percent-coverage data within one calculation (Magurran, **1988**). One data set, hereafter referred to as the "mobile" community, consisted of those species that were counted: *Carcinus maenas*, *Littorina littorea*, *Littorina obtusata*, *Mytilus edulis*, *Nucella lapillus* and *Tectura testudinalis*. The other data set included species that were quantified using percent cover: *Ascophyllum nodosum*, *Hildenbrandia rubra*, *Chondrus crispus*, *Fucus vesiculosus*, *Verrucaria* spp.

Dynamenapumila, *Halichondria* spp., *Semibalanus balanoides*, *Phymatolithon* spp., *Pilayella littoralis* and *Spirorbis spirorbis*. This data set will be referred to as the "sessile" community. Only species whose average numerical abundance was greater than one (1) or whose mean percent cover was greater than 0.1% were included in the community analyses. Thus, all rare species were excluded from these community analyses though they are included in the richness data.

A two-way crossed ANOSIM examining 'Treatment' and 'Site' effects was conducted on the untransformed community data for each time period. The community data collected at each sampling time can be considered to be independent because the same exact location was not sampled in subsequent time periods and the composition of organisms in these community assemblages varies temporally (Chapman and Underwood, 1999).

To emphasize the distribution of less common species in the analysis, the PFUMER manual suggests transforming raw counts using the 4th root ($x^{0.25}$) which is similar to a $\log(x+1)$ transformation. Transforming the data using the 4th root has a fairly severe effect in down-weighting the importance of very abundant species so that the less dominant, and even rare species, play some role in determining the similarity between samples (Clarke and Warwick, 1994). This suggestion was followed although there was no biological justification for transforming the data in this manner. Analyses were performed on both untransformed and transformed data sets as a means of comparing the effects of species weighting on the results.

Two-way factorial ANOSIMs on the transformed community data were also performed at the individual sampling dates. Analyses of the similarity matrices used in

ANOSIM was also used to identify the species making the largest contribution to between-treatment differences (Clarke, 1993). The program SIMPER partitions the average Bray-Curtis dissimilarity between the treatment groups, into components from different species in a similarity/dissimilarity percentage breakdown (Clarke, 1993). Species are ordered by their average contribution to the total average dissimilarity. The values are then re-scaled to percentages, i.e., SIMPER computes the percentage of the total dissimilarity each species contributes. The significance level for all global tests was set at 0.05 while for post-hoc treatment comparisons the level was Bonferroni-adjusted to 0.017 to account for the three possible pair-wise contrasts (Winer et al., 1991).

5.4. Results

The highest mean surface water temperatures were reached during the late summer and the lowest in mid-winter (Fig. 5.2). Salinity values were fairly stable at Blue Hill, Lamoine and Rackliff Island (29-34 ppt.; Fig. 5.3). Slight seasonal variation did occur with highest salinities being recorded in late fall and lowest in early spring. The greater variability in salinity at Castine reflects the site's more estuarine nature due to its proximity to the Penobscot River.

During the two-year, post-harvesting sampling period, 58 different algal, invertebrate and fungal **taxa** were found in the experimental plots (Table 5.1). Overall species richness was tested using a three-factor, repeated-measures MANOVA and found to be significantly lower in the harvested plots compared to the controls ($P = 0.0246$). Community composition also differed based on treatment effects. The number of significant effects that were detected using ANOSIM varied according to the **type** of

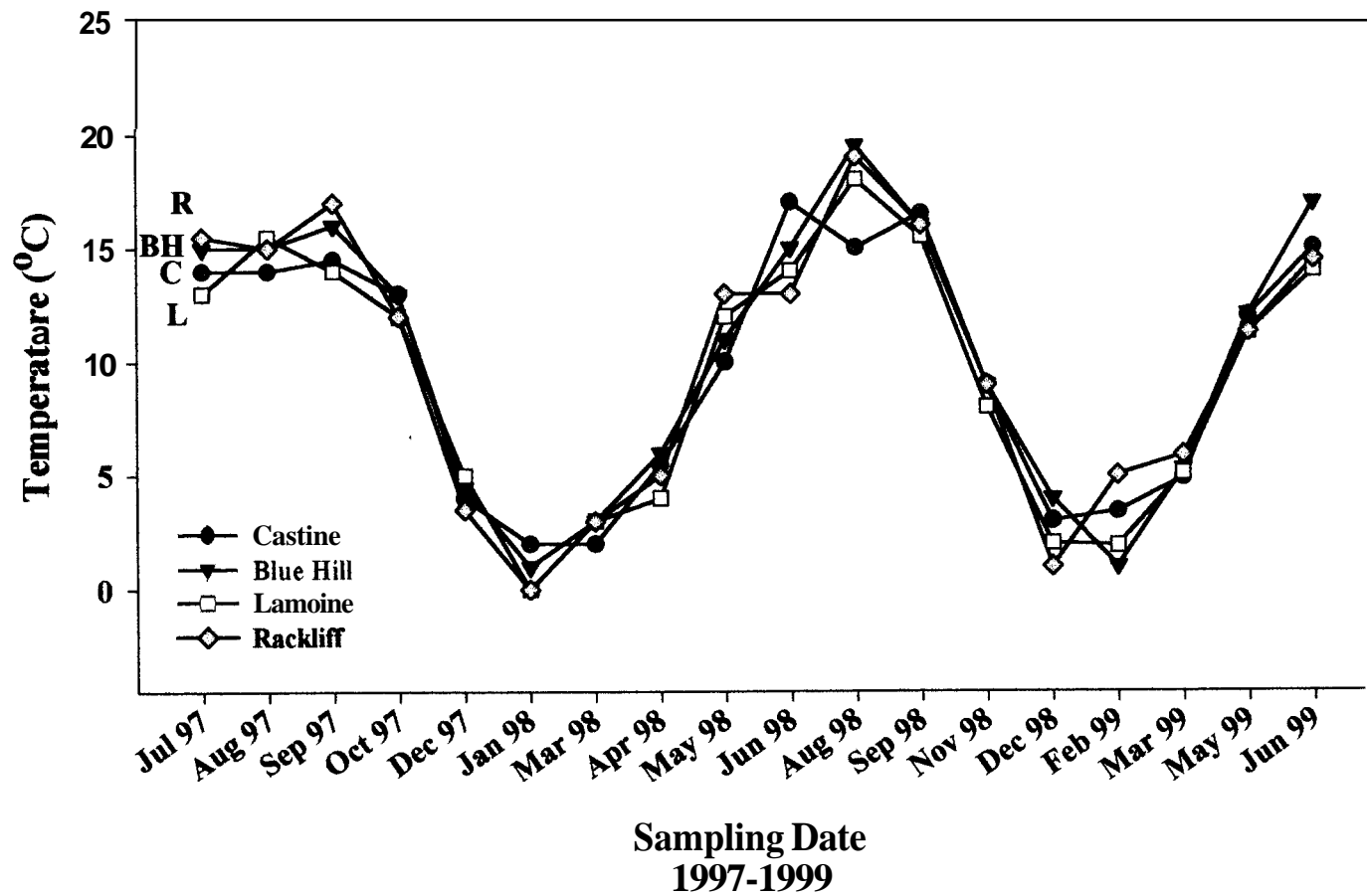


Figure 52. Monthly water temperatures (°C) measured at low tide at the study sites, July 1997 - June 1999.

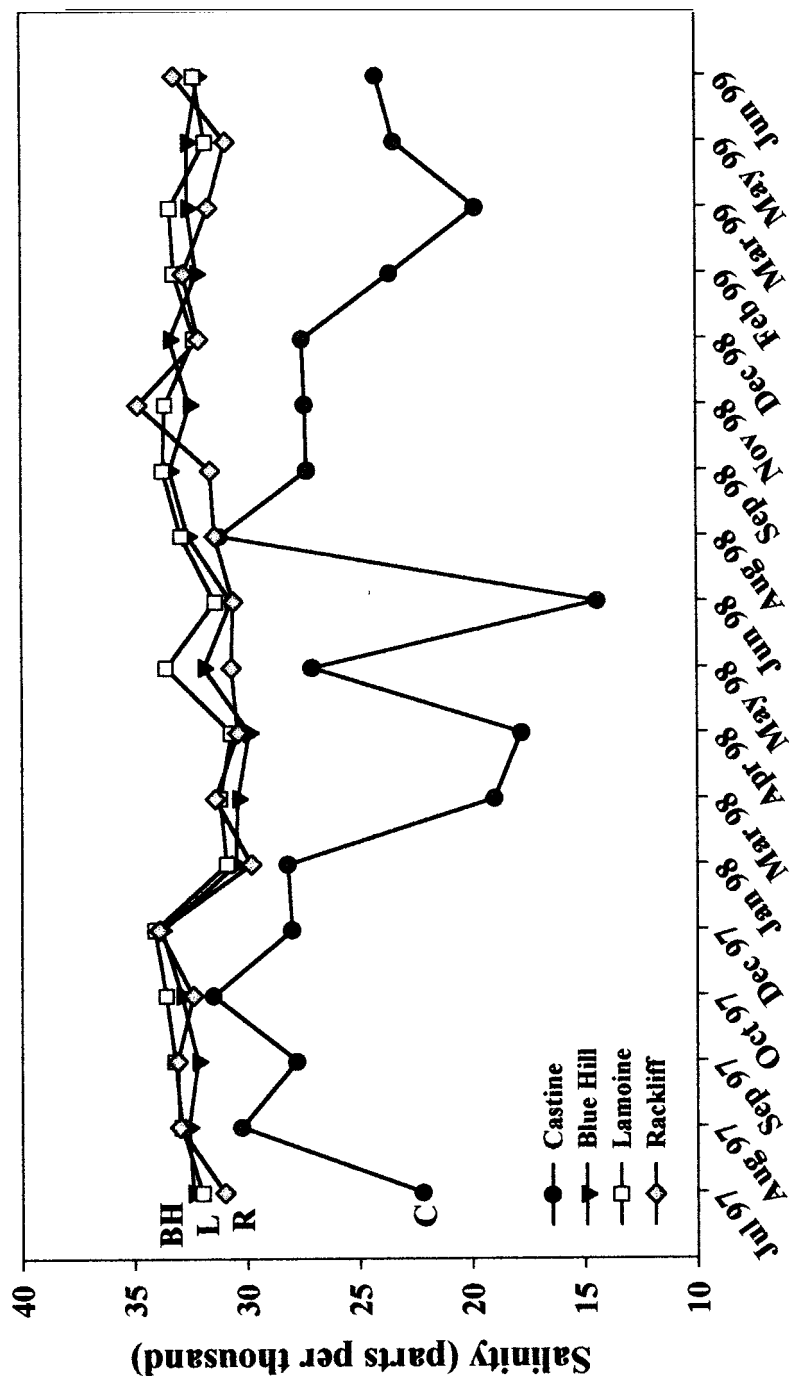


Figure 5.3. Monthly salinity measurements (ppt.) taken at low tide at the study sites, July 1997 - June 1999.

Table 5.1. Taxonomic list of algal, invertebrate and fungal species recorded in the experimental plots during the two-year study. All species were included in the richness analysis. Only those species that have a * were included in the community analyses.

Algal species	Invertebrate Species	Invertebrate species
PHAEOPHYCEAE	PORIFERA	MOLLUSCA
<i>Ascophyllum nodosum</i> *	<i>Halichondria</i> sp. *	<i>Aeolidia papillosa</i>
<i>Elachista fucicola</i>	<i>Halisarca</i> sp.	<i>Anomia simplex</i>
<i>Fucus vesiculosus</i> *	CTENOPHORA	<i>Colus stimpsoni</i>
<i>Petaloniafascia</i>	<i>Beroe cucumis</i>	<i>Crepidulaformicata</i>
<i>Pilayella littoralis</i> *	CNIDARIA	<i>Dendronotus frondosus</i>
<i>Ralfsia</i> sp.	<i>Cerianthus borealis</i>	<i>Flabellina</i> sp.
<i>Scytosiphon lomentaria</i>	<i>Clava multicornis</i>	<i>Hiatella arctica</i>
FLORIDEOPHYCEAE	<i>Diadumene lineata</i>	<i>Lacuna vineta</i>
<i>Chondrus crispus</i> *	<i>Dynamena pumila</i> *	<i>Littorina littorea</i> *
<i>Clathromorphum</i> spp.	<i>Metridium senile</i>	<i>Littorina obtusata</i> *
<i>Devaleraea ramentacea</i>	<i>Urticina felina</i>	<i>Modiolus modiolus</i>
<i>Hildenbrandia rubra</i> *	PLATYHELMINTHES	<i>Mytilus edulis</i> *
<i>Mastocarpus stellatus</i>	<i>Notoplana atomata</i>	<i>Nucella lapillus</i> *
<i>Phymatolithon</i> sp. *	ECTOPROCTA	<i>Onchidoris bilamellata</i>
<i>Polysiphonia lanosa</i>	<i>Alcyonidium</i> sp.	<i>Onchidoris muricata</i>
<i>Porphyra</i> sp.	<i>Flustrellidra hispida</i>	<i>Tectura testudinalis</i> *
ULVOPHYCEAE	<i>Electra pilosa</i>	<i>Urosalpinx cinerea</i>
<i>Monostroma grevillei</i>	ECHINODERMATA	ANNELIDA
<i>Rhizoclonia tortuosum</i>	<i>Asterias rubens</i>	<i>Lepidonotus squamatus</i>
<i>Ulothrix</i> sp.	<i>Strongylocentrotus droebachiensis</i>	<i>Spirorbis spirorbis</i> *
Fungal species	ARTHROPODA	
ASCOMYCOTINA		<i>Balanus balanus</i>
<i>Verrucaria</i> sp. *	CHORDATA	<i>Carcinus maenas</i> *
	<i>Molgula</i> sp.	<i>Pandalus borealis</i>
		<i>Semibalanus balanoides</i> *

assemblage ('sessile' or 'mobile') and whether or not the raw data were transformed.

Significant 'Site' effects were present at nearly every time period.

5.4.1 Species richness

Immediately following the experimental harvest, species richness decreased by **25%** in the cut plots (Fig. **5.4**). This pattern persisted for approximately 8 months (based on Tukey's *post-hoc* tests). Overall 'Treatment' effects were detected by the three-factor, repeated-measures MANOVA ($P = 0.0460$; Table **5.2**). Since there were no significant two- or three-way interactions, we can conclude that harvesting significantly reduces the species richness in the cut plots when compared to the controls regardless of spatial and temporal differences ($P = 0.0246$; Fig. **5.5**). A *priori* orthogonal contrasts did not detect differences in the mean species richness when comparing the two treatments ($P = 0.2218$).

'Site', 'Time' and 'Time \times Site' effects were also detected by the MANOVA. Although I cannot fully evaluate 'Site' effects because a significant higher order interaction is present, it should be noted that Lamoine had significantly higher species richness than all other sites (Table **5.3**). Throughout the two-year study, Lamoine consistently had the highest species richness at each time period. The significant two-way interaction occurs because the species richness varies spatially and temporally at the other three sites (Castine, Blue Hill, and Rackliff Island). Recovery of species richness was correlated with the regeneration of the canopy.

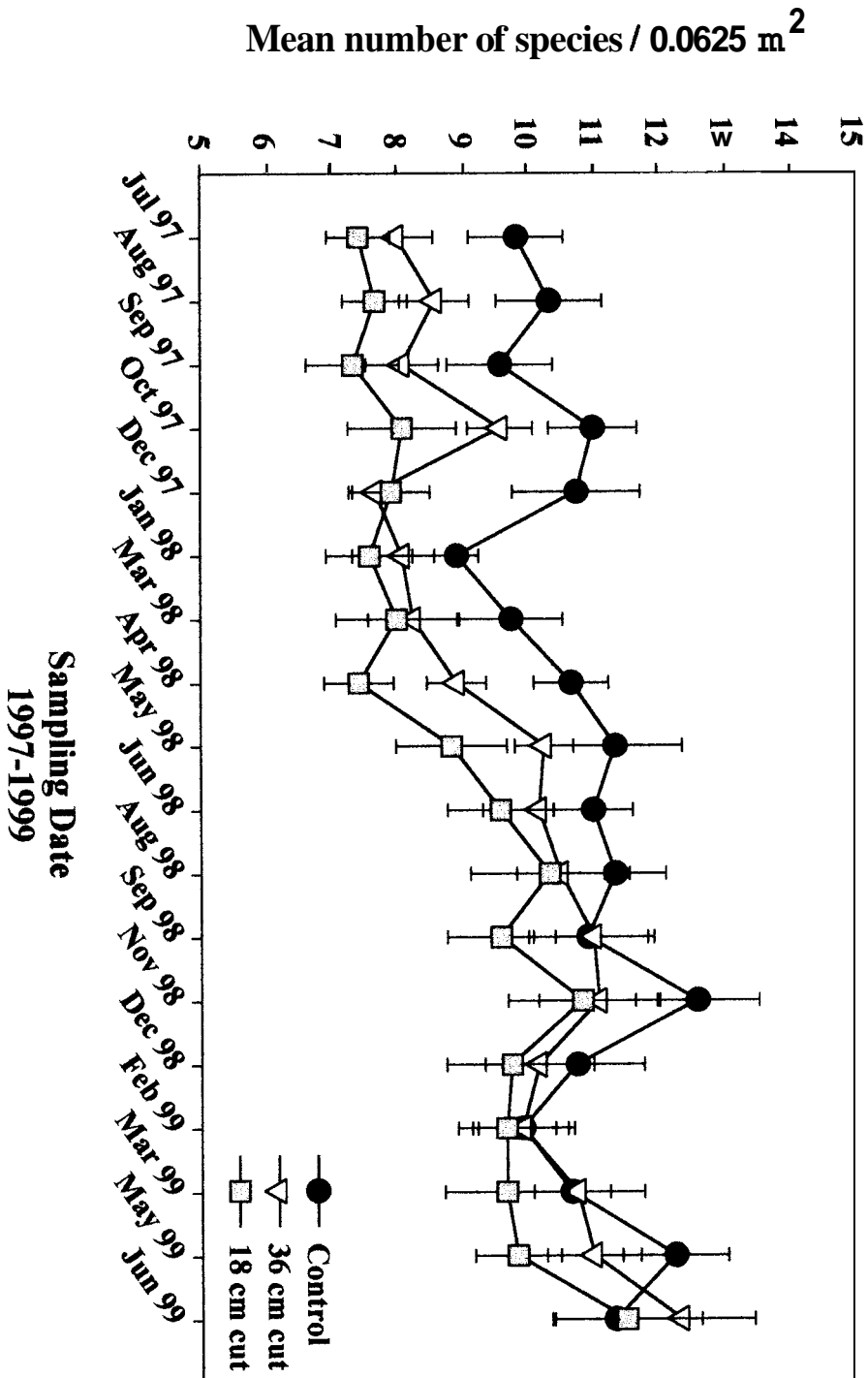


Figure 5.4. Temporal changes in the mean species richness per 0.0625 m² at various treatment levels. Values represent means \pm S.E. (n = 4 sites \times 3 reps/site = 12/treatment/time period).

Table 5.2. Results of a three-factor, mixed model, repeated-measures MANOVA on the influence of site, harvesting treatment and time on intertidal mean species richness. A priori orthogonal contrasts appear below the treatment main effect. Within-subject effects were tested using Wilks' Test Statistic where possible (MS values are not provided for these terms). Univariate tests were conducted on 'Time' and 'Time x Treatment' since the data matrices were nearly singular and could not be inverted. Sites were considered a random factor. Significant effects are in bold. (α level = 0.05; n = 3)

MANOVA TABLE	df	MS	Test	Critical value	P - value
Source of variation					
Between-subject effects					
SITE (A)	3	500.74	$MS_{A/Error(between)}$	17.110	0.0000
TREATMENT (B)	2	171.31	$MS_{B/A*B}$	5.372	0.0460
Control vs. cut (1)	1	283.36	$MS_{B1/A*B}$	8.89	0.0246
36cm vs. 18cm (2)	1	59.26	$MS_{B2/A*B}$	1.86	0.2218
SITE x TREATMENT (A x B)	6	31.89	$MS_{A*B/Error(between)}$	1.090	0.3967
ERROR (BETWEEN)	24				
Within-subject effects					
TIME (C)	17	44.03	$MS_{C/C*A}$	5.187	0.0000
TIME x SITE (C x A)	51		$SS\&CP_{C*A/Error(within)}$	0.003	0.0028
TIME X TREATMENT (C x B)	34	4.09	$MS_{C*B/C*A*B}$	1.167	0.2734
TIME X SITE X TRT (C x A x B)	102		$SS\&CP_{C*A*B/Error(within)}$	0.002	0.4789
ERROR (WITHIN)	408				

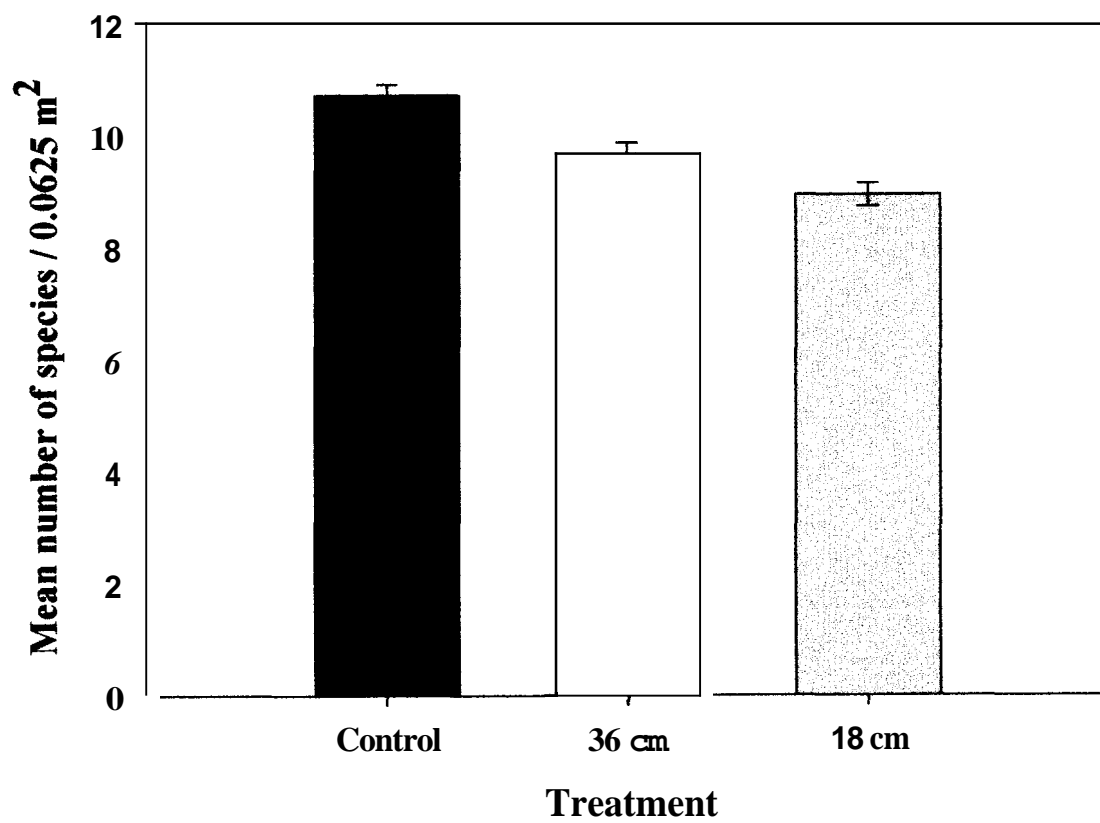


Figure 5.5. The effects of harvesting treatment level on species richness. Values represent means \pm S.E. ($n = 4$ sites \times 3 reps/site \times 18 time periods = 216 / trt)

Table 53. The number and type of different taxa that occurred at each experimental site during the two-year study. The number of algal and invertebrate species unique to each site is also presented. Details on unique species are in the text.

Site	Total # of species	# of algal species	# of invert. species	# of fungal species	# of unique algal species	# of unique invert. species
Castine	30	10	19	1	1	0
Blue Hill	40	13	26	1	0	6
Lamoine	46	13	32	1	1	8
Rackliff	30	13	16	1	3	0

5.4.2. 'Sessile' community analyses

Two-way crossed ANOSIM conducted on the 'sessile' *Ascophyllum* community at different time periods indicated that there were significant differences among treatment levels and among sites (Table 5.4). Treatment differences in the 'sessile' community were detected during the first eight sampling periods following the experimental harvest. Differences were also detected in September 1998 ($P = 0.014$). *Post-hoc* treatment comparisons indicate that most treatment differences were between the control plots and those cut 18 cm from the holdfast. *Ascophyllum nodosum* contributed the most (from 34-61%) to average measures of dissimilarity among treatment replicates at eight of the nine time periods. Other important species contributing to dissimilarity among replicates were *Hildenbrandia rubra*, *Verrucaria* spp., and *Fucus vesiculosus*. Significant 'Site' effects were detected at 14 of the 18 time periods. Several negative global test statistics (R values) occurred in the analyses which indicates greater dissimilarity within than among samples (Clarke, 1993; Chapman and Underwood, 1999).

The community data were transformed using the 4th root to preserve information concerning relative abundance or cover of species across samples as well as to reduce differences in scale (and therefore relative weight) among variables (Clarke, 1993; Anderson and Underwood, 1997). The two-way crossed ANOSIM on the transformed data did not detect as many treatment differences as the untransformed analyses (Table 5.5). The effects of harvesting on the 'sessile' community were detected in March and April of 1998 ($P = 0.033$ and $P = 0.002$, respectively) and June of 1999 ($P = 0.039$). Using a 4th root transformation altered the composition of species that accounted for the separation of the treatments. *Verrucariu* played a prominent role in the observed

Table **5.4.** Results of two-way crossed ANOSIM tests at each sampling period examining 'Treatment' and 'Site' differences between untransformed community samples. Samples consisted of dominant sessile species (both algal and invertebrate) found in *Ascophyllum* beds. Main species contributing to the treatment differences are shown with their percentage contribution to the separation of the treatments. (global α level = 0.05; *post-hoc* comparison α levels < 0.017) (n = 12/treatment/time period)

¹ Global test statistic (R) was negative.

² Species abbreviations: *Asco.* = *Ascophyllum nodosum*
 Hild. = *Hildenbrandia rubra*
 Verr. = *Verrucaria* spp.
 Dyna. = *Dynamena pumila*
 Phym. = *Phymatolithon* spp.
 Fucus = *Fucus vesiculosus*
 Pila. = *Pilayella littoralis*

Sampling period	Global ANOSIM 'Treatment' (P-value)	'Site' (P-value)	Post-hoc 'Treatment' differences ($\alpha < 0.017$)	Main species contributing to 'Treatment' differences (% contribution) ²
July 1997	0.000	0.000	C v 18 36 v 18	<i>Asco.</i> (52), <i>Hild.</i> (25), <i>Verr.</i> (7), <i>Dyna.</i> (6) <i>Asco.</i> (50), <i>Hild.</i> (23), <i>Verr.</i> (10), <i>Phym.</i> (10)
August 1997	0.020	0.294	C v 18	<i>Asco.</i> (57), <i>Hild.</i> (26), <i>Verr.</i> (10)
September 1997	0.017	0.151	C v 18	<i>Asco.</i> (57), <i>Hild.</i> (25), <i>Verr.</i> (7), <i>Fucus</i> (6)
October 1997	0.000	0.001	C v 18	<i>Asco.</i> (49), <i>Hild.</i> (22), <i>Verr.</i> (14), <i>Fucus</i> (7)
December 1997	0.001	0.024	C v 18	<i>Asco.</i> (61), <i>Hild.</i> (18), <i>Fucus</i> (8), <i>Verr.</i> (7)
January 1998	0.006	0.001	C v 18	<i>Asco.</i> (57), <i>Hild.</i> (26), <i>Verr.</i> (9)
March 1998	0.001	0.001	C v 18	<i>Asco.</i> (43), <i>Hild.</i> (28), <i>Verr.</i> (14), <i>Fucus</i> (7)
April 1998	0.001	0.000	C v 36 C v 18	<i>Asco.</i> (34), <i>Hild.</i> (31), <i>Verr.</i> (12), <i>Fucus</i> (9), <i>Pila.</i> (7) <i>Asco.</i> (46), <i>Hild.</i> (25), <i>Verr.</i> (12), <i>Fucus</i> (7)
May 1998	0.085	0.001		
June 1998	0.068	0.000		
August 1998	0.649 ¹	0.000		
September 1998	0.014	0.000	C v 36	<i>Hild.</i> (40), <i>Asco.</i> (23), <i>Verr.</i> (16), <i>Dyna.</i> (7)
November 1998	0.053	0.001		
December 1998	0.305	0.143		
February 1999	0.141	0.170		
March 1999	0.448	0.005		
May 1999	0.608'	0.028		
June 1999	0.277	0.036		

Table **5.5**. Results of two-way crossed ANOSIM tests at each sampling period examining 'Treatment' and 'Site' differences between 4th root transplanted community samples. Samples consisted of dominant sessile species (both algal and invertebrate) found in *Ascophyllum* beds. Main species contributing to the treatment differences are shown with their percentage contribution to the separation of the treatments. (global α level = 0.05; *post-hoc* comparison α levels < 0.017) (n = 12/treatment/time period)

- ¹ Species abbreviations:
- Verr.* = *Verrucaria* spp.
 - Pila.* = *Pilayella littoralis*
 - Phym.* = *Phymatolithon* spp.
 - Fucus* = *Fucus vesiculosus*
 - Dyna.* = *Dynamena pumila*
 - Hild.* = *Hildenbrandia rubra*
 - Semi.* = *Semibalanus balanoides*

Sampling period	Global ANOSIM 'Treatment' (P-value)	'Site' (P-value)	Post-hoc 'Treatment' differences ($\alpha < 0.017$)	Main species contributing to 'Treatment' differences (% contribution)
July 1997	0.086	0.000		
August 1997	0.361	0.001		
September 1997	0.093	0.001		
October 1997	0.274	0.000		
December 1997	0.152	0.000		
January 1998	0.076	0.000		
March 1998	0.003	0.000	C v 3 6	Verr.(19), Phym.(16), <i>Fucus</i> (15), <i>Hild.</i> (10)
April 1998	0.002	0.000	C v 18 36 v 18	Verr.(18), <i>Pila.</i> (15), <i>Fucus</i> (15), <i>Phym.</i> (10) <i>Pila.</i> (17), Verr.(16), Phym.(15), <i>Hild.</i> (10)
May 1998	0.209	0.000		
June 1998	0.074	0.000		
August 1998	0.355	0.000		
September 1998	0.166	0.000		
November 1998	0.119	0.000		
December 1998	0.071	0.000		
February 1999	0.265	0.000		
March 1999	0.218	0.000		
May 1999	0.120	0.000		
June 1999	0.039	0.000	C v 18	<i>Verr.</i> (15), <i>Dyna.</i> (14), <i>Fucus</i> (14), <i>Semi.</i> (13)

difference in similarity as did *Phymatolithon*, *Pilayella* and *Dynamena*. *Fucus vesiculosus* was also a discriminating species. Significant 'Site' effects were detected at all 18 time periods.

5.4.3. 'Mobile' community analyses

The 'mobile' assemblage was virtually unaffected by the *Ascophyllum* harvesting. The two-way ANOSIM on the untransformed community data yielded only three time periods where species assemblages varied by treatment (Table 5.6). *Post-hoc* comparisons, however, failed to detect specific treatment differences. Two-way ANOSIM on 4th root transformed data generated no significant treatment effects (Table 5.7). The 'mobile' community was significantly different between sites at every time period regardless of treatment and **type** of data transformation.

5.5. Discussion

5.5.1 Species richness

Macroalgal canopies provide a structurally complex habitat for numerous understory algal and invertebrate species in intertidal and shallow subtidal zones worldwide. The increased structural complexity afforded by the canopy is considered a contributing factor to increased species diversity (Hicks, 1980; Sebens, 1991; Gee and Warwick, 1994; Jarvis and Seed, 1996). *Ascophyllum's* large size and highly branched morphology provides not only a secondary substratum for epiphytic organisms to colonize, but also serves **as** an important habitat and refuge for a wide range of

Table **5.6.** Results of two-way crossed ANOSIM tests at each sampling period examining 'Treatment' and 'Site' differences between untransformed community samples. Samples consisted of dominant mobile (invertebrate) species found in *Ascophyllum* beds. Main species contributing to the treatment differences are shown with their percentage contribution to the separation of the treatments. (global α level = 0.05; *post-hoc* comparison α levels < 0.017) (n = 12/treatment/time period)

¹ Global test statistic(R) was negative.

Sampling period	Global ANOSIM 'Treatment' (P-value)	'Site' (P-value)	Post-hoc 'Treatment' differences ($\alpha < 0.017$)	Main species contributing to 'Treatment' differences (% contribution)
July 1997	0.043	0.000	NS	<i>L. littorea</i> (72), <i>L. obtusata</i> (15), <i>Tectura</i> (5)
August 1997	0.520'	0.017		
September 1997	0.921'	0.007		
October 1997	0.188	0.000		
December 1997	0.637'	0.000		
January 1998	0.431	0.000		
March 1998	0.259	0.000		
April 1998	0.175	0.000		
May 1998	0.012	0.001	NS	<i>L. littorea</i> (87), <i>L. obtusata</i> (6), <i>Mytilus</i> (5)
June 1998	0.979'	0.000		
August 1998	0.636'	0.000		
September 1998	0.755'	0.000		
November 1998	0.442	0.000		
December 1998	0.540'	0.000		
February 1999	0.905'	0.000		
March 1999	0.032	0.000	NS	<i>L. littorea</i> (50), <i>Mytilus</i> (44)
May 1999	0.193	0.000		
June 1999	0.249	0.000		

Table **5.7.** Results of two-way crossed ANOSIM tests at each sampling period examining 'Treatment' and 'Site' differences between 4th root transformed community samples. Samples consisted of dominant mobile (invertebrate) species found in *Ascophyllum* beds. Main species contributing to the treatment differences are shown with their percentage contribution to the separation of the treatments. (global α level = 0.05; post-hoc comparison α levels < 0.017) (n = 12/treatment/time period)

¹Global test statistic (R) was negative.

Sampling period	Global ANOSIM	
	'Treatment' (P-value)	'Site' (P-value)
July 1997	0.307	0.000
August 1997	0.267	0.000
September 1997	0.802'	0.003
October 1997	0.270	0.000
December 1997	0.748'	0.000
January 1998	0.051	0.000
March 1998	0.709	0.002
April 1998	0.161	0.000
May 1998	0.394	0.001
June 1998	0.427	0.000
August 1998	0.415	0.000
September 1998	0.373	0.000
November 1998	0.316	0.000
December 1998	0.927 ¹	0.000
February 1999	0.213	0.000
March 1999	0.093	0.000
May 1999	0.179	0.000
June 1999	0.372	0.000

organisms. The added structural complexity also alters the physical environment, thereby influencing the abundance and distribution of associated species (Bertness, 1999).

A single harvest disturbance had the immediate effect of reducing species richness. The reduction in richness was correlated to the intensity of exploitation. This decline was not surprising given that the primary goal of harvesting is to remove biomass, which also removes any species attached to it or residing within the canopy. Species richness remained depressed in the cut plots throughout the two-year, post-harvesting sampling period. The partial recovery observed in the cut plots is correlated to the regeneration of the canopy species (Chapter 3).

The diversity of species also varied temporally and spatially. Overall species richness increased in the summer and decreased in the winter. The seasonal patterns are due to migrational habits of mobile residents (e.g. *Carcinus maenas* and *L. littorea*) and to annual recruitment events (e.g. *Pilayella*, *Dynamena* and *Mytilus*). Although all four sites were located in mid-coast Maine (within 110km of each other), the number of species present at each site varied significantly. Habitats of identical structural complexity that are exposed to different regimes of environmental disturbances and/or to a different pool of species will likely differ in their species diversities (Safriel and Ben-Eliahu, 1991).

5.5.2. Community analyses

Although species richness provides an important basis for comparisons among communities, it provides no information regarding the relative abundances of the species. Over the years, various diversity indices have been developed to account for variation in

both the number of species in a community and their relative abundances (Magurran, 1988). Each of the indices characterizes the diversity of a sample or community by a single number (Magurran, 1988). ANOSIM, a multivariate statistical method, supercedes these indices by being able to not only characterize the diversity of a sample, but also statistically test for changes in community structure. Community data used in ANOSIM tests can be transformed in a variety of ways to down-weight the effects of common species (e.g., varying the degree of evenness). For a more complete discussion on the effects of data transformations on ANOSIM results see Clarke (1993) and Clarke and Warwick (1994).

The 'sessile' *Ascophyllum* community was analyzed on both untransformed and 4th root transformed data using ANOSIM. The untransformed analyses revealed significant 'treatment' effects for 10 months following the harvest. Not surprisingly, *Ascophyllum nodosum* contributed the most to the separation of the treatments. Although the canopy of *Ascophyllum* was reduced in the harvested plots, it was still a dominant member of the community in terms of percent coverage. *Hildenbrandia* and *Verrucaria* were also extremely abundant in the experimental plots. Another significant treatment effect was detected in September 1998 where *Hildenbrandia* contributed the most to the observed differences. The reduced contribution of *Ascophyllum* to treatment differences with time is due to the regeneration of plants in the cut plots. Several community samples had negative global test (R) statistics indicating greater dissimilarity within replicate treatment samples than between samples (Chapman and Underwood, 1999). Using untransformed data in ANOSIM is analogous to obtaining a dominance measure (such as Simpson's index) since the analysis is weighted toward the abundances of the

most common species rather than providing a measure of species richness. Generally, it is undesirable to base an assessment of changes in community structure on a small number of very abundant species. Transforming the data using the 4th root has a fairly severe effect in down-weighting the importance of the very abundant species so that the less dominant, and even rare species, play some role in determining the similarity between samples (Clarke and Warwick, 1994).

Examination of the ANOSIM tests where the ‘sessile’ community was 4th root transformed revealed only three significant ‘treatment’ effects (March and April 1998 and June 1999). The species that contributed most to treatment differences were *Verrucaria*, *Phymatolithon*, *Pilayella*, *Fucus*, *Dynamena* and *Hildenbrandia*. Thus species weighting has a substantial impact on the results of the analyses, not only in terms of the detection of ‘treatment’ effects but also in terms of the species contribution to treatment differences. The community patterns detected by ANOSIM are related to individual species effects (Chapter 3 and Chapter 4).

The ‘mobile’ *Ascophyllum* community was also analyzed using both untransformed and 4th root transformed data. ANOSIM detected significant global ‘treatment’ effects during three sampling periods spread throughout the two-year study. *Post-hoc* tests, however, failed to detect differences at the adjusted α level. *L. littorea* was the numerically dominant mobile species in the *Ascophyllum* beds, and this is reflected in the percent contribution to treatment differences. ANOSIM failed to detect any treatment differences when using transformed data. The high variability associated with the abundances of the mobile species is reflected in the large number of analyses where negative global test (R) statistics were present. It should be noted that ‘site’

differences were detected in **68** out of 72 ANOSIM tests. The community structure clearly differs based on 'site' attributes.

5.5.3. Site differences

Sites were considered a random factor at the beginning of the experiment, which would allow the results of the study to be generalized to other "similar" sites with populations of *Ascophyllum*. The high spatial heterogeneity associated with the species richness and community data was an unanticipated result. Although there was little interest initially in individual 'Site' effects, the fact that significant effects were detected in 95% of the community analyses cannot be ignored. The apparent structural homogeneity of the *Ascophyllum* beds does not necessarily mean that the associated communities are similar.

To assess the degree of changes in species from one habitat to another I examined the degree of association or similarity of sites (Magurran, **1988**; Cox, 1996). The easiest way to measure the diversity of pairs of sites is by the use of similarity coefficients. Sorenson's index of similarity (S) was calculated **as** follows to determine the degree of similarity of the *Ascophyllum* communities at the different sites:

$$S = \frac{2w}{(A + B)}$$

Where: A = number of species in community A
 B = number of species in community B
 w = number of species in common

Sites that have the same composition of species will have a Sorenson's index equal to **1.0**, denoting complete similarity. Conversely, dissimilar sites that have no species in common will have an index value equal to 0. In this **type** of diversity measure all species count equally in the equation irrespective of whether they are abundant or rare.

Comparisons of Blue Hill and Lamoine with Rackliff led to low degrees of species associations compared to the other pairs of sites (Table 5.8). Castine and Rackliff had the lowest overall diversity ~~of~~ species, yet the degree of species overlap was smallest when comparing Rackliff to all other sites.

Examination of the total number of species recorded at each site and the number of species unique to each location provides additional insight into the observed spatial differences in the communities (Table 5.3). While Castine had only one unique species (*Porphyra* sp.), Rackliff had three (*Scytosiphon lomentaria*, *Polysiphonia lanosa* and *Ulothrix flacca*), Blue Hill had six (*Halisarca* sp., *Cerianthus borealis*, *Diadumene lineata*, *Urticina felina*, *Aeolidia papillosa* and *Crepidula fornicata*) and Lamoine had nine (*Ralfsia* sp., *Beroe cucumis*, *Notoplana atomata*, *Colus stimpsoni*, *Dendronotus frondosus*, *Flabellina* sp., *Hiatella arctica*, *Urosalpinx cinerea* and *Molgula* sp.). The variety and relative abundances of species within *Ascophyllum nodosum* beds varies significantly within a narrow (10 km) geographical region.

5.6 Conclusion

Ascophyllum nodosum has been harvested for decades, yet few studies have assessed the impact of this disturbance on the associated assemblage of species. This paper specifically documents the community-level response of rockweed harvesting at various exploitation levels. Removal of the seaweed canopy resulted in the loss of habitat, which caused an initial decrease in the number of species occupying the affected areas. The reduction in species richness corresponded to the intensity of the disturbance. Not surprisingly, the recovery of species richness, which took approximately 8 months,

Table **58.** The degree of association of the *Ascophyllum nodosum* communities at the different sites using Sorenson's Index (S). The number of species in each community and the number of species in common are also presented.

Site comparisons (A vs. B)	# of species in community A	# of species in community B	# of species in common (w)	Sorenson's Index (S)
Castine vs. Blue Hill	30	40	26	0.74
Castine vs. Lamoine	30	46	28	0.74
Castine vs. Rackliff Is.	30	30	22	0.73
Blue Hill vs. Lamoine	40	46	31	0.72
Blue Hill vs. Rackliff Is.	40	30	23	0.66
Lamoine vs. Rackliff Is.	46	30	25	0.66

was correlated to the regeneration of the canopy. Numerous studies have linked increased structural complexity within a habitat to increased species diversity (Hicks, 1980; Sebens, 1991; Gee and Warwick, 1994; Jarvis and Seed, 1996). Thus, harvesting at a lower intensity (e.g., leaving more canopy) will likely decrease the effects.

The effects of *Ascophyllum* harvesting on the overall community structure were equivocal. Whether or not treatment effects were detected clearly depended on how species abundances were weighted in the analyses. Multivariate analyses, such as the one used in this paper, attempt to reduce the complexity of the (high-dimensional) community data by collapsing the data into a low-dimensional “view” of the structure it exhibits (Clarke and Warwick, 1994). A view in which most of the emphasis is on the pattern of occurrence of rare species will be very different than one in which the emphasis is wholly on a handful of species that numerically dominate the samples (Clarke and Warwick, 1994). Thus, the choice of transformation can significantly alter the conclusions of an analysis. The subjectivity with which community data is analyzed makes it difficult to draw irrefutable conclusions about changes to community structure.

The variety and relative abundance of organisms found in *A. nodosum* beds was spatially heterogeneous. The fact that the community structure varied between sites made it difficult to detect overall harvesting effects. This is not to say that individual sites were not affected by the harvesting disturbance but that the effects on a broader geographical scale were undetectable. The specific effects of *Ascophyllum* harvesting on the associated species still cannot be quantitatively predicted in unstudied areas.

Chapter 6

An assessment of *Ascophyllum nodosum* as a resource in mid-coast Maine and the effects of harvesting on demographic characteristics

6.1. Abstract

Variation in the biomass of the perennial brown alga *Ascophyllum nodosum* (L.) Le Jolis was examined at several commercially viable sites in mid-coast Maine during 1996, 1997 and 1999. Spatial differences in fresh weights were not detectable due to high within-site variability. A significant increase in biomass ~~was~~ detected in 1999 and was attributed to the mild winter of the previous year, which had less intertidal ice rafting and thus caused lower winter mortality. Temporal and spatial differences were also detected in the wet-weight/dry-weight relationship.

Effects of three harvesting regimes (cut 18 cm from the holdfast; cut 36 cm from the holdfast; and unharvested/control) on *Ascophyllum* population and morphological characteristics were also examined. The growth rate of *Ascophyllum* one-year after the harvesting event was highly variable and depended on cut intensity and site. Data gathered two-years post-harvest revealed increased shoot densities in the harvested plots that was likely a result of increased inadiance levels in the sub-canopy, causing a significant increase in the growth of the young, understory fronds. The number of branches at 18 cm and the number of apical dichotomies increased in the harvested plots. Control plants were also significantly longer than the plants in either of the cut plots indicating a lack of recovery to preexisting conditions.

Key words: algae; *Ascophyllum nodosum*; biomass; macroalgal characteristics; macroalgal harvesting; rocky intertidal.

6.2 Introduction

Fleshy brown algae (rockweeds) dominate intertidal shores throughout much of the world's colder oceans. The brown alga *Ascophyllum nodosum* (L.) Le Jolis is a prominent component of the intertidal flora in the North Atlantic, where its distribution extends from northern New Jersey to the Baffin Islands in the west and southern Portugal to the White Sea in the east (Baardseth, 1970). Commonly referred to as “knotted wrack,” this species is generally found in rocky intertidal areas protected from intense wave action (Boney, 1966). At the center of its distribution this alga is abundant and forms dense, homogeneous stands in estuaries and sheltered bays. *Ascophyllum* accounts for 80 to 90% of the plant cover on sheltered shores in estuaries and produces dry-weight standing crops of 5 to 6 kg/m² (Keser et al., 1981). Mean substrate cover and biomass estimates for more exposed shores are lower (50 to 70% and 3 to 4 kg/m², respectively) (Vadas et al., 1976; Topinka et al., 1981).

Easy access to large quantities of *Ascophyllum* has led to the commercial exploitation of this species in many countries where it is used for alginates, organic fertilizers, and fodder. The largest industrial harvests of *Ascophyllum* are in Western Norway, Britain, Ireland, Northern France, Iceland and Eastern Canada (Baardseth, 1970). Although *Ascophyllum* has been harvested commercially in these areas for decades, only recently have large-scale harvests begun in the U.S.A., especially in Maine. Despite the absence of harvests in the past, biomass values in the Gulf of Maine are as

high as those of the most productive Canadian and European shores (Keser et al., 1981; Cousens, 1984; Sharp, 1987).

Commercial harvesting of *Ascophyllum* is governed by many considerations, some of which are biological. Data on the temporal and spatial variability associated with seaweed constituents, in particular the percentage of *dry* matter, can offer important insight regarding the best timing and placement for harvesting activities. For example, sites that contain older populations will produce a higher percentage of *dry* matter per acre, and this allows better exploitation per unit effort than sites with younger populations (Baardseth, 1970a). Despite the importance of this information from a commercial perspective, relatively few studies have explored this relationship in depth (Baardseth, 1970a). Baardseth (1970a) examined two *Ascophyllum* populations in Norway and found that the wet-weight/dry-weight relationship varied by locality and season. Lack of temporal and spatial replication, however, limits generalizing from these results. Previous investigations in New England have shown that fucoiid biomass (kg/m^2 wet weight) is highly variable among sites (Keser et al., 1981; Topinka, et al., 1981). Unfortunately, these studies focused on the variation of wet biomass values instead of the relationship between wet weight and *dry* weight, which is a more important measurement commercially.

Despite extensive information regarding the phenology and autecology of *Ascophyllum*, few studies have been conducted in the Gulf of Maine. This study was designed to determine the baseline standing crop of *Ascophyllum nodosum* at several commercially viable sites in mid-coast Maine and to examine the between-site and inter-annual variability associated with these measures. In addition, I was interested in

examining the effects of various harvesting regimes on such characteristics as growth, density, length of shoots, number of apical dichotomies, and number of branches in *Ascophyllum*.

6.3. Materials and Methods

6.3.1. Study sites

Four *Ascophyllum nodosum* beds with similar standing crops were selected in the mid-coast region of Maine (Fig. 6.1). All four sites were moderately sheltered, had a slope 15° or less, and support a dense, continuous cover of *Ascophyllum* (>70% cover). Although an attempt was made to standardize sites by visually selecting stands of similar biomass, differences in standing crop between sites could not be avoided. Initial mean standing crop was approximately 9 kg/m² (wet weight), but individual sites ranged from 7 to 12 kg/m². Mean tidal amplitude of this region is 3.1 m and the mean tidal level is 1.7 m. Substrate at three of the sites (Castine - 44°27'8"N; 68°47'29"W, Blue Hill Falls - 44°22'21"N; 68°33'9"W, and Lamoine Beach - 44°27'18"N; 68°16'34"W) consisted mainly of small to medium-sized rocks interspersed with sand and pebbles. Ledge was occasionally present. The substrate at the remaining site, Rackliff Island (43°59'28"N; 69°9'6"W), consisted of large bedrock outcroppings embedded in muddy substrate. Three of the four sites were established in May 1996 (Castine, Blue Hill, and Lamoine). The remaining site, Rackliff Island, was established in May 1997.

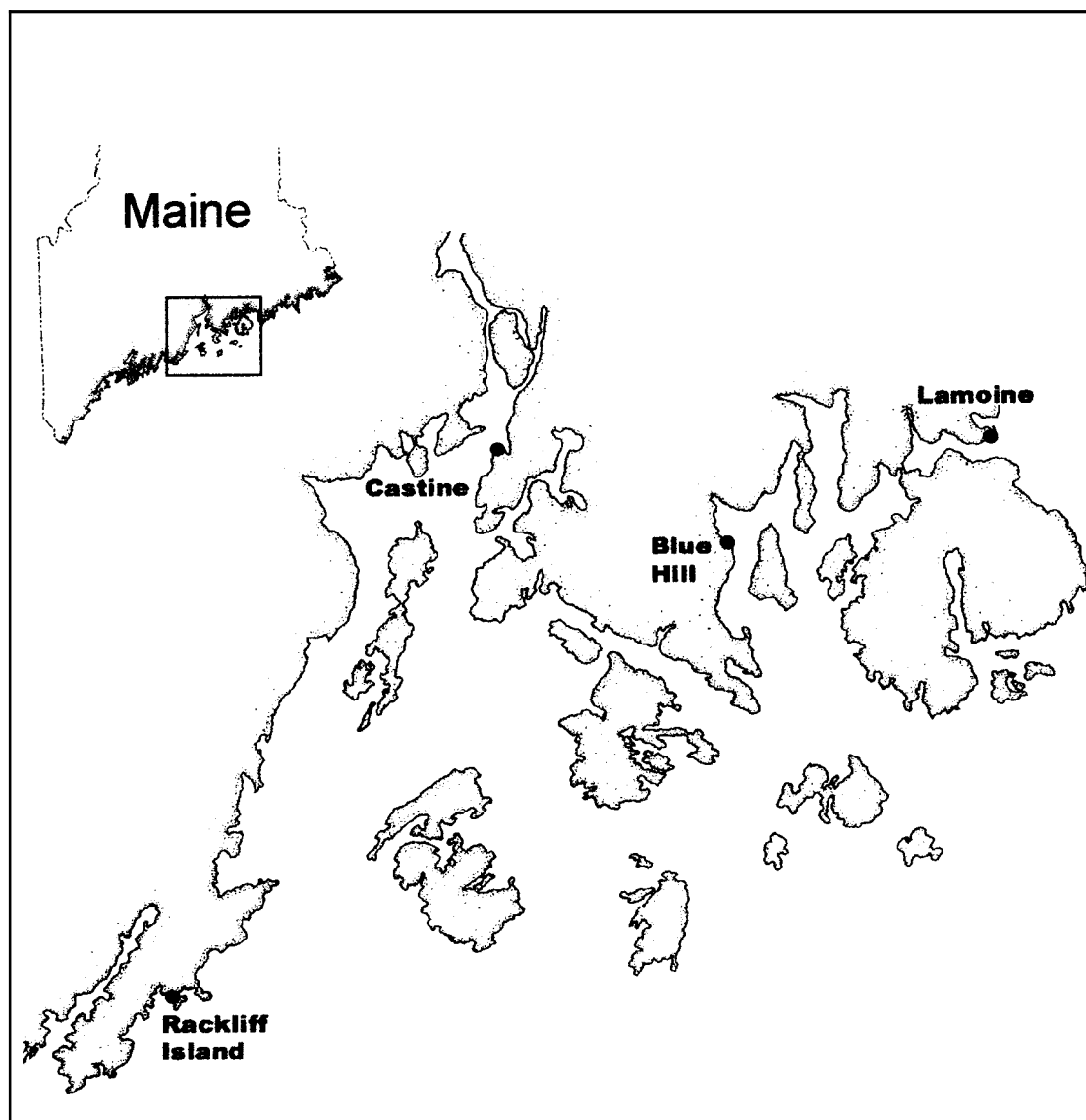


Figure 6.1. Location of experimental sites along the mid-coast region of Maine, USA.

6.3.2. Biomass estimation

To assess spatial and annual variability associated with the standing crop, biomass samples were taken from the low *Ascophyllum* zone at three experimental sites in June **1996** (Castine, Blue Hill, and Lamoine) and from all four sites in June **1997** and June **1999**. Random samples were taken using a 25 cm x 25 cm quadrat. All plants whose holdfasts originated within the quadrat were cut at the base of the holdfast, placed in a plastic bag and returned to the laboratory for weighing. Eighteen samples per site were collected in June **1996**, 27 per site in **1997**, and 14 per site in **1999**. If the random quadrat landed in an area that contained no plant holdfasts, then the biomass determination for that sample ~~was~~ zero. In quadrats that contained holdfasts, the complete plants, from stipe to tip, were cut and weighed in the fresh state. To reduce the influence of seasonal variation in biomass, all samples were collected during late June of each year.

Receptacles and epiphytes were manually removed from all *Ascophyllum* plants prior to obtaining a wet weight since their weight contribution could add considerably to the biomass value. In addition, since industry typically avoids plants that are reproductive and that have epiphytes, I followed the same general principle but manually removed the nuisance organisms so that sampling would still be random. In particular, removal of the receptacles reduced the between-site and inter-annual variability. The fruiting bodies contain a high content of water when they are ripe. Maturation and gamete release in Maine occurs during the months of April, May and early June (Bacon and Vadas, **1991**). The season starts with a considerable uptake of water by the receptacles, followed by release of gametes, and ends with shedding of receptacles. By

late June when the biomass samples were taken, most of the plants were post-reproductive and had **begun** to shed the receptacles. **In** Maine, the reproductive period of *Ascophyllum* is known to follow a latitudinal gradient from west to east that is correlated with increasing water temperatures (Bacon and Vadas, **1991**). Another reason to remove the receptacles is that the percent of fruiting bodies in *Ascophyllum* plants is known to vary from year to year (Baardseth, **1970**).

Biomass samples were kept in cold storage (**4°C**) until they were processed (up to five days post-harvest). Fresh weights on cleaned plants were determined after blotting the material dry. Plants were dried for a minimum of **48** hours at **60°C**, which allowed all samples to reach a constant dry mass. Plants were then removed from the drying chamber and reweighed immediately to prevent uptake of moisture.

6.3.3. Post-harvest morphological sampling

The experimental design included **4** sites (described above) each containing **9** permanently marked **5 m x 5 m** plots placed perpendicular to the shoreline at mean low water. All plots were located at the same relative tidal height to ensure that the sample areas were emersed for the same amount of time. Each plot was haphazardly placed and separated from the other plots by a minimum of **5** meters to assure treatment independence (Hurlbert, **1984**). Three different treatments were imposed on the plots in June of **1997**: (1) *Ascophyllum* uncut (control), (2) *Ascophyllum* cut **36** cm above the holdfast (36-cm cut), and (3) *Ascophyllum* cut **18** cm above the holdfast (18-cm cut). At each site, three plots were randomly assigned to each of the three treatments while assuring that the treatments were adequately interspersed (Hurlbert, **1984**).

In late June of **1998**, one-year post-harvest growth rates were measured on 25 plants randomly selected from each treatment at each site. I was interested in determining whether the uncut lateral branches on the harvested plants increased their growth rate when the canopy was removed. Growth rate measurements were collected in the field (nondestructive sampling) from the tallest unbroken shoot or lateral. The plants were measured from the distal end of the **1997** vesicle to the distal end of the **1998** vesicle. The internode length represents the amount of growth that occurred from March **1997** to March **1998** plus three months of additional elongation.

Post-harvest biomass and morphological sampling was conducted in June of **1999** (two years after harvesting). Biomass data were collected to examine the amount of recovery that occurred in the cut plots during the two years following the harvest. Morphological data were collected to determine whether plant structure was affected by harvesting. Using the same biomass sampling technique as before, all plants whose holdfasts originated within the quadrat were cut at the base of the holdfast, placed in a plastic bag and returned to the laboratory for measurements. If the random quadrat landed in an area that contained no plant holdfasts then another random sampling location within the grid system was selected. This procedure was continued until three samples were collected that contained plant material. This sampling technique ensured adequate treatment by site replication for the morphological measurements. In the case of post-harvest biomass sampling, if a quadrat landed in an area that contained no plant holdfasts, then the biomass for that sample was determined to be zero.

In the laboratory, plants were measured for morphological characteristics including shoot density, shoot length, number of apical dichotomies and number of

branches at 18 cm and **36** cm. The density of shoots was determined by counting the number of shoots in each quadrat and then converting this number to a per-square-meter basis. Null samples were included in the analyses. Shoot density was further subdivided into three size classes: small shoots (< 25 cm), medium shoots (25-50 cm), and large shoots (> 50 cm). Two random shoots per sample per size class were selected for further morphological measurements. The total length of each shoot and the number of branches that occurred at 18 cm and **36** cm from the base were recorded. From each shoot the average number of apical dichotomies was determined. If the shoot had only one apical branch then only one measurement was recorded. If multiple branches were present then the number of dichotomies was recorded for each branch and the average for that shoot was used in the analysis.

6.3.4. Ancillary measurements

Shore slope was measured using graded staffs and survey levels. Nine slope measurements were made per site (1 per plot). The resulting slope was a measure of the mean shore slope low in the *Ascophyllum* zone.

Temperature and salinity data were collected every six weeks from June 1996 through June 1999. Surface water temperature was determined at low tide at the time of sampling. Water temperature was measured with a column thermometer at approximately **30** cm depth in water **75** cm deep. At the same time, salinity samples were collected for analysis in the laboratory. A density hydrometer was used to determine salinity (correcting for temperature) and read to the nearest 0.1 ppt.

6.3.5. Statistical analysis

Biomass ~~data~~ were analyzed using a two-factor ('Site' and 'Year') mixed model analysis of variance (ANOVA). Since experimental sites were randomly selected from a larger population of commercially viable *Ascophyllum* beds, sites are considered a random factor in the model. Linear regression was used to determine the relationship between wet weight and *dry* weight. To test for differences in the wet/dry relationship by 'Year' and 'Site', analysis of covariance (ANCOVA) was used. The assumption of constancy of slopes was tested for all covariance analyses. Data were log-transformed to meet the assumptions of homogeneity and normality of the error terms.

One-year post-harvest growth rate data was also analyzed using a two-factor ('Site' and 'Treatment') mixed model analysis of variance (ANOVA). To meet the assumptions of the model, the data were log-transformed. All other post-harvest morphological and biomass data were analyzed using a non-parametric rank F-test since the assumptions of ANOVA could not be met despite transformations. Two-factor, mixed model analyses on the ranked data were performed. Where significant differences were detected, Tukey's post-hoc, pairwise comparison tests were employed.

6.4. Results

Highest mean surface-water temperatures occurred during late summer, whereas lowest temperatures were in mid-winter (Fig. 6.2). Salinity values were fairly stable at Blue Hill, Lamoine, and Rackliff Island (29-34 ppt.; Fig. 6.3). Slight seasonal variation did occur with highest salinities being recorded in late fall and lowest in early spring.

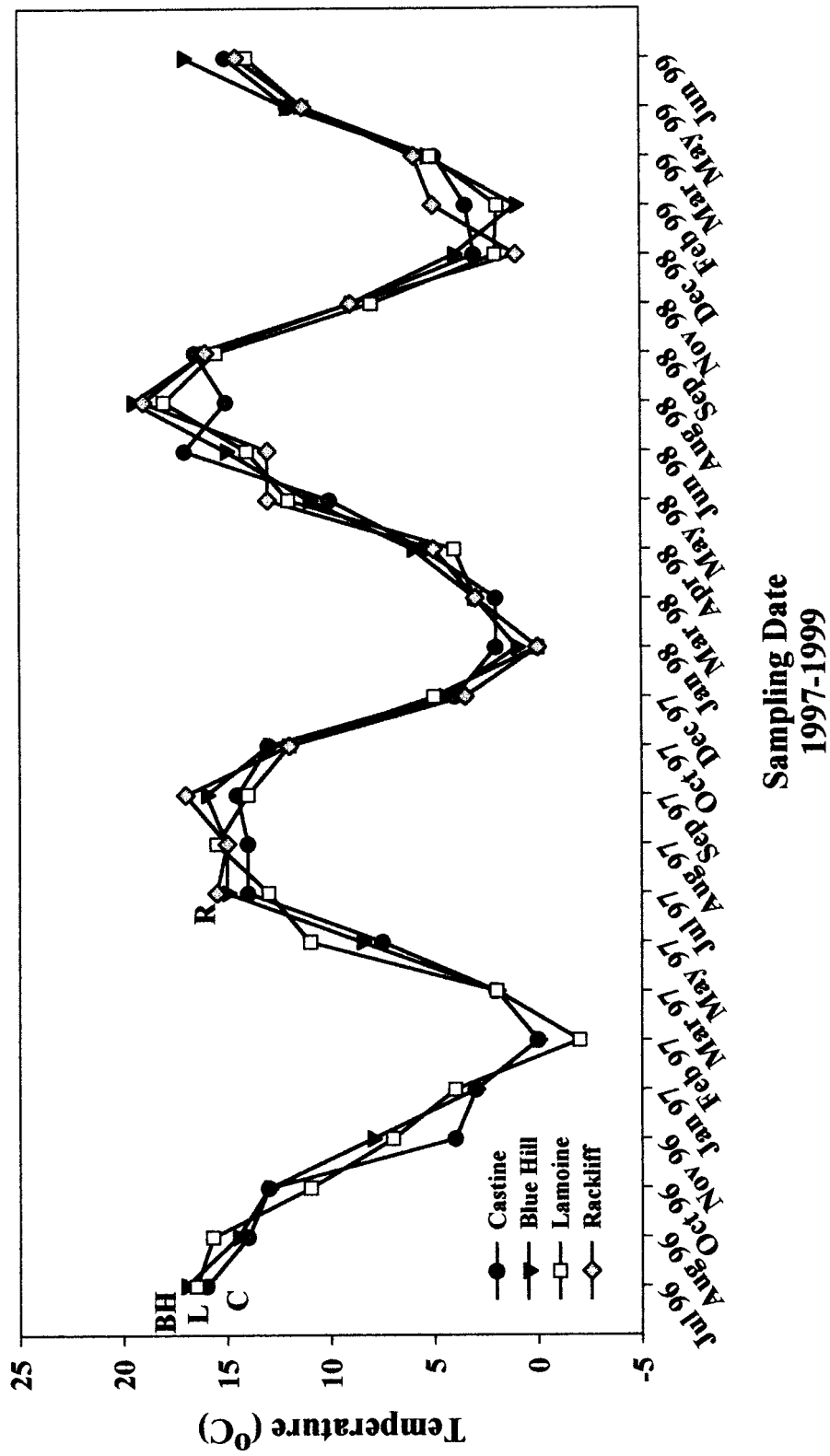


Figure 6.2. Monthly water temperatures (°C) measured at low tide at the study sites, July 1996 - June 1999.

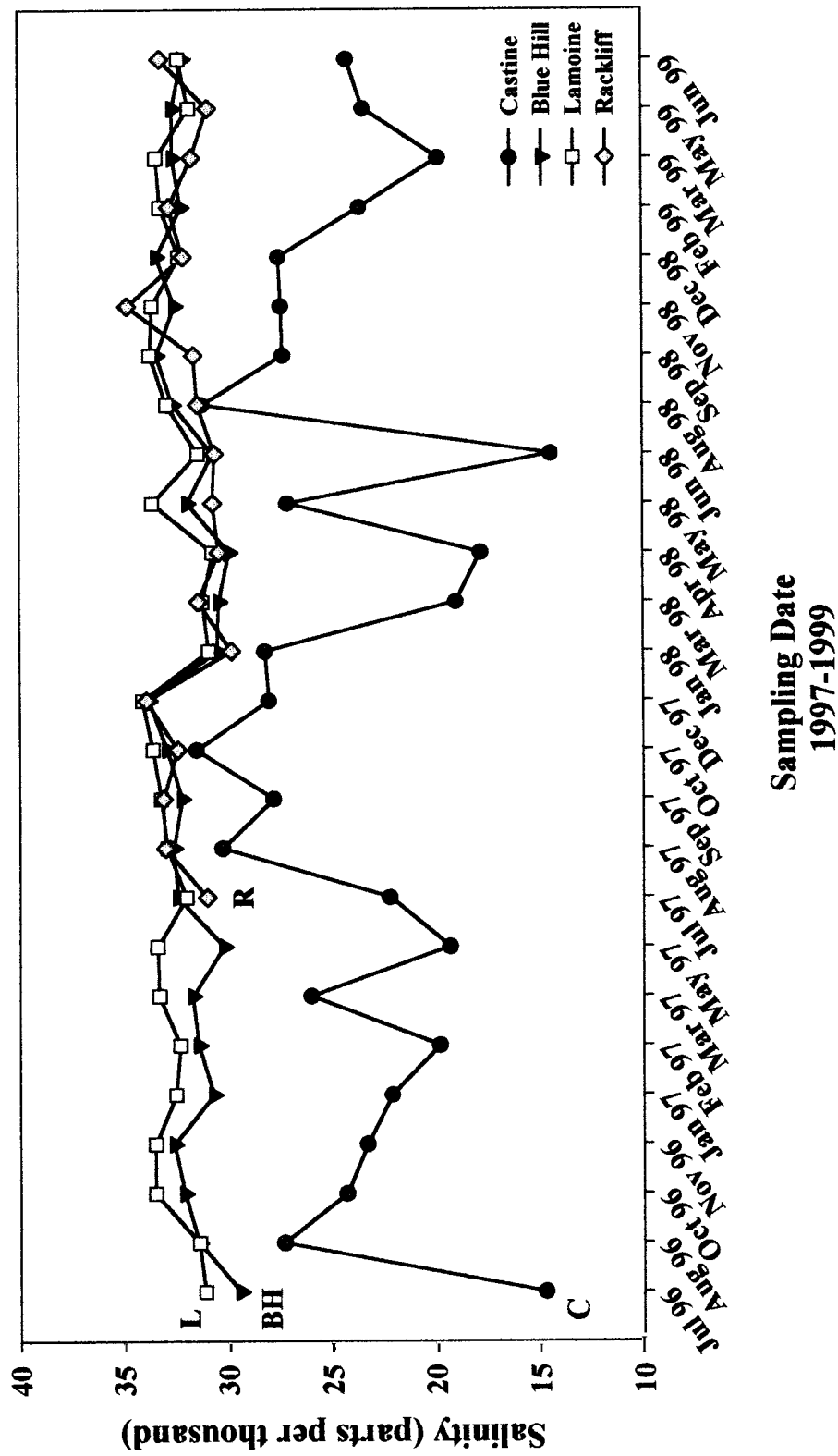


Figure 6.3. Monthly salinity measurements (ppt.) taken at low tide at the study sites, July 1996 - June 1999.

The greater variability in salinity at Castine reflects the site's more estuarine nature due to its proximity to the Penobscot River.

The average slope of the low intertidal experimental plots at each site ranged from 5" - **15.6°**. Castine had the shallowest slope (5°), Blue Hill and Lamoine were only slightly steeper (**5.4"**). The steepest slope occurred at the most western site, Rackliff Island (**15.6°**).

6.4.1. Biomass values

Overall mean biomass (wet weight) of *Ascophyllum* at the four experimental sites varied temporally from **7 +/- 4 kg/m²** in **1996** to **17 +/- 3 kg/m²** in **1999** (Fig. 6.4).

Biomass values at individual sites followed the same general trend with estimates ranging from 7 +/- 3 kg/m² in **1996** to over **25 +/- 11 kg/m²** in **1999**. A two-factor, mixed model analysis of variance detected significant 'Year' effects ($P = 0.040$; Table 6.1).

Post-hoc comparisons, however, failed to detect differences at an overall (family) confidence level of $\alpha = 0.05$ due to the high variance associated with the mean values.

Regression analysis was used to determine the linear relationship between fresh (wet)-weight and dry-weight of *Ascophyllum* during each year that biomass samples were collected (Fig. 6.5). The coefficient of determination (r^2) was **0.99** for all three regressions, indicating a high degree of log-linear association between the variables. The least-squares regression are as follows:

$$\mathbf{1996} \quad \log (\text{dry weight}) = \mathbf{-0.975 + 0.953^* \log (\text{wet weight})}$$

$$\mathbf{1997} \quad \log (\text{dry weight}) = \mathbf{-1.002 + 0.976^* \log (\text{wet weight})}$$

$$\mathbf{1999} \quad \log (\text{dry weight}) = \mathbf{-1.245 + 1.008^* \log (\text{wet weight})}.$$

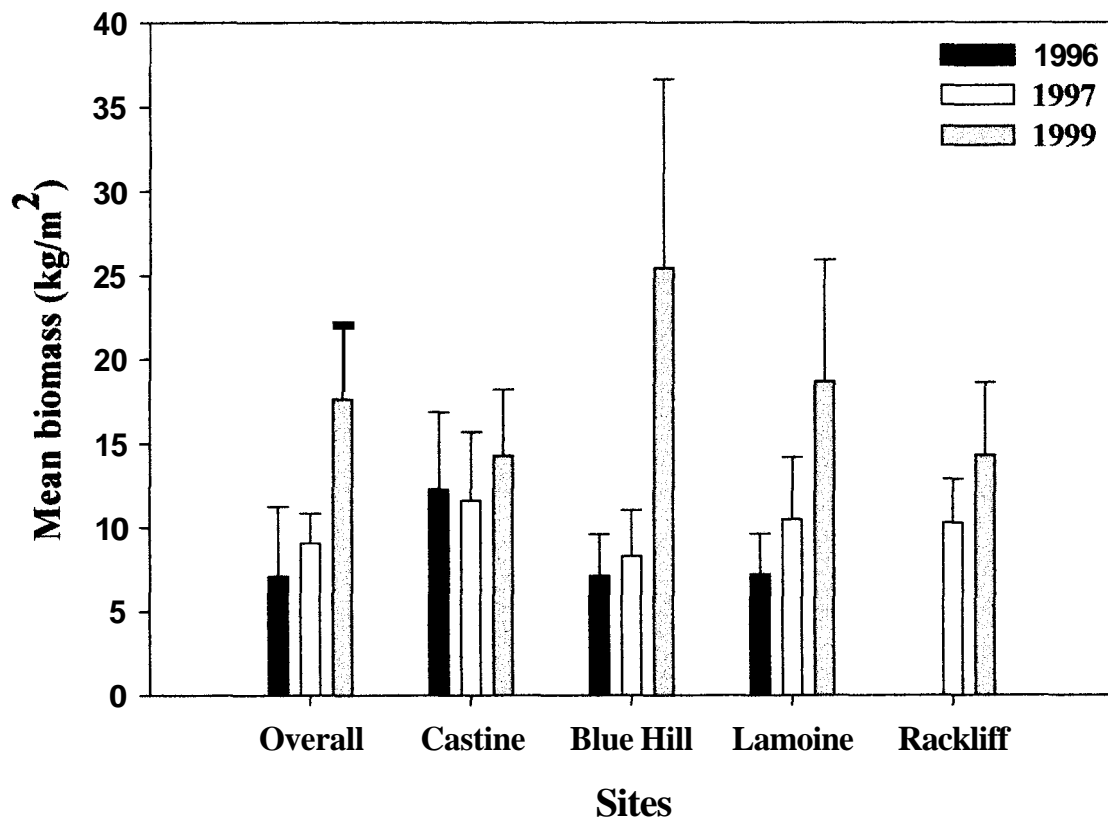


Figure 6.4. Mean biomass value (wet weight) per meter squared for *Ascophyllum nodosum* overall and at the four experimental sites (+ S.E.) for 1996, 1997 and 1999. Data were log-transformed to meet model assumptions. Back-transformed values are graphed. (n ranged from 9-19)

Table 6.1. Results of a two-factor, mixed model analysis of variance on biomass during 1996, 1997 and 1999 at the four experimental sites. Sites are considered a random factor. Data were log-transformed to meet the assumptions of normality and homogeneity of error variances. (n ranged from 9-19)

Source of Variation	df	Mean Square	F	P
Sites	3	0.882	0.452	0.716
Year	2	6.584	6.584	0.040
Site x Year	5	0.953	0.488	0.785
Error	207	1.953		

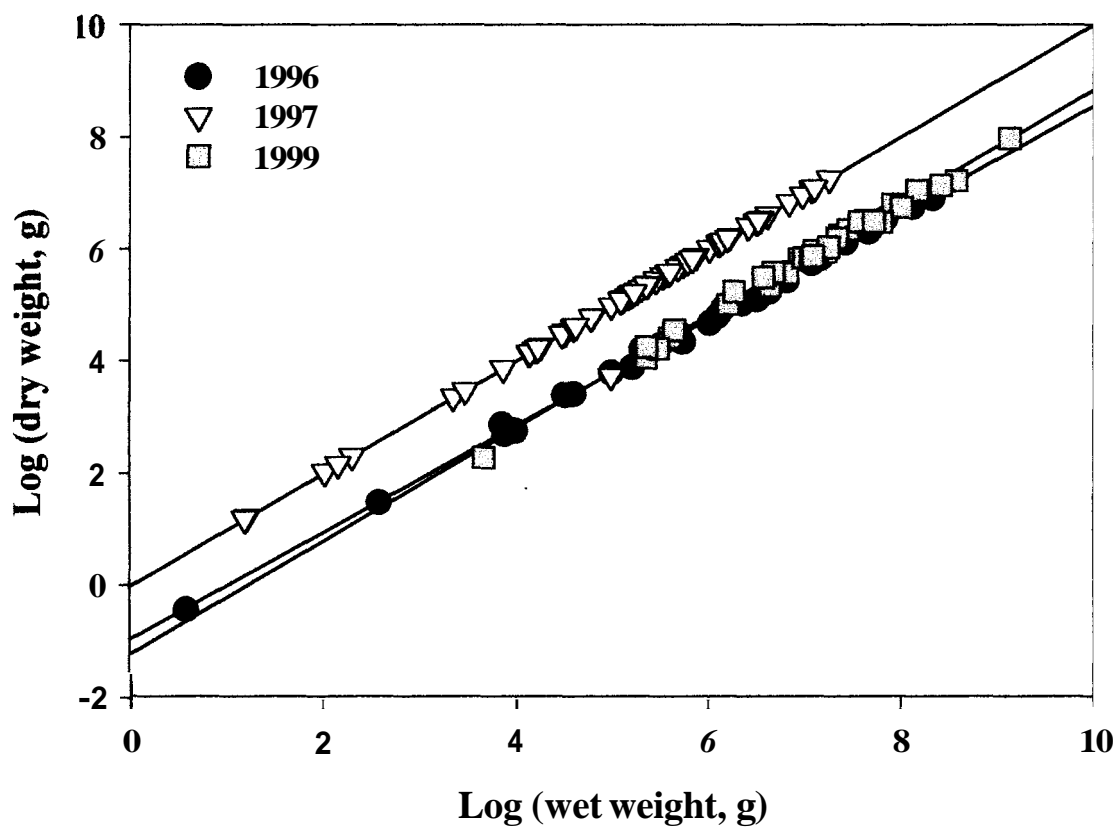


Figure 6.5. Log-linear relationship between wet-weight and dry-weight biomass samples (measured in grams) of *Ascophyllum nodosum* during 1996, 1997 and 1999. Lines represent least-squares regressions for 1996($\log(y) = -0.975 + 0.953 \log(x)$), 1997 ($\log(y) = -1.002 + 0.976 \log(x)$) and 1999($\log(y) = -1.245 + 1.008 \log(x)$). (n = 35 for 1996; n = 63 for 1997; and n = 37 for 1999)

To test for inter-annual differences in the relationship, an analysis of covariance (ANCOVA) model with years as the concomitant variable was examined for its appropriateness. The model condition of constancy of slopes, however, was not met, indicating that covariance analysis was not appropriate for these data (Neter et al., 1996). Lack of parallelism in the regression lines indicates an interaction effect, which suggests that the nature of the relationship changes each year. The magnitude of the relationship also appears to change through time (Fig. 6.5). A non-parametric rank F-test was conducted on the ratio of the weights (dry/wet) to test for annual differences in the mean percent dry matter. Significant differences between the years were detected ($P = 0.000$). Tukey's post-hoc tests indicate that the percentage of dry matter in 1997 was significantly higher than the percentage of dry matter in 1996 and 1999 ($P = 0.000$ and $P = 0.047$, respectively).

Spatial differences were detected in the wet/dry relationship in 1996 ($P = 0.001$) and 1997 ($P = 0.008$) using ANCOVA with sites as the concomitant variable (Fig. 6.6). The slopes of the regression lines were parallel in both covariance analyses. No significant difference in the wet/dry relationship was detected in 1999 ($P = 0.332$). Tukey's multiple comparisons indicate that the wet/dry relationship at Lamoine in 1996 was significantly higher than Castine ($P = 0.000$). In 1997, the wet/dry relationship at Blue Hill was significantly higher than at Castine ($P = 0.004$). Although statistically significant differences were detected between sites, graphical examination of the relationship failed to show the differentiation (Fig. 6.6). To further elucidate the magnitude of the site differences, the percentage of dry matter was calculated for each site and year (Table 6.2). In terms of a practical application of this information, if a

Figure 6.6. Log-linear relationship between wet-weight and dry-weight biomass samples (measured in grams) of *Ascophyllum nodosum* during 1996,1997 and 1999 at the experimental sites. Data were log-transformed to meet the assumptions of the model. (n = 11-13 in 1996; n = 13-19 in 1997; and n = 6-12 in 1999).

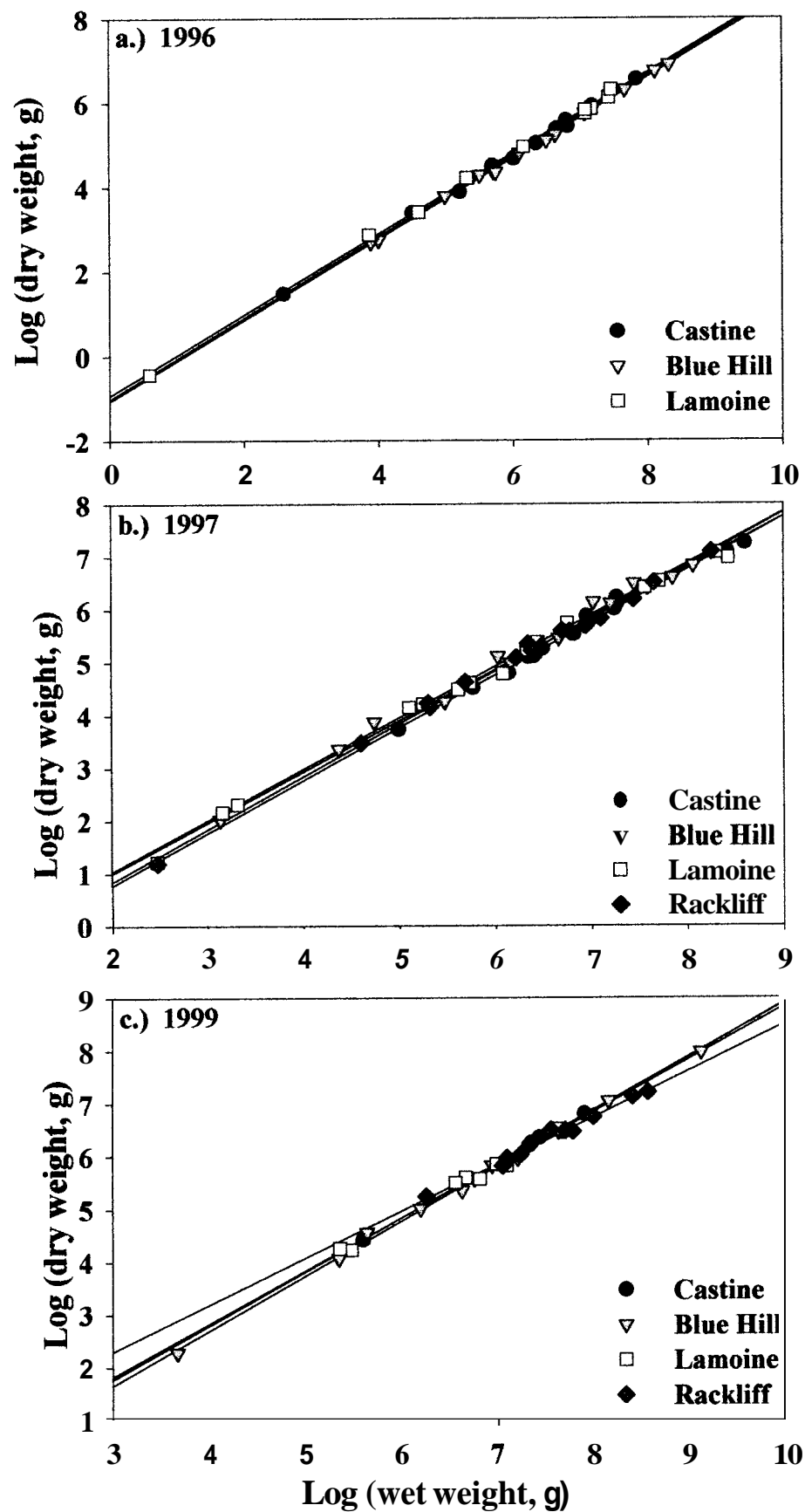


Table 6.2. The mean percentage of *Ascophyllum nodosum* dry matter [(dry weight/wet weight)*100] by year and by site.

Year	% dry matter	n
1996	28.6	35
Castine	26.8	13
Blue Hill	28.5	11
Lamoine	30.9	11
1997	31.8	63
Castine	29.2	14
Blue Hill	34.4	13
Lamoine	32.4	17
Rackliff	31.4	19
1999	30.5	37
Castine	30.7	10
Blue Hill	33	9
Lamoine	28	9
Rackliff	30.3	9

company needed **1000** kg of dried *Ascophyllum* in **1996**, harvesters at Castine would have needed to collect **3,731** kg of fresh seaweed whereas those at Lamoine would have only needed to harvest **3,236** kg.

6.4.2. Post-harvest biomass recovery

Two-years following the experimental harvest, mean biomass in the 36-cm and 18-cm cut plots was 88% and **67%** of the mean biomass of the control plots, respectively (Fig. **6.7**). Despite the large difference associated with the mean values, a statistical difference was not detected using a non-parametric rank F-test ($P = \mathbf{0.692}$). The high variance associated with the collection of the biomass data likely contributed to the lack of statistical difference.

6.4.3. Post-harvest morphological measurements

Undisturbed fronds grew **-12** cm in length during the first year following the harvest (Fig. **6.8**). A two-factor, mixed model ANOVA revealed that treatment effects were not significant ($P = \mathbf{0.703}$; Table **6.3**). The analysis did detect differences in 'Site' and 'Treatment x Site' growth rates. In situations where significant interactions are present, main factors cannot be fully evaluated (Winer et al., **1991**). Examination of the interaction, however, reveals that Castine had a much higher growth rate (**-16** cm/year) than the other sites (Fig. **6.9**). Tukey's multiple comparisons detected no treatment difference in the growth rates at Castine and Blue Hill. Significant treatment effects were detected at Lamoine where the growth rate in the control plots was greater than the

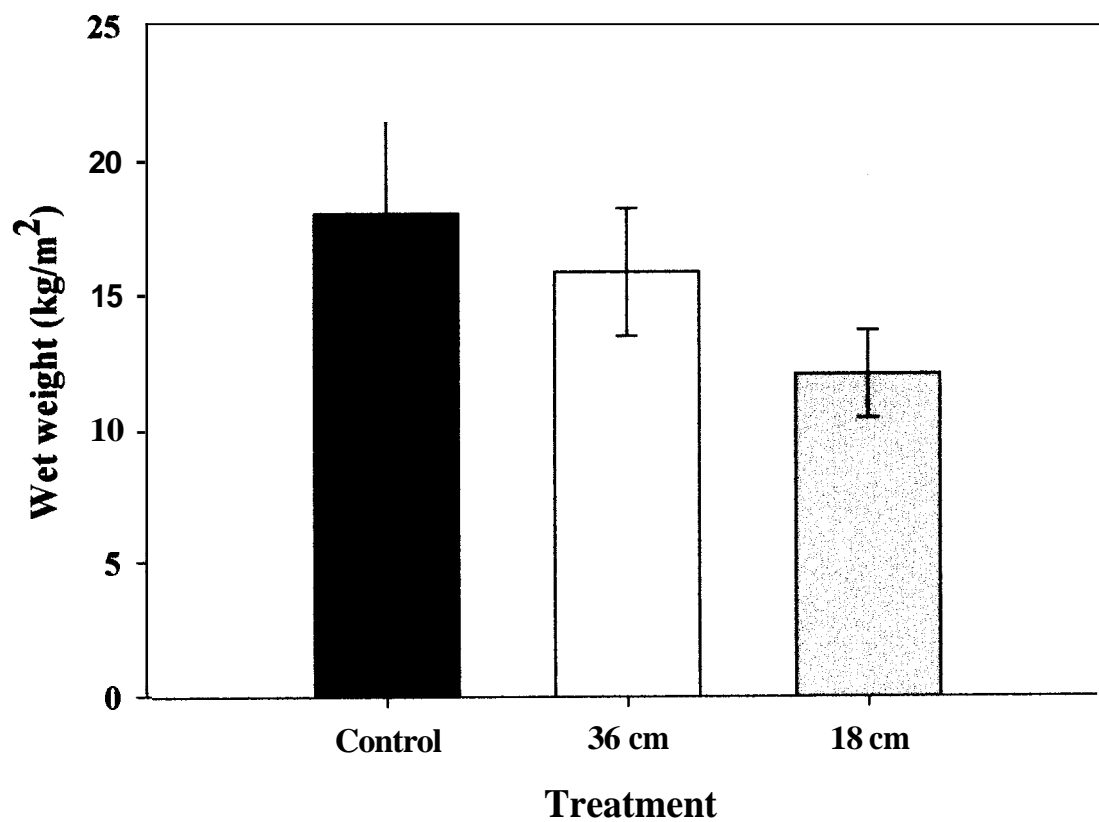


Figure 67. Two-year post-harvest biomass recovery ~~data~~ by treatment. Samples were taken in July of 1999. Values represent means \pm S.E. ($n = 56/\text{treatment}$).

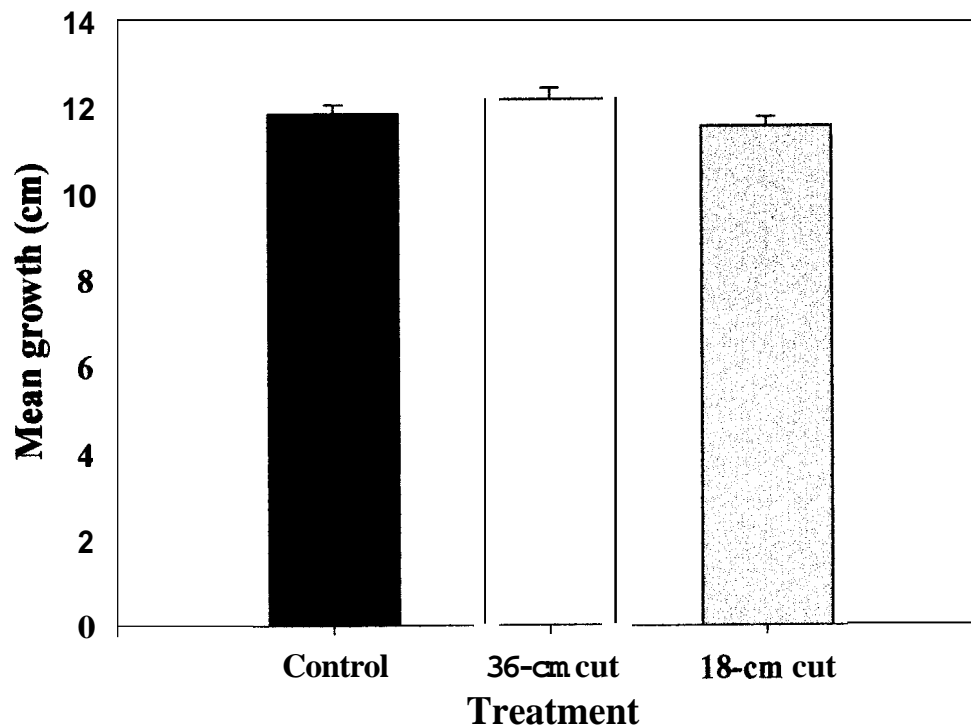


Figure 6.8. Average growth rate of *Ascophyllum nodosum* at different treatment levels during the first year post-harvest. Values represent back-transformed means + S.E. (n = 100/treatment).

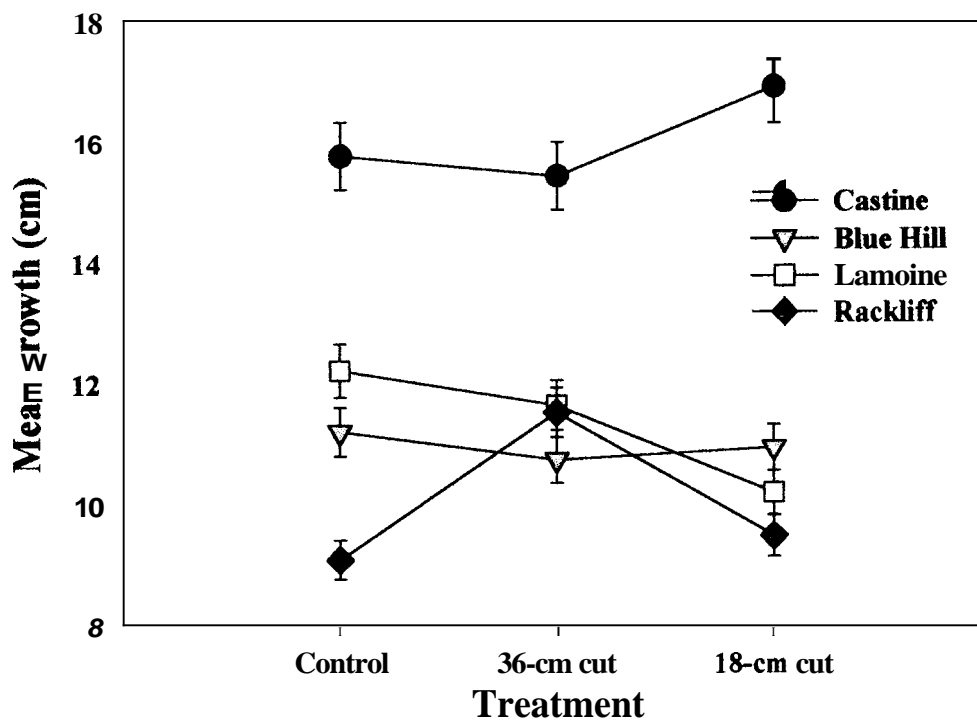


Figure 6.9. The effects of harvesting treatment level on the annual growth rate, one-year post-harvest at different sites in Maine. Values represent back-transformed means +/- S.E. (n = 25/treatment/site).

Table 6.3. Results of a two-factor mixed model analysis of variance on one-year post-harvest growth rates of the three harvesting treatments at the four experimental sites. Sites are considered a random factor. Data were log-transformed to meet the assumptions of normality and homogeneity of error variances. (n = 25/treatment/site)

Source of Variation	df	Mean Square	F	P
Treatment	2	0.076	0.374	0.703
Site	3	3.054	100.205	0.000
Treatment x Site	6	0.202	6.629	0.000
Error	287	0.030		

growth rate in the 18-cm cut plots ($P = 0.012$). Treatment effects were also detected at the Rackliff site. Growth was highest in the 36-cm cut plots compared to both of the other treatments.

Non-parametric rank F-tests used to analyze the two-year post-harvest morphological data detected several significant treatment effects (Table 6.4). Although 'Site' differences were present, since sites are considered a random factor and no significant interaction effects were detected, only overall treatment effects will be discussed. Overall shoot density in the three treatments was not significantly different although there appears to be a trend toward increasing numbers in the harvested plots (Fig. 6.10). Shoots were broken down into different size classes with the smallest ($< 25\text{cm}$ in length) being the most prevalent and following the same density pattern as above (Fig. 6.11). The number of medium and large shoots were significantly affected by the harvesting treatment ($P = 0.033$ and $P = 0.024$, respectively). More medium-sized shoots were present in the 18-cm cut plots compared to the control plots ($P = 0.008$). The density of large shoots was greater in the 36-cm cut treatment compared to the 18-cm cut treatment ($P = 0.012$).

The large plants in the control plots were greater in length than those found in the harvested plots ($P = 0.001$; Fig. 6.12) two years after the harvest event. All treatments were statistically different from one another. The mean number of apical dichotomies did not differ by treatment in the small and large-sized shoots (Table 6.4). Although a treatment effect was detected in the medium-sized shoots, the number of dichotomies in the two harvested treatments did not differ from the control values. There was, however,

Table 6.4. Results of a two-factor, mixed model analysis of variance on several morphological characteristics at various harvesting levels at the four experimental sites. Sites are considered a random factor. Data were analyzed using rank transformations to meet the assumptions of normality and homogeneity of error variances.

Morphological Characteristics	Treatment (P-value)	Site (P-value)	Trt x Site (P-value)
Density of shoots/ m²			
Overall (all shoots)	0.547	0.506	0.546
Small shoots (< 25cm)	0.626	0.568	0.448
Medium shoots (25-50cm)	0.033	0.258	0.898
Large shoots (> 50cm)	0.024	0.963	0.819
Length of longest shoot			
Small plants (<25cm)	0.176	0.045	0.819
Medium plants (25-50cm)	0.531	0.988	0.716
Large plants (>50cm)	0.001	0.001	0.376
Number of apical dichotomies			
Small shoots (<25cm)	0.189	0.086	0.205
Medium shoots (25-50cm)	0.036	0.000	0.297
Large shoots (>50cm)	0.401	0.098	0.723
Number of branches			
18cm from the holdfast (all shoots)	0.016	0.000	0.331
36cm from the holdfast (all shoots)	0.438	0.154	0.139

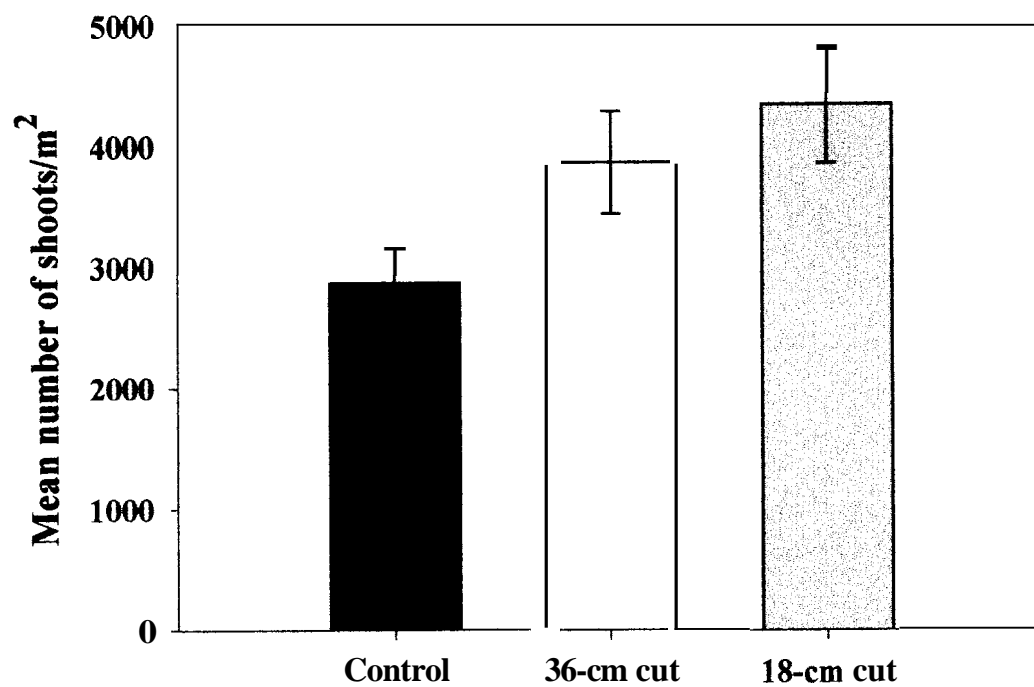


Figure 6.10. Overall density of shoots per meter squared in the three treatments. (n = 56/treatment)

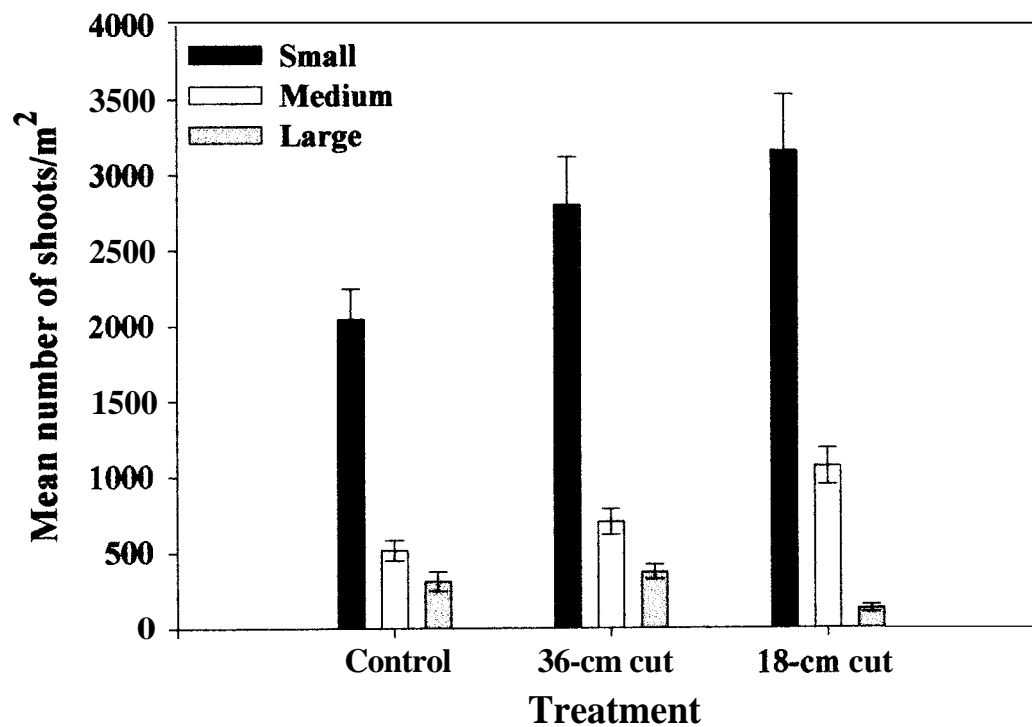


Figure 6.11. Effect of treatment on the mean number of small (< 25cm), medium (25-50cm) and large (> 50 cm) shoots per meter squared. (n = 56/treatment)

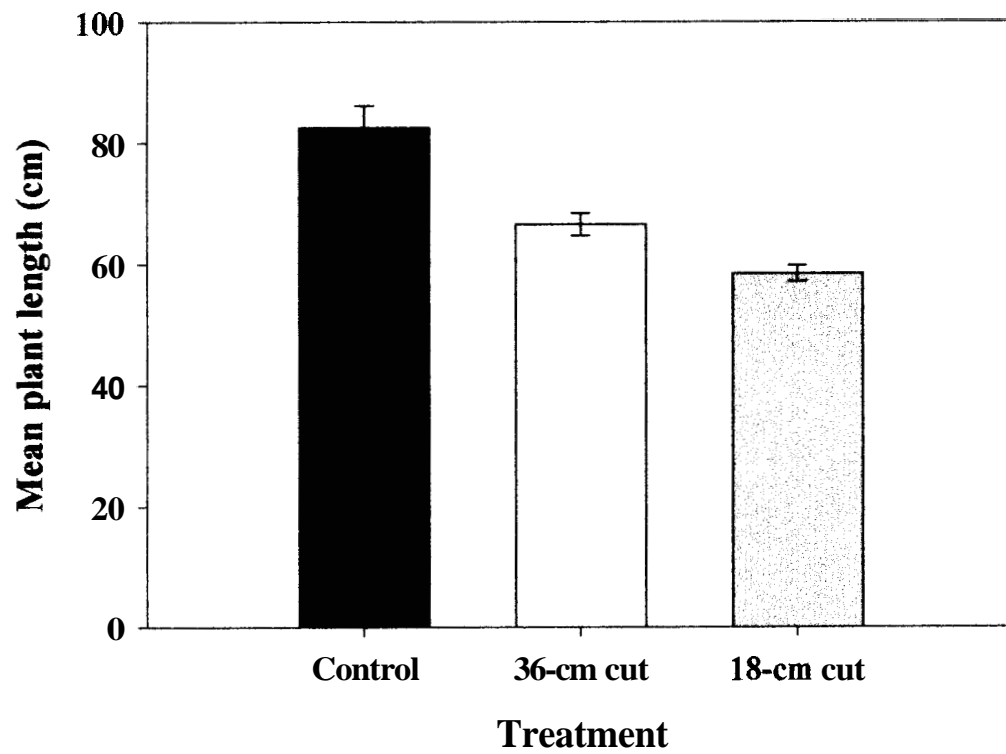


Figure 6.12. Mean length of the large plants in the different treatments. [n = 34 (control), 33 (36-cm) and 31 (18-cm)]

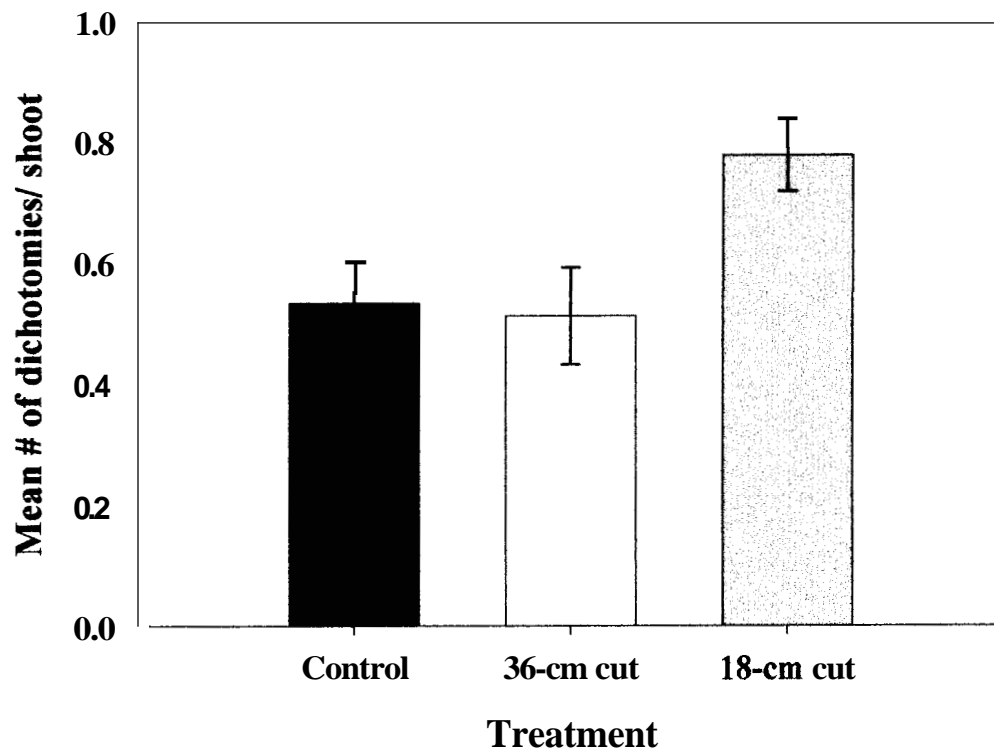


Figure 6.13. Mean number of dichotomies per shoot in medium sized plants (25-50cm in length) in the different treatments. (n = 36/ treatment)

a significant difference in the number of dichotomies when comparing the 18-cm cut treatment to the 36-cm cut treatment ($P = 0.044$; Fig. 6.13). No difference was detected when comparing the number of dichotomies in the control plots to either treatment. The mean number of branches 18-cm from the holdfast was significantly higher in the shoots that were intensely harvested compared to the number of branches at that height in both the control plots and the plots cut at 36-cm (Fig. 6.14). Treatment level did not affect the branching pattern at a height of 36 cm from the holdfast two years after harvesting.

6.5. Discussion

6.5.1. Biomass values

Fucoid macroalgae are the dominant flora of rocky intertidal temperate shores. Despite their conspicuousness in the littoral zone, the distribution of fucoid biomass along the shore is highly variable (Baardseth, 1970; Keser et al., 1981; Topinka et al., 1981; Cousens, 1986). Although fucoid growth and distribution is influenced by many chemical, physical and biological factors, exposure to wave action and the availability of suitable substrata are regarded as two of the most important factors governing the local distribution of fucoid algae (Baardseth, 1970). In this study, site differences in biomass values were not detected although the means differed substantially. The considerable within-site variability most likely masked any geographic trend. Cousens (1982) found that even within a single site, small changes in wave exposure could result in great variation in plant growth and morphology leading to within-site differences in biomass. In addition, patchy distribution of the holdfasts can lead to high within-site variability in biomass. The overall biomass values in this study varied inter-annually. In 1999, the

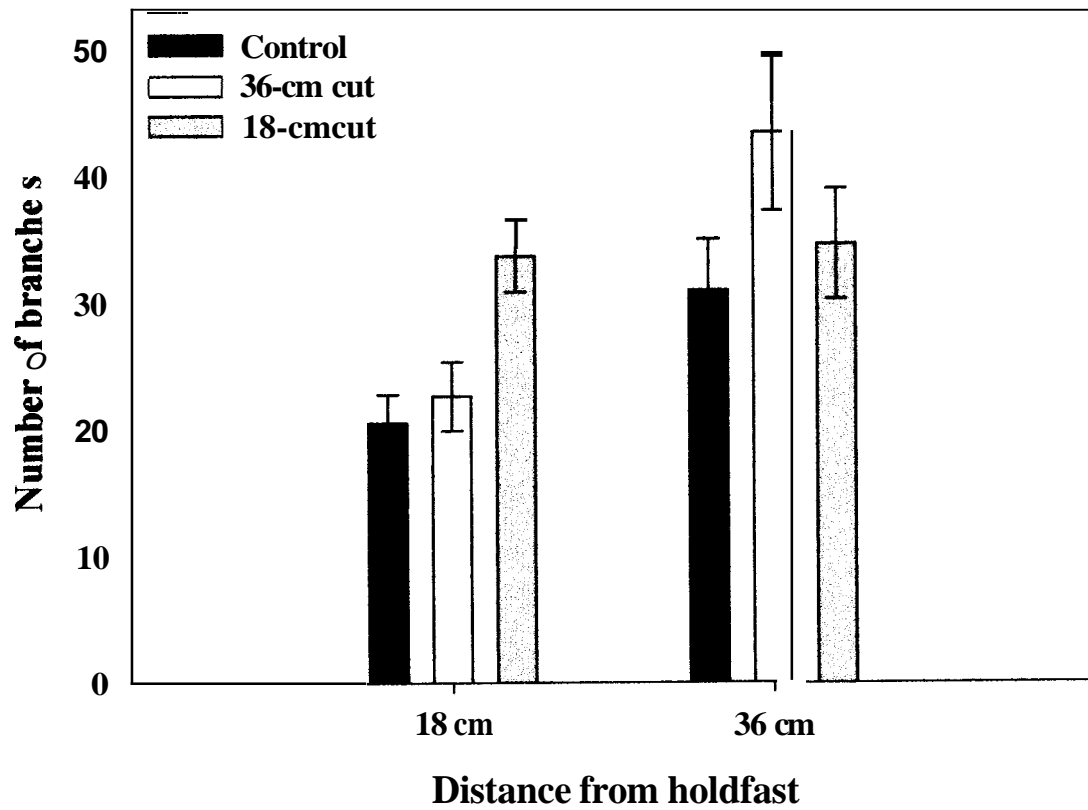


Figure 6.14. Mean number of branches at 18 cm and 36 cm from the holdfast at the three treatment levels, two-years post-harvest (\pm S.E.). (n = 36/treatment)

mean biomass increased at all of the experimental sites. This increase may be due, in part, to the mild winter of 1998/99. From November to March the mean surface water temperature at experimental sites was 4.8°C whereas during the winter of 1997/98 the mean temperature was 2.6°C and in 1996/97 it was 2.8°C. The warmer temperatures in 1998/99 may have resulted in less ice rafting in the intertidal, a factor **known** to contribute substantially to loss of biomass in winter (Baardseth, 1970; Vadas et al., 1976, 1978; Cousens, 1981; Mathieson et al., 1982). In addition, increased temperatures may have resulted in increased **growth** (Sheader and Moss, 1975; Vadas et al., 1978; Stromgren, 1981).

Spatial and temporal differences were detected in the relationship between *Ascophyllum* fresh (wet) weight and dry weight. The percent of dry matter is **known** to vary from one part of the *Ascophyllum* plant to another, with stumps having a higher biomass than actively growing shoots (Baardseth, 1970a). The percent dry matter also increases with increasing number of vesicles or plant age (Baardseth, 1970a). The observed differences in the wet/dry relationship may simply reflect spatial and temporal differences in plant population and morphological characteristics. Whatever the cause, the fact that this relationship is not constant is of commercial importance. Industry is generally interested in a dried product. Data on the spatial and temporal differences in the seaweed composition that will lead to a higher yield of dry matter per unit effort is valuable information.

Two-years after the experimental harvest, the biomass values in the three treatments were not statistically different from one another despite the fact that the mean biomass in the 18-cm cut plots was only 66% of the mean of the control plots. Keser et

al. (1981) also harvested *Ascophyllum* in Maine and found similar biomass recovery rates. Plants in their study were cut at the holdfast, at 15 cm, and at 25 cm. The average biomass recovery in the 15-cm cut plots three years after harvesting was 62% of the original biomass. Thus, although no statistical difference was detected in the mean biomass values between treatments, caution must be employed in using this information for management purposes. The **high** variability associated with the biomass sampling decreases the power of the statistical analysis making it harder to reject the null hypothesis. The intrinsic variability of the population is the only component of sampling and experimentation that affects the power of the experiment and is not a function of the hypothesis nor is it under the control of the experimenter (Underwood, 1997).

6.5.2 Post-harvest morphological differences

The growth rate of *Ascophyllum* one-year after the harvesting event was somewhat variable depending on cut intensity and site. Other post-harvest studies on *Ascophyllum* detected increased frond growth in plots that were harvested, presumably due to the release of suppressed shoots (Boaden and Dring, 1980; Lazo and Chapman, 1996). Only one site, Rackliff Island, had a significant increase in *Ascophyllum* growth rate after being harvested. Plants at other sites either experienced no change in growth (Castine and Blue Hill) or a decrease in the growth rate corresponding to the cut intensity. No clear overall treatment response was observed. Fronds with intact apical meristems, regardless of the treatment, grew approximately 12 cm in length during the first year following the harvest. The post-harvest growth estimates are approximately the

same as those reported by Sharp (1981) whose monthly growth rates for a semi-exposed population in Nova Scotia ranged between 0.7 and 1.1 cm.

A. nodosum populations are generally dominated by a small number of large fronds that monopolize the canopy layer causing intense shading beneath. The highest densities of fronds are found in the sub-canopy where they experience little irradiation, grow slowly and reproduce little, if at all (Cousens, 1985). It has been hypothesized that this "meristem bank" of basal or suppressed shoots, if released from competition by the canopy, will grow rapidly and become overstory shoots (Cousens, 1985; Vadas and Wright, 1986). The increased densities observed in the harvested plots is likely a result of increased irradiance levels in the sub-canopy, causing a significant increase in the growth of the young, understory fronds. The data on the number of branches at 18 cm and 36 cm in the three different treatments shows an increase in branching in the harvested plots. In addition, I observed an increase in the number of apical dichotomies in the cut plots. Both measurements confirm the hypotheses put forth by Cousens (1985) and Vadas and Wright (1986).

6.6. Conclusion

Determining the "recovery" of harvested populations is of particular interest to resource managers. In many populations, "recovery" is often assessed using a population biomass measure (Krebs, 1994). Harvested macrophyte populations are typically considered "recovered" when the standing crop regenerates to pre-harvest biomass values. As demonstrated in this study, biomass sampling of *Ascophyllum* is highly variable and thus not a very robust measure of "recovery." Because the holdfasts of

Ascophyllum plants are patchily distributed, a high degree of variability is associated with not only the distribution of the plants but also the associated weight measurements. This variability makes it difficult to accurately determine when "recovery" **has** occurred. Other measures, such **as** plant population and morphological characteristics, should be used in conjunction with biomass estimates to provide a more accurate assessment of recovery. Although no treatment difference was detected in biomass values two-years after the harvest, I did detect significant differences in the plant length based on cutting intensity. The control plants were significantly longer than the plants in either of the cut plots. "Recovery," if defined **as** returning to baseline conditions, did not occur in the *Ascophyllum nodosum* populations in this study. Information on the demography of the species harvested is needed, not **only** to determine recovery rates, but also to assess the health of the species being exploited. In recent years the focus for management has shifted to consideration of the sustainability of the resource and the potential population and ecological effects that harvesting may have.

Chapter 7

Synthesis

Dense canopies of *Ascophyllum nodosum* are characteristic of sheltered rocky shores throughout the Gulf of Maine. They are one of the most conspicuous features of these shores, and yet they have been relatively understudied (Bertness et al., 1999). This work contributes to our understanding of the importance of habitat-modifying organisms, such as *Ascophyllum*, in the structuring and organization of natural communities. Anthropogenic disturbances, such as harvesting, significantly alter not only the target species but also the structure of associated communities.

The ecological importance of seaweeds as habitats and habitat modifiers often parallels their value as potential resources (Santelices and Griffiths, 1994). In general, the species most sought after for exploitation tends to be those that grow to an exceptionally large size or those that form dense monocultures. Frequently, the most economically valuable seaweeds are those same species that are ecologically most important. The existence of concentrated stands of *Ascophyllum* has encouraged commercial harvesting in many countries. The effect of harvesting on this species has much broader implications due to its structural role.

A single harvesting disturbance significantly affected the abundances of numerous common intertidal species. Both algal and invertebrate assemblages were altered by the canopy removal (Chapters 2, 3 and 4). In addition, overall species richness declined following the harvest (Chapter 5). It is clear that habitat structure, provided by the dominant plant, has an important influence on the functional value of the habitat for

resident organisms. Removal of the algal canopy caused a reduction in structural complexity, which altered the physical environment, thereby influencing the abundance and distribution of associated species.

Despite the fact that numerous species within the community experienced short-term effects (**1-2** years), few effects persisted through time. In addition, many important members of the intertidal community were unaffected by the perturbation. This suggests that a single harvest event can cause short-term changes to the community structure but that the community is resilient to this type of disturbance at this spatial scale (25 m²) and time of year. However, this level of disturbance at larger spatial scales or with a higher frequency could have greater and longer lasting effects.

The ecological impacts of harvesting appear to have site-specific components, which makes it difficult to generalize the findings to an ecosystem level (Chapter **5**). **Only** four species (*Ascophyllum*, *Fucus*, *Carcinus* and *Dynamena*) showed significant harvest effects regardless of site differences (Chapters 3 and **4**). It is likely that the spatial heterogeneity associated with the composition of the communities and with species abundances made it difficult to detect overall individual and community-level treatment effects.

Seaweed resource managers measure the recovery of harvested macrophyte populations by assessing the standing crop and comparing it to a pre-harvest, baseline value. There are problems associated with using this method on *Ascophyllum* populations because the plant's holdfasts are patchily distributed, leading to a high degree of variability associated with the biomass values on a per-square-meter basis (Chapter **6**). This variability makes it difficult to accurately determine when "recovery" has occurred.

A statistical test on two-year post-harvest biomass values indicated no significant difference in the means. From this information we would normally conclude that the plants had "recovered." A closer examination of the data reveals that plant biomass in the 18-cm cut plots was only 66% of the biomass in the control plots. So, have the plants "recovered or not? Data on plant morphology showed that the control plants were significantly longer than the plants in either of the cut plots, indicating a lack of "recovery" to pre-existing morphological conditions. Resource managers will have to wrestle with the question of how to define "recovery" and hopefully their definition and actions will follow a precautionary principle (Underwood, 1995). **An** integrative management approach including information on biomass regeneration, morphological recovery and overall habitat/ community recovery should be used for this species.

Temporal and spatial differences were detected in the wet weight/ *dry* weight biomass relationship at the four experimental sites (Chapter 6). Information regarding the variation associated with seaweed constituents, in particular dry matter, can offer important insight regarding the best timing and placement of harvesting activities. The observed differences in the relationship may simply reflect spatial and temporal differences in plant population and morphological characteristics. Whatever the cause, the fact that this relationship is not constant is of commercial and biological interest.

The results of this research have raised several additional questions regarding the impacts of anthropogenic disturbances on habitat recovery. Although my Qssertation examined harvesting effects in 25 m² plots, which are larger than plots typically used by marine researchers, the experimental areas were much smaller in scale than areas commercially exploited. The effects of large-scale persistent harvesting on the intertidal

community are likely to be greater than those quantified in this study. Thus, landscape-scale studies are needed to fully understand the impact of this **type** of disturbance.

Additional research is also needed to determine the ecological effects of harvesting using traditional removal methods (e.g., hand rakes). To allow for repeatable treatment levels, *Ascophyllum* plants in the harvested plots were cut at a set height (either 18 cm or 36 cm from the holdfast). Although this allowed me to replicate treatments, it was not a realistic harvesting scenario since most harvesters use hand rakes and cut the plants at an angle leaving variable lengths of shoots. The ecological effects of *Ascophyllum* harvesting based on different exploitation rates should be examined.

The cumulative ecological effect of harvesting *Ascophyllum* also needs to be studied. Cumulative effects occur over a period of time when the same perturbation occurs with high frequency such that the separate perturbations are not dampened by the ecosystem. Although my dissertation research suggests that, for the most part, *Ascophyllum* communities recover within two years, repeated harvests in shorter intervals may not allow for habitat recovery. Long-term ecological studies examining differing frequencies of harvest beg additional investigation.

The link between habitat structure and community structure also deserves more attention. Harvesting frequency is generally related to the rate of biomass regeneration. As long as biomass recovery does not occur at a faster rate than the recovery of the community, the frequency of harvesting will not likely generate cumulative ecological effects. Knowledge of how habitat structure affects the functioning of the ecosystem is important, not only to manage and conserve the nearshore habitat, but also to provide ideas and techniques for remediation.

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Biography of the Author

Tides have been a prominent feature in Jill's life. She was born in June 1967 in coastal New Jersey. She grew up in the seaside community of Cape May. The beaches of southern New Jersey were her playgrounds; they were some of her earliest teachers. When she graduated from Lower Cape May Regional High School in 1985 having won both scholastic and athletic (tennis) honors, a future career in medicine directed her beginning college years. But the outdoor experiences and fascination with nature beckoned and Jill graduated from the Richard Stockton College of New Jersey in 1989 with a Bachelor of Science degree in biology with a concentration in environmental science. She used her extensive coastal experience while working first for the State of New Jersey as a wetland specialist and then for Cape May County in designing their first well-head protection program. Her marriage to a marine ecologist (Stephen Fegley) in 1990 led to her move to coastal Maine in 1991. For several years she took a respite from professional efforts to raise her two children, Bryan and Erin, through their formative years. Then the tides called again. Jill entered the University of Maine, Ecology and Environmental Sciences program in the fall of 1995 and steeped herself in the breadth and depth of marine ecology. In addition to successfully completing her Sea Grant funded dissertation research, during her graduate school years she taught summer courses in marine invertebrates or field techniques at the College of the Atlantic, she served as a fellow to the Maine State Legislature's Marine Resources Committee, and she has been a board member of the Maine Seaweed Council. With all these experiences and accomplishments, it is clear that the tides will continue to be a part of Jill's future. Jill is

**a candidate for the Doctor of Philosophy degree in Ecology and Environmental Science
from The University of Maine in May, 2001.**