

AN ABSTRACT OF THE THESIS OF

Carla M. D'Antonio for the degree of Master of Science
in Zoology presented on September 3, 1982
Title: Population and Community Ecology of the Red Alga
Rhodomela larix (Turner) C. Agardh, on the Central Oregon Coast
Redacted for Privacy
Abstract approved: Dr. Jane Lubchenco

Aspects of the life history and ecology of the intertidal turf-forming alga *Rhodomela larix* (Turner) C. Agardh were examined over a two year period at several sites on the Oregon coast. *Rhodomela* occurred over a broad tidal range and exhibited different growth and morphology characteristics with respect to tidal height. Growth was most rapid in spring and summer for mid and low zone sites. A large amount of variation in growth occurred both between and within sites. Within site variation was partially explained by diversity in the age of erect portions of thalli within a given plant. Basal portions of post-reproductive axes may be retained by a plant without directly contributing further to reproductive output. Male gametophytes (haploid) begin developing early in spring, and appear to be restricted to mid and high intertidal areas. Tetrasporophytes (diploid) and fertilized female gametophytes (cystocarps) follow later in the spring and continue to be produced into the fall. Despite the extensive development of reproductive structures, little recruitment was observed. *Rhomomela* regained dominance following removal by vegetative

proliferation from surrounding plants and through regeneration from microscopic basal cells.

Many epiphyte species were found in association with Rhodomela larix. Peak abundance of larger forms occurred in the late summer. Several of these species were shown to have a negative affect on the growth and survival of Rhodomela axes. Epiphytes were utilized by herbivores living within the beds of R. larix as a food source. The gastropod Littorina scutulata and several species of gammarid amphipods consume diatoms from the surface of Rhodomela. Amphipods were shown to significantly decrease the growth of epiphytic, chain-forming diatoms on R. larix in laboratory tanks.

Rhodomela larix reaches maximum abundance on low zone benches subjected to sand scour and/or burial. Laboratory experiments confirmed that Rhodomela can survive at least three months of burial in fine-grained, anoxic sediment. Epiphytes and several species of saxicolous algae were eliminated by sand coverage both in the laboratory and in situ. In addition, large herbivores were absent from sand-swept benches where Rhodomela was common. Thus it is hypothesized that sand may benefit Rhodomela by (1) eliminating potential competitors and epiphytes and (2) eliminating large herbivores which might otherwise consume the plant. The life history and morphology of the plant contribute to its success in sand-influenced habitats.

Population and Community Ecology of the Red Alga
Rhodomela larix (Turner) C. Agardh, on the Central Oregon Coast

by

Carla M. D'Antonio

A THESIS

submitted

Oregon State University

in partial fulfillment of
the requirements for the
degree of

Master of Science

Completed 3 September 1982

Commencement June, 1983

APPROVED:

Redacted for Privacy

Professor of Zoology in charge of major

Redacted for Privacy

Chairman, Department of Zoology

Redacted for Privacy

Dean of Graduate School

Date thesis is presented September 3, 1982

Typed by Dianne Rowe for Carla M. D'Antonio

ACKNOWLEDGEMENTS

I would like to acknowledge the support and enthusiasm of my major professor Dr. Jane Lubchenco. Her continued encouragement and thoughtful criticism helped me through many of the difficulties I encountered. Other members of my committee provided valuable input including Ken Chambers, Pete Dawson, Peter McEvoy and Bruce Menge. Many friends gave me feedback on earlier drafts including Teresa Turner, Harry Phinney, Annette Olson and Chris Marsh.

This work would not have been possible without the valuable assistance of Marlys Cappeart and Tom Dudley. They provided me with hours of cheerful field assistance under frequently cold and stormy conditions. Tom Dudley also deserves warm thanks for his patience and feedback on all aspects of this project. Marlys Cappeart and John Lucas assisted in making figures, Dr. Lavern Webber provided laboratory space at the Oregon State University Marine Science Center, and Dianne Rowe showed patience and an unhesitating willingness to type this thesis. To all of them I am most grateful.

TABLE OF CONTENTS

Page

I.	GENERAL INTRODUCTION	
II.	ECOLOGICAL ASPECTS OF THE LIFE HISTORY OF THE MARINE ALGA, <u>RHODOMELA LARIX</u> (TURNER) C. AGARDH.	
	Abstract.....	4
	Introduction.....	5
	General Distribution and Description of the Plant.....	8
	Methods.....	11
	Results.....	15
	Discussion.....	26
	Summary and Conclusions.....	33
	Future Studies.....	34
	References.....	35
III.	EPIPHYTES ON THE ROCKY INTERTIDAL RED ALGA <u>RHODOMELA LARIX</u> (CERAMIALES): NEGATIVE EFFECTS ON THE HOST AND FOOD FOR HERBIVORES.	
	Abstract.....	60
	Introduction.....	61
	Methods.....	65
	Results.....	70
	Discussion.....	77
	Summary and Conclusions.....	83
	References.....	84
IV.	THE INFLUENCE OF SAND ON A ROCKY INTERTIDAL ALGAL COMMUNITY	
	Introduction.....	103
	Description and General Distribution of Plant.....	105
	Methods.....	107
	Results.....	112
	Discussion.....	120
	Summary and Conclusions.....	128
	References.....	130
V.	BIBLIOGRAPHY.....	144
VI.	APPENDIX.....	153

LIST OF FIGURES

<u>Figure</u>	<u>Page</u>
 Chapter II.	
1. External morphology of <u>Rhodobryopsis</u> <u>larix</u>	39
2. Life cycle of a typical Florideophyte species (Class Rhodophyta).....	41
3. Location of study sites on the central Oregon coast.....	42
4. Seasonal changes in size of randomly collected axes.....	43
5. Sea surface temperatures for the Boiler Bay area, Oregon....	44
6. Seasonal occurrence of damaged axes in samples taken from mid zone populations of <u>R. larix</u> in Boiler Bay, Oregon.....	45
7. Survivorship of damaged and undamaged axes in the mid zone..	46
8. Growth of individual plants in the low zone.....	47
9. Horizontal expansion of <u>Rhodobryopsis</u> <u>larix</u> patches in the low zone between June 1981 and April 1982.....	49
10. Seasonal changes in the occurrence of reproductive phases of <u>Rhodobryopsis</u> <u>larix</u>	51
 Chapter III	
11. Arrangement of seawater tanks for amphipod/epiphyte experiment.....	87
12. Changes in the percent cover of epiphytes on <u>Rhodobryopsis</u> <u>larix</u> at Boiler Bay.....	88
13. Survival of individually marked axes with and without epiphytes in the low zone at Boiler Bay.....	90
14. Percent of total tissue length reproductive for axes with and without epiphytes.....	92
15. Distribution of diatom cover rankings for axes exposed and not exposed to amphipods.....	93

Chapter IV.

15. Description of intertidal areas surveyed for Rhodomela larix.....138
16. Sessile organisms commonly found in association with Rhodomela larix on emergent substrates.....139
17. Herbivore density transects in sites containing Rhodomela larix.....140
18. Percent cover of Rhodomela larix in quadrats within the main R. larix bed at Strawberry Hill, Oregon.....141
19. Species composition (percent cover) and sand cover along horizontal transect northwest of main Rhodomela larix bed at Strawberry Hill, Oregon.....142
20. Algal tissue changes after periods of sand coverage in the laboratory.....143

LIST OF TABLES

Chapter II.

1. Variability in maturation of tagged axes within individual plants in the low zone.....54
2. Maximum seasonal growth rates for individually tagged low and mid zone axes.....55
3. Axis breakage rates in each season.....56
4. Morphological characteristics of randomly collected axes during period of maximum growth.....57
5. Growth pattern of low zone transplants during spring and summer 1981.....58
6. Mean weight and height of (a) axes collected in October 1980 and (b) tetrasporophytes collected in June 1981.....59

Chapter III

7. Epiphyte species associated with the red alga Rhodomela larix.....94
8. Biomass of selected species of erect epiphytes and host (Rhodomela larix).....95
9. Tissue loss frequencies for individually marked axes with and without epiphytes.....96
10. Growth of individually marked axes with and without Isthmia nervosa epiphytes.....97
11. Wilcoxon paired sample tests for rate of tissue loss per day for axes with and without Ceramium sp. and Ulva sp. epiphytes.....98
12. Size and biomass of Rhodomela larix axes with and without Ulva sp. epiphytes.....99
13. Analysis of diet of selected small invertebrates from beds of Rhodomela larix.....100
14. The effect of different levels of amphipod grazing on the cover of diatoms on Rhodomela larix.....101

Chapter IV.

15. Description of intertidal areas surveyed for Rhodomela larix.....138
16. Sessile organisms commonly found in association with Rhodomela larix on emergent substrates.....139
17. Herbivore density transects in sites containing Rhodomela larix.....140
18. Percent cover of Rhodomela larix in quadrats within the main R. larix bed at Strawberry Hill, Oregon.....141
19. Species composition (percent cover) and sand cover along horizontal transect northwest of main Rhodomela larix bed at Strawberry Hill, Oregon.....142
20. Algal tissue changes after periods of sand coverage in the laboratory.....143

Appendix

1. Herbivore species associated with mid and low zone populations of Rhodomela larix.....102

POPULATION AND COMMUNITY ECOLOGY OF THE
RED ALGA, RHODOMELA LARIX ON THE OREGON COAST

CHAPTER I.

INTRODUCTION

In marine intertidal habitats, investigators have examined and manipulated communities to understand the patterns of spatial dominance (see Paine 1977 for a review). A species may be numerically dominant, functionally dominant (i.e., although not the most common species it controls the growth and recruitment of other species) or both. This dominance may be achieved through a number of mechanisms. In habitats with regular disturbance (including herbivory, carnivory and/or physical disturbances), a species may become dominant because of its relative resistance to the disturbance agent. In benign environments, a species may achieve dominance because of its growth characteristics or competitive ability. In order to clarify factors favoring the development of communities dominated by a single species, it is necessary to understand the life history characteristics of that species and how it responds or is affected by the prevailing disturbance regime.

On the central Oregon coast horizontal sandswept benches are frequently dominated by the red alga Rhodomela larix. Until recently very little has been known about the biology of this plant. In this thesis I present a portion of a study I have conducted on the natural history and ecology of this species. The thesis is divided into three

chapters. In the first chapter I investigate the life history of the alga; specifically addressing the growth and persistence of Rhodomela larix within large monocultures and as isolated individuals. Rhodomela thalli are perennial and erect portions of a single axis may live for several years. Although thalli become reproductive each year, sexual recruitment is rare. However Rhodomela larix. has the ability to regrow from a small number of basal cells and thus can recover readily from certain types of disturbance.

In many marine habitats epiphytes have been found to negatively affect the growth and survivorship of their host (Wing & Clendenning 1971, Lobban 1978, Dixon et. al. 1981, Harkin 1981). In the second Chapter I examine the importance of epiphytes on Rhodomela larix. Because Rhodomela is host for a large variety of epiphytes, the potential effects on host survivorship and reproduction are great. I demonstrate a negative correlation between epiphyte presence and both growth and survivorship of R. larix axes. Both sand coverage and herbivore grazing may help to decrease epiphyte cover on Rhodomela.

In the final chapter I delineate several mechanisms whereby Rhodomela develops and maintains dominance on sandswept reefs. These mechanisms are based upon data indicating (1) that Rhodomela can survive both lengthy burial and extensive scour by sand, (2) that large herbivores are absent from these sand-influenced areas and (3) that other species either lack the ability to tolerate sand scour or may not be able to achieve dominance because of life history limitations such as the inability to spread vegetatively. Thus sand-influenced rocky habitats may serve as refuges for R.larix from large grazers and

competitors. Once established Rhodomela monocultures may be maintained for long periods of time because of their resistance to the prevailing disturbance (sand burial or scour) regime and the ability of R. larix to recover and spread through vegetative growth.

CHAPTER II

Ecological Aspects of the Life History of the
Marine Alga, Rhodomela larix (Turner) C. Agardh.

ABSTRACT

Aspects of the growth and life history of the red alga, Rhodomela larix (Turner) C. Agardh were studied over 18 months in a mid and a low intertidal habitat on the central Oregon coast. Growth was measured by following: 1) individually marked fronds, 2) clumps of thalli thought to be individual plants and 3) the spreading of large patches of R. larix. Plants grew most rapidly in the spring and summer in the mid and low sites, however, a large amount of variation occurred both between and within sites. Phenology of reproductive stages was determined by monthly sampling of the population at both sites. Male and female gametophytes (haploid) occurred primarily in the mid zone, while tetrasporophytes (diploid) were common in both the mid and low zone. Reproductive thalli were present throughout the spring, summer and fall. Males appeared in the early spring and were senescent by late June, while cystocarpic and tetrasporic plants were present from April through January. Recruitment was poor throughout the observation period. Growth studies suggested that persistence of individual plants in the intertidal is accomplished mainly by vegetative proliferation and perennation.

INTRODUCTION


The life history characteristics of a given population may be viewed as "a set of adaptive responses accumulated over evolutionary time" (Wilbur et al. 1974). These characteristics include the number and size of young, the age distribution of reproductive effort and the interaction between reproductive effort and adult mortality (Stearns 1976). Knowledge of the life history of a group of organisms is critical to the understanding of the role of that species in a community, and aids in predicting the response of a community to disturbance.

Many marine plants survive and reproduce in several different microhabitats. A study of the growth and life history characteristics of a species in more than one habitat can provide information on the ability to respond to the heterogeneity of environmental influences. In turn, such variable responses may help to interpret the potential role of that species in the different microenvironments.

The life histories of many terrestrial plants and most marine algae are complex. Our understanding of some of the basic life history traits has been complicated by the presence of alternating free living haploid (gametangial) and diploid (sporangial) phases. Interpretation of these patterns within an adaptive framework therefore requires clarification of the timing and distribution of the various phases, their growth, reproduction and mortality schedules, and environmental influences upon the expression of the life history traits.

In the Rhodophyta, a wide variety of life history patterns have been described and yet for many species we lack adequate data to establish a complete life cycle (Dixon 1973). A large number of red algae, particularly those in the class Florideophyceae, have three distinct life phases. The gametophyte and a tetrasporophyte phase alternate with a third stage called the carposporophyte. The diploid cells making up the carposporophyte are formed following syngamy, and develop parasitically on the female gametophyte as a structure called the cystocarp. Upon release the carpospore usually develops into the free living tetrasporophyte. The evolutionary significance of this third phase remains obscure, although Searles (1979) suggested that it may be related to the lack of motile spermatangia in the Rhodophyta.

The turf-forming red alga, Rhodomela larix (Turner) C. Agardh is a major component of moderately exposed rock benches in intertidal areas on the Pacific coast of North America. Many investigators have examined the phenolic chemistry of the plant (Katsui et al. 1967, Weinstein et al. 1975, and Phillips and Towers 1981, 1982a, b) and its use as a source of bromine and antibiotics has been suggested (Phillips and Towers 1982a, b). Although it occurs commonly in a variety of habitats, little information has been published on the growth and life history of the species (for brief general descriptions see Smith 1944, Abbott and Hollenberg 1976).

 This paper describes growth characteristics, reproduction and recruitment of R. larix. I specifically address the following questions: (1) Is the growth of R. larix seasonal and how does the growth pattern differ in two different zones where Rhodomela is

present? (2) Is the distribution of reproductive phases constant between zones? (3) During what portions of the year do reproduction and recruitment occur? and (4) What are the relative roles of vegetative proliferation, perennation and sexual reproduction in the maintenance of R. larix individuals in intertidal communities?

GENERAL DISTRIBUTION AND DESCRIPTION OF THE PLANT

Rhodomela larix occurs abundantly in mid and low intertidal habitats from Japan to Pt. Conception, Calif. (Smith 1944, Abbott and Hollenberg 1976 and Saito 1980). Although it occurs on emergent substrata and in rocky intertidal pools, this paper focuses on emergent substrata plants. For a treatment of seasonal changes in biomass and abundance of R. larix in pools in the Pacific Northwest see Dethier 1982.

Along the central Oregon coast R. larix is most common on sand-swept horizontal benches between .3 and 1.5 m above mean low water. It often forms dense monospecific stands or occurs in patches intermixed with the surfgrass Phyllospadix scouleri. It is also common in moderately protected outer coast boulder fields although it does not appear to reach as great an abundance in these areas (pers. observation).

The general appearance and gross morphology of R. larix are described with the following terminology (Figure 1). The plant issues upright axes consisting of slender (<2 mm diameter) cylindrical main axes from a perennating basal holdfast. Branches of the axis may occur at any point along the main axis and appear to be of indeterminate growth. Both the branches and the main axis are covered with small branchlets of determinate growth. Clusters of small branchlets form when the plant becomes reproductive. The life cycle follows that of the "polysiphonous-type" Florideophyceae (Dixon 1973, Bold and Wynne 1978, Figure 2), with the independent reproductive stages having a similar vegetative morphology.

Because R. larix grows in turf-like beds and the basal tissue of adjacent axes appear to be fused, it is impossible to distinguish individuals in continuous beds in the intertidal. It was occasionally possible to study what appeared to be individual plants. These plants were small and well separated from the rest of the R. larix bed. The terms sprig, erect portions of thalli, and axes are used interchangeably in this paper to describe a single main axis and its branches and branchlets rather than a single individual plant.

Study Sites

Specimens of R. larix were examined and collected from two sites within Boiler Bay, a north facing bay in Lincoln Co., on the central Oregon coast (lat. 44° 50' N) (Fig. 3). The sites differed primarily in their height above mean low water and secondarily in their degree of exposure to sand scour and grazing pressure. As part of the eastern shore of the north Pacific basin, the central Oregon coast is subject to mixed semi-diurnal tides with the lower low tide occurring after daybreak in spring and summer and after sunset in fall and winter. Sea surface temperature data was obtained from the U.S. weather bureau at triweekly intervals.

The low intertidal site is a horizontal mudstone bench rising gently from 0 to .7 m above mean low water. A large rocky point protects the bench from direct wave action during storms. Rhodomela larix occurs in both isolated and extensive patches and with Phyllospadix scouleri dominates space in the community. Rhodomela at this site is subject to

sand scour during the winter (Chapter 4) and to a variety of herbivores throughout the year (Chapter 3).

The middle intertidal site is oriented perpendicular to and directly east of the low zone site. It is a gently sloping mudstone shelf projecting from 1 to 3 m above mean low water. Rhodomela larix occurs over the majority of the shelf but I studied the populations between 1.3 and 1.7 m above MLW. The shelf receives wave action directly from the northwest but is moderately protected from southwesterly swells. Rhodomela in this zone appears to experience little if any sand scour and appears to be regularly grazed by only one species of herbivore (Chapter 3).

A third site called Strawberry Hill in Lane Co., Oregon (Figure 3) was used to collect Rhodomela for periodic determination of reproductive states. This area is 27 kms south of Newport and has extensive patches of R. larix between .3 and 1.0 m above MLW. The area is subject to seasonal sand cycles of the type described by Komar (1976) for the central Oregon coast.

METHODS

Growth Rates

A variety of techniques were employed to describe the growth of R. larix in the field. These involved measuring in situ growth rates of individually marked sprigs, estimating mean length and biomass for a number of axes randomly collected each month and measuring the number of erect thalli and combined length thereof in what appeared to be entire individual plants. Using a variety of techniques allowed me to clarify the dynamics of R. larix within large beds and as distinct individuals.

Growth rates of individual axes were determined in the field by marking individual axes and measuring the length of the main axis and all branches. During the first 5 months of the study, plants were marked by placing flexible plastic discs 5 mm in diameter around the base of each thallus (J. Pederson, University of Oregon). This method was difficult to use without injuring plants and was thus terminated. I then tied monofilament line bracelets containing some combination of 2 colored beads, around the base of each axis within 5 mm of the holdfast. Measurements of the axis were taken at irregular intervals for one year. A high rate of tag loss necessitated marking new erect thalli on a bimonthly basis.

In addition, R. larix populations were sampled monthly to ascertain seasonal changes in axis length, biomass and reproductive condition. Each month approximately twenty axes were haphazardly removed along a

horizontal transect line through both sites. Reproductive condition was noted and epiphyte cover and overall axis length measured before each sprig was dried for 2 weeks at 90°C. All large epiphytes were removed from the thalli before drying.

To estimate growth rates of individual plants, isolated clumps of axes were selected. Most of these clumps were small (<10 cm in diameter), and showed no evidence of connection with nearby plants. All of them were situated in the low zone. I was unable to locate mid zone plants which I could be reasonably certain were separate, distinct individuals. All axes and branches within a given plant were measured and the total number of axes counted at approximately monthly intervals. This technique was feasible only for small clumps because those with a diameter of greater than 10 centimeters frequently contained more than 100 axes and proved difficult to measure accurately. Differences in growth rates between axes from the same individual were compared by marking 8 to 10 sprigs of approximately the same size within one clump and monitoring their subsequent growth.

Growth rates were also calculated for groups of 5 to 10 axes transplanted between the two zones on pieces of rock substrate. Depressions were made in the rock surface so that transplanted rocks would be flush with the surface of the surrounding substrate. Transplants were secured in the depressions with Sea Goin' Pox Putty. Three rocks were transplanted within each zone as a control and 3 were transplanted between zones.

Horizontal expansion of the main bed was studied in four locations in the low zone by initially marking the substrate at four points along

a 30-40 centimeter section of the edge of the bed. Each edge was traced monthly onto a clear piece of vinyl and the position of all markers noted. Growth of established plants into adjacent clearings provided additional information on vegetative expansion.

The ability of Rhodomela to grow back from basal cells was tested by removing all visible portions of thalli with a putty knife and observing subsequent regrowth. In many cases this involved scraping the rock surface until several millimeters of the rock itself were removed. Clumps of Rhodomela were removed from 2 mid and 2 low intertidal sites in the summer of 1980, 8 mid intertidal sites in the summer of 1981 and 4 low intertidal sites in the spring of 1982.

Reproduction and Recruitment

All the axes collected for the monthly analysis of biomass were examined for their reproductive status. In order to accurately assess those times of the year when reproductive output was the highest, it was necessary to supplement critical evaluations of reproductive state with an estimate of the amount of mature reproductive tissue per thallus. This was done by collecting axes that looked reproductive and examining them under magnification. The density of mature reproductive structures was subjectively estimated, and the length of main axis over which these structures were present was measured.

To measure recruitment of R. larix into the intertidal I made eight 900 cm² clearings, four at each of the two Boiler Bay sites, during the summer of 1980. Clearings were scraped with a putty knife and painted

with lye to remove all algal cells adhering to or imbedded in the substrate. Clearings were monitored bimonthly for the first 6 months and trimonthly thereafter. In addition recruitment was monitored in five similarly prepared 225 cm² clearings made in January of 1981, where all herbivores were removed every 2 weeks to decrease their possible effect on recruitment patterns. Naturally created clearings near patches of R. larix were also monitored throughout the year for the presence of newly recruited individuals.

RESULTS

Growth Studies

Axes varied greatly both in length during any given month and in patterns of growth over the year (Fig. 4, Table 1, 3). For example, 10 out of 17 axes marked in December 1980 and January 1981 in the low zone never grew taller than 5 centimeters, while the remaining axes grew to lengths greater than this and became reproductive by early summer 1981. A similar pattern was observed in the high zone where only 4 out of 9 axes marked in January 1981 grew and became reproductive in the following summer. In addition, several axes marked in December 1980 were still present in February 1982 and showed no signs of growth after the first season. Two axes marked in April 1981 which became reproductive in summer 1981 were also still present 14 months later although they showed little growth in spring 1982. Hence axes may be retained by a plant after they have released their spores or gametes.

Data from marked axes within known individual plants supports the hypothesis that variation in growth is common among axes and that portions of an axis are perennial (Table 1). Axes which did not become reproductive during this study either slowly lost tissue or grew less than .1 cm per month. In one case I was able to document the sexual maturation in spring 1982, of three axes which were present but not reproductive, during the preceding summer while other axes on the same plant which were reproductive in summer 1981 were present as 1-3 cm stubs in early summer 1982 and did not become reproductive again. This

suggests that some axes may not mature until their second year and others may be retained by a plant after senescence of the reproductive parts.

Data obtained from marked individual axes suggest that some thalli respond to breakage of the main axis by sprouting lateral branches or through the elongation of lateral branches already present. It was often difficult to tell whether branches present after breakage of the main axis were new because individual branches on an axis were not marked. Consequently, I was only able to demonstrate elongation of lateral branches after main axis breakage in erect thalli that had one or no lateral branches. In eight cases, growth of new lateral branches clearly occurred after breakage of the main axis, but 15 other marked axes did not grow over a one year period after the main axis broke. Artificial clipping of axes also produced variable results. One quarter to one third of 120 axes clipped in June of 1980 sprouted lateral branches while there was little or no growth in the remaining portion over an entire year. This also suggests that erect portions of a given plant differ physiologically.

To estimate periods of potential maximum growth, changes in erect thallus length were calculated for those axes that did not lose tissue during the period of measurement (Table 2). The greatest growth rates in the low zone occurred during the 'spring and summer' period. Water temperatures showed a net increase of only 1°C during this period (Figure 5) and are frequently very low on the Oregon coast during the late spring and summer due to upwelling (NOAA publications). Hence temperature changes were assumed not to be the direct cause of the

spring growth period. In the mid zone, maximal rates of growth occurred in the summer, but the spring and summer growth rates are statistically indistinguishable. Growth rates differed significantly between zones during winter and spring (Table 2), when low zone thalli grew at rates almost twice those of mid zone thalli. Slight growth occurred in both zones during the fall and winter months, but many thalli lost tissue during these seasons (Table 3).

Like the studies of marked axes, the study of monthly population samples suggests that the largest sizes are reached in the spring and summer (Figure 4). A significant increase in mean length occurred from early May to mid June in the low zone (Mann-Whitney, $Z = 4.58$, $p < .05$) and from early March to mid May in the mid zone (Mann-Whitney, $Z = 4.14$, $p < .05$). Changes in mean biomass of samples for the most part coincided with changes in the mean length of axes. In the low zone both the biomass and the overall peaks in length occurred in June. However, mid zone plants had two peaks in biomass, only one of which corresponds to a peak in axis length. The possible reasons for this phenomenon are discussed later.

Large variation occurred in the mean axis length and biomass of axes within zones during most of the year (Figure 4). This variation can be explained by the presence of small, non-reproductive axes throughout the year. Variation was the lowest during the winter after the senescence of the previous year's reproductive thalli and before the growth of new thalli, and increased in the spring as some axes began to mature.

The mean axis length of low zone thalli was larger than that of mid zone thalli from June through October. A comparison of the mean size of

the longest central axis on a given upright, among axes from the two zones also suggested that mid zone thalli were shorter in stature than those from the low zone (Table 4). Low zone axes also had a larger number of branches during the summer suggesting further differences in plant morphology between the zones.

Analysis of monthly samples suggested that prolonged exposure to air and sun injures mid zone plants during the summer. The mean length of these plants decreased significantly between July and August when low zone plants were still near their June peak (Fig. 4, Mann-Whitney test, $Z = 1.30$, $.p < .20$). Close inspection of the samples revealed that a large percent of mid zone axes showed evidence of exposure damage from May through July (Fig. 6). Damaged plant tissue appeared whitened, shriveled and deteriorated easily when handled. Very few specimens collected in August showed signs of bleaching although most contained damaged or broken axes suggesting that the reduction in length of the August samples reflected damage suffered during previous months. Exposure damage did not appear to be as common in the low zone. In the monthly samples from this zone, only one axis was ever found with whitened tissue, and marked low zone axes were less apt to lose tissue during the summer than mid zone axes (Table 3).

To quantify the impact of exposure damage in the mid zone I marked 24 individual axes along a horizontal transect approximately 1.7 m feet above mean low water during July, 1981. Twelve of these axes already contained more than 1 cm of whitened plant tissue. The remaining 12 axes showed no visible evidence of exposure damage. Growth and survival of all 24 axes were monitored for the next three months. The

significant difference in slopes of the two survivorship lines suggest damaged axes have lowered survivorship (Fig. 7, $t = 13.01$, $p < .001$). Of those axes which survived in each treatment between 16 June and 16 July, 83.3 percent of the damaged thalli lost tissue while significantly fewer (16.7 percent) undamaged sprigs lost tissue (Chi-square = 7.5, $p < .01$). The only damaged axis which grew during this time period increased .4 cm. In contrast the nine undamaged sprigs that grew increased a mean of 2.33 cm.

The lower growth rates and typically smaller stature of axes in the mid zone appear to result from environmental conditions experienced within that zone. Evidence from transplant experiments supports this contention. Both control and experimental transplants in the mid zone suffered exposure stress within one week after they were moved suggesting that transplant techniques caused damaging exposure in both sets of transplants. However, in summer 1981, one year after being moved, both control and between zone transplants in the mid zone showed a similar pattern of growth. Mid zone plants transplanted to the low zone did not suffer exposure stress. However the mean axis length per clump of transplanted axes did not increase as greatly as low zone controls during summer 1981 (Table 5) suggesting that the environment was not the sole determinant of growth patterns in this zone.

Growth data from entire individual plants parallel the patterns in the individual thalli and suggests that vegetative growth is potentially important in spatial monopolization by R. larix. Both the total number of axes and the total length of tissue present increased in all plants between March and July (Figure 8). Most plants increased their total

number of axes over the time period observed and showed similar patterns of growth. However, larger plants appeared to gain proportionately more axes each year than very small plants. In the size range of plants examined, a growth asymptote was not reached.

The importance of vegetative growth was also demonstrated in the pattern of lateral expansion of the main low zone Rhodomela bed. Between June of 1981 and April 1982 all markers originally placed along the edges of the main bed were overgrown by 1 to 2 centimeters due to the generation of new erect portions of thalli. However growth did not appear to be constant along a given edge (Figure 9). This was also evident in the patterns of invasion of R. larix into clearings made for recruitment studies. Vegetative growth was most evident in clearings made in July 1980. By summer 1982 in one of the four low zone clearings Rhodomela occupied more than 50 percent cover of the rock surface. This Rhodomela was continuous with the Rhodomela surrounding the clearing and appeared to be the result of vegetative proliferation of adjacent plants, although some small recruits were observed. The remaining 3 clearings in the low zone contained 15, 6 and 4% Rhodomela respectively. Again most of this Rhodomela appeared to be the result of vegetative proliferation from plants adjacent to the clearings. The large variation between clearings may have resulted from differences in the amount of Rhodomela surrounding each clearing. In both of the clearings where R. larix regrowth occupied less than 10% of the rock surface, only one clearing edge consisting of R. larix. The remaining two clearings had almost continuous Rhodomela along their edges.

In addition to vegetative proliferation, R. larix appears to have the ability to regenerate from a very small number of basal cells. Putty knife removals of upright portions of Rhodomela in July 1981 at Boiler Bay, resulted in the regrowth of scattered patches of Rhodomela thalli with upright axes of less than one cm in height within two weeks. New thalli grew from the rock substrate even after up to five mm of rock surface and all visible traces of plant holdfast were removed, suggesting that the basal cells or filaments of the plant can penetrate the surface of the mudstone. Four 900 cm² clearings made at Strawberry Hill in April 1982 followed a similar pattern. Scattered patches of Rhodomela regenerated (within one month) from a freshly scraped rock surface. However in this case the surface of the substrate was basalt and was not as easily abraded by the putty knife. Thus basal cells of the Rhodomela holdfasts may have adhered tightly to the irregular substrate surface without having actually penetrated it.

Reproductive Phases and Timing

Individual axes could be classified into five categories with respect to reproduction: (1) tetrasporic, bearing at least one identifiable tetrasporic branchlet; (2) cystocarpic, containing at least one identifiable cystocarp; (3) male gametophyte, with clusters of spermatangia; (4) immature reproductive plants bearing clustered branchlets (Figure 1) but no identifiable reproductive structures and; (5) vegetative, bearing main axis branchlets only.

Reproductive condition of thalli varied both in time and between sites. In August 1980, tetrasporophytes predominated at both sites. Male gametophytes were found to occur primarily at the higher site and their occurrence was temporally more restricted than that of female or tetrasporic plants (Figure 10). Cystocarpic plants were also more common in the higher site where they occurred abundantly between May and October. In the low intertidal most plants with clustered branchlets were tetrasporic.

Plants examined from Strawberry Hill in February and July 1981 showed patterns similar to the Boiler Bay sites. In February only eight percent of the 104 axes collected were reproductive. These few axes were tetrasporic and came from a mid zone area. However in July >80% of all axes from both mid and low areas at Strawberry Hill were reproductive. Sixty-five and 73 percent of these were tetrasporic in the mid and low zones respectively. Cystocarpic axes accounted for 23% of the mid zone samples, but only 3% of low zone samples. This pattern corresponds to the dominance of tetrasporophytes on the low zone bench and the larger percent of cystocarpic plants in the mid zone at Boiler Bay.

Immature reproductive thalli were present throughout spring, fall and winter at both Boiler Bay tidal heights (Fig. 10). In the mid zone the greatest abundance of reproductively immature plants immediately preceded the fall peak in cystocarp production, suggesting that these were immature female axes. The presence of immature thalli in this zone in May also preceded cystocarp production in early summer. Since both

male and tetrasporic plants decreased in abundance during this time, it is also likely that these immature axes were female gametophytes.

Several individually marked axes in both zones developed from a non-reproductive condition without clustered branchlets to the tetraspore stage within one month suggesting that tetraspores develop shortly after clustered branchlets are formed on a diploid thallus. Female plants on the other hand remain unidentifiable until development of the cystocarp occurs. However, the presence of unidentifiable immature thalli in the low zone where carposporophytes were always rare (Fig. 10) suggests that these were immature tetrasporophytes.

An assessment of reproductive capacity should include not only the number of reproductive plants (Fig. 10), but also the abundance of reproductive structures on each axis (Prince 1971). This latter information was garnered by examining field-collected reproductive sprigs under a 30x dissecting lens. The following patterns were observed: (1) mature tetrasporic sori were present on low zone thalli in May and June but were rare (<10) on each axis. (2) Tetraspores were most dense on erect portions of thalli in July and August within both zones. (3) Carpospores were never dense on low zone samples and (4) occurred in the densest assemblages in mid zone samples collected in October. Thus a peak in overall tetraspore production occurred in August of both years while the major peak in cystocarp production occurred in the mid zone in October 1980. In November mid zone axes often contained cystocarps but many of the reproductive structures were deteriorating and their overall density was low. The senescence of

reproductive material might explain the decline in the biomass of mid zone samples between October and November (Fig. 4).

Within a given zone there were slight differences in the mean sizes of the different reproductive phases. Tetrasporangial axes were longer than cystocarpic ones in the mid zone although significantly smaller than low zone tetrasporangial axes (Table 6).

Recruitment

This 18-month study produced little evidence of recruitment. In the eight 900 cm² clearings made in July 1980, no settlement was observed until winter 1982, when 10 small plants were found in one of the four low zone clearings. S. Spenser Univ. of California, Santa Cruz (pers. comm.) has found that laboratory cultures of Rhodomela tetrasporophytes send out small runners and spread vegetatively in this manner. I found no rhizoidal-like connections between plants in this low zone clearing and the surrounding Rhodomela plants so concluded that these plants were in fact newly recruited individuals. Rhodomela did not recruit over 15 months in the five 225 cm² clearings made in the winter 1981.

In bare patches along the edges of the main low zone beds of Rhodomela, four small R. larix plants appeared during spring 1981 and no recruits were found during the following year. These plants had between one and three axes when found and presumably were newly recruited individuals because of their absence throughout summer and fall of 1980. They showed growth during the period of time in which they were present and at least one axis per plant showed signs of

becoming reproductive but all of the recruits disappeared by early July. Hence, recruitment may occur but recruits have difficulty persisting in a population. In addition, recruitment and the fate of newly established plants may vary from year to year.

DISCUSSION

Growth Rates and Plant Morphology

The growth and reproductive patterns of R. larix exhibited both distinct seasonal cycles and differences related to tidal height. For both zones maximal growth occurred in the spring and summer, corresponding with the period of the year of maximal day length. Growth rates were not thought to correlate with increasing water temperature, as has been found for many other species (Conover, 1958, 1964; Edwards and Kaupran 1973; Whittick and Hooper, 1977) because of the generally low water temperatures present along the Oregon coast in the spring and early summer. This is probably also true of reproductive development.

Many marine algae have been found to display differences in growth rate and morphology associated with differences in intertidal elevation (for examples see Lilly 1968; Stewart 1968; Mathieson and Prince 1973, and Santelics 1978), with a trend towards decreased stature with increasing height in the intertidal. Chapman (1946, 1962) pointed out that the higher an alga grows on the shore, the shorter the time available for growth and metabolism. Previous studies have also correlated the morphology of individuals within a given species to their exposure to wave action (Lilly 1968), to salinity (Mathieson and Burns, 1975) and to light intensity (MacFarlane 1956). Such patterns could be created by differential settlement of genetically different spores and zygotes or by environmental influences upon the phenotype. The effect of the environment may also be limited to juvenile plants, resulting in

adults that are genetically programmed for a specific morphology. Few studies have examined changes in morphology when algal individuals are transplanted between zones. One exception is a study by Floc'h (1969) cited in Mathieson and Prince (1973) in which specimens of two morphological extremes of the red alga, Chondrus crispus, were transplanted into different environments. Specimens appeared to retain their respective morphologies for at least seven months after transplantation. This suggests that not only may environmental modifications of growth form be slow in occurring (Floc'h 1969 as cited in Mathieson and Prince 1973) but that individual morphologies may have a strong genetic component.

The results of my transplant experiments with Rhodomela larix suggest that the higher intertidal environment has a more dramatic influence on the phenotype than does the lower intertidal environment. Low zone plants transplanted to the mid zone never achieved the axis lengths observed in both low zone control transplants and unmanipulated low zone thalli. However the axes of mid zone thalli transplanted to the low zone did not achieve the lengths characteristic of low zone plants, a situation similar to that observed by Floc'h (1969). This supports the hypothesis that control of morphology may have a strong genetic element, or is programmed in response to early environmental influences.

Differences in morphology associated with tidal height have been found to result from differences in the distribution of reproductive phases between zones for several species of marine algae (Kilar and Mathieson 1978, Norall et al. 1981). The latter authors found that

tetrasporangial and gametangial thalli of the red alga, Ptilota serrata, showed different growth responses to the same increases in depth. Thus stature differences associated with tidal height were to some extent the result of a skewed distribution of the reproductive phases. On the other hand, Kilar and Mathieson (1978) found that differences in the morphology of Dumontia incrassata individuals between tide pools was due to a staggered distribution of reproductive phases in the different pools.

Although the different life stages of R. larix are described as isomorphic (Bold and Wynne 1978) subtle differences in the morphology of gametophytes and tetrasporophytes may account for some of the morphological variation between the populations at different tidal heights. Gametophytes in the mid zone appear to have a slightly smaller stature than tetrasporangial thalli in the same zone (Table 6). Hence the high frequency of occurrence of gametangial plants in the mid zone may have a dampening effect on the mean stature of thalli collected in this zone. However diploid plants themselves were significantly smaller in the mid zone than in the low zone (Table 6, $p < .01$).

Distribution of Reproductive Phases

Skewed distributions of reproductive phases over tidal heights and seasons characterizes many groups of algae (Fritsch 1945). Tetrasporangial phases dominate algal populations in several species within the Florideophyceae orders Ceramiales, Cryptonemiales and Gigartinales (Fritsch 1945, Dixon 1963, Mathieson and Burns 1975, Hansen

and Doyle 1976, Whittick and Hooper 1977, Hoyle 1978, Kilar and Mathieson 1978, Ngan and Price 1980, and Kaupran 1980). Examples have also been found in the Phaeophyta (Allender 1977). The causes of diploid dominance are not well understood; however, several hypotheses have been proposed to explain this phenomenon. These include, (1) poor germination conditions for settling tetraspores; (2) high mortality of tetraspores before settlement preventing the establishment of gametophytes, (3) adverse environmental conditions preferentially affecting gametophyte growth and survival and (4) the ability of tetrasporangial thalli to reproduce themselves through apomeiosis (Hansen and Doyle, 1976, Hansen, 1977). It is unclear how many of these hypotheses apply to R. larix. A large number of tetrasporophytes appeared to release mature spores in both 1980 and 1981, suggesting that there is no barrier to the production of spores. However the ploidy level of these "spores" is unknown and the potential for apomeiosis cannot be ruled out.

The small amount of recruitment of either phase observed in this study suggests that establishment of new individuals is a bottleneck for R. larix populations. Thus tetrasporophyte dominance may result from greater relative tolerance of environmental hardships by juvenile tetrasporangial thalli and/or greater relative ability to proliferate vegetatively. Further experiments are needed to elucidate the importance of each of these factors. Also low zone thalli of R. larix appear to be subject to a greater variety of environmental stresses including sand scour and burial (Chapter 4), potentially increased exposure to herbivores (Chapter 3), and possibly greater wave action

(pers. observation) than thalli in the higher area. Thus the more restricted distribution of gametophytes supports the tolerance hypothesis.

Male thalli were considerably less common than female thalli over the course of the reproductive season. This pattern is also characteristic of many red algae (Fritsch 1945, Ngan and Price 1980) although the latter authors suggest that in many cases this may be the result of inadequate sampling techniques. The high percent of mature carpogonia observed suggest that even if males are relatively rare, production of spermatia is adequate to insure fertilization of a large number of female oogonia.

Istock (1967) argued that complex life cycles are inherently unstable because of "the independent evolution of the ecologically distinct portions of the life cycle". Thus the numerical dominance of tetrasporangial thalli may reflect advantages of diploidy over haploidy including the apparent lack of ability by the haploid phase to exploit a variety of habitats. If apomeiosis does take place in R. larix, its occurrence in the field may be the result of selective forces favoring the diploid phases of the life cycle. Production of gametophytes may be retained because of the advantages of sexual reproduction (see Williams 1975, Maynard Smith 1979).

Vegetative vs. Reproductive Proliferation

The low rate of recruitment of R. larix during the period of this study suggests that vegetative growth, although slow, is the primary

means by which Rhodomela maintains space in these intertidal areas. In a study of recolonization of denuded rock surfaces on Vancouver Island, B.C., Rhodomela larix did not reestablish in two plots where it was previously present (Lee 1966). However, DeWreede (1981) reported that Rhodomela larix did recruit into clearing made in stands of Sargassum muticum on the coast of Vancouver Island if the clearings were made at a time when Sargassum was not reproductive and if patches of adult Rhodomela plants were nearby. Dethier (in prep.) observes rapid recruitment of Rhodomela larix into tide pools in the San Juan Islands in Washington. However, these pools were denuded of R. larix and other plants by the scraping of macrophytes followed by a soaking of the pool in boiling water. My own experience with removal of Rhodomela larix from rock surfaces suggests that the only effective means of eliminating it from rocks is by removing several cms of the rock itself or by spreading several coats of lye on the rock surface to eliminate algal cells that may have penetrated into or are closely adherent to the rock. If not removed, these cells will proliferate into macroscopic thalli. In a recent study of succession in surfgrass beds on the Oregon coast, Turner (1982) created clearings by scraping the plants present off of the rock surface with a crowbar. She found that R. larix achieved > 20% cover over three years in those clearings where it was previously present but only rarely invaded clearings where it was previously absent. This again suggests that the ability of Rhodomela to perennate from basal cells is more important to its persistence in intertidal communities, than is reproduction.

Until recently very little attention has been paid to the importance of vegetative proliferation in the maintenance of space in the rocky intertidal. However it is clear from this study and others (Dixon 1963, Hansen and Doyle 1976, Whittick and Hooper 1977, Lubchenco and Menge 1978, Hansen, 1982) that vegetative proliferation and perennation may be important life history characteristics for marine algae which live in environments where recruitment is generally poor or at best unpredictable. The low availability of space in the habitats where Rhodomela occurs (pers. obs.) also points out the importance of ability to perennate. The availability of cleared space at a time when propagules are present may be essential to successful colonization. R. larix plants do reproduce sexually each year and therefore have not lost the ability to invade new habitats should they become available.

SUMMARY AND CONCLUSIONS

Rhodomela larix occurs over a broad tidal range in rocky intertidal habitats. Erect axes grow to reproductive maturity from early spring throughout the summer and into the fall. Plants in the mid zone suffer losses to exposure in the summer but undergo a second peak in the production of spores and gametes in the fall. Gametangial plants are less common than tetrasporangial plants and in general are restricted to higher intertidal areas. Recruitment appeared to be quite low in spite of the large number of reproductive structures produced by thalli in both zones. Vegetative proliferation on the other hand appeared to be important in the acquisition and maintenance of space.

FUTURE STUDIES

Further long term studies are needed to document year to year variation in recruitment and differences in recruitment among habitats. The growth and longevity of basal portions of all phases of Rhodomela larix also needs to be elucidated.. Combined laboratory and field studies are needed to demonstrate the susceptibility of young sporophytes and gametophytes to environmental influences. The potential for apomeiosis in tetrasporangial thalli also needs to be explored.

REFERENCES

- Abbott, I.A. and G. J. Hollenberg. 1976. Marine algae of California. Stanford University Press, Stanford, California.
- Allender, B.M. 1977. Ecological experimentation with the generations of Padina japonica Yamada (Dictyotales: Phaeophyta). J. Exp. Mar. Biol. Ecol. 26: 225-234.
- Bold, H. and M. Wynne. 1978. Introduction to the algae. Prentice-Hall, Inc., Englewood Cliffs, N.J.
- Chapman, V.J. 1946. Marine Algal Ecology. Bot. Rev. 12:682-672.
- Chapman, V.J. 1962. The Algae. Macmillan and Co., London.
- Conover, J.T. 1958. Seasonal growth of benthic marine plants as related to environmental factors in an estuary. Publ. Inst. Mar. Sci. Univ. Texas 5:97-147.
- Conover, J.T. 1964. The ecology, seasonal periodicity and distribution of benthic plants in some Texas lagoons. Bot. Mar. 7:4-41.
- Dethier, M. 1982. Pattern and process in tidepool algae: Factors influencing seasonality and distribution. Bot. Mar. 25: 55-66.
- DeWreede, R. 1981. The effects of sea urchin grazing, clearing, and competition on the distribution of three low zone intertidal algae in British Columbia, Canada. J. Phycol. 16 (suppl). p. 10.
- Dixon, P.S. 1965. Perennation, vegetative propagation and algal life histories, with special reference to Asparagopsis and other Rhodophyta. Bot. Gothob. Acta. Univ. Gothob. 3: 67-74.
- Dixon, P.S. 1973. Biology of the Rhodophyta. Hafner Press, N.Y.
- Edwards, P. and Kaupran, D.F. 1973. Benthic marine algal ecology in the Port Aransas Texas area. Contr. Mar. Sci. Univ. Texas. 17:15-52.
- Fritsch, F.E. 1945. The structure and morphology of the algae. vol. 2.
- Hansen, J.D. 1977. Ecology and natural history of Iridaea cordata (Gigartinales, Rhodophyta) growth. J. Phycol. 13: 395-402.
- Hansen, J.E. and W.T. Doyle. 1976. Ecology and natural history of Iridaea cordata (Rhodophyta: Gigartinales): Population structure. J. Phycol. 12: 273-278.

- Hoyle, M.D. 1978. Reproductive phenology and growth rates in two species of Gracilaria from Hawaii. J. Exp. Mar. Biol. Ecol. 35(3): 273-283.
- Istock, C. 1967. The evolution of complex life cycle phenomena: An ecological perspective. Evol. 21:592-605.
- Katsui, N., Y. Suzuki, S. Kitamura and T. Irie. 1967. 5,6-Dibromoprotocatechualdehyde and 2,3-dibromo-4,5-dihydroxybenzylmethyl ether. New dibromophenols from Rhodomela larix. Tetrahedron 23: 1185-1188.
- Kaupran D.F. 1980. Floristic affinities of North Carolina inshore benthic marine flora. Phycologia 19: 245-252.
- Kilar, J.A. and A.C. Mathieson. 1978. Ecological studies of the annual red alga Dumontia incrassata (O.F. Muller) Lamouroux. Bot. Mar. 12: 423-437.
- Komar, P. 1976. Beach processes and sedimentation. Prentice Hall, Englewood Cliffs, N.J.
- Lee, R.K. 1966. Development of marine benthic algal communities on Vancouver Island, British Columbia. In, The Evolution of Canada's Flora. R. Taylor and R.A. Ludwig eds. Univ. of Toronto Press, Toronto, Canada.
- Lilly, G.R. 1968. Some aspects of the ecology of Irish Moss, Chondrus crispus (L.) Stackhouse, in Newfoundland waters. Fish. Res. Bd. Can. Tech. Rep. 43.
- Lubchenco, J. and B. Menge. 1978. Community development and persistence in a low rocky intertidal zone. Ecol. Monogr. 48:67-94.
- MacFarlane, C.I. 1956. Irish Moss in the maritime Provinces, Nova Scotia Res. Fdn. Publ. 20 pp.
- Mathieson, A. and R. Burns. 1975. Ecological studies of economic red algae. V. Growth and reproduction of natural and harvested population of Chondrus crispus Stackhouse, in New Hampshire. J. Exp. Mar. Biol. Ecol. 17: 137-156.
- Mathieson, A. and J. Prince. 1973. Ecology of Chondrus crispus Stackhouse. Proc. N.S. Inst. Sci. 27: 53-79.
- Maynard Smith, J. 1979. The evolution of sex. Cambridge Univ. Press, Cambridge, England.
- National Weather Service Publications, Sea Surface thermal analysis. U.S. Dept. of Commerce, National Oceanographic and Atmospheric Association.

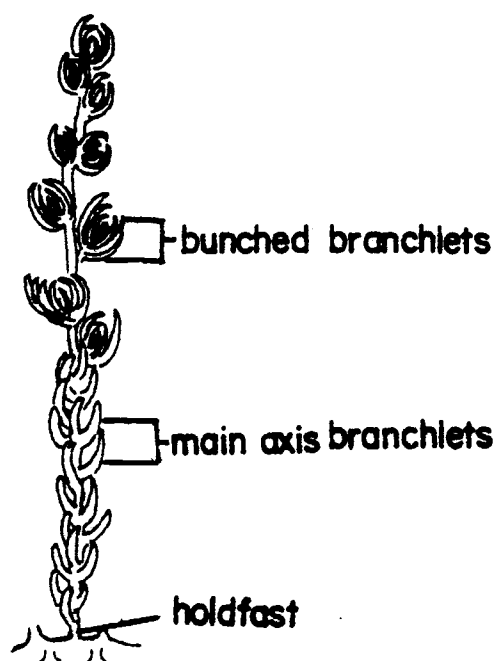
- Ngan, Y. and I.R. Price. 1980. Seasonal growth and reproduction of intertidal algae in Townsville region (Queensland, Australia). *Aquat. Bot.* 9: 117-134.
- Norall, T.L., A.C. Mathieson and J.S. Kilar, 1981. Reproductive ecology of four subtidal red algae. *J. Exp. Mar. Biol. Ecol.* 54: 119-136.
- Phillips, D.W. and G.N. Towers. 1981. Bromophenols of Rhodomela larix: Chemotaxonomy of morphological forms. *Biochem. Syst. Ecol.* 9:1-3.
- Phillips, D.W. and G. N. Towers. 1982a. Chemical ecology of red algal bromophenols. I. Temporal, interpopulational and within-thallus measurements of lanosol levels in Rhodomela larix (Turner) C. Agardh. *J. Exp. Mar. Biol. Ecol.* 58: 285-293.
- Phillips, D.W. and G. N. Towers. 1982b. Chemical ecology of red algae bromophenols. II. Exudation of bromophenols by Rhodomela larix (Turner) C. Agardh. *J. Exp. Mar. Biol. Ecol.*
- Prince, J.S. 1971. An ecological study of the marine red alga Chondrus crispus in the waters off Plymouth, Mass. Ph.D. Thesis, Cornell Univ. Ithaca, N.Y. 193pp.
- Saito, Y. 1980. Suitable habitats for certain algae with respect to their growth on the vertical surface of breakwaters. *Jap. J. Phycol.* 28(3): 171-176.
- Santelics, B. 1978. The morphological variation of Pterocladia caerulescens (Gelidiales, Rhodophyta) in Hawaii. *Phycologia* 17(1): 53-59.
- Searles, R. B. 1980. The strategy of the red algal life history. *Am. Nat.* 115: 113-120.
- Smith, G. M. 1944. Marine algae of the Monterey peninsula. Stanford University press, Stanford, California.
- Stearns, S. 1976. Life history tactics: A Review of the ideas. *Quart. Rev. Biol.* 51: 3-47.
- Steward, J.G. 1968. Morphological variation in Pterocladia pyramidale. *J. Phycol.* 4: 76-84.
- Taylor, A.R. and L. M. Chen. 1973. The Biology of Chondrus crispus Stackhouse: Systematics, Morphology and life history. *Proc. N.S. Inst. Sci* 27:1-33.

- Turner, T. 1982. Community organization and succession in rocky intertidal surfgrass beds. Ph.D. Thesis, Oregon State University.
- Weinstein, B.T. Rold, D.E. Harrell Jr., M. Burns III, and J.R. Waaland. 1975. Reexamination of the bromophenols in the red alga Rhodomela larix. *Phytochemistry* 14:2667-2670.
- Whittick, A. and R. Hooper. 1977. The reproduction and phenology of Antithamnion cruciatum (Rhodophyta: Ceramiaceae) in insular Newfoundland. *Can. J. Bot.* 55: 520-524.
- Wilbur, H. M., D.W. Tinkle and J.P. Collins. 1974. Environmental certainty, trophic level, and resource availability in life history evolution. *Am. Nat.* 108: 805-817.
- Williams, G. 1975. Sex and evolution. Princeton Univ. Press, Princeton, N.J.

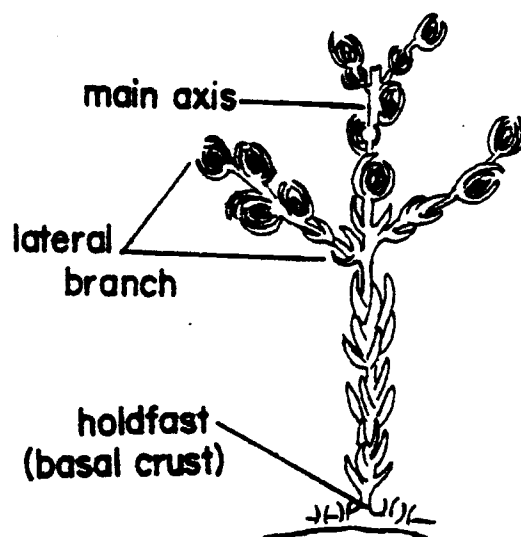
Figure 1. External morphology of Rhodomela larix. Erect axes and their holdfasts make up the algal thallus. A. unbranched erect axis. B. Axis with branching morphology. C. Bunched branchlet with developing cystocarp. D. Bunched branchlet developing into tetrasporic condition.

Figure 1

A.



B.



C.



D.



Figure 2. Life cycle of a typical Florideophycean species (Division Rhodophyta).

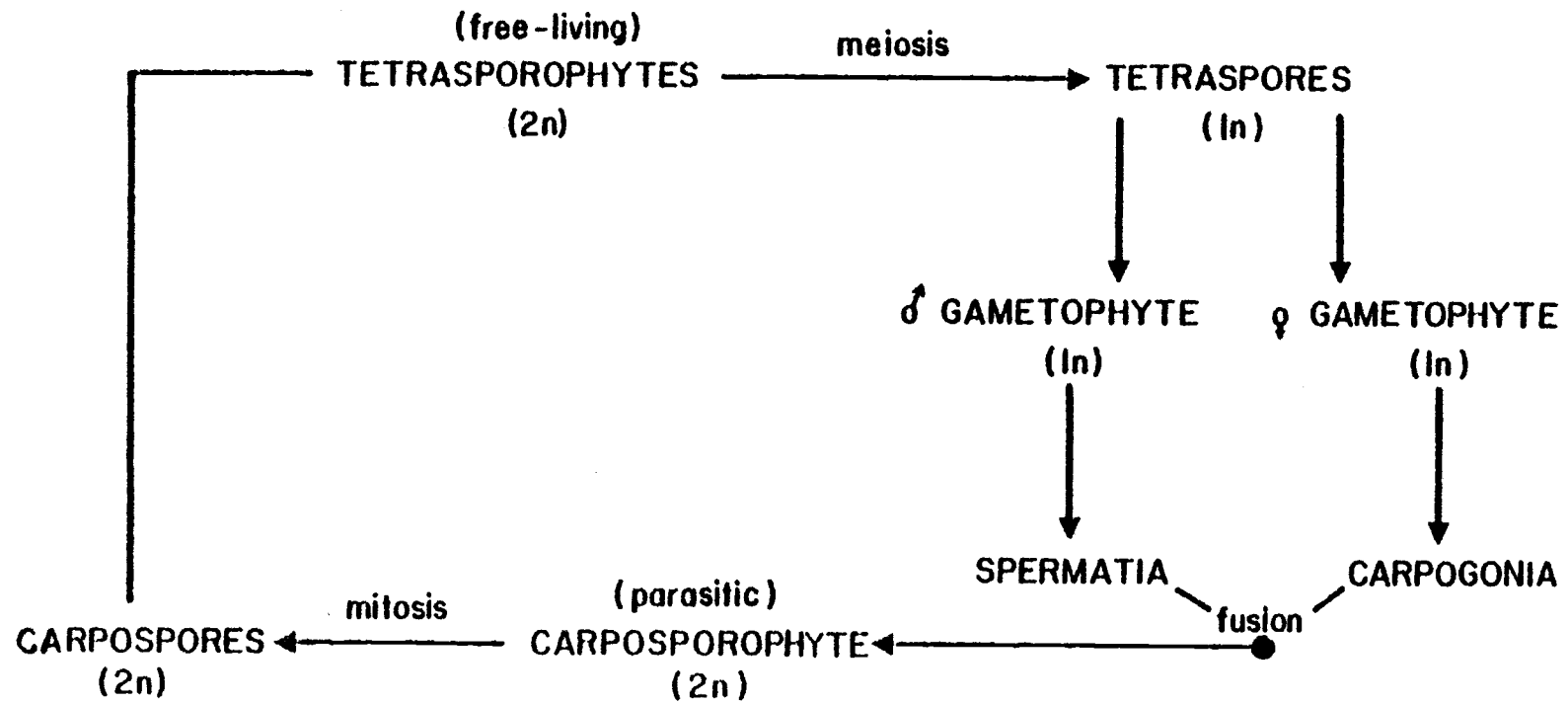


Figure 3. Location of study sites on the central Oregon coast. Dashed lines indicate county boundaries. Solid stars represent exact study site locations.

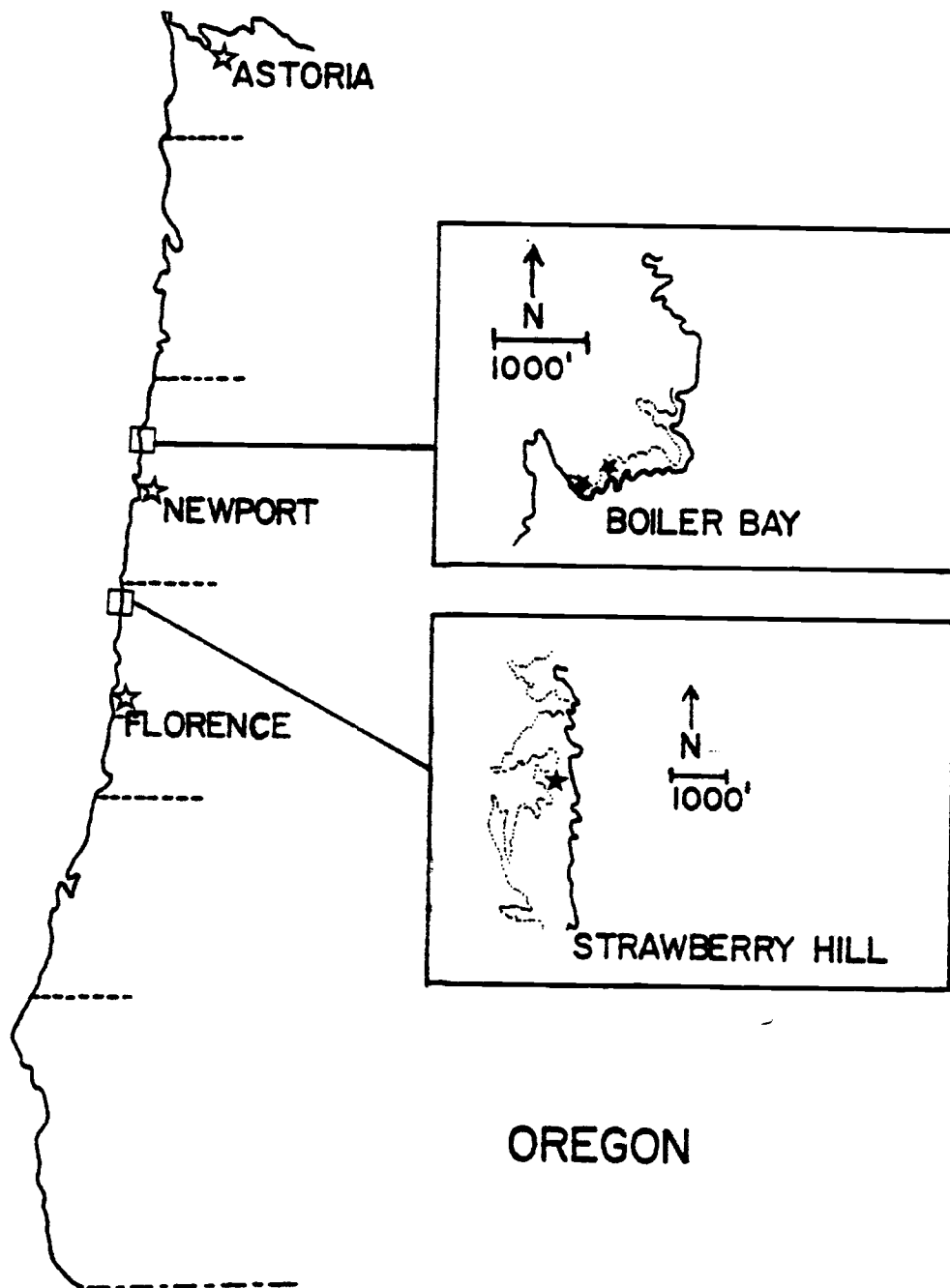


Figure 4. Seasonal changes in size of randomly collected axes. $n=20$ for each sample. A. Mean axis length per sample for each month. B. Mean dry weight per sample for each month. Bars represent standard deviations.

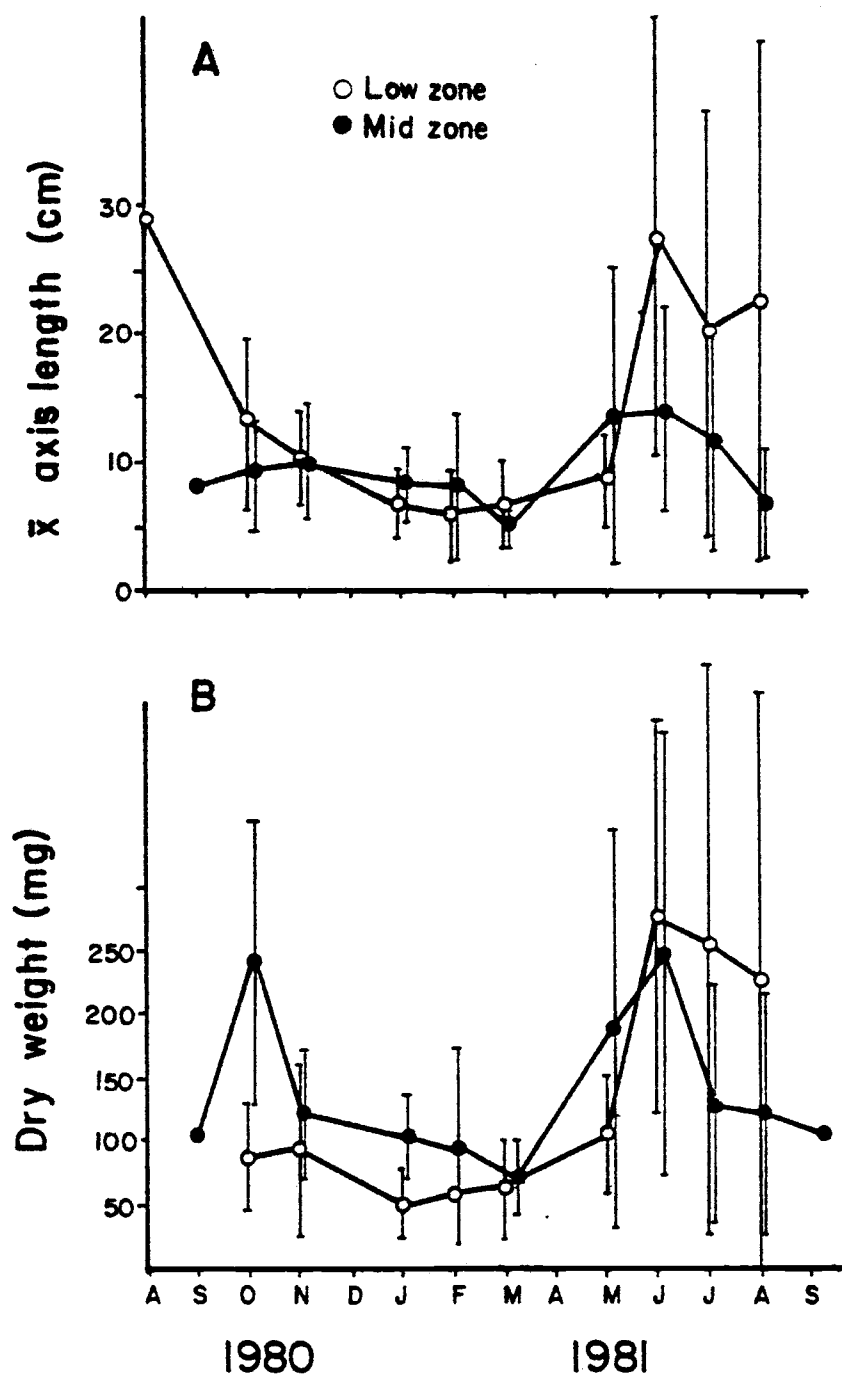


Figure 5. Sea surface temperatures for the Boiler Bay area, OR. Data were obtained from the National Oceanographic and Atmospheric Association.

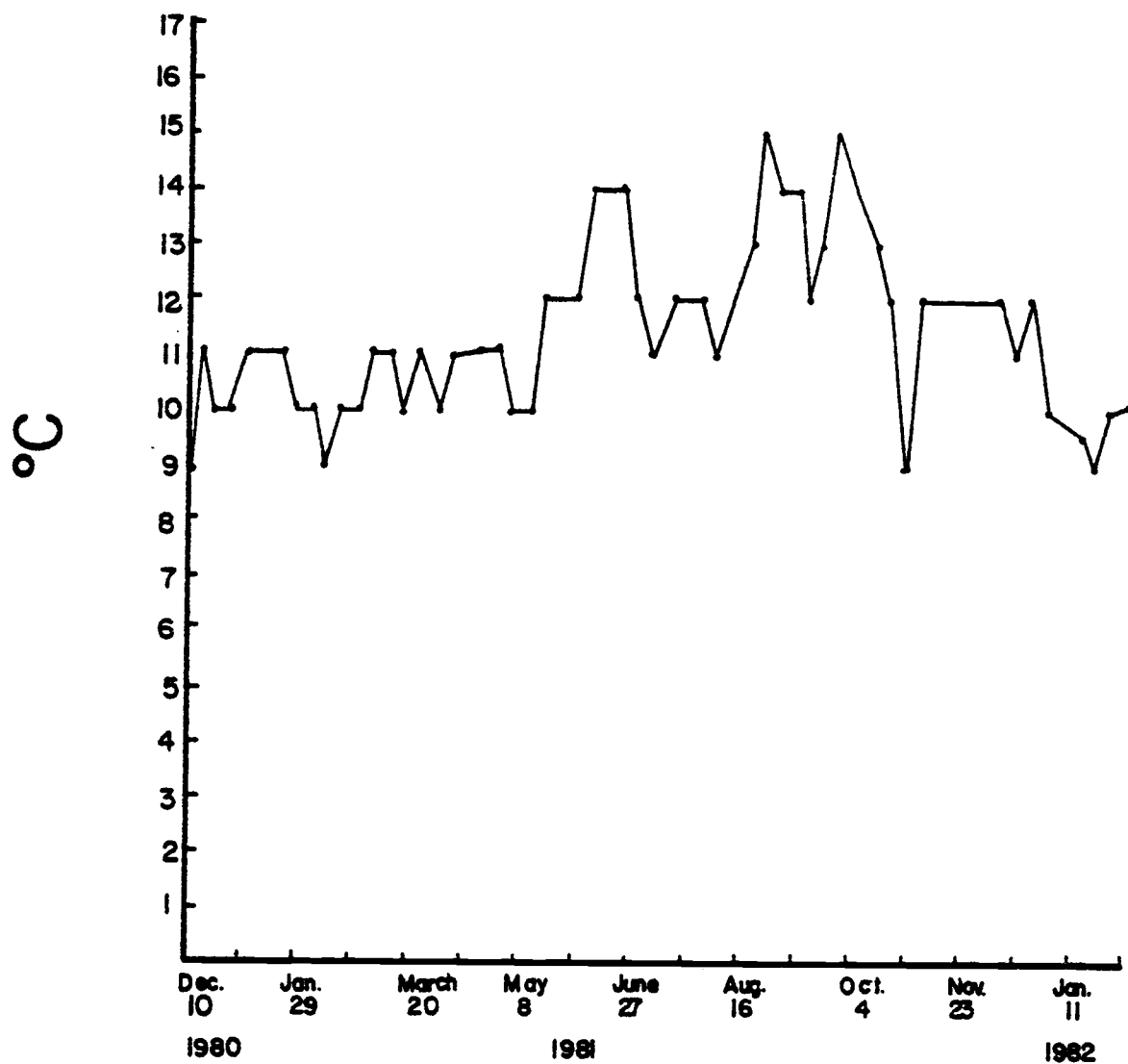


Figure 6. Seasonal occurrence of damaged axes in samples from mid zone population of Rhodomela larix at Boiler Bay, OR.

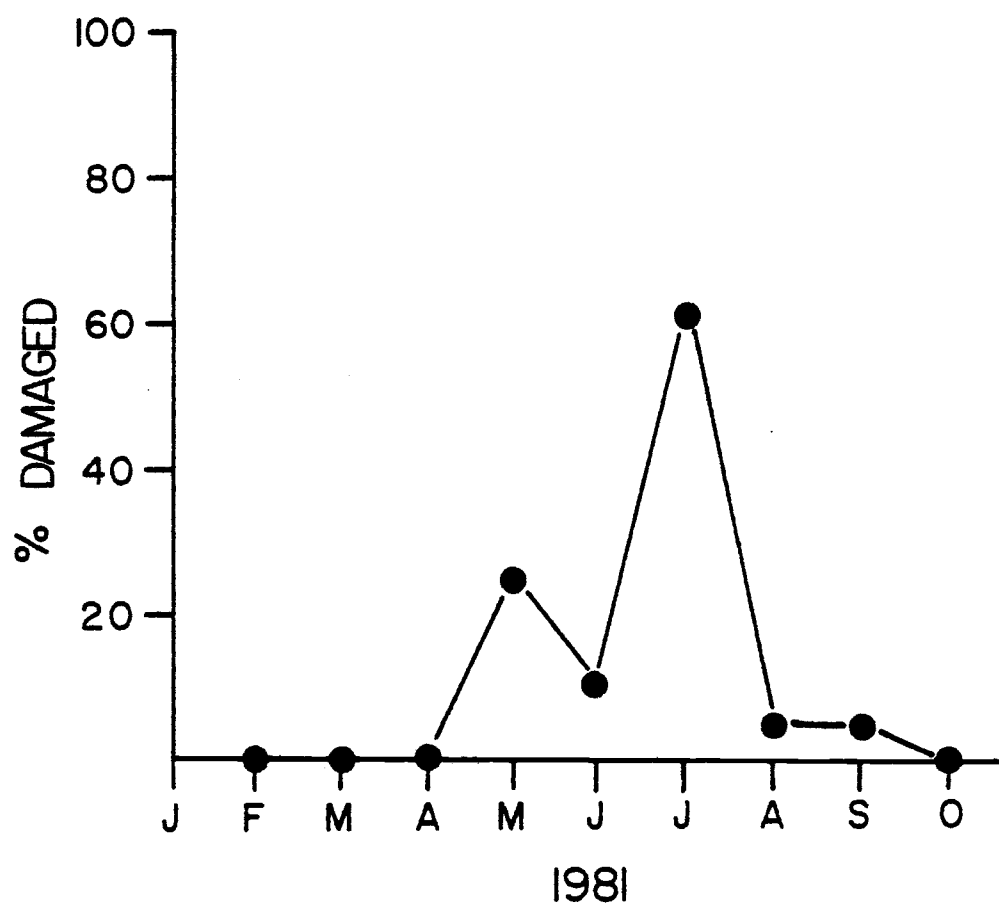


Figure 7. Survival of damaged and undamaged axes in the mid zone at Boiler Bay, where $n=12$ for each category.

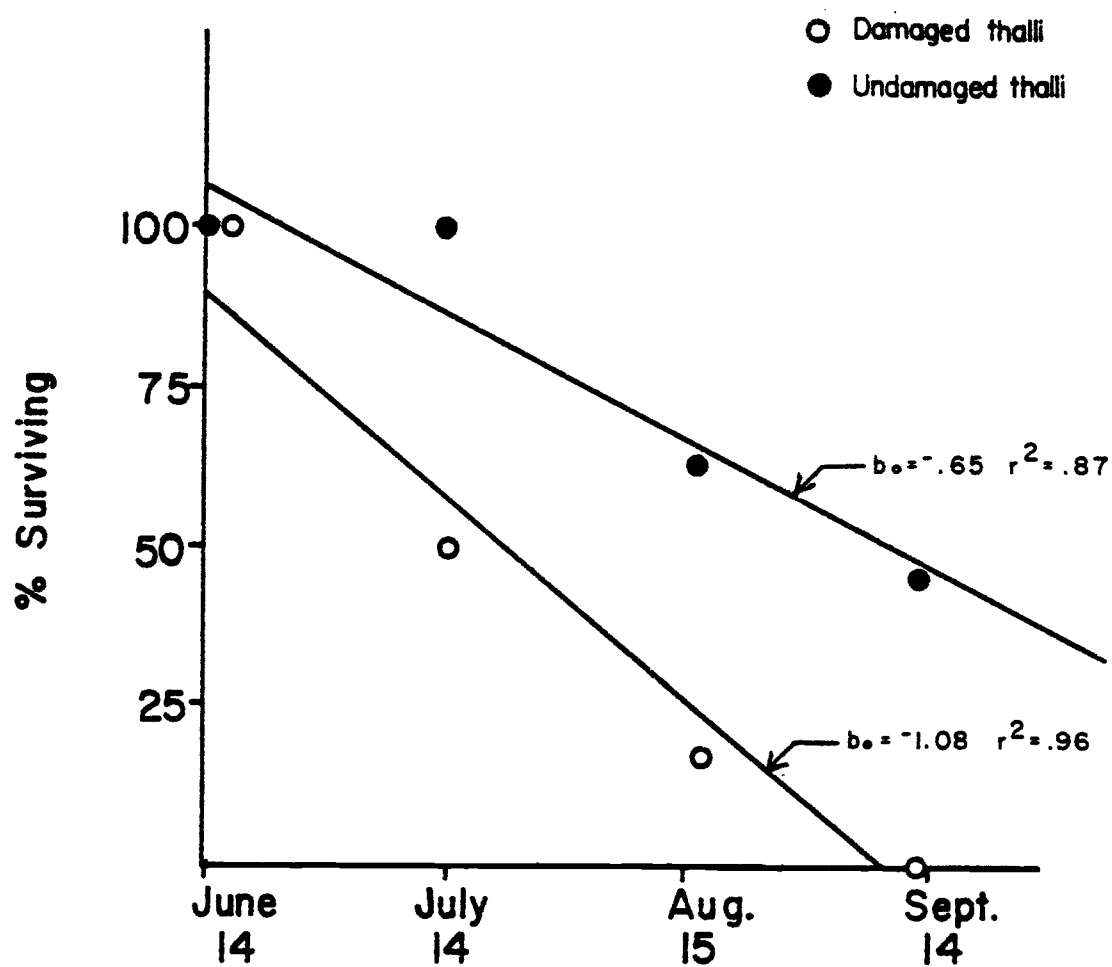


Figure 8. Growth of individual plants in the low zone.
A. Changes in total axis length for each plant.
Dashed lines indicate missing data points. Triangles
indicate the disappearance of entire plants. B.
Changes in the number of axes per plant.

Figure 8

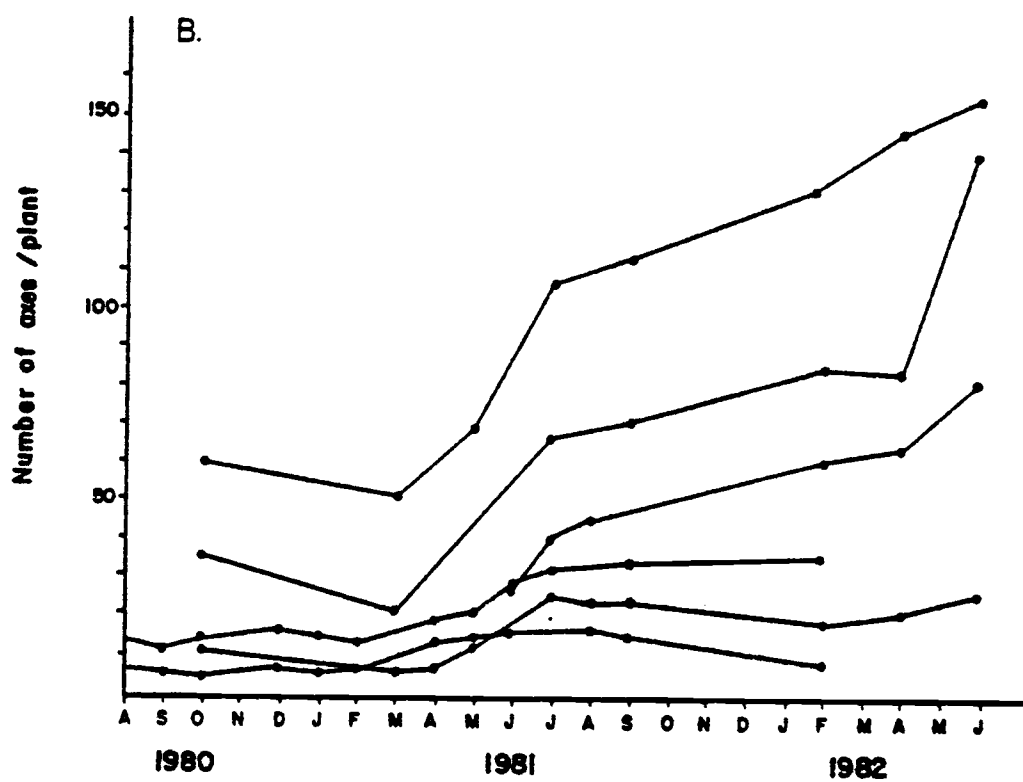
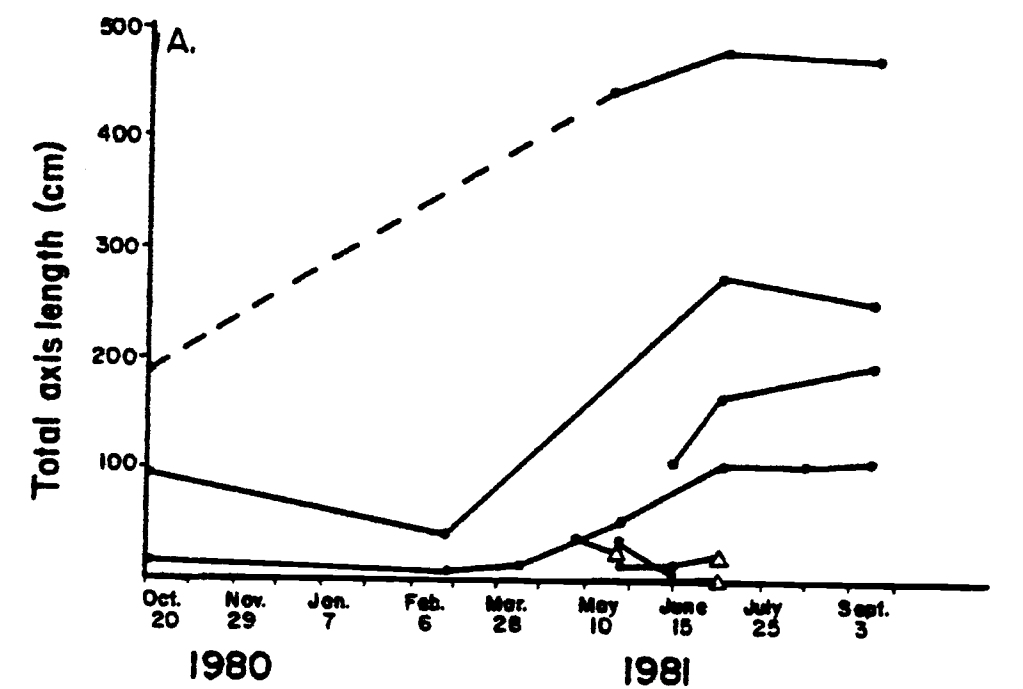


Figure 9. Horizontal expansion of Rhodomela larix patches in the low zone between June 1981 and April 1982. Solid lines indicate the location of patch edges in June 1981. -.-.- indicate positive changes and ---- indicate negative changes.

Figure 9

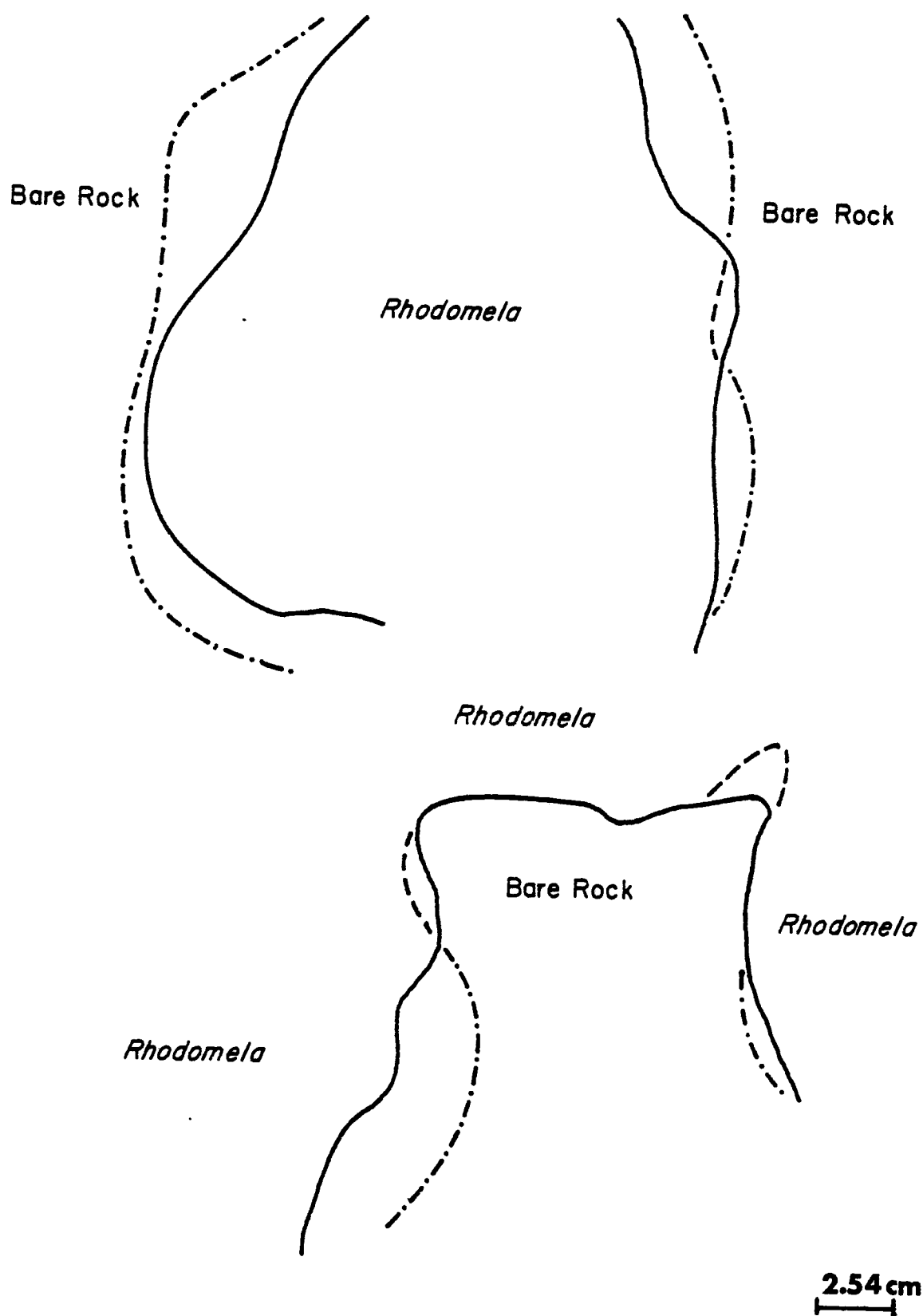


Figure 10. Seasonal changes in the occurrence of reproductive phases of Rhodomela larix. A(1). Mid zone data for randomly collected axes. A(2). Mid zone data for collections of axes with bunched branchlets present (these samples excluded juvenil axes or those axes containing only main axis branchlets). B(1). Low zone data for randomly collected axes. B(2). Low zone data for collections of axes with bunched branchlets present. For samples A(1) and B(1) percentages do not add up to 100 on the graphs because juvenile axes (i.e. axes with only main axis branchlets) are not presented.

Figure 10

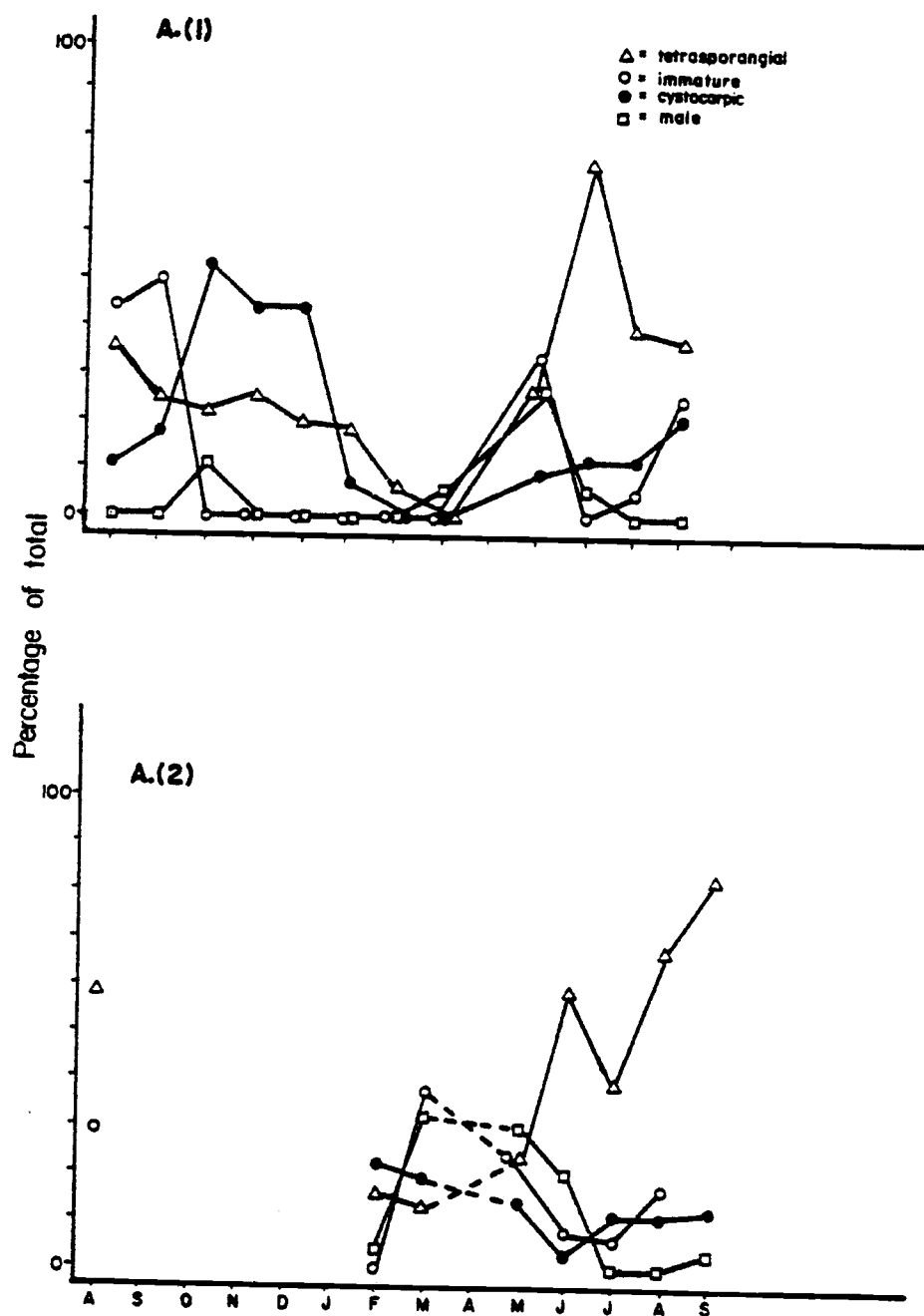


Figure 10

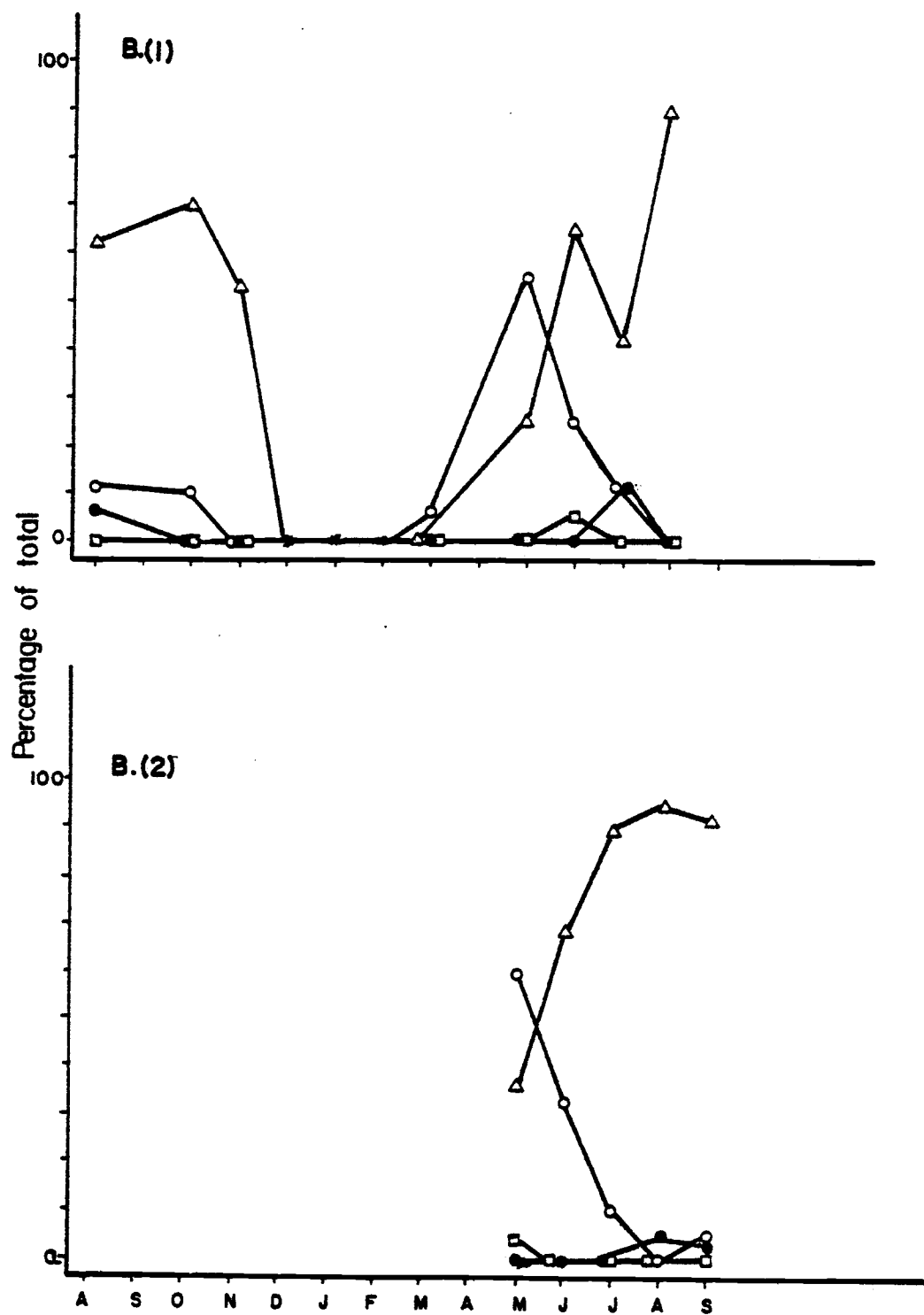


Table 1. Variability in maturation of tagged axes within individual plants in the low zone. All axes were of similar size when marked. Axes not becoming reproductive showed little or no growth. 1 = period over which markers remained in place.

Plant #	Time period ¹	#thalli marked*	potentially becoming repro.**
1	Dec. 10, 1980- April 7, 1981	10	3
1	July 16, 1981- Feb. 5, 1982	7	2
1	Feb. 23, 1982- May 26, 1982	14	6
2	Feb. 7, 1981- June 14, 1981	3	1
4	Dec. 10, 1980- April 7, 1981	8	2
4	June 15, 1981- Oct. 17, 1981	11	4
6	June 15, 1981- Oct. 17, 1981	6	2
A	Feb. 23, 1982- June 22, 1982	10	3
B	Feb. 23, 1982- June 22, 1982	8	2

* all thalli were under 5 cm and were not reproductive when marked

**developing clusters of bunched branchlets

Table 2. Maximum seasonal growth rates for individually tagged low and mid zone axes. All axes which experienced a net loss of tissue during the observation period were excluded from this analysis. Standard deviations are in parentheses. NS = not significant ($p > .05$) using a Mann-Whitney test. When the same letter appears next to two means, the rates of increase are significantly different from one another.

Season	n	Low Zone \bar{x} increase (cm) day ⁻¹	n	Mid Zone \bar{x} increase (cm) day ⁻¹	Between zone Comparison
Winter (Dec.-Feb.)	13	.0248 (.0476) a	12	.0074 (.0077) c	$p < .05$
Spring (March-May)	32	.1229 (.1024) a	9	.0518 (.0532) c	$p < .05$
Summer (June-Aug.)	33	.1077 (.1004) b	14	.0649 (.1270)	N.S.
Fall (Sept.-Nov.)	30	.0401 (.0670) b	39	.0293 (.0225)	N.S.

Table 3. Axis breakage rates in each season. n=total number of axes tagged within the zone during each season. N.S. = not significant. * major source of deviation due to fall samples.

	Frequency of axes with net tissue loss:		Between zone Comparison
	Low Zone	Mid zone	(Chi squared tests)
Winter (Dec.-Feb.)	.46 (n=26)	.50 (n=20)	N.S.
Spring (March-May)	.33 (n=80)	.34 (n=56)	N.S.
Summer (June-Aug.)	.40 (n=65)	.55 (n=66)	N.S.
Fall (Sept.-Nov.)	.76 (n=33)	.47 (n=40)	p < .02
Between season comparison	p < .005*	N.S.	

Table 4. Morphological characteristics of randomly collected axes during period of maximum growth. Between zone comparisons were done using the Mann-Whitney test because of unequal variances between samples. N.S. = not significant ($p < .05$).

Month	\bar{x} length(cm)	longest branch	Comparison	\bar{x} number branches per thallus	Comparison
	Low	Mid		Low	Mid
March	4.92(1.67)	3.85(0.85)	N.S.	0.70(0.92)	0.90(1.02)
May	7.20(1.94)	6.82(1.95)	N.S.	1.00(1.08)	6.65(8.49)
June	13.10(3.97)	7.36(2.90)	$p < .001$	7.42(6.60)	3.55(4.22)
July	9.50(4.00)	5.19(2.28)	$p < .001$	4.40(4.90)	3.94(4.00)
August	11.48(3.75)	4.37(1.73)	$p < .01$	6.00(5.25)	2.00(1.92)

Table 5. Growth pattern of transplants into the low zone during spring and summer 1981. Changes are expressed in percentages and represent increases in the total axis length present.

Origin of transplant	April-June	June-August
Mid zone	+62%	+6.7%
Mid zone	+44%	-3.3%
Low zone	+122%	+34%
Low zone	+172%	+36%

Table 6

Mean weight and height of (a) axes collected in October 1980 and (b) tetrasporophytes collected in June 1981. 1= Cystocarpic axes. Statistical comparisons were made using the Mann-Whitney test. N.S. = non significant ($p < .05$).

	(a). Within mid zone comparisons			(b) Between zone comparisons		
	Cystocarps ¹	Tetrasporophytes	difference	Low	Mid	difference
\bar{x} height(cm)	8.43	13.20	N.S.	35.06	14.43	$p < .01$
s	3.16	5.89		15.31	7.45	
n	6	5		13	13	
\bar{x} dry weight(g)	.1568	.2216	N.S.	.3495	.2473	N.S.
s	.0388	.1424		.1465	.1544	
n	6	5		13	13	

CHAPTER III.

Epiphytes on the Rocky Intertidal Red Algal Community

Rhodomela larix (Ceramiales): Negative effects

on the host and food for herbivores.

Abstract

The epiphytes associated with the red alga, Rhodomela larix, were examined by surveying intertidal areas for the presence of epiphytes, and by following changes in epiphyte cover in marked quadrats of R. larix. The alga is host for at least 17 species of sessile plants and animals. To determine the role of some of the larger epiphytes in the community, Rhodomela plants were marked and monitored and herbivore feeding was examined. Data indicate that epiphytes decrease the growth rate of their host, increase the probability of axis breakage and decrease reproductive output. Epiphytes provide food for littorine snails and gammarid amphipods that live in the beds of the plant. Amphipods were found to decrease epiphyte cover in laboratory tanks of R. larix, thus suggesting that these herbivores may have beneficial effects on the host plant.

INTRODUCTION

The presence of epiphytes has been noted in communities worldwide, however their role in the community has often been difficult to assess. In aquatic environments epiphytes have been found to contribute to the primary productivity of ecosystems (Brock 1970, Finke 1978, and Jones 1980), supply food for grazers (Randall 1964, Reyes-Vasques 1970, Berg 1974, Morgan 1980, Brawley and Adey 1981a, and Zimmermann et al., 1979), and decrease the growth rates of their hosts (Brawley and Adey 1981b, and Dixon et al. 1981). Several investigators have also suggested that the physical drag caused by high densities of epiphytes may decrease the survivorship of host plants (Lilly 1968, Menge 1975, Humm 1974, Yates 1981, Dayton et al., 1980) in particular in environments subject to moderate to severe wave action. Hence epiphytes may be important components of food webs while potentially decreasing fitness of the host plant.

In marine rocky intertidal communities space is often a limiting resource for sessile plants and animals (e.g. Connell 1961a, b, Paine 1966). This is particularly true in areas where disturbance agents are rare, allowing the monopolization of space by dominant plants or animals. In these habitats some organisms may be forced to grow as epiphytes. These epiphytes in turn may increase the resistance of the host plant to water movement, eventually pulling up both the host plant and adjacent or attached plants. This effect may be amplified in perennial plants which acquire increasing numbers of epiphytes with age.

On the central Oregon coast, moderately exposed intertidal benches are characterized by a high percent cover of algae and surfgrass. The red alga Rhodomela larix occurs abundantly in these areas and together with the surfgrass, Phyllospadix scouleri, dominates space in the low intertidal. Both species are perennial, resulting in low seasonal variability in the space available for colonization. Artificial removal of R. larix and P. scouleri resulted in rapid colonization of newly cleared space by several species of plants and animals (Turner 1982, D'Antonio, unpublished), suggesting that space is a limiting resource in these environments. Thus algae which have the ability to exist as epiphytes may persist in these habitats, and those occupying the rock surface itself may be subject to a high degree of fouling.

The following study was conducted to examine the community of epiphytes associated with Rhodomela larix. While a large number of flora and fauna have been found to use Phyllospadix scouleri as a host (Harlin 1971), the occurrence of epiphytes on R. larix and the role of epiphytes in communities dominated by R. larix has received little attention. Preliminary observations suggest that the alga is colonized by a variety of species including several that are often are saxicolous. Here I will examine (1) the temporal and spatial distribution and abundance of these epiphytes, (2) the influence of selected epiphyte species on the growth, reproduction and survivorship of R. larix axes and (3) the potential role of epiphytes as a food source for invertebrates.

Description of the host

Rhodomela larix is a turf-forming red alga with an upright and irregularly branching morphology (Chapter 2, Fig. 1). Erect axes as much as 30 cm long arise from a small perennating basal holdfast. New axes are added to a plant each year and several axes within a plant grow to reproductive maturity during the spring and summer. These axes are gradually beaten back or torn loose by winter storms. Because basal cells of adjacent axes are fused, axes are often removed in small clumps (pers. obs.). However, if the erect portion of a thallus is broken off rather than pulled up from the base the remaining attached portion may persist throughout the following spring and summer (Chapter 2). Preliminary data suggests that individual axes may live one to three years while the boundaries of R. larix clumps may be maintained for > 25 years (J. Peterson, pers. comm., Univ. of Oregon).

Study Sites

The occurrence of epiphytes on R. larix was monitored at two intertidal sites, on the central Oregon coast (Chapter 2, Fig. 2). Both sites were located within Boiler Bay, a north facing bay, one mile north of Depoe Bay, Oregon (lat. 44°50'N). Site 1 is a sloping mudstone shelf where R. larix is present between 1 and 1.5 m above mean low water. The shelf is directly exposed to wave action in winter storms and is exposed to prolonged emersion during summer low tides. Site 2 is located directly west of site 1 and is a horizontal shelf between 0 and .7 m

above mean low water. The R. larix populations sampled were around +.5 m. The area received moderately intense wave action and severe sand scour throughout the winter (Chapter 4). A third site Strawberry Hill (lat. 44° 15'16'') was visited irregularly throughout the study to monitor the presence of epiphytes and for some of the diatom studies. Strawberry Hill is an extensive intertidal habitat characterized by basaltic rock outcroppings and horizontal benches. The main bed of R. larix studied is approximately .5 m above mean low water. The site is subject to seasonal sand depositions (Chapter 4) and moderate wave action.

In addition, 23 sites in Oregon and northern and central California were surveyed during September 1981 for the presence of epiphytes on Rhodomela.

METHODS

To quantify the occurrence of epiphytes on R. larix, 20 axes were randomly collected along horizontal transects at both of the Boiler Bay sites between August 1979 and November 1982. The presence and location of all epiphytes was noted at each sampling date. Large epiphytes were removed from thalli using watchmaker's forceps and dried with their hosts at 90°C for 2 weeks. At this time the weight of epiphytes relative to their host was determined. The biomass of small epiphytes, such as crustose coralline algae, blue green algae and diatoms could not be determined although a subjective scoring procedure was used to estimate the relative abundance of these algae between months. The presence of macroscopic epiphytes was quantified in eight marked quadrats in the low zone and four marked quadrats in the mid zone each month between April 1981 and July 1982. The percent cover of epiphytes within these 900 cm² quadrats was estimated by counting the percent of 100 randomly placed dots falling on each species (Menge 1976).

To estimate the effect of large epiphytes on the survivorship of Rhodomela thalli, individual axes with and without epiphytes were marked using monofilament line and colored plastic beads. Bracelets were tied around the base of each axis as close to the holdfast as possible. Studies were conducted on two sets of R. larix thalli: (1) those with Ceramium sp. and Ulva sp. epiphytes and (2) those with the chain-forming diatom Isthmia nervosa epiphytes. The first set of plants was marked in mid August 1981 when epiphyte abundance was high and many axes were reproductively mature. Changes in the amount of tissue present were

compared between the two types of axes during August and September. Many of the axes which had a high cover of epiphytes at the start of the observation period broke off below the level at which the epiphyte(s) was present. These were no longer considered axes with epiphytes and were added to the axes without epiphytes column in the survivorship graph. For plants with epiphytes, survivorship was estimated as the percent of axes present which had epiphytes at the previous observation time. Survivorship of plants without epiphytes was estimated as the percent of axes present that at the previous observation time did not contain epiphytes. The second set of plants was marked in the low zone at Strawberry Hill in May 1982. Axes with and without epiphytes were marked and followed for two months. Differences in mean percent growth were then compared between treatments.

To obtain an indication of the effect of epiphytes on the reproductive output of the host, axes with and without epiphytes were collected from an area with dense Ulva sp. at Boiler Bay. Epiphytes were removed by hand from the epiphyte group with watchmakers forceps and the length of reproductive tissue present on the host estimated by measuring the length of the main axis containing reproductive branchlets. Measurements were taken of the total plant length, and the length of mature versus immature reproductive tissue. Thalli were collected in late August and again in mid September. After separation both epiphytes and host plants were dried at 90°C for two weeks. In September the reproductive portions of both groups of axes were separated from the remaining portion before weighing. The percentage of total axis length that was reproductive and the weight of that tissue

per cm of reproductive tissue present was compared between plants with and without epiphytes.

To examine the potential importance of epiphytes as food for invertebrates in beds of R. larix, fecal pellet and gut content analyses were carried out on the most common invertebrates found in these beds (for a list of associated species see Appendix I). These included the herbivorous gastropods Littorina scutulata and Lacuna marmorata and two species of gammarid amphipods (Ampithoe simulans and Parallorchestes ochotonis). Animals were collected from R. larix in the field and placed in a small vial of seawater for up to four hours. At this time several fecal pellets from each snail were placed on a microscope slide and examined under 400X. Analyses were carried out at a time when the herbivores and several of their potential epiphyte food sources were common. For littorines this analysis was in July and August 1979 and July 1982. For Lacuna marmorata analyses were conducted in November from animals found on plants heavily encrusted with Isthmia nervosa, coralline crusts and Dermocarpa sp. and tufts of Microcladia borealis and Plocamium sp.

The most abundant macroinvertebrates in beds of Rhodomela larix are gammarid amphipods. At least three species are present during the late summer and fall but only the largest species (Amphithoe simulans) is present most of the year. The gut contents and fecal pellets of amphipods consisted largely of unidentifiable amorphous material; hence two laboratory experiments were conducted to determine the interaction between amphipods, R. larix and its epiphytes.

In the first experiment large numbers of amphipods were collected from Rhodomela larix sprigs at Seal Rock, Oregon in mid August 1981. Animals were collected by briefly holding the sprigs under running freshwater. This causes them to move to the outer portions of the plant where they are easily dislodged by shaking. Amphipods were kept in aerated containers of seawater overnight while the experimental apparatus was assembled. Two 10-gallon aquaria were partitioned into quarters using 1 mm nylon mesh. Both tanks were fed from the same line of the Oregon State University Marine Science Center open seawater system, and both were aerated in two corners with gravel filters (Fig. 11). A timed ultraviolet grow lamp was suspended above and between the tanks to coincide with ambient daylight hours. The tanks were partially submerged in cold seawater to insulate them from temperature fluctuations. Eight experimental plants were collected from Seal Rock, Oregon, using a hammer and chisel to remove a portion of the substrate bearing the basal holdfast of the plants. All rocks were collected along a 30 m transect at approximately +.6 m, matched for number and size of sprigs, and randomly assigned to treatments. Every rock contained five thalli greater than 5 cm in length, up to 19 smaller thalli, a light to moderate covering of the chain-forming diatom Isthmia nervosa and a moderate cover of the blue-green epiphyte Dermocarpa sp. The four experimental rocks were dipped into containers each holding approximately 100 amphipods. The plants act as a 'magnet' for the crustaceans, which quickly settle into the plants. Plants were removed after 10 days from their respective sectors, and monitored for numbers and species of epiphytes, general condition, and percent coverage by

diatoms. Diatom coverage was estimated subjectively by examining the six tallest sprigs from each plant under a 20X dissecting scope against a .5 cm linear grid. In each .5 cm section the coverage of diatoms ranked as (0) Absent, (1) Low, (2) Moderate, and (3) Heavy depending on the amount of Rhodomela tissue covered and the density of the diatoms. Any epiphytes present were noted as well as the state of the plant in terms of coverage by main axis branchlets.

The second experiment was performed simultaneously to more closely assess the impact of amphipods on the Rhodomela itself. Individual sprigs were collected and separated into two sections: (1) upper portions containing reproductive bundles and branchlets surrounding them and (2) lower portions containing main-axis branchlets only. All plant portions were examined under a dissecting scope to count the number of damaged versus undamaged branchlets for each section and to estimate diatom cover. Sprigs were weighed after damp-drying for 60 sec. with a bath towel, then randomly assigned to treatments. Six individuals of the amphipod species Parallorchestes ochotonis, commonly found on Rhodomela, were placed in each experimental vial, while the control group did not receive herbivores. Plants were set into chambers 2.5 cm wide by 4 cm tall, covered with 1 mm nylon mesh, and placed in an aerated running seawater tank for 10 days. After this time all axis portions were examined for damage to branchlets and diatom cover, and damp-weighed to quantify alterations in biomass of tissue present.

RESULTS

Timing and distribution of epiphytes

Rhodomela is host for a large variety of both plant and animal epiphytes and many of these epiphytes were found on Rhodomela over a large geographic range (Table 7). Although numerous epiphyte species occur on R. larix, only a few commonly reach a large size relative to their host (Table 8). Of the epiphytes found on the plant more than half are commonly saxicolous. Most the remaining species do not appear to be obligate epiphytes on R. larix(pers. obs.). Thus Rhodomela larix supports a diverse array of epiphytes although few of these appear to have evolved as specialists on Rhodomela.

Examination of plants carrying epiphytes revealed that several epiphytes take up very characteristic positions on their host (Table 7). Plocamium sp. for example was always found within 3.5 cm of the base of an axis whereas Ulva sp. grew in sheets with small areas of attachment along the main axis. Halosaccion glandiforme and Leathesia were found primarily along the upper erect portions of thalli attached to the main axis. Although erect axes frequently had epiphytes on the main axis and nearby large branchlets, very few epiphytes were found on reproductive structures of mature Rhodomela. Most axes in the low zone contained blue green algal epiphytes and scattered patches of coralline crusts, but rarely did a single axis contain more than one of the erect epiphyte species.

The distribution of epiphytes appeared to be affected by tidal height. Very few macroscopic epiphytes were observed in the higher Boiler Bay site (site 1), and those that settled in the early summer suffered severe exposure damage by July. Plants in the low zone had the most epiphytes in later summer before the onset of fall storms (Fig. 12). By late December 1981, the epiphyte Ulva sp. and many of the smaller macroscopic epiphytes, such as Leathesia nana and Ceramium sp were gone from the area. The remaining macroscopic epiphytes tended to be those which either grew near the base of the thallus or in close proximity to the central axis. In this zone, only the coralline crust, the blue green alga Dermocarpa sp. and small amounts of Microcladia borealis and Plocamium sp. persisted throughout the winter.

The spatial distribution of many epiphyte species was patchy. For Ulva, Leathesia and Ceramium this patchiness is reflected in the large standard deviations in Figure 12. For example, in August 1981 the percent cover of Ulva varied from 0 in four quadrats to more than 60 percent in three others. Several other species appeared to have patchy distributions but could not be quantified in the permanent quadrat study. These included Microcladia borealis, Plocamium sp., and the diatom Isthmia nervosa. During the period of this study these species were uncommon in the permanent quadrats although present and often abundant as epiphytes on R. larix in other regions of the Boiler Bay intertidal.

Growth, Survivorship and Reproduction

Both chain-forming diatoms and upright fleshy eiphytes appeared to negatively affect the growth and persistence of R. larix thalli. A significantly larger proportion of axes with heavy encrustations of I. nervosa lost tissue between May and June, and between June and July 1982, than did unfouled axes (Table 9A.). Considering only those axes that grew, fouled axes grew at a much slower rate (Table 10). The same trend was evident between August and September 1981 for those axes fouled by Ceramium sp. and Ulva sp. (Table 9B.). For this group plant size was negatively correlated with rate of tissue loss ($r^2=.50$, $b=-2.5$, $p < .05$). To account for this relationship and to compare fouled and unfouled axes, plants were paired on the basis of their size at the outset of the observation period. Axes without epiphytes either grew more or lost less tissue than those with epiphytes between mid August and mid September (Table 11). Between September and October the same trend was evident although most plants in both categories lost tissue during this time period (Table 7).

The survivorship of axes without epiphytes was greater over a 3-month period than those with epiphytes (Fig. 13). Both curves are best fitted by a linear regression and the slope of the two lines are significantly different ($t = 21.53$, $p < 0.05$). No axes previously without epiphytes acquired them during the survivorship study, and axes that lost their epiphytes were lumped with those that never had epiphytes.

Examination of plants with Ulva sp. epiphytes indicated that axes without epiphytes are longer and weigh significantly more than axes with epiphytes (Table 12). Furthermore, a larger percent of their total tissue length was reproductive (Fig. 14) and the per centimeter weight of this tissue was greater (Table 12). Although these data do not demonstrate a causal relationship, they do suggest that epiphytes negatively influence the development of host reproductive tissue.

Feeding Studies

Littorines are abundant throughout the year but appear to be concentrated mainly in the higher zone (Appendix I). An examination of L. scutulata fecal pellets revealed that these snails graze both cell layers of R. larix and small pennate diatoms on the surface of the plant (Table 13). 100% of all pellets contained pennate diatoms while only 76% contained Rhodomela. Of the pellets containing Rhodomela more than half contained clusters of undigested Rhodomela cells (Table 13). Two pellets contained colonies of the blue green epiphyte Dermocarpa sp. but no other epiphytes were present in the pellets of the snails. Hence pennate diatoms are the only epiphytes which are eaten in any quantity by L. scutulata and appear to be a large part of their diet.

The gastropod Lacuna marmorata is abundant in the intertidal throughout the later summer, fall, and winter yet appeared to utilize Rhodomela larix itself as a food source, rather than any of its epiphytes. The fecal pellets of individual snails were very consistent in their content. All pellets examined, even those examined from snails

collected from R. larix encrusted with Isthmia nervosa contained a large amount of Rhodomela-like cells and few diatoms (Table 13). Of the 36 pellets examined, five contained a mass of cells of an unknown alga although the majority of the fecal material was R. larix. Since R. larix was the only saxicolous alga present where the snails were collected, these unidentified groups of cells probably belonged to epiphytic algae. However the low abundance of these epiphytes in the fecal samples indicates that snails are probably not actively foraging for the epiphytes but may graze them if encountered.

Amphipod Feeding Experiments

Laboratory experiments indicated that amphipods can exert strong grazing pressure on both Rhodomela and the epiphyte Isthmia nervosa. Coralline crust epiphytes did not appear to be affected by the amphipod grazing; while Dermocarpa sp., which was in low to moderate abundance on all plants before the experiments, was virtually absent from all axes with amphipods at the end of the experiments.

In the first experiment, plants without amphipods acquired a conspicuous cover of Isthmia nervosa during the 10-day experiment. This cover differed significantly from that found on thalli exposed to amphipods (Fig. 15, $p < .05$). Since the cover of diatoms was equivalent (approx. 1.5) on all axes at the outset of the experiment, subsequent observations were due to experimental effects. In addition, three sprigs in the plants without amphipods bore tufts of Plocamium sp., and 2 had tufts of Ulva sp. at the beginning and end of the experiments. In

contrast, scattered tufts of Microcladia borealis and Plocamium sp. initially present in thalli exposed to herbivores disappeared by the end of the experiment.

The erect axes of R. larix themselves were severely damaged by amphipod grazing. Several of the axes from the tanks with amphipods broke during the diatom scoring procedure and most of the longer sprigs had lost their main axis branchlets. However, mature carpogonia were apparent on grazed axes and appeared undamaged. Because I did not score the amount of reproductive tissue present before and after the experiment, I cannot quantify effects induced by the amphipods; nonetheless, it appeared that carposporophyte development was accelerated in those thalli which had been exposed to the amphipods and that amphipods do not consume the mature cystocarp structures.

In the second experiment, control vials became contaminated by small amphipods. Therefore, I designed an herbivore index based on the ratio of three small (carapace length, 1.5 mm) amphipods to one large amphipod (carapace length \geq 3 mm) using large amphipod equivalents as an index. A significant linear regression existed between level of herbivory (herbivore index) and the change in amount of plant tissue present for the upper sections of plants ($r^2 = .67$, $b = 2.1$, $p < 0.5$). Amphipods destroyed significantly more of the upper portion of the plants than the lower portions ($t = 3.38$, $p < .02$). This difference was also reflected in a difference in the mean percent of main axis branchlets that were damaged between upper and lower portions before and after exposure to herbivores ($t = 6.51$, $p < .005$). The percent cover of diatoms also decreased in the upper sections of the plants with herbivores present

(Table 14). Herbivore density and change in diatom cover were significantly correlated ($r^2=.75$, $b=.65$, $p < .05$). The two plants that remained uncontaminated by small amphipods had approximately the same percent cover of diatoms after the experiment as before.

DISCUSSION

R. larix serves as a host for a large variety of algal species, many of which are potential space competitors. These species may reach a large size relative to their host (Table 8) and appear to negatively affect the growth and survivorship of individual axes. Similarly, many marine investigators have shown that epiphytes may cause decreased growth rates or loss of entire fronds of algae (Humm 1964, Wing and Clendenning 1971, Lobban 1978, Dixon et al. 1981, Harkin 1981).

The distribution of epiphytes was found to be spatially and temporally variable (Fig. 12). The spatial variability suggests (1) that algal spores settle in groups and/or (2) that patches of Rhodomela vary in their susceptibility to specific epiphytes. Within a given year a single R. larix clone may contain many axes with epiphytes. Thus, the effects of epiphytes on a single axis may reflect the effects on the entire individual plant.

Because of the potentially large effect of epiphytes on host growth and subsequent reproduction, the timing of epiphyte attachment is crucial to the potential reproductive output of a given thallus. Reproduction in Rhodomela larix begins in the late spring and continues into the fall. A heavy epiphyte cover early in the year may prevent the development of reproductive tissue, as occurred with axes encrusted with Isthmia nervosa. Axes that acquire epiphytes during mid and late summer may already have reproductive structures but will probably acquire little additional reproductive tissue and have a higher probability of breakage than those without epiphytes. Epiphytes acquired in the fall

and winter will probably have a less dramatic effect unless they persist at a great enough size to prevent growth of their host in the spring.

It is difficult to assess the role of epiphytes in contributing to the formation of bare patches in R. larix beds. Manipulative studies are needed to demonstrate this relationship. Patches of bare space appear in Rhodomela beds in the winter (Chapter 4), and I have observed that the pulling up of one erect axis can result in the removal of a patch of axes. It is therefore conceivable that epiphytes, by increasing the probability that an axis will be pulled up or broken off, contribute to the creation of bare space within Rhodomela monocultures. These spaces are then available for colonization by other algae. A similar mechanism has been suggested to help explain the diversity of trees in tropical rainforests (Strong 1976). Several investigators have reported heavy epiphyte loads on tropical trees (see Strong 1976 for a review), and Strong suggests that these plants contribute to high tree fall rates, therefore opening up space for colonization or growth of understory seedlings.

The observation that reproductive structures of R. larix are generally free of epiphytes is consistent with several hypotheses. Ballantine (1979) found that epiphyte species composition and abundance decreased with proximity to meristematic regions in several species of tropical algae. He suggested that this pattern was due to a difference in exposure time to the environment, between young and old portions of a plant. Decreased exposure may result in less alteration of plant surfaces and as a consequence, greater resistance to fouling. However, these results might also be explained by a differential distribution of

anti-fouling compounds within the host plant. Sieburth and Conover (1965) suggest that antibiotic substances produced in active meristematic regions may account for observed epiphyte distributions in two species of Sargassum. In R. larix, the distribution of brominated phenols, suspected to have anti-fouling capability, is not uniform throughout all plant tissues (Phillip and Towers 1982): Reproductive structures contain higher levels of phenolic compounds than non-reproductive regions. However, in R. larix several epiphytes do settle on portions of the main axis adjacent to reproductive structures (Table 7) suggesting that the distribution of anti-fouling compounds, if they exist, is very localized.

Epiphytes as Food

Epiphytes within Rhodomela beds are an important source of food for the gastropod L. scutulata and the gammarid amphipods. These herbivores apparently consume primarily epiphytic diatoms. The chain-forming diatoms consumed by the amphipods, in turn may decrease the growth rates of R. larix. Thus grazing may help to eliminate detrimental epiphytes.

While littorine snails did consume epiphytic pennate diatoms, a large percentage of the fecal pellets I examined contained Rhodomela cells. Previous investigators have shown that in general Littorina scutulata populations survive mainly on diatoms (North 1954, Foster 1964, Dahl 1964, Behrens 1971). However, these studies have generally been done in areas where very little macroalgae is present. Dethier

(1982) found that tidepool populations of littorines preferred grazing on R. larix over several other algal species, although she does not characterize the basis for this "preference". Littorines may prefer to "associate" with Rhodomela for a number of reasons including both food and shelter, and graze diatoms off of the surface of the alga consuming macroalgae in the process. My observation that a large number of fecal pellets contained undigested Rhodomela cells, suggests that littorines may have a low assimilation efficiency on Rhodomela. Thus diatoms may be an important source of nutrition for snails living in Rhodomela beds.

That littorines have a significant effect on the growth of diatoms on R. larix is supported by several observations. In a bed of R. larix littorines are often dense, yet the algae do not show signs of being damaged. Fecal pellets from these snails contain a high percentage of diatom matter suggesting that littorines may affect diatom abundance (Table 13). In addition Castenholz (1961) demonstrated that L. scutulata could control the abundance of diatoms in intertidal pools in the spring and summer on the Oregon coast, and Behrens (1971) demonstrated a similar situation on emergent substrate on San Juan Island, Washington. Thus it is conceivable that littorines may greatly influence the growth of epiphytic diatoms on R. larix.

Many recent studies have demonstrated the effect of amphipod grazing in marine environments (Brenner et al., 1976, Young and Young 1978, Zimmerman et al. of 1979, Brawley and Adey 1981a). With the exception of Brenner et al., 1976, investigators have found that amphipods graze a variety of epiphytic filamentous algae. However the actual effects of the amphipods on in situ communities have not been easily measured

because of the difficulty of manipulating these small crustaceans. Because amphipods are highly mobile but could move only a limited distance in my laboratory tanks, the experimental densities I used may have been effectively much higher than those found under natural conditions. Hence the negative effect of the amphipods on R. larix, observed in the laboratory, may have been an artifact of the lab setup. Although field densities of amphipods can be quite high (Appendix I), they may migrate between clumps of macroalgae after lowering the density of their favored food items. Thus in situ amphipods may increase macroalgal growth rates by removing epiphytes without causing significant damage to the host plant.

The decline in abundance of the blue green algal epiphyte, Dermocarpa sp., observed in the amphipod study may result from amphipod grazing. Several investigators have examined the influence of amphipods on blue green algae with somewhat contradictory results. A salt marsh amphipod, Talorchestia longicornis, was found to graze heavily on blue green algae (Brenner et al., 1976). Other studies have shown that amphipods either avoided blue green algae or that these algae pass undigested through their guts (Hargrove 1970, Moore 1975, Brawley and Adey 1981a). In this study amphipods appeared to consume the Cyanophyta, but I was not able to determine their ability to digest the algal material. Blue green algal cells can pass undigested through the gut of several gammarid amphipod species, and some showed up to a 20% survival rate after excretion (Moore 1975).

Epiphytes may indirectly cause damage to host tissues by attracting predators such as amphipods which damage the host while preying on the

epiphytes. This situation has been described for carnivorous fish grazing on bryozoan epiphytes on kelps. Fish preferred kelp blades with dense coverings of the bryozoan and severely damaged the kelp while preying on the epiphytes (Bernstein and June 1979). Goff and Cole (1976) have suggested that grazing by isopods and amphipods increases the susceptibility of R. larix to parasitism by the red alga Harveyella mirabilis. Thus, the possibility that epiphytes attract amphipods or other grazers, which then have a negative effect on the host plant needs to be explored.

Further Considerations

It is difficult to assess factors which determine the susceptibility of a given algal species and a given thallus to epiphytes. The lack of information on epiphyte species associated with other major algal species on the Oregon Coast, hinders a comparison of epiphyte diversity and abundance on R. larix with epiphytes in other local communities. Casual observations of Odonthalia lyalli, a closely related species with a very similar morphology, which often occurs in close proximity to R. larix suggests a comparatively depauperate epiphyte community. A more detailed comparative study could provide valuable information on the importance of such factors as life history, morphology, and biochemistry in governing susceptibility to epiphitism.

SUMMARY AND CONCLUSIONS

A study of the epiphytes associated with the perennial red alga Rhodomela larix indicated that, (1) the alga is colonized by at least 17 species of plants and animals, (2) these species vary in their morphology, size and distribution, (3) epiphytes were most common in the late summer and declined in abundance during the fall, and (4) at least three species negatively affect the growth, reproduction and/or survivorship of individual R. larix axes. In addition several species of invertebrates utilized both Rhodomela and some of the epiphytes as food.

Additional studies are needed to assess long term effects of epiphytes on R. larix. It is conceivable that epiphytes, by increasing the probability of mortality of their host, accelerate successional sequences. In addition epiphytes may increase species diversity in communities otherwise dominated by one or two species.

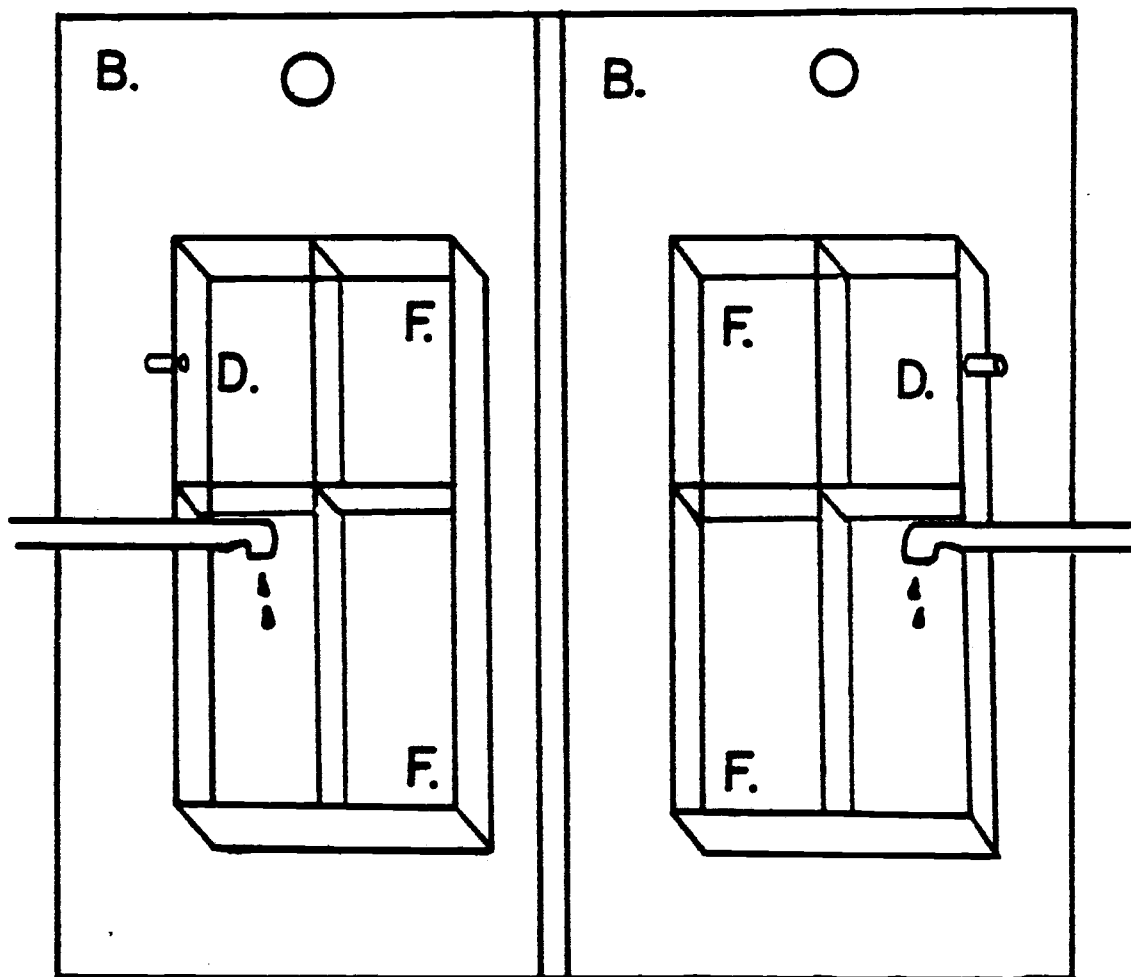
REFERENCES

- Ballantine, D.L. 1979. The distribution of algal epiphytes on macrophyte hosts offshore from La Parguera, Puerto Rico. *Bot. Mar.* 22: 107-111.
- Behrens, S. 1971. The distribution and abundance of the intertidal prosobranchs Littorina scutulata (Gould 1849) and L. sitkana (Philippi 1845). MS Thesis. Univ. of British Columbia.
- Berg, C.J. Jr. 1974. A comparative ethological study of strombid gastropods. *Behavior* 51: 274-322.
- Bernstein B. and M. Jung. 1979. Selective pressures and coevolution in a kelp canopy community in Southern California. *Ecol. Monogr.* 49: 335-355.
- Brawley, S. and W. Adey. 1981a. The effect of micrograzers on algal community structure in a coral reef microcosm. *Mar. Biol.* 61: 167-177.
- Brawley, S. and W. Adey. 1981b. Micrograzers may affect macroalgal density. *Nature* 292: 177.
- Brenner, D., I. Galiela, C. van Raalte and E. Carpenter. 1976. Grazing by Talochestia longicornus on an algal mat in a New England salt marsh. *J. Exp. Mar. Biol. Ecol.* 22: 161-169.
- Brock, T.D. 1970. Photosynthesis by algal epiphytes of Utricularia in Everglades National Park. *Bull. Mar. Sci.* 20(4): 952-956.
- Castenholz, R.W. 1961. The effect of grazing on marine littoral diatom populations. *Ecology* 42: 783-794.
- Connell, J. 1961a. The influence of interspecific competition and other factors on the distribution of the barnacle Chthamalus stellatus. *Ecol.* 42: 710-723.
- Connell, J. 1961b. Effects of competition, predation by Thais lapillus, and other factors on natural populations of the barnacle Balanus balanoides. *Ecol. Monogr.* 31: 61-104.
- Dahl, A.L. 1964. Macroscopic algal foods of L. planaxis Philipps and L. scutulata Gould (Gastropoda: Prosobranchiata). *Veliger* 7(2): 139-143.
- Dayton, P.K., B.D. Keller, and D.A. Van Tresca. 1980. Studies of a nearshore community inhabited by sea otters. U.S. Marine Mammal Conference, Final Report No. MMC-78/14.

- Dethier, M. 1982. Pattern and process in tidepool algae: Factors influencing seasonality and distribution. *Bot. Mar.* 25: 55-66.
- Dixon, J., S. Schroeter and J. Kastendiek. 1981. Effects of the encrusting byrozoan, Membranipora membranacea, on the loss of blades and fronds by the giant kelp Macrocystis pyrifera (Laminariales). *J. Phycol.* 17: 341-345.
- Finke, L.R. 1978. Nitrogen fixation (acetylene reduction) by epiphytes of freshwater macrophytes. *Appl. Environ. Microbiol.* 36(1): 129-135.
- Foster, M.S. 1964. Microscopic algal food of Littorina planaxis Philippi and Littorina scutalata Gould (Gastropoda: Prosobranchiata). *Vel.* 7(2) 149-152.
- Goff, L. and K. Cole. 1976. The biology of Harveyella mirabilis (Crytonemiales, Rhodophyceae). IV. Life history and phenology. *Can. J. Bot.* 54: 281-292.
- Hargrave, B. 1970. The utilization of benthic microflora by Hyaella azteca (amphipoda). *J. Anim. Ecol.* 39: 427-437.
- Harkin, E. 1981. Fluctuations in epiphyte biomass following Laminaria hyperborea canopy removal. Xth Internatl. Seaweed Symposium Proceedings. 303-308.
- Harlin, M. 1971. Epiphytic marine algae: Interactions with their hosts. Ph.D. Thesis, Univ. of Washington.
- Humm, J.H. 1964. Epiphytes of the sea grass, Thalassia testudinum, in Florida. *Bull. Mar. Gulf Carib.* 14(2): 306-341.
- Jones, R.C. 1980. Productivity of algal epiphytes in a Georgia salt marsh: Effect of inundation frequency and implications for total marsh productivity. *Estuaries* 3(4): 135-317.
- Lilly, G.R. 1968. Some aspects of ecology of Irish Moss, Chondrus crispus (L). Stack., in Newfoundland waters. *Fish. Res. Bd. Can. Tech. Rep.* 43.
- Lobban, C.S. 1978. Growth of Macrocystis integrifolia in Barkley sound, Vancouver, IS., B.C. *Can. J. Bot.* 56: 2707-11.
- Menge, B.A. 1976. Organization of the New England rocky intertidal community: Role of predation, competition and environmental heterogeneity. *Ecol. Monogr.* 46:355-393.
- Menge, J.L. 1975. Effects of herbivores on community structure of the New England rocky intertidal region: Distribution, abundance and diversity of algae. Ph.D. Thesis. Harvard University.

- Moore, J. 1975. The role of algae in the diet of Asselus aquaticus L. and Gammarus pulex L. J. Anim. Ecol. 44: 719-730.
- Morgan, M.D. 1980. Grazing and predation of the grass shrimp Palaemonetes pugio. Limnol. & Oceanogr. 25(5): 896-902.
- North, W.J. 1954. Size distribution, erosive activities, and gross metabolic efficiency of the marine intertidal snails, Littorina planaxis and L. scutulata. Biol. Bull. 106: 185-197.
- Paine, P.T. 1966. Food web complexity and species diversity. Am. Nat. 100: 65-75.
- Phillips, D.W. and G.N. Towers. 1982. Chemical ecology of red algal bromophenols. I. Temporal, interpopulational and within-thallus measurements of lanosol levels in Rhodomela larix (Turner) C. Agardh. J.E.M.B.E. 58: 285-293.
- Randall, J.E. 1964. Contributions to the biology of the queen conch, Strombus gigas. Bull. Mar. Sci. Gulf & Carib. 14(2): 246-295.
- Reyes-Vasquez, G. 1970. Studies on the diatom flora living on Thalassia testudinum König in Bicayne Bay, Florida. Bull. Mar. Sci. 20(1): 105-134.
- Sieburth, J.M. and J.T. Conover. 1965. Sargassum tannin, an antibiotic which retards fouling. Nature 208(1-5): 52-53.
- Strong, D.R. 1977. Epiphyte loads, tree falls, and perennial forest disruption: a mechanism for maintaining higher tree species richness in the tropics without animals. J. Biogeogr. 4: 215-218.
- Turner, T. 1982. Community organization and succession in rocky intertidal Surfgrass beds. Ph.D. Thesis, OSU.
- Wing, B. and K. Clendenning. 1971. Kelp surfaces and associated invertebrates. In North, W.J. (Ed.). The Biology of Giant kelp beds (Macrocystis) in California. Nova Hedwigia 32: 319-341.
- Yates, K. 1981. A limpet kelp interaction: Description and definition. Masters Thesis, Oregon State University.
- Young, D. and M. Young. 1978. Regulation of species densities of sea grass associated macrobenthos: Evidence from field experiments in the Indian River Estuary, Florida. J. Mar. Res. 36: 569-593.
- Zimmerman, R., R. Gibson and J. Harrington. 1979. Herbivory and detritivory among gammaridan amphipods from a Florida seagrass community. Mar. Biol. 54: 41-47.

Figure 11. Arrangement of seawater tanks for amphipod/epiphyte experiment.



B. = Buffer Tank

D. = Drain

F. = Aeration Filter

Figure 12. Changes in the percent cover of epiphytes on Rhodomela larix at Boiler Bay, OR. Data were taken in marked permanent quadrats in the low zone. Bars represent standard deviations.

Figure 12

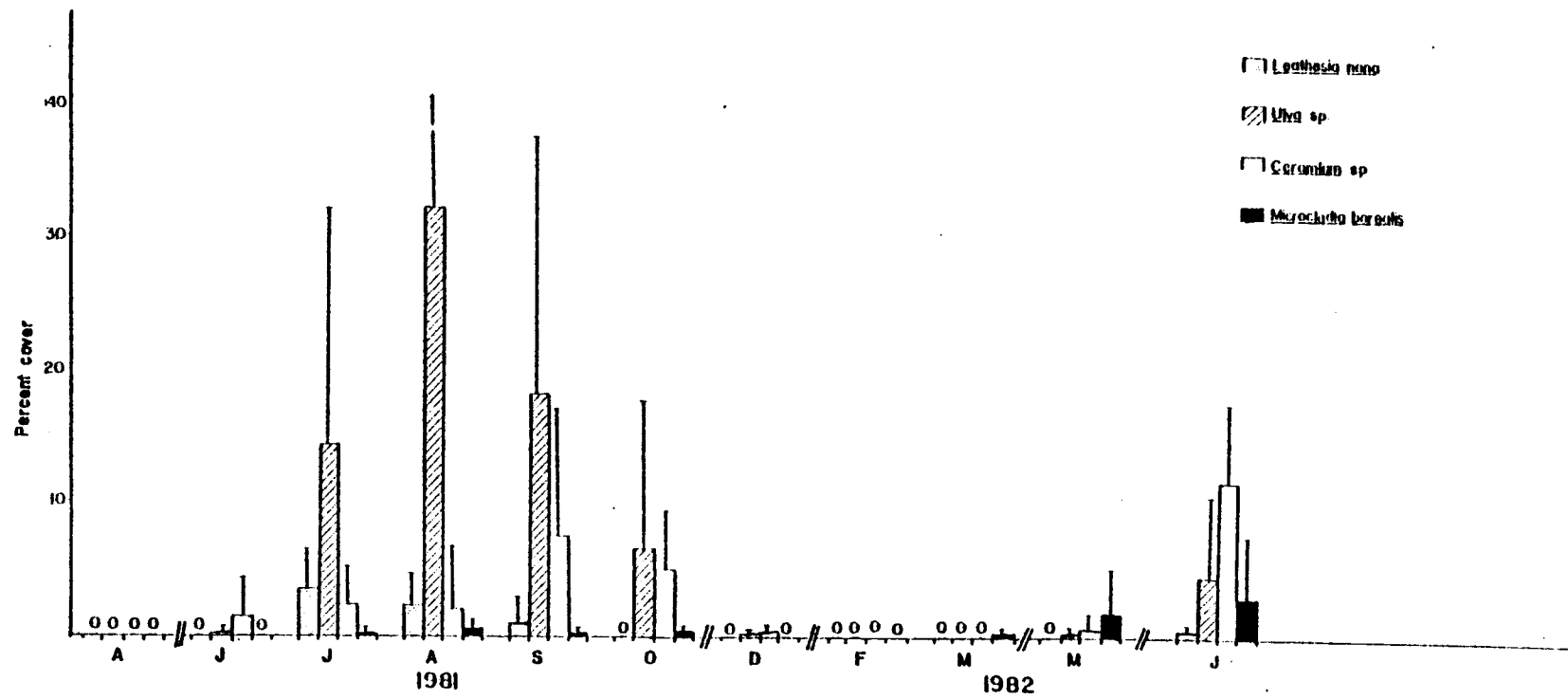


Figure 13. Survival of individually marked axes with and without epiphytes in the low zone at Boiler Bay, OR.

Figure 13.

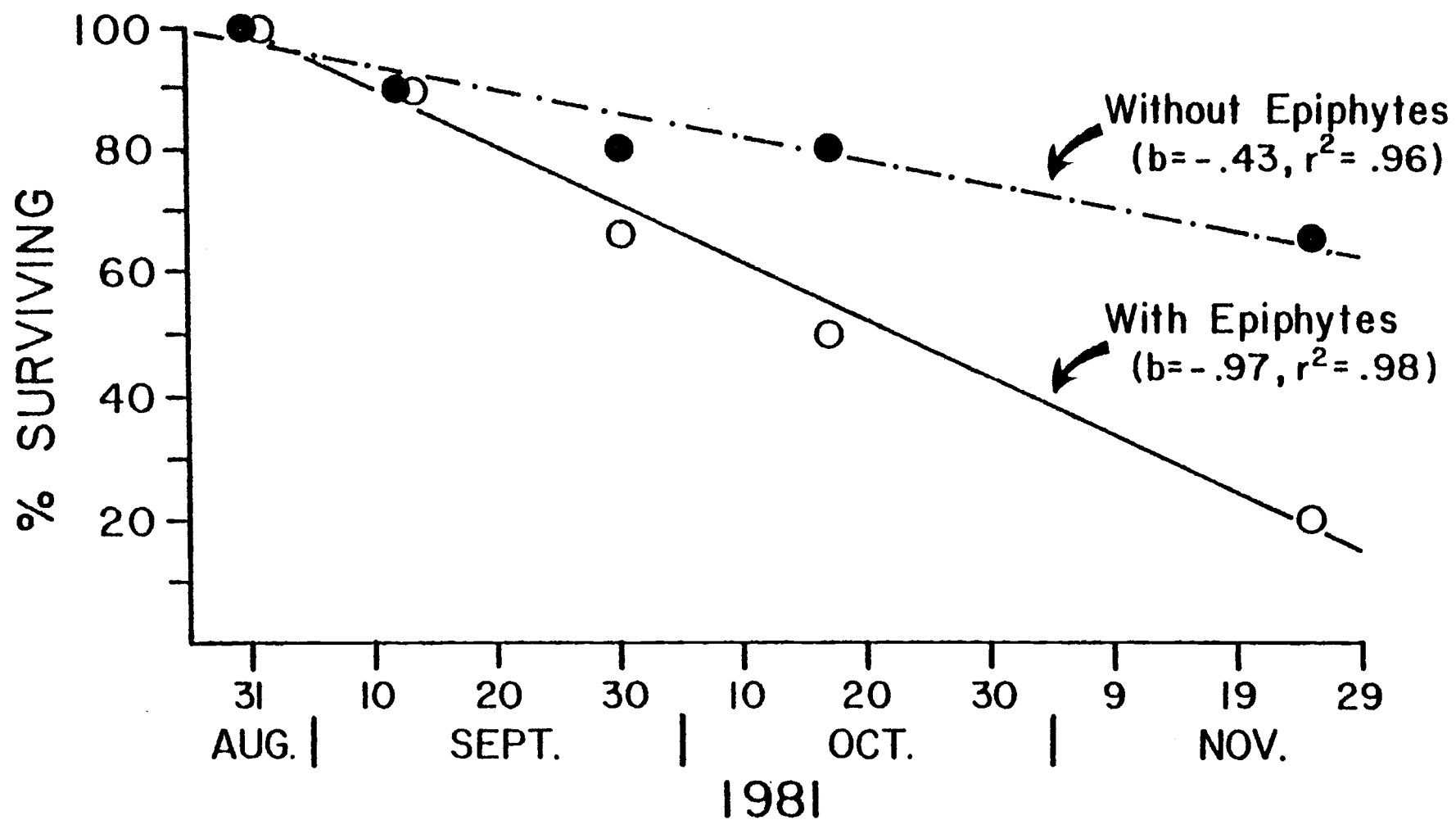


Figure 14. Percent of total tissue length containing reproductive structures for axes with and without epiphytes.

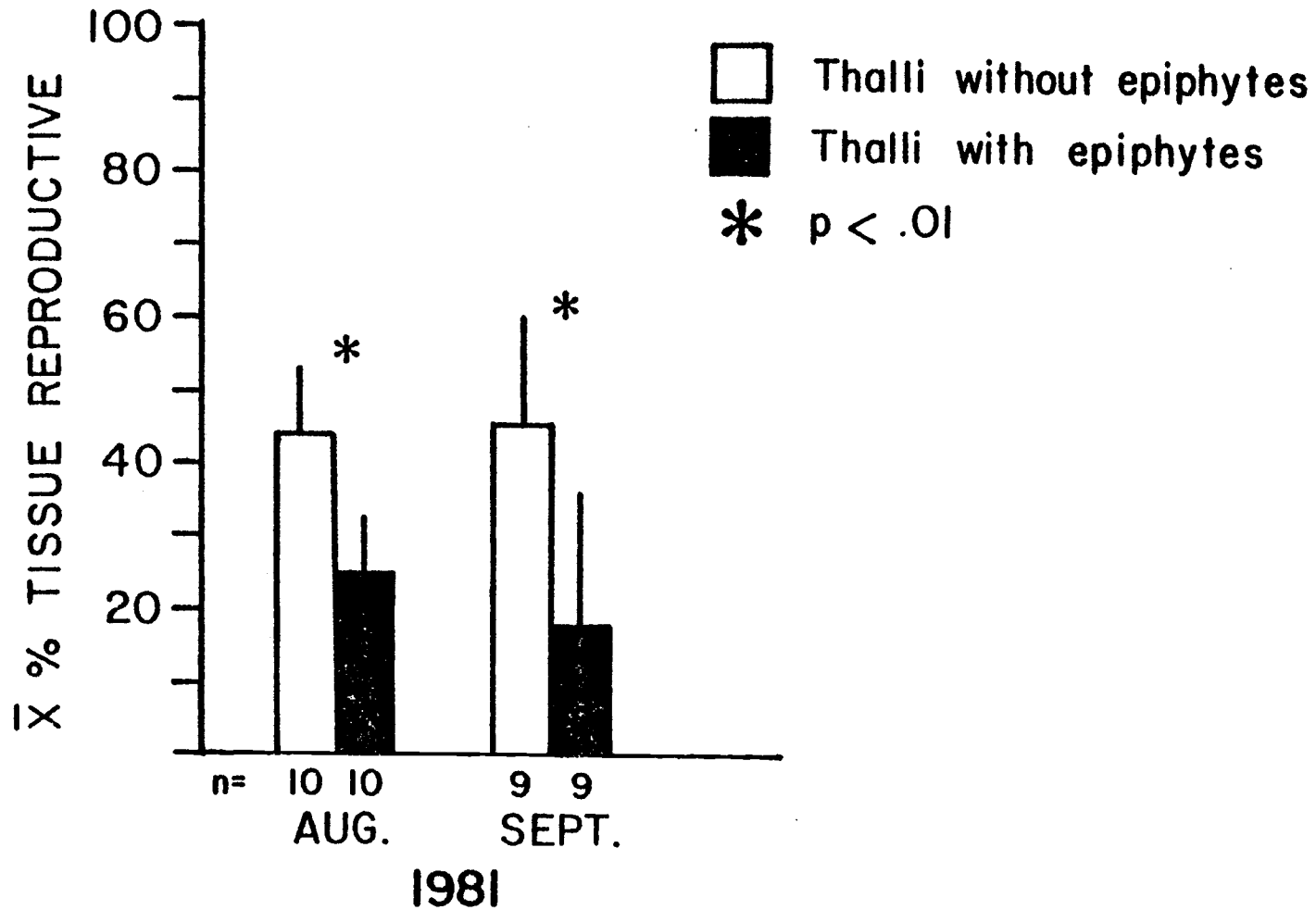


Figure 15. Distribution of diatom cover rankings for axes exposed and not exposed to amphipods. See text for experimental design.

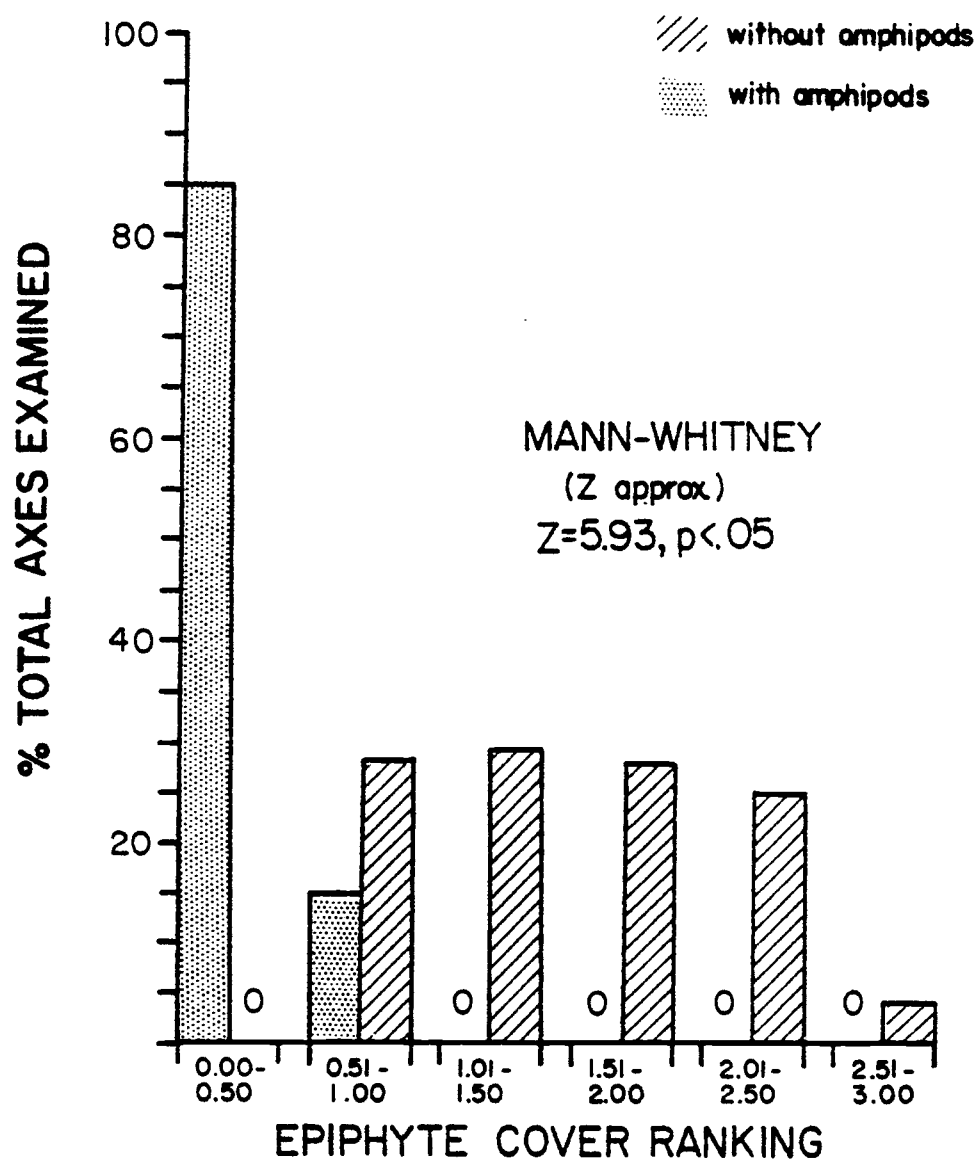


Table 7. Epiphyte species associated with the red alga, *Rhodomela larix*.

Species	Zone	Geographic region*	Peak abundance	Abundance pattern	Location on host	Growth form	Life span
CYANOPHYTA							
<i>Dermocarpa</i> sp.	L,M	OR-c. CA	summer	A	all, excl. r.s.	small (2mm) encrusting colonies	?
CHRYSOPHYTA							
<i>Isthmia nervosa</i>	L	OR-c. CA	late summer, fall	P,A	all	chain-forming, dense aggregations	Pe?
Mixed pennates	L,M,H	OR-c. CA	unknown	A	all, excl. r.s.	variable	?
CHLOROPHYTA							
<i>Cladophora columbiana?</i>	M,H	OR-n. CA	late summer	P,A	main axis, mab. basal 2cm	turf-forming, grows over lower portions	Pe
<i>Ulva</i> sp.	L	OR-n. CA	summer	P,A	all, excl. r.s.	thin blades	An
PHAEOPHYTA							
<i>Soranthra ulvoidea</i>	pools	OR-n. CA	summer	P,A	upper main axis	globose, hollow	An
<i>Leathesia nana</i>	L,M	OR-n. CA	summer	P,A	main axis, mab. occas. on r.s.	globose aggregations	An
RHODOPHYTA							
<i>Cryptosiphonia woodii</i>	L,M	OR-c. CA	summer, spring	R	main axis, gen. lower 5cm	erect, profusely branched, saxic.	Pe
Coralline crust	L	c. OR	winter	A	main axis, mab., gen. basal 5cm	encrusting growths (1-4mm)	An?
<i>Plocamium violaceum</i>	L	c. OR	fall	P,0	main axis, 1-3.5cm above holdfast	erect, plumose, from stoloniferous branches, saxic.	Pe
<i>Iridaea cordata</i>	L	c. OR	summer	R	low main axis	flat blade, saxic.	Pe
<i>Halosaccion glandiforme</i>	L,M	OR-c. CA	summer, early fall	0	main axis, nr. axis tips	sac-like thalli, saxic.	Pe
<i>Microcladia borealis</i>	L,M	c. OR	summer	P,A	main axis, gen. lower 5cm	erect, finely branched tufts	Pe
<i>Ceramium californicum?</i>	L	OR-c. CA	summer	P,A	all	finely branched, dense aggregations	An
ANIMAL SPECIES							
<i>Balanus crenatus</i>	L,M	c. OR	winter	P,A	main axis	attached by basal plate	?
<i>Mytilus edulis</i>	M	OR-c. CA	winter, spring	P,A	main axis	attached by byssal threads	Pe
<i>Mytilus californianus</i>	L,M	OR-C. CA	unknown	P,0	main axis	attached by byssal threads	Pe

abbreviations: L,M,H=low, mid, high intertidal; P=patchy, A=abundant (within patch or entire area), 0=occasional, R=rare (seen only a few times); all=all portions of plant, r.s.=reproductive structures, mab.=main axis branchlets (Fig. 1, Chapter 1); saxic.=commonly saxicolous; Pe=perennial, An=annual; *=regions where collected in this study.

Table 8. Biomass of selected species of erect epiphytes and host (Rhodomela larix). Samples were taken during period of peak abundance for each epiphyte species and represent maximum weights found. Standard deviations in parentheses.

Epiphyte	n	<u>\bar{x} Dry weight (g)</u>		<u>Epiphyte:Host ratio</u>	
		Host	Epiphyte	\bar{x}	Range
<u>Microcladia borealis</u>	8	0.36 (0.31)	1.04 (0.68)	6.30 (9.86)	1.20-29.81
<u>Plocamium</u> sp.	7	0.10 (0.06)	0.08 (0.05)	1.12 (1.11)	0.23-2.94
<u>Ulva</u> sp.	10	0.15 (0.06)	0.11 (0.07)	0.78 (0.44)	0.30-1.69
<u>Ceramium</u> sp.	7	0.13 (0.13)	0.09 (0.02)	1.23 (0.88)	0.27-2.36

Table 9. Tissue loss frequencies for individually marked axes with and without epiphytes. N.S.=not significant.

Study site	Primary epiphyte	<u>Frequency of net tissue loss</u>		Chi-squared
		No epiphytes	With epiphytes	
A.				
Strawberry Hill (May-June 1982)	<u>Isthmia nervosa</u>	0	.30	7.95 p<.005
Strawberry Hill (June-July 1982)	<u>Isthmia nervosa</u>	.08	.64	9.18 p<.005
B.				
Boiler Bay (Aug.-Sept. 1981)	<u>Ceramium</u> sp.	.19	.79	10.75 p<.005
Boiler Bay (Sept.-Oct. 1981)	<u>Ceramium</u> sp.	.69	.75	0.019 N.S.

Table 10. Growth of individually marked axes with and without Isthmia nervosa epiphytes. Growth is calculated in terms of percent of original axis length present and analyzed using a Mann-Whitney test.

Without epiphytes	with epiphytes	Rank Without	Rank With
May-June 1982:			
.73	.04	8	19
.24	.13	14	16
1.43	.02	2	20
1.35	.31	3	13
1.22	1.25	5	4
1.18	.05	6	18
.55	.12	10	17
.57		9	
1.09		7	
.38		12	
.13		15	
2.32		1	
.44		11	

$U=90, n_1=13, n_2=7 \quad p<.001$

June-July 1982:

.11	.08	11	14
.28	.01	6	16
.51	0	3	17
.21	.23	8	7
.76	.17	1	9
.14	.09	10	13
.48		4	
.03		15	
.72		2	
.10		12	
.38		5	

$U=55. \quad n_1=11, \quad n_2=6 \quad p<.05$

Table 11. Wilcoxon paired sample tests for rate of tissue loss per day for axes with and without Ceramium sp. and Ulva sp. epiphytes. Data are paired on the basis of initial size of axis.

Plants without epiphytes(E_o)	Plants with epiphytes(E_w)	D ($E_o - E_w$)	Rank Score
.011	0	.011	8
-.004	-.0012	-.0052	-4
.0004	.006	-.0056	-6
-.002	-.003	.001	1
.002	0	.002	2
-.0033	-.0077	.0044	3
.0002	-.014	.0142	9
.006	-.0048	.0054	5
.009	-.010	.019	11
.0085	-.0062	.0147	10
.0007	-.005	.0057	7

Sum of negative values = -10, $p < .05$. August to Sept. 1981

.0007	0	.0007	2
.0097	-.0024	.0121	7
-.008	-.0300	.0220	10
0	-.0047	.0047	5
-.0013	-.0094	.0081	6
-.0018	.0160	-.0142	8
-.0300	-.0300	0	1
-.0068	-.0300	.0232	11
-.0215	-.0236	.0021	3
-.0260	-.0300	.0040	4
-.0130	-.0300	.0170	9

Sum of negative values = -8, $p < .05$. Sept. to Oct. 1981

Table 12. Size and biomass of R. larix axes with and without Ulva sp. epiphytes. Standard deviations in parentheses and differences between means analyzed with Mann-Whitney test. Data for August and September, *=data available for September only.

	<u>Dry wt. (g)</u>		<u>Length (cm)</u>		<u>Wt/cm length</u>		<u>Wt/cm repro- ductive axis</u>	
	n	\bar{x}	n	\bar{x}	n	\bar{x}	n	\bar{x}
Plants with epiphytes	18	0.15 (0.06)	19	15.5 (5.4)	10	0.0090 (0.0014)	8	0.0087 (0.0020)
Plants without epiphytes	19	0.23 (0.07)	19	17.3 (6.4)	10	0.0172 (0.0035)	9	0.0133 (0.0052)
Difference	p<.05		N.S.		p<.05		p<.06	

Table 13. Analysis of diet of selected small invertebrates from beds of Rhodomela larix.

Fecal pellet analysis Species	Date	#pellets examined	%with <u>R. larix</u>	% 50% <u>R. larix</u>	%with diatoms	% 50% diatoms	% 50% unknown
<u>Lacuna marmorata</u>	28-XI-81	28	100	82	29	0	32
<u>L. marmorata</u>	2-II-81	8	100	50	13	0	50
<u>Littorina scutulata</u>	25-VII-80	26	77	62	100	42	23
<u>L. scutulata</u>	24-VII-82	12	100	42	100	75	8
Gut Content analysis		#individuals examined					
<u>Ampithoe simulans</u>	10-IX-80	3	66	0	66	0	100
<u>A. simulans</u>	2-II-81	2	0	-	0	-	100
<u>A. simulans</u>	25-VII-82	2	0	-	0	-	100

Table 14. The effect of amphipod grazing on the diatom cover of Rhodomela larix. Grazing index was calculated by counting the number of small and large amphipods and adjusting for size(see description in text). Diatom cover was scored by estimating the density of chain-forming diatoms along the main axis of R. larix thalli, where 3=very dense and axis totally covered and 0=no diatoms present.

Grazing level	Diatom Cover:		
	Before	After	Difference
0	3	2.5	-.5
0	3	2.5	-.5
1.7	3	2.5	-.5
3.7	3	1	-2.0
4.0	3	1	-2.0
4.3	2	0	-2.0
5.7	3	0.5	-2.5
7.0	3	1.5	-1.5
9.0	3	0	-3.0

Appendix 1. Herbivore species from beds of *R. larix*. Data presented as mean number/g dry weight of host; n=2 for each sample; standard errors in parentheses. M=mid zone, L=low zone. Sampling dates May1981 to February 1982.

Taxon	May		June		July		August		October		December		February	
	M	L	M	L	M	L	M	L	M	L	M	L	M	L
GASTROPODA														
<i>Littorina scutulata</i>	15.78 (6.00)	0	29.00 (2.72)	0.47 (0.66)	23.80 (2.23)	0	43.39 (19.29)	0.43 (0.16)	17.73 (5.96)	0.58 (0.29)	10.17 (1.58)	0.52 (0.55)	10.08 (7.31)	0
<i>Lacuna marmorata</i>	2.65 (0.50)	3.00 (0.71)	4.51 (3.05)	6.81 (4.98)	0.51 (0.71)	1.60 (0.17)	2.69 (3.80)	2.20 (0.82)	9.50 (10.70)	2.87 (0.19)	4.38 (0.49)	25.36 (0.67)	1.72 (1.17)	34.69 (21.65)
INSECTA														
<i>Diptera larvae</i>	2.16 (0.19)	0	3.77 (1.33)	4.67 (6.02)	2.63 (3.57)	15.10 (3.80)	3.19 (2.17)	2.63 (0.66)	2.73 (0.45)	1.54 (0.59)	0	0.29 (0.23)	7.94 (5.55)	6.21 (3.00)
CRUSTACEA														
<i>Amphipoda</i>	1.00 (1.42)	9.66 (0.40)	0	11.92 (3.59)	2.53 (2.86)	93.57 (7.00)	1.40 (0.23)	155.21 (107.13)	5.48 (4.33)	25.00 (9.94)	5.98 (0.66)	80.63 (48.52)	2.14 (1.77)	16.78 (8.02)
<i>Isopoda</i>	2.77 (1.75)	1.83 (0.94)	8.07 (0.60)	0.47 (0.66)	2.27 (2.50)	0	0.83 (1.17)	0.56 (0.35)	0	0	0.20 (0.28)	0.29 (0.23)	0.65 (0.28)	5.19 (4.45)

CHAPTER IV

The Influence of Sand on a Rocky Intertidal Algal Community

INTRODUCTION

The role of disturbance in maintaining or influencing species diversity has received both theoretical and empirical attention in recent years (for examples see Levin and Paine 1974, Sutherland 1974, 1981, Connell 1975, 1978, Platt 1975, Sousa 1979a, b, Highsmith et al. 1980, Paine and Levin 1981). In fact, Sousa (1979a) has claimed that disturbance events, whether small scale and/or patchy in space and time, probably characterize most natural systems. One such system is the marine rocky intertidal. The temperate rocky intertidal zone has frequently been described as a space limited system, such that in the absence of agents which remove biomass (= disturbance as defined by Grime 1977), space becomes monopolized by one or a few species (Paine 1966, Dayton 1971, 1975, Paine and Levin 1981). In habitats with regular disturbances, a species may become numerically or functionally dominant because of its relative resistance to the disturbance agent. Examples of regular disturbances in rocky intertidal environments include log battering, wave shock, and desiccation (Dayton 1971), predation (see Paine 1977 and Connell 1975 for reviews) and the turning over of boulders (Sousa 1979a, b). A factor which to date has received little empirical attention is the influence of sand on rocky shore organisms (for preliminary information see Cimberg et al. 1973, Foster 1975, Daly and Mathieson 1977, Phinney 1977, Taylor and Littler 1982).

Several authors have noted the decreased diversity of organisms associated with sand-influenced rocky intertidal habitats (Chapman 1946, Stephenson and Stephenson 1972, Phinney 1977). In addition many investigators have described species associated with sandswept habitats (Doty 1947, Mathieson 1965, 1967, Markham and Newroth 1972, Markham 1973, Daly and Mathieson 1977, Phinney 1977). Markham and Newroth (1972) suggest that several of these species may be dependent upon sandy conditions.

Moving sand may scour or bury intertidal substrata. Its effects as a disturbance agent include removing plant tissue, epiphytes, or invertebrates with poor attachment to the rock surface (scouring), and decreasing light, oxygen, and substratum available to organisms (burial). The depth and duration of burial or wave shock severity will be important in determining the intensity of the disturbance.

In this study I examine the influence of sand on the occupation of space by a red alga Rhodomela larix (Turner) C. Agardh in the Oregon rocky intertidal zone. R. larix has not previously been described as a "psammophyllic" or sand-loving species. However, on the Oregon coast it is abundant on moderately exposed sandswept benches (personal observations), and sand appears potentially important as a disturbance agent in the development and persistence of Rhodomela monocultures. Here I look specifically at (1) the distribution of R. larix with respect to rocky areas subject to sand scour or burial, (2) the distribution of potential herbivores with respect to these habitats, (3) changes in the abundance of Rhodomela and associated species throughout

the year, and (4) the resistance to burial of potential competitors on sand influenced shores.

Description and General Distribution of Plant

Rhodomela larix is an upright red alga which sprouts erect axes from a small perennating basal holdfast. Individual axes, or sprigs, grow to lengths of 30 or more centimeters during the late spring and summer. Maximum length is generally achieved by mid summer after which time plant tissue is lost due to a variety of factors (Chapter 2). Individual sprigs may persist for more than one year although the majority of large ones are lost by mid October. Very few axes $> 8\text{cm}$ survive the winter (Chapter 2). New erect axes are sprouted each spring and plants may reach a density of 350 thalli/ 225 cm^2 by mid summer. Although reproductive plants can be found from April through November, evidence of recruitment as presented in the literature is ambiguous. Recruitment appeared to be low during the time of this study (August 1980 - June 1982). Vegetative growth and perennation appear to be important in the maintenance of space occupancy and are probably responsible for the formation of large beds of the plant (Chapter 2).

Rhodomela larix occurs in the low and mid intertidal zones from Japan, throughout Alaska, British Columbia, the Pacific Northwest, and northern California (Abbott and Hollenberg 1976, Saito 1980). Its southern distribution in North America ends ten miles southeast of Point Conception, California (Richard Doyle, unpublished data, Univ. Calif., Santa Barbara). Although its distribution is variable, Rhodomela is

generally common and frequently very abundant on moderately wave exposed horizontal benches around .3m above mean lower low water. It is generally in low abundance or absent from intertidal areas with high urchin densities or with wave exposed vertical faces. The largest and most continuous patches of R. larix that I have observed occur on sandswept, low intertidal benches on the central Oregon coast.

METHODS

Survey of Intertidal Habitats and Herbivore Densities

To describe habitats in which R. larix occurs, 26 rocky intertidal areas were surveyed between 1 August and 22 September 1981 (Fig. 16). For all sites the following factors were noted: (1) presence and texture of sand, (2) sand scoured rocks, (3) organisms characteristic of sandy environments, (4) steepness of rock surfaces, and (5) wave exposure conditions. Herbivore densities were sampled in continuous $.25\text{m}^2$ quadrats along horizontal transects in 15 of the locations with Rhodomela. Transect length varied from 18 to 30 meters depending on the topography of the area sampled. All herbivores (excluding small snails and amphipods) were counted and mean densities calculated for each site. The abundance of R. larix was estimated by counting the number of 10 x 10cm subunits in which Rhodomela occurred within each $.25\text{m}^2$ quadrat, and taking a mean for each transect line.

Changes in R. larix Communities Over Time

To examine the ability of Rhodomela to persist under different sand-related disturbance regimes, beds of Rhodomela larix were examined at two study sites, Strawberry Hill and Boiler Bay, along the central Oregon coast. Rhodomela is a major component of the rocky intertidal community at both sites although the presence and abundance of other plants and animals varies between the sites. In addition sand texture

and movement is different at the two sites. Sand grain size was determined with a U.S. standard sieve series and classified according to Wentworth scale (Thurman, 1975).

Strawberry Hill is an extensive intertidal region of basaltic rock 27 miles south of Newport, Oregon (lat. 44°15'16") (Fig. 17). The intertidal zone is made up of irregular rock outcroppings and gently sloping rock benches. On the largest of these benches Rhodomela forms an extensive monoculture 40 meters in diameter. Patches of the species are present throughout most of the exposed rock habitat between .3 and 1.0 meters above mean low water. The entire area is subject to moderate to heavy wave action although the main Rhodomela bed is protected from direct surf by a series of low horizontal basaltic dikes. It is also subjected to seasonal sand cycles such as those described by Komar (1976). Sand accumulates as wave steepness declines in the spring, with major burials occurring in the summer. Sand is then moved seaward by wave action during fall storms.

The second site is located 15 miles north of Newport, Oregon on the western end of Boiler Bay, Oregon (lat. 44°50'N) (Fig. 18). The site consists of a horizontal mudstone bench between 0 and .7 M above MLW bordered by a boulder field to the west and a series of shallow surge channels to the east. Rhodomela occurs in patches on the horizontal surfaces in the surge channels and intermixed with Phyllospadix scouleri on the mudstone bench. The area does not appear to experience the dramatic sand cycles apparent at Strawberry Hill, although coarse sand is present throughout most of the year.

To observe community changes over time, two permanent transects were established at the Strawberry Hill site. The transects ran parallel to the shore and were censused seasonally between July 1981 and April 1982. The first of these transects ran for 75 meters directly northwest of the main Rhodomela bed through an area of more diverse algal cover. The diversity and abundance of algae was sampled along the transect line by recording the secondary (canopy) and primary cover (rock) of organisms (Menge 1976) at 30 cm intervals. The other transect line extended for 18 m across the widest portion of the main Rhodomela bed. Here, percent cover was monitored by recording the identity of the species underneath each of 100 randomly placed dots in 900 cm² quadrats at three meter intervals along the transect line. I sampled herbivore densities in three 25 cm² quadrats within each larger quadrat. During periods of sand coverage, holes were dug at estimated 3 m intervals, sand depth measured and the presence and condition of Rhodomela beneath the sand noted.

At Boiler Bay, eight permanent quadrats, 900 cm² were established in the main bed of Rhodomela in April 1981 to follow seasonal changes in the community. The percent cover of all species and primary cover of sand and rock was monitored monthly for 16 months, using a vinyl sampling quadrat with 100 randomly placed dots. In addition the growth rate of erect portions of thalli buried by sand was compared with that of thalli which did not experience burial at this site. Monthly observations of growth rates were made on marked individual Rhodomela axes in patches near the edges of the main Rhodomela bed. Axes were marked by placing small plastic tags around the base of the main axis.

To distinguish individual sprigs, four colors of tags were used in varying orders. The presence of sand on or around the base of the plants, and the presence and size of each marked sprig were noted at irregular intervals between December 1980 and March 1982. The survival of entire patches of Rhodomela was monitored by carefully mapping individual patches along the edges of the main bed and noting duration of sand coverage.

Laboratory Studies on Sand Tolerance by Intertidal Algae

To test the ability of Rhodomela to survive lengthy sand inundation and to observe changes in the plant during sand coverage, two sets of laboratory experiments were performed. In the first experiment four rocks containing 20 to 30 erect axes were examined and the presence of epiphytes noted. Eight axes on each rock were individually marked with monofilament line-plastic bead bracelets, and measured. All plants were placed under six inches of fine sand in a running seawater tank with oxygen aeration. Two rocks were examined after two weeks and then replaced under the sand. At six weeks after initial submergence they were placed in a well lit and aerated seawater tank without sand for continued observations on survival. After 14 weeks the remaining two rocks were removed from under the sand, examined and placed in the well-lit seawater tank for further observation.

The second experiment was designed to test the relative survivorship under sand of several species of algae commonly found in mid and low intertidal habitats and often interspersed with Rhodomela. Plants of seven species, including Rhodomela, were collected by chipping away a

portion of the rock to which they were attached. At least seven specimens of each species were collected so that plants could be divided into seven sets with one specimen of each species per set. Four sets were placed in a running seawater tank under 15 to 20 cm of fine sand. The remaining three sets were placed in a well lit aerated seawater tank to serve as controls. After one month, two of the experimental sets were removed from the sand and examined to determine the amount of plant material remaining. Controls were also examined at this time. The two remaining experimental sets were removed from the sand after three months and monitored in the same way.

RESULTS

Latitudinal Distribution of Rhodomela larix

Rhodomela was present at 21 of the 26 sites visited in summer 1981 (Table 15). The remaining five sites were very exposed sloping rocky outcroppings. Where horizontal surfaces were present at these sites, they often contained large numbers of sea urchins and/or clumps of mussels. There was no evidence of sand or sediment movement at any of these wave exposed sites.

Sixteen of the 21 sites where Rhodomela was present showed evidence of sediment accumulation or seasonal sand cycles (e.g. sites 2, 6, 8, 11-14). The community of plants and animals at these sites (Table 16) was also characteristic of that described for sand-influenced rocky shores (Doty 1947, Phinney 1977, Taylor and Littler 1982, Abbott and Hollenberg 1976). The remaining five sites (with Rhodomela larix, but no sand), were more exposed to wave action and were .3 to .6 M higher above mean LW than most of the other 15 sites. Thus Rhodomela occasionally occurs without sand, but is present at all sites with sediment accumulations.

Herbivore Densities

The highest densities of herbivores, which graze algae at the rock surface, occurred at sites without sediment accumulations (Table 17). No large herbivores were observed at the sites with the greatest sand

accumulations. During an intensive search of the Strawberry Hill, Seal Rock, and Otter Crest areas where sand coverage of the substrate was high, I found the chiton Katharina tunicata only on elevated benches or vertical walls that were never observed to be covered by sand. Urchins (Strongylocentrotus purpuratus) were absent from all such areas although common at more exposed areas with Rhodomela. Sites with coarse grained sand or intermediate amounts of the finer grained sand had an occasional chiton and sometimes high densities of the herbivorous gastropod Tegula funebris but otherwise lacked large herbivores and limpets (Table 17). At many of these areas chiton and urchin abundance appears to vary little seasonally (pers. obs.; T. Turner pers. comm.).

Chiton density is inversely correlated with Rhodomela abundance ($r^2 = .43$, $b = 1.61$). Those sites with high chiton densities had large amounts of bare space and were frequently dominated by the kelp Hedophyllum sessile with an understory of erect coralline algae (Bossiella plumosa and Corallina vancouveriensis). These observations suggest that, (1) chitons negatively effect R. larix, (2) sand has a negative effect on chitons and a positive effect on R. larix or (3) both.

Survival of Rhodomela After Sand Burial in the Field

The percent cover of Rhodomela on the permanent transect lines and permanent quadrats at Strawberry Hill and Boiler Bay respectively, changed little over time (Tables 18, ,19, Fig. 19). Percent cover of Rhodomela on primary space declined at both sites during the winter

months. However Rhodobrya was still the most abundant species in all areas throughout the year.

Sand levels changed dramatically with season at Strawberry Hill (Figure 17). In February 1981, very little sand was observed around the base of Rhodobrya plants and no large deposits of sand were observed at the study site. By late July, 1981, 2.5 to 7.5 cms of sand had accumulated around the basal holdfasts of the Rhodobrya in the main bed and intrusions of sand were common along both transect lines. By mid August, 30 to 60 cm of densely packed, fine-grained (1/8 to 1/4 mm) sand covered most of the main bed. Sand removal occurred during early to mid November; by late November very little sand was present at the base of the Rhodobrya thalli. Sand withdrawal continued throughout December leaving little or no sand in the region of the main bed by early January. At the time this study was terminated in July 1982, 3 to 10 cm of sand had already accumulated over the main Rhodobrya bed.

Little damage was evident on Rhodobrya removed from beneath the sand at Strawberry Hill within two weeks of the major burial in August, 1981 although dense populations of diatoms and amphipods on Rhodobrya in July were absent (pers. obs.). A large percent of plants removed from under the sand had mature tetraspores on their axes. I saw no evidence of decay. However, Rhodobrya examined in mid September (> 1 month after burial) appeared to be experiencing anoxic conditions. The sand at the depths to which the Rhodobrya was buried was blackened and the odor was typical of that produced by anoxic sediment layers. Although the upper portions of these Rhodobrya thalli disintegrated when touched the lower 5-7 centimeters appeared healthy.

Sand apparently did not affect the percent cover of Rhodomela on primary space along either transect line; however, the appearance of Rhodomela did change after sand coverage. Changes observed were: (1) few of the diatom epiphytes and virtually none of the algal epiphytes associated with Rhodomela (such as Leathesia nana and Halosaccion glandiformes) persisted throughout the burial period, although they remained at nearby unburied areas; (2) virtually all of the reproductive portions of Rhodomela thalli decayed during the period of burial; (3) the mean size of a Rhodomela axis was much smaller after burial (\bar{x} before = 20 cm, $n = 27$, \bar{x} after = less than 5 cm); and (4) Rhodomela thallus density appeared to be reduced after burial (i.e. the % of Rhodemela in the primary space declined Table 18). In February 1982 the plants in the region where sand coverage had been the deepest looked healthy and appeared to have new growth along the tips of their main axes.

Effects of sand coverage on other plants in the area was variable. Some species appeared unchanged. For example, near the main bed, patches of Phyllospadix sp., and Gymnogongrus linearis, appeared similar before and after sand burial. On the transect line northwest of the Rhodomela bed, the percent cover of several species was not negatively affected by sand cover (Table 19). The increase in percent cover of many of these species between July and December 1981 (e.g. R. larix, B. plumosa, C. vancouveriensis, G. linearis and Plocamium sp.) to a large extent reflects the disappearance of sand previously covering patches of these algae. Other species, specifically the perennial red

algae Microcladia borealis, Dilsea californica and Cryptosiphonia woodii disappeared during sand coverage (Table 19).

Sand also appears to affect some large invertebrates at Strawberry Hill. For example, the starfish Pisaster ochraceus is abundant there, and during the period of sand coverage a large number of starfish were found dead on the sandy substrata. Most of these appeared to have had their ampullae eaten by gulls and the presence of sand may have hindered the ability of the starfish to cling to the rocks. Under these circumstances one would expect that effective starfish foraging might only occur above the level of sand accumulation. I was unable to gauge the effect of sand on the mussel Mytilus californianus because these mussels are confined to rocky pinacles, at Strawberry Hill, all of which were always above the September sand level.

At Boiler Bay, sand movement differed from the pattern at Strawberry Hill. Rather than large scale summer movements of fine-grained sand, a 5 to 15 cm layer of very coarse (1-2 mm) sand moved back and forth across the Rhodomela bed in winter between December, 1980 and March, 1981. Portions of the bed were intermittently covered with sand and all marked plants outside of the main bed were under 7.6 to 13 cm of sand between January and March 1981. No indication of anoxia was ever observed beneath the sand. After the sand receded, 13 out of 14 marked sprigs remained in the region of total coverage. Within the main bed where sand coverage was never complete, 20 out of 32 marked axes survived during the same time period. Although three of these 12 losses were probably tag losses, erect axis losses were higher in the areas

subjected to sand scour (9 of 32 or 28%) than in areas of total sand coverage (1 of 14 or 7%).

A similar pattern of sand movement at Boiler Bay occurred in winter 1982. Photographs of the area revealed increases in the percent of bare rock exposed in what were formerly patches of Rhodomela. This was also apparent in the primary cover data from the permanent quadrats (Fig. 19). Many patches of Rhodomela in the surge channel area contained erect axes only 1 to 3 centimeters tall, which were barely visible above the thin cover of coarse sand. An examination of these axes under a dissecting scope revealed gouges full of sand grains in the main axes. Rhodomela thalli in nearby unscoured areas appeared healthier and showed fewer signs of scour damage.

A small but apparent summer pattern of sand movement did occur at the Boiler Bay site. Again, however, the sand was of a coarse rather than fine nature and sand depth never exceeded 5 cm. Many marked sprigs became covered with sand in late July and early August. When sand levels receded in October, 9 out of 9 marked sprigs were present. It was not possible to estimate axis losses from areas without sand cover during this same time interval because such areas were at different tidal heights or had a large cover of epiphytes. A similar pattern of sand movement occurred in summer 1982. Nails fixed into the rock indicated sand accumulations up to 7 cm deep in the main Rhodomela bed.

Laboratory Experiments on Sand Tolerance - Experiment 1 - Survival of Rhodomela

In the laboratory R. larix also tolerated sand burial. All 16 of the initial markers were present on the plants examined after 2 weeks and no marked axes increased in length. Diatom (both sets of erect axes) and L. nana (one set) epiphytes were still present although the latter disintegrated when handled and emanated a rotten odor. The cover of diatoms was not quantified but appeared much reduced. After six weeks the same plants were reexamined and 13 of 16 marked axes were still intact. The plant had not grown and both diatom and Leathesia epiphytes were absent. After 14 weeks of burial all sprigs of plants three and four greater than 2 cm had become detached and/or had suffered marked disintegration. None of the remaining sprigs had diatom epiphytes as they had at the outset of the experiment. Two blades of the red alga Iridaea cordata growing adjacent to plant three were absent when the Rhodomela was uncovered. All plants subsequently survived the winter in the laboratory tanks without sand, although no new growth was apparent.

Experiment 2 - Survival of Rhodomela and Other Algae

R. larix is more tolerant of sand burial than the other species tested (Table 20). After one month, all four of the upright algae other than Rhodomela showed decline in the amount of plant tissue present

although at least some portion of most specimens remained. Controls at this time were similar in appearance to their initial condition.

Examination of the plants buried for three months revealed an even more striking difference between R. larix and other species. R. larix and Ulva lactuca were the only specimens of upright plants that retained any visible tissue. Both of the rocks with Ulva retained only small (5 mm) tufts of the blades. On the other hand, although both the Rhodomela and the coralline crust were reduced in size and slightly discolored, they were otherwise similar to their initial state. After 3 more months in running seawater the Rhodomela had regained their original dark red color. Although these experiments could not mimic field conditions because of the lack of wave action, conditions in the laboratory may have been harsher than in the field because anoxia may have been greater. Therefore, my results support the contention that R. larix is better adapted to withstand dark and anaerobic conditions than the other species of algae listed in Table 20.

DISCUSSION

The Role of Sand in Community Structure

The common occurrence of Rhodomela larix on sandswept intertidal benches (Table 15) suggests that sand may be linked with the development and persistence of Rhodomela beds. Since Rhodomela also occurs in areas where sand accumulations do not occur, it is unlikely that individuals are directly dependent upon the presence of sand for survival. However, the indirect benefits of sand may create the patterns of distribution and abundance of R. larix observed at these sites. Several mechanisms, none of which are mutually exclusive, may be operating to maintain Rhodomela monocultures: (1) sandy areas may serve as refuges for Rhodomela from the potentially detrimental effects of large herbivores (chitons, sea urchins) ; (2) seasonal sand coverage may eliminate many of the smaller herbivores (amphipods, isopods, gastropods) which are able to colonize and eat Rhodomela thalli; (3) sand coverage may eliminate detrimental epiphytes while protecting the lower portions of Rhodomela thalli from exposure stress during the summer months, (4) sand may eliminate at least some potential competitors which cannot withstand anoxic burial or sand scour and, (5) sand coverage may limit algal recruitment, giving an advantage to those species which perennate and grow vegetatively.

The two major, large herbivores that are absent from sandy sites, the chiton Katharina tunicata and the urchin Strongylocentrotus purpuratus (Table 17) have been shown elsewhere to have important

effects on algal populations (Paine and Vadas 1969, Paine 1977, Dayton 1975, Sousa et al. 1981, Gaines in prep.). For example, in the Pacific Northwest rocky intertidal, dense populations of urchins occur in many areas and produce a community dominated either by crustose coralline algae and ephemeral green and red algae (Paine and Vadas 1969) or coralline algae and the grazer-resistant plants Codium and Phyllospadix (Paine 1977). In the absence of urchins, large brown algae and perennial reds predominate (Dayton 1975, Paine and Vadas 1969). Also, in two southern California intertidal areas, removal of urchins resulted in rapid recruitment of upright algae and eventual domination of plots by turfy perennial red algae (Sousa et al. 1981).

The precise effect of urchins on Rhodomela larix itself has not been well documented. DeWreede (1980) observed the movement of a population of urchins through a low intertidal habitat where Rhodomela was common. Grazing by urchins almost completely eliminated stands of Sargassum muticum but had little apparent effect on Rhodomela. However, urchin occupation of the area was temporary, and it is unclear what effect urchins might have had if they had remained in the area after the supposed preferred food item was eliminated. Although I have observed S. purpuratus eating Rhodomela in the laboratory, they do not usually co-occur in the field. Rhodomela is largely confined to horizontal emergent substrata, while urchins occur primarily in tide pools and shallow surge channels. In those locations where urchins are found on emergent substrata, little erect macroalgae is present. Urchins in these areas may prevent the settlement and growth of new Rhodomela sporelings.

The lack of large chitons in sandswept areas and the low abundance of Rhodomela in high chiton density areas (Table 17) suggests that the survival and growth of Rhodomela is enhanced by the lack of this molluscan grazing pressure. Preliminary data from field enclosures of Katharina suggest that these molluscs are able to eat adult Rhodomela plants (D'Antonio, unpublished). Dethier (1982) has made similar observations for R. larix in pools. However, the primary effects of chitons may be (1) to eliminate algal sporelings preventing Rhodomela recruitment (Dayton 1975) and (2) keeping preexisting plants from spreading vegetatively. Gaines (in prep.) observed a noticeable increase in the percent cover of Rhodomela on intertidal benches following the removal of Katharina. Thus the absence of chitons in sandy areas may increase the likelihood of growth and recruitment of Rhodomela.

The precise role of sand on the decreased chiton and urchin densities observed at the sandy sites is unclear. Experiments examining the affect of sand burial on adult chiton survivorship at Strawberry Hill indicate that the mantle of Katharina suffers severe abrasion during one week of sand coverage. Long term effects are unknown. Sand may also have a negative effect on the larval or juvenile phases of the herbivores.

Small herbivores, such as the prosobranch gastropod Lacuna marmorata, the isopod Idotea wosnosenskii and an array of gammarid amphipod species colonize Rhodomela larix and are able to consume it (Chapter 3). The small crustaceans and gastropods begin to increase in density in the Rhodomela fronds in mid to late summer. In areas where

sand coverage was never complete, densities remained high throughout the fall and into the winter. Sand burial at Strawberry Hill eliminated all crustaceans and gastropods from the affected patches of R. larix, thus decreasing their possible detrimental effects on the alga. These small herbivores may recolonize R. larix after the sand is gone; however, the coverage of Rhodomela beds by sand during the late summer, may decrease the total number of these herbivores grazing the plant throughout the winter.

The reduction in epiphyte cover caused by sand burial may also increase the survivorship of Rhodomela thalli. At Boiler Bay, where sand coverage was never complete, many epiphytes persisted throughout the year. This was also apparent in two patches of Rhodomela at Strawberry Hill which escaped total sand burial. These patches remained covered with epiphytes and grew little in the spring of 1982 (Chapter 3). Epiphytes were also found to increase the probability of axis breakage and often the pulling up of one Rhodomela axis resulted in the removal of several adjacent axes. Thus the removal or decay of epiphytes due to sand may decrease the loss of clumps of axes during fall and winter storms.

The ability of R. larix to withstand prolonged sand coverage better than many other algal species is undoubtedly important in the development and maintenance of Rhodomela monocultures. Several algal species that did not survive in laboratory cultures are common in low intertidal habitats. In addition, they are sometimes found as epiphytes on Rhodomela particularly in areas where bare space is uncommon (Chapter 3). The elimination of these potential space occupiers and potential

epiphytes by sand may increase the likelihood of dominance by Rhodomela.

The elimination of potential space competitors cannot be the whole explanation for Rhodomela monocultures because several other species can tolerate sand. These include Ahnfeltia plicata, Gymnogongrus linearis, Phaeostrophion irregulare, Egregia menziesii, Laminaria sinclairii, and Hedophyllum sessile. The latter species has been described as a functional dominant in moderately exposed rocky intertidal communities on the coast of Washington (Dayton 1975). It is common in intertidal habitats on the coast of Oregon, and understory plants in both areas include Corallina vancouveriensis, Bossiella plumosa and occasionally Iridaea cordata and R. larix. Removal of Hedophyllum results in an increase in several algal species including Rhodomela. Once established, these algae appear to inhibit the reestablishment of a Hedophyllum canopy (Dayton 1975). While Hedophyllum is common, it is not dominant on the sandswept reefs where Rhodomela is abundant. Sand may limit its ability to achieve dominance, and the establishment and persistence of perennial reds such as R. larix in these habitats, will in turn inhibit the ability of Hedophyllum to invade.

The capacity of a plant to reproduce vegetatively may be a feature important to its persistence on sand-influenced rocky shores. A variety of psammophyllic plants, such as R. larix, P. scouleri, Ahnfeltia plicata and G. linearis, and Laminaria sinclairii can grow in this manner while Egregia menziesii and Hedophyllum sessile cannot. Markham (1973) has suggested that rhizomatous growth is important to the development and persistence of large populations of Laminaria sinclairii

in the low zone on northern Oregon shores. Species which cannot grow vegetatively must recruit into these intertidal areas during the period of the year when sand is not present and reach a large enough size for at least the basal portions to withstand the forthcoming burial or scour.

That sand influences recruitment patterns of plants in rocky intertidal areas was also apparent in colonization of clearings made in the low zone at Boiler Bay. These clearings were initially made to test the effect of varying densities of limpets on recruitment and vegetative growth of Rhodomela (D'Antonio, unpublished). Between January 1981 and April 1982 several of these clearings showed evidence of severe sand scour and three of the clearings were under 1 to 2 cms of sand for most of the year. With the exception of a small amount (<5% cover) of Phaeostroiphion, no algal recruitment was observed in these clearings. Yet recruitment of many species of macroscopic algae was apparent in the clearings not suffering sand scour.

Geographic Considerations

Much of our knowledge of community structure in rocky intertidal habitats comes from studies in Washington state. These Washington study sites may not be characteristic of the entire northwest region. For example the studies of Connell (1970), Paine (see 1977 for review), and Dayton (1971 and 1975) have focused on very exposed communities at the northern tip of Washington state or the protected inland waters of the San Juan Islands. In the latter area the lowest low tides occur during

mid day when exposure to the sun is the most extreme. Rhodomela is confined mainly to intertidal pools in these habitats (Muenscher 1915), and the occurrence of many plant and animals species on emergent substrata is lower in the intertidal than on the outer coast (Dethier, pers. comm.). In addition, the Oregon coast may be more strongly influenced by sand because of the greater number of rivers there, and sediments from the Columbia river which are transported south in surface waters (Runge 1966, Hartlett 1972). Thus the composition of communities in rocky intertidal habitats should reflect this influence. Phinney (1977) presents an algal species list for Oregon and suggests that the lower algal diversity in this region, is the result of a greater amount of sand influence relative to Washington and central California.

Persistence Stability in R. larix beds

This study indicates that the percent cover of R. larix stayed constant over two summers at both the Boiler Bay and the Strawberry Hill sites. Pictures of the Boiler Bay site indicate that these beds have been in roughly the same location for a minimum of four years (T. Turner, OSU, personal communication). Photographs from 1960 of an additional site where Rhodomela is common on the southern Oregon coast also indicate that R. larix beds, once established, may persist for long periods of time (J. Pederson, pers. comm., Univ. of Oregon).

Individual Rhodomela thalli have the ability to perennate and R. larix shows a remarkable ability to regrow from a minimal number of basal cells (Chapter 1). Thus the minor fluctuations and general constancy of

cover the Rhodomela beds followed in this study probably reflect conditions which have persisted for many years.

In sand-influenced rocky intertidal habitats in Oregon it appears that Rhodomela is eventually outcompeted by the surfgrass Phyllospadix scouleri (Turner 1982). However, the rate at which the surfgrass takes over areas dominated by Rhodomela appears to be slow. I have observed settlement and germination of Phyllospadix seeds at Boiler Bay; however, survival of seedlings is poor and vegetative growth of established individuals is slow (Turner 1982). At Strawberry Hill I did not observe settlement of any Phyllospadix seeds during this study, even though patches of Phyllospadix occur adjacent to patches of Rhodomela. Seed settlement occurs in the fall on the Oregon coast (Turner 1982) and in 1981 may have occurred before the seaward movement of the intertidal sand bar at Strawberry Hill. Phyllospadix may eventually take over through vegetative growth, however the amount of sand accumulating in a single summer and the duration of its stay may influence the ability of Phyllospadix to invade patches of Rhodomela through sexual recruitment.

SUMMARY AND CONCLUSIONS

The results of this study indicate:

- (1) Rhodomela larix occurs predominantly on sandswept low intertidal benches and apparently maintains a constant cover throughout the year in these areas;
- (2) Rhodomela can survive at least three months of total burial in medium to fine-grained sand as well as extensive scour by coarse-grained sand, thus indicating that it is well adapted to survive in several types of sand influenced habitats;
- (3) Few large herbivores live in these areas and I suggest that sand limits the recruitment and survival of such herbivores, making sandy sites a refuge from these consumers;
- (4) Diatom epiphytes and other epiphytes appear to be negatively affected by sand burial, leaving the surface of Rhodomela plants cleaner than before burial; and
- (5) Several species of perennial reds appear to be unable to survive under sand-stressed conditions while other species of both red and brown algae survive on sandswept benches.

Further long term studies are needed to document year to year variation in sand coverage, and the potential importance of such

variation to patterns of distribution and abundance of organisms in these habitats. Clearing experiments are presently underway to determine the pattern of colonization of cleared areas in these sandy habitats. Preliminary results suggest that R. larix regains dominance in clearings where it was previously present by vegetative proliferation and perennation from basal cells left during the clearing process. Hence Rhodomela monocultures, once established may be maintained because of the growth characteristics of the plant and its tolerance to environmental hardships such as sand.

REFERENCES

- Abbott, I.A. and G.J. Hollenberg. 1976. Marine algae of California. Stanford Univ. Press, Palo Alto.
- Chapman, V.J. 1946. Marine algal ecology. Bot. Rev. 12: 628-672.
- Cimberg, et al. 1973. In Proceedings of Joint Conference on Prevention and Control of Oil Spills. March 13-15, 1973, Wash. D.C., sponsored by Amer. Petrol. Institute, EPA, US Coast Guard. 697-702.
- Connell, J. 1970. A Predator-prey system in the marine intertidal region. I. Balanus glandula and several predatory species of Thais. Ecol. Monogr. 40:49-78.
- Connell, J. 1975. Some mechanisms producing structure in natural communities: A model and evidence from field experiments. Pages 460-490. In M. Cody and J. Diamond, eds. Ecol. and Evol. of Communities, Belknap Press, Cambridge, Mass., USA.
- Connell, J.H. 1978. Diversity in tropical rain forests and coral reefs. Science 199: 1302-1310.
- Daly, M.A. and A.C. Mathieson. 1977. The effects of sand movement on intertidal seaweeds and selected invertebrates at Bound Rock, New Hampshire, USA. Mar. Biol. 43: 45-55.
- Dayton, P. 1971. Competition, disturbance and community organization: the provision and subsequent utilization of space in a rocky intertidal community. Ecol. Monogr. 41: 351-389.
- Dayton, P.K. 1975. Experimental evaluation of ecological dominance in a rocky intertidal community. Ecol. Monogr. 45: 137-159.
- Dethier, M. 1982. Pattern and process in tidepool algae: factors influencing seasonality and distribution. Bot. Mar. 25: 55-66.
- DeWreede, R. 1981. The effects of sea urchin grazing, clearing and competition on the distribution of three low intertidal algae in B.C. Canada. J. Phycol. (Supple). p. 10, Abstract.
- Doty, M.S. 1947. The marine algae of Oregon. Part I. Chlorophyta and Phaeophyta. Farlowia 3, 1-65.
- Foster, M.S. 1975. Algal succession in a Macrocystis pyrifera forest. Mar. Biol. 32: 313-329.
- Grime, J.P. 1977. Evidence for the existence of 3 primary strategies in plants and its relevance to ecological and evolutionary theory. Am. Nat. 111: 1169-1194.

- Hartlett, J.D. 1972. Sediment transport on the northern Oregon continental shelf. Ph.D. Thesis. Oregon State University
- Highsmith, R., A. Riggs and C. D'Antonio. 1980. The survival of hurricane-generated coral fragments and a disturbance model for reef calcification/growth rates. *Oecologia* 46: 322-329.
- Komar, P. 1976. Beach processes and sedimentation. Prentice Hall, Englewood Cliffs, NJ.
- Levin, S. and R.T. Paine. 1974. Disturbance, patch formation, and community structure. *Proc. Nat. Acad. Sci.* 71: 2744-2747.
- Markham, J. 1973. Observation on the ecology of Laminaria sinclarii on three northern Oregon beaches. *J. Phycol.* 9: 336-341.
- Markham, J.W. and P.R. Newroth. 1972. Observations on the ecology of Gymnogongrus linearis and related species. *Interntl. Seaweed Symposium 7*: 127-130.
- Mathieson, A.C. 1965. Contributions to the life history and ecology of the marine brown alga, Phaeostrophion irregulare. S. et G. Ph.D. Thesis, Univ. of B.C., Canada.
- Menge, B.A. 1976. Organization of the New England rocky intertidal community: Role of predation, competition and environmental heterogeneity. *Ecol. Monogr.* 46:355-393.
- Muenschler, W.L. 1915. A study of the algal associations of San Juan Island. *Puget Sound Biol. Stat. Publ.* 1:59-83.
- Paine, R.T. 1966. Food web complexity: species diversity. *Am. Nat.* 100: 65-75.
- Paine, R.T. Controlled manipulations in the marine intertidal zone, and their contributions to ecological theory. *The changing scenes in natural sciences*, 245-270.
- Paine, R.T. and S. Levin. 1981. Intertidal landscapes: disturbance and the dynamics of pattern. *Ecol. Monogr.* 51: 145-178.
- Paine, R.T. and R. Vadas. 1969. The effects of grazing by sea urchins, Strongylocentrotus spp., on benthic algal populations. *Limnol. Oceanogr.* 14: 710-719.
- Phinney, H.K. 1977. The macrophytic marine algae of Oregon. in *The Marine Plant Biomass of the Pacific Northwest Coast*. R.W. Krauss (ed.) O.S. Univ. Press. p. 93-116.

- Platt, W.J. 1975. The colonization and formation of equilibrium plant species associations on badger disturbances in a tall grass prairie. *Ecol. Monogr.* 45: 285-305.
- Runge, E.J. 1966. Continental shelf sediments, Columbia River to Cape Blanco, Oregon. Ph.D. Thesis. Oregon State University.
- Saito, Y. 1980. Suitable habitats for certain algae with respect to their growth on the vertical surface of breakwaters. *Jpn. J. Physiol.* 28(3): 171-176.
- Sousa, W. 1979a. Experimental investigations of disturbance and ecological succession in a rocky intertidal algal community. *Ecol. Monogr.* 49(3): 227-254.
- Sousa, W. 1979b. Disturbance in marine intertidal boulder fields: the nonequilibrium maintenance of species diversity. *Ecol.* 60(6): 1225-1239.
- Sousa, W., S. Schroder and S. Gaines. 1981. Latitudinal variation in intertidal algal community structure: the influence of grazing and vegetative propagation. *Oecologia* 48: 297-307.
- Stephenson, T.A. and A. Stephenson. 1972. Life between tidemarks on rocky shores. W.H. Freeman and Co. San Francisco.
- Sutherland, J. 1974. Multiple stable points in natural communities. *Am. Nat.* 108: 859-873.
- Sutherland, J.P. 1981. The fouling community at Beauford, North Carolina: a study in stability. *Am. Nat.* 118: 488-498.
- Taylor, P.R. and M.M. Littler. 1982. The roles of compensatory mortality, physical disturbance, and substrate retention in the development and organization of a sand-influenced, rocky-intertidal community. *Ecology* 63: 135-146.
- Thurmen, H.V. 1975. Introductory Oceanography. Merrill Publ. Co. Columbus, Ohio.
- Turner, T. 1982. Community organization and succession in rocky intertidal surfgrass beds. Ph.D. Thesis, Oregon State University.

Figure 16. Location of intertidal sites surveyed for the presence of Rhodomela larix. Dashed lines indicate county boundaries. Numbers correspond to sites listed in Table 15. Vancouver Island sites are not included on this map.

Figure 16

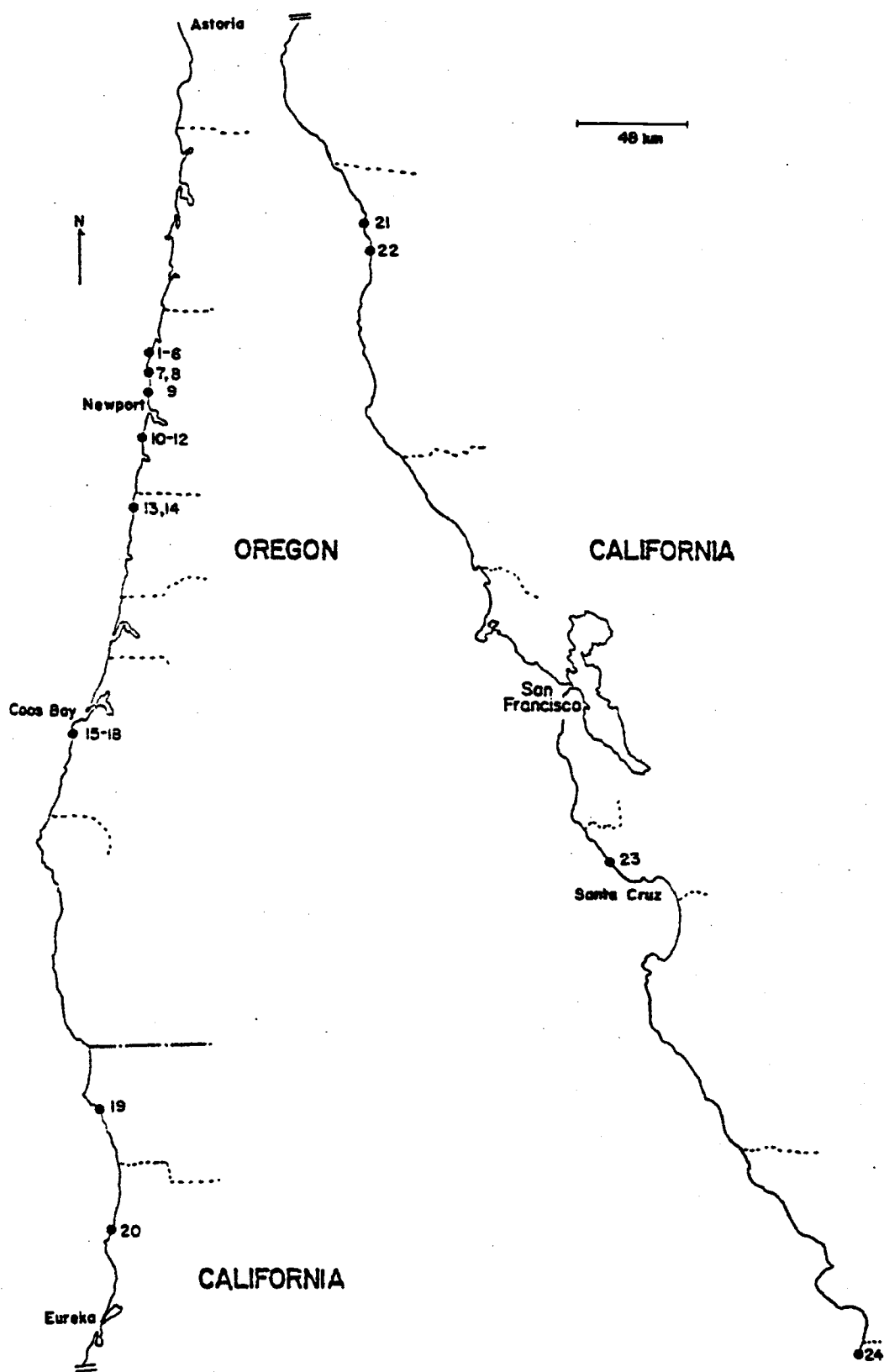


Figure 17. Study site at Boiler Bay, OR. Region over which coarse sand moves is in the foreground.



Figure 18. Study site habitat and changes in sand cover at Strawberry Hill, OR. A. September 1981. B. Feb. 1982.

A.



B.



Figure 19. Changes in the percent cover of primary (i.e. rock) surface by Rhodomela larix and sand at Boiler Bay, OR. Bars represent standard deviations.

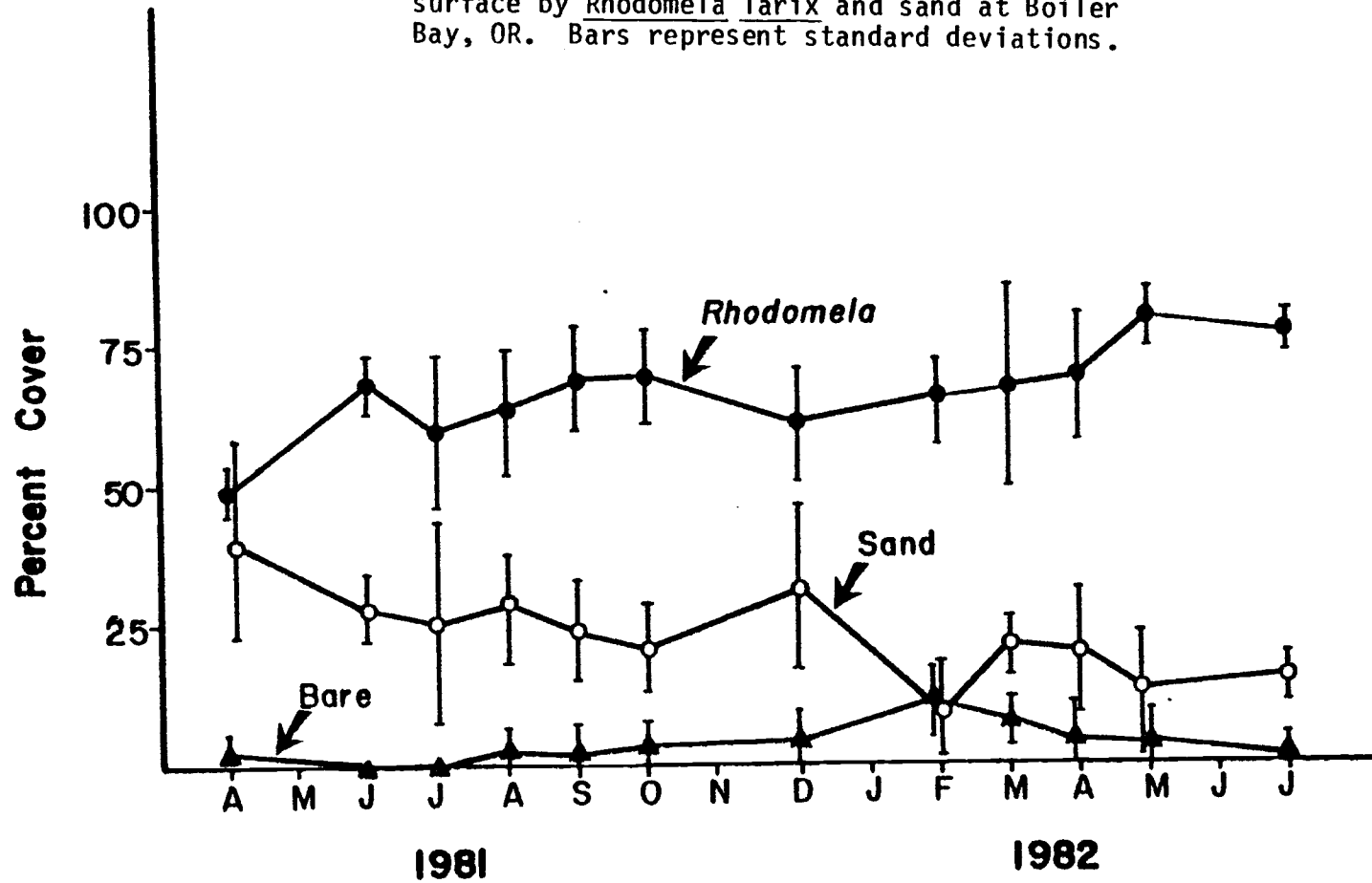


Table 15. Location and description of intertidal areas surveyed for *R. larix*. Tidal height estimated by tide tables and timing of visit to site, and values indicate either area surveyed, or if *R. larix* is present, then the zone of occurrence.

Location	Exposure	Seasons visited	Sediment	<i>R. larix</i>	Tidal height (m)
LINCOLN CO., OR					
1. Boiler Bay, NE	VE	all	abs	abs	0--1.6
2. Boiler Bay, NE	P	all	C,Sp-S	+	0.7--1.0
3. Boiler Bay, Central	E	all	abs	abs	0--1.0
4. Boiler Bay, Central	ME	all	abs	+	1.0
5. Boiler Bay, West end	ME	all	abs	+	1.0--1.7
6. Boiler Bay, West end	ME	all	C,Y	+	0--0.7
7. Otter Crest, North end	E	A,W	abs	+	0--1.6
8. Otter Crest, Back reef	P	S,W	F,Y	+	0.7
9. Yaquina Head, South side	E	all	abs	+	1.3
10. Seal Rock, North end	ME	all	abs	+	0.7--1.0
11. Seal Rock, Central reef	ME	all	F,Y	+	0--0.7
12. Seal Rock, Back reef	ME	all	F,Y	+	1.0--1.3
LANE CO., OR					
13. Strawberry Hill, Surge channels	ME	S,W	F,S	+	0--1.0
14. Strawberry Hill, South benches	ME	all	F,Y	+	0--1.0
COOS CO., OR					
15. Cape Arago, North Cove	E	Sp,S	abs	abs	0.3--1.0
16. Cape Arago, Simpson's Reef	ME-P	S	C	+	0.7--1.0
17. Cape Arago, S. Sunset Bay	ME	S,W	F,Y	+	0--0.7
18. Cape Arago, Squaw Island	ME	S,W	C,W	+	0--0.7
DEL NORTE CO., CA					
19. 5km S. Crescent City	ME	S	F	+	0.7--1.0
HUMBOLDT CO., CA					
20. Mussel Rock, nr. Trinidad	E	S	abs	abs	1.3--2.0
MENDOCINO CO., CA					
21. Rockport area	ME	S	F	+	1.0
22. N. Westport area	E	S	C	+	0.7--1.3
SANTA CRUZ CO., CA					
23. Davenport Landing	ME	S	C	+	0--0.5
SANTA BARBARA CO., CA					
24. Point Sal	ME	S,W	F,S	+	0--1.3
VANCOUVER ISLAND, B.C.					
25. Kirby Point, Barclay Sound	ME-E	S	abs	abs	0.3--2.0
26. Execution Pt., Barclay Sound	ME	S	F,S	+	0.3--0.7

abbreviations: VE=very exposed, ME=moderately exposed, E=exposed, P=protected; all=all seasons, W=winter, Sp=spring, S=summer; abs=absent, C=coarse sand, F=fine sand, Y=year round; + indicates presence of *R. larix*.

Table 16. Sessile organisms commonly found with R. larix on emergent substrates. List was compiled from observations at 21 intertidal areas in Oregon and California where R. larix was present. Longevity data from Abbott and Hollenberg 1976 and personal observation.

Species	Longevity	Season when blades abundant
CHLOROPHYTA		
<u>Ulva</u> sp	A*	S
<u>Cladophora</u> sp	P	S
PHAEOPHYTA		
<u>Leathesia</u> sp.	A	S
<u>Hedophyllum</u> sessile	P	S
<u>Egregia</u> menziesii	P	S
<u>Fucus</u> distichus	P	L
<u>Phaeostrophion</u> irregulare	P	W
RHODOPHYTA		
<u>Cryptosiphonia</u> woodii	P	S
<u>Corallina</u> vancouveriensis	P	L
<u>Bossiella</u> plumosa	P	L
<u>Plocamium</u> sp.	P	W
<u>Iridea</u> cordata	P	S
<u>I. heterocarpa</u>	P	S
<u>Halosaccion</u> glandiforme	P	S
<u>Gigartina</u> papillata	P	S
<u>Microcladia</u> borealis	P	S
<u>Odonthalia</u> floccosa	P	S
<u>Gymnogongrus</u> linearis	P	L
<u>Ahnfeltia</u> plicata	P	W
ANGIOSPERMAE		
<u>Phyllospadix</u> scouleri	P	L
<u>P. torreyi</u>	P	L
CNIDARIA--ANTHOZOA		
<u>Anthopleura</u> elegantissima	P	U
MOLLUSCA--BIVALVIA		
<u>Mytilus</u> californianus	P	L
<u>M. edulis</u>	P	Spring

Abbreviations: A=annual, P=perennial; S=summer, W=winter, L=little seasonal variation, U=unknown; *=known to have some perennial cells.

Table 17. Herbivore density transects in sites containing *R. larix*. Quadrat=0.25 m² and density is as #/quadrat. ¹ includes *Katharina tunicata* and *Mopalia* sp.; *=sites with most extreme sand level fluctuations: ²= mean % cover primary space; standard deviations in parentheses.

Site & Description	Tidal ht.(m)	Sediment	# of quadrats	<i>R. larix</i> ² abundance	Chiton ¹ density	Other herbivores
LINCOLN CO., OR						
Boiler Bay, sloping shelf, exp.	1.0	abs	21	0.72(2.31)	3.57(2.18)	--
Boiler Bay, flat bench, prot.	0.5	C,Y	28	31.65(26.84)	0	3 T.f. 1 qt.
Boiler Bay, central, mod. exp.	1.0	abs	41	17.49(24.20)	1.34(1.28)	S.p. 2 qt.
Otter Crest, exp. shelf	1.3	abs	38	17.0 (20.8)	0.83(1.17)	sm.limp.abund.
Otter Crest, mod. exp. ridge	0.5	abs	29	8.8 (12.8)	0.78(1.17)	Sp. 6.52/qt.
* Otter Crest, back reef	0.7	F,Y,S	32	18.0 (14.7)	0	T.f. 2 qt.
Seal Rock, mod. exp. ridge	1.0	abs	29	11.20(14.00)	0.61(0.91)	lg.C.p. 5 qt.
Seal Rock, mod. exp. central reef	1.0	F,S	48	26.35(23.33)	0.17(0.52)	--
* Seal Rock, prot. back reef	1.0	F,Y,S	37	33.33(21.16)	0	--
LANE CO., OR						
* Strawberry Hill, mod. exp.						
horiz. shelf	0.5	F,S	36	45.0 (2.84)	0	--
S. Hill, mod. exp. below main bed	0.3	F,S	72	27.0	0	--
COOS CO., OR						
Cape Arago, Sunset Bay, mod. exp.	0.6	C,W	19	61.0 (5.7)	0	T.f. 5.22/qt.
C. Arago, mod. exp. horiz. shelf	0.6	F,Y	10	31.67(15.70)	0	occas. T.f.

abbreviations: exp.=exposed, mod. exp.=moderately exposed, prot.=protected; abs=no sediment present, C=coarse sand, F=fine sand, Y=sediment present year round, S=sediment deepest in summer, W=deepest in winter; T.f.=*Tegula funebris*, S.p.=*Strongylocentrotus purpuratus*, limp.=limpets, C.p.=*Collisella pelta*, qt.=quadrats.

Table 18. Percent cover of *R. larix* in quadrats within main Rhodomela bed, Strawberry Hill, Lane Co., Or. Arc sin transformed, and standard deviations in parentheses.

	Partial Sand (July 1981)	No Sand (Dec. 1981)	No Sand (March 1982)	Partial Sand (July 1982)
Secondary cover (canopy)	83.75 (7.33)	76.00 (3.72)	69.52 (5.29)	80.70 (7.24)
Primary cover (rock surface)	---	45.24 (4.56)	45.00 (2.84)	56.35 (3.43)

Table 19. Species composition (% cover) and sand cover along transect northwest of main R. larix bed at Strawberry Hill, OR. Both July sets were during partial sand coverage, December was after, and April before coverage.

Cover component	July 1981	Dec. 1981	Apr 1982	July 1982
Sand	58.0	6.6	10.6	27.0
<u>Rhodomela larix</u>	22.0	27.0	24.0	25.0
<u>Bossiella plumosa</u>	3.5	6.6	5.3	4.4
<u>Corallina vancouveriensis</u>	2.8	5.2	3.0	0.7
Coralline crust	2.1	14.8	3.0	0.5
<u>Gymnogongrus linearis</u>	2.1	5.2	6.0	6.0
<u>Phyllospadix</u> 2 spp. rhizomes	2.1	9.6	3.0	7.4
<u>Iridea cordata</u>	1.4	3.0	3.8	4.4
<u>Ptilota filicina</u>	1.4	1.5	1.5	3.0
<u>Microcladia borealis</u>	1.4	0	0	0
<u>Plocamium</u> sp.	0.7	8.1	10.0	2.2
<u>Leathesia difformis</u>	0.7	0	0	0
<u>Dilsea californica</u>	0.7	0	0	0.5
<u>Cryptosiphonia woodii</u>	0.7	0	0	0
<u>Ulva</u> sp.	0.7	0	0.7	1.5
<u>Ahnfeltia plicata</u>	0	1.5	1.5	0
<u>Phaeostrophion irregulare</u>	0	0.5	3.8	0
<u>Codium setchelli</u>	0.5	1.5	4.5	1.5
Bare space	0	0	1.5	0
<u>Polysiphonia</u> sp.	0	0	0.7	0
<u>Porphyra</u> sp.	0	0	0	0.5
<u>Anthopleura elegantissima</u>	0	0	0	2.2

Table 20. Algal tissue changes after periods of sand coverage in the laboratory.

Species	One Month		3 Months	
	Control	Experimental	Control	Experimental
<u>Rhodomela</u> <u>larix</u>	no change	no change	little change	upright portions decaying, sl. discolored, holdfast and crust intact
<u>Microcladia</u> <u>borealis</u>	no change	no trace	holdfast remains	no trace
<u>Cryptosiphonia</u> <u>woodii</u>	little change	basal <1cm remains	basal 1-2 cm remain	no trace
<u>Ulva</u> sp.	little change	one gone, 2 nd plant $\geq \frac{1}{2}$ initial size	present, blades $\frac{1}{2}$ initial	basal tufts on both rocks (90% lost), discolored
<u>Gigartina</u> <u>papillata</u>	little change	blade present, no papillae	present, no papillae	no trace
Coralline crust	no change	no change	no change	red-orange in color

BIBLIOGRAPHY

- Abbott, I.A. and G.J. Hollenberg. 1976. Marine algae of California. Stanford Univ. Press, Palo Alto.
- Allender, B.M. 1977. Ecological experimentation with generations of Padina japonica Yamada (Dictyotales: Phaeophyta). J. Exp. Mar. Biol. Ecol. 26: 225-234.
- Ballantine, D.L. 1979. The distribution of algal epiphytes on macrophyte hosts offshore from La Parguera, Puerto Rico. Bot. Mar. 22: 107-111.
- Behrens, S. 1971. The distribution and abundance of the intertidal prosobranchs Littorina scutulata (Gould 1849) and L. sitkana (Philippi 1845). MS Thesis. Univ. of British Columbia.
- Berg, C.J. Jr. 1974. A comparative ethological study of strombid gastropods. Behavior 51: 274-322.
- Bernstein, B. and M. Jung. 1979. Selective pressures and coevolution in a kelp canopy community in Southern California. Ecol. Monogr. 49: 335-355.
- Bold, H. and M. Wynne. 1978. Introduction to the algae. Prentice-Hall, Inc., Englewood Cliffs, N.J.
- Brawley, S. and W. Adey. 1981a. The effect of micrograzers on algal community structure in a coral reef microcosm. Mar. Biol. 61: 167-177.
- Brawley, S. and W. Adey. 1981b. Micrograzers may affect macroalgal density. Nature 292: 177.
- Brenner, D., I. Galiela, C. van Raalte and E. Carpenter. 1976. Grazing by Talochestia longicornis on an algal mat in a New England salt marsh. J. Exp. Mar. Biol. Ecol. 22: 161-169.
- Brock, T.D. 1970. Photosynthesis by algal epiphytes of Utricularia in Everglades National Park. Bull. Mar. Sci. 20(4): 952-956.
- Castenholz, R.W. 1961. The effect of grazing on marine littoral diatom populations. Ecology 42: 783-794.
- Chapman, V.J. 1946. Marine algal ecology. Bot. Rev. 12: 628-672.
- Chapman, V.J. 1962. The algae. Macmillan and Co., London.

- Cimberg, et al. 1973. In Proceedings of Joint Conference on Prevention and Control of Oil Spills. March 13-15, 1973, Wash. D.C., sponsored by Amer. Petrol. Institute, EPA, US Coast Guard. 697-702.
- Connell, J. 1961a. The influence of interspecific competition and other factors on the distribution of the barnacle Chthamalus stellatus. Ecol. 42: 710-723.
- Connell, J. 1961b. Effects of competition, predation by Thais lapillus, and other factors on natural populations of the barnacle Balanus balanoides.
- Connell, J. 1970. A Predator-prey system in the marine intertidal region. I. Balanus glandula and several predatory species of Thais. Ecol. Monogr. 40: 49-78.
- Connell, J. 1975. Some mechanisms producing structure in natural communities: A model and evidence from field experiments. Pages 460-490. In M. Cody and J. Diamond, eds. Ecol. and Evol. of Communities, Belknap Press, Cambridge, Mass., USA.
- Connell, J.H. 1978. Diversity in tropical rain forests and coral reefs. Science 199: 1302-1310.
- Conover, J.T. 1958. Seasonal growth of benthic marine plants as related to environmental factors in an estuary. Publ. Inst. Mar. Sci. Univ. Texas 5:97-147.
- Conover, J.T. 1964. The ecology, seasonal periodicity and distribution of benthic plants in some Texas lagoons. Bot. Mar. 7:4-41.
- Dahl, A.L. 1964. Macroscopic algal foods of L. planaxis Philipps and L. scutulata Gould (Gastropoda: Prosobranchiata). Veliger 7(2): 139-143.
- Daly, M.A. and A.C. Mathieson. 1977. The effects of sand movement on intertidal seaweeds and selected invertebrates at Bound Rock, New Hampshire, USA. Mar. Biol. 43: 45-55.
- Dayton, P. 1971. Competition, disturbance and community organization: the provision and subsequent utilization of space in a rocky intertidal community. Ecol. Monogr. 41: 351-389.
- Dayton, P.K. 1975. Experimental evaluation of ecological dominance in a rocky intertidal community. Ecol. Monogr. 45: 137-159.
- Dayton, P.K., B.D. Keller, and D.A. Van Tresca. 1980. Studies of a nearshore community inhabited by sea otters. U.S. Marine Mammal Conference, Final Report No. MMC-78/14.

- Dethier, M. 1982. Pattern and process in tidepool algae: factors influencing seasonality and distribution. Bot. Mar. 25: 55-66.
- DeWreede, R. 1981. The effects of sea urchin grazing, clearing and competition on the distribution of three low intertidal algae in B.C. Canada. J. Phycol. (Supple). p. 10, Abstract.
- Dixon, J., S. Schroeter and J. Kastendiek. 1981. Effects of the encrusting byozoan, membranipora membranacea, on the loss of blades and fronds by the giant kelp Macrocystis pyrifera (Laminariales). J. Phycol. 17: 341-345.
- Dixon, P.S. 1965. Perennation, vegetation propagation and algal life histories, with special reference to Asparagopsis and other Rhodophyta. Bot. Gothob. Acta. Univ. Gothob. 3: 67-74.
- Dixon, P.S. 1973. Biology of the Rhodophyta. Hafner Press, N.Y.
- Doty, M.S. 1947. The marine algae of Oregon. Part I. Chlorophyta and Phaeophyta. Farlowia 3, 1-65.
- Edwards, P. and Kaupran, D.F. 1973. Benthic marine algal ecology in the Port Aransas Texas area. Contr. Mar. Sci. Univ. Texas. 17:15-52.
- Finke, L.R. 1978. Nitrogen fixation (acetylene reduction) by epiphytes of freshwater macrophytes. Appl. Environ. Microbiol. 36(1): 129-135.
- Foster, M.S. 1964. Microscopic algal food Littornia planaxis Philippi and Littorina scutalata Gould (Gastropoda: Prosobranchiata). Vel. 7(2) 149-152.
- Foster, M.S. 1975. Algal succession in a Macrocystis pyrifera forest. Mar. Biol. 32: 313-329.
- Fritsch, F.E. 1945. The structure and morphology of the algae. vol. 2.
- Goff, L. and K. Cole. 1976. The biology of Harveyella mirabilis (Cryotonomiales, Rhodophyceae). IV. Life history and phenology. Can. J. Bot. 54: 281-292.
- Grime, J.P. 1977. Evidence for the existence of 3 primary strategies in plants and its relevance to ecological and evolutionary theory. Am. Nat. 111: 1169-1194.
- Hansen, J.D. 1977. Ecology and natural history of Iridaea cordata (Gigartinales, Rhodophyta) growth. J. Phycol. 13: 395-402.

- Hansen, J.E. and W.T. Doyle. 1976. Ecology and natural history of Iridaea cordata (Rhodophyta: Gigartinales): Population structure. J. Phycol. 12: 273-278.
- Hargrave, B. 1970. The utilization of benthic microflora by Hyaella azteca (amphipoda). J. Anim. Ecol. 39: 427-437.
- Harkin, E. 1981. Fluctuations in epiphyte biomass following Laminaria hyperborea canopy removal. Xth Internatl. Seaweed Symposium Proceedings. 303-308.
- Harlin, M. 1971. Epiphytic marine algae: Interactions with their hosts. Ph.D. Thesis, Univ. of Washington
- Hartlett, J.D. 1972. Sediment transport on the northern Oregon continental shelf. Ph.D. Thesis. Oregon State University
- Highsmith, R., A. Riggs and C. D'Antonio. 1980. The survival of hurricane-generated coral fragments and a disturbance model for reef calcification/growth rates. Oecologia 46: 322-329.
- Hoyle, M.D. 1978. Reproductive phenology and growth rates in two species of Gracilaria from Hawaii. J. Exp. Mar. Biol. Ecol. 35(3): 273-283.
- Humm, J.H. 1964. Epiphytes of the sea grass, Thalassia testudinum, in Florida. Bull. Mar. Gulf Carib. 14(2): 306-341.
- Istock, C. 1967. The evolution of complex life cycle phenomena: An ecological perspective. Evol. 21: 592-605.
- Jones, R. C. 1980. Productivity of algal epiphytes in a Georgia salt marsh: Effect of inundation frequency and implications for total marsh productivity., Estuaries 3(4): 135-317.
- Katsui, N., Y. Suzuki, S. Kitamura and T. Irie. 1967. 5,6-Dibromoprotocatechualdehyde and 2,3-dibromo-4,5-dihydroxybenzylmethly ether. New dibromophenols from Rhodomela larix. Tetrahedron 23: 1185-1188.
- Kaupran, D.F. 1980. Floristic affinities of North Carolina inshore benthic marine flora. Phycologia 19: 245-252.
- Kilar, J.A. and A.C. Mathieson. 1978. Ecological studies of the annual red alga Dumontia incrassata (O.F. Muller) Lamouroux. Bot. Mar. 12: 423-437.
- Komar, P. 1976. Beach processes and sedimentation. Prentice Hall, Englewood Cliffs, NJ.

- Lee, R.K. 1966. Development of marine benthic algal communities on Vancouver Island, British Columbia. In, The Evolution of Canada's Flora. R. Taylor and R.A. Ludwig eds. Univ. of Toronto Press, Toronto, Canada.
- Levin, S. and R.T. Paine. 1974. Disturbance, patch formation, and community structure. Proc. Nat. Acad. Sci. 71: 2744-2747.
- Lilly, G.R. 1968. Some aspects of the ecology of Irish Moss, Chondrus crispus (L.) Stackhouse, in Newfoundland waters. Fish. Res. Bd. Can. Tech. Rep. 43.
- Lobban, C.S. 1978. Growth of Macrocystis integrifolia in Barkley sound, Vancouver, IS., B.C. Can. J. Bot. 56: 2707-11.
- Lubchenco, J. and B. Menge. 1978. Community development and persistence in low rocky intertidal zone. Ecol. Monogr. 48:67-94.
- MacFarlane, C.I. 1956. Irish Moss in the maritime Provinces. Nova Scotia Res. Fdn. Publ. 20 pp.
- Markham, J. 1973. Observation on the ecology of Laminaria sinclarii on three northern Oregon beaches. J. Phycol. 9: 336-341.
- Markham, J.W. and P.R. Newroth. 1972. Observations on the ecology of Gymnogongrus linearis and related species. Internatl. Seaweed Symposium 7: 127-130.
- Mathieson, A.C. 1965. Contributions to the life history and ecology of the marine brown alga, Phaeostrophion irregulare. S. Ph.D. Thesis, Univ. of B.C., Canada.
- Mathieson, A. and R. Burns. 1975. Ecological studies of economic red algae. V. Growth and reproduction of natural and harvested population of Chondrus crispus Stackhouse, in New Hampshire. J. Exp. Mar. Biol. Ecol. 17: 137-156.
- Mathieson, A. and J. Prince. 1973. Ecology of Chondrus crispus Stackhouse. Proc. N.S. Inst. Sci. 27: 53-79.
- Maynard Smith, J. 1979. The evolution of sex. Cambridge Univ. Press, Cambridge, England.
- Menge, B.A. 1976. Organization of the New England rocky intertidal community: Role of predation, competition and environmental heterogeneity. Ecol. Monogr. 46: 355-393.
- Menge, J.L. 1975. Effects of herbivores on community structure of the New England rocky intertidal region: Distribution, abundance and diversity of algae. Ph.D. Thesis. Harvard University.

- Moore, J. 1975. The role of algae in the diet of Asselus aquaticus L. and Gammarus pulex L. J. Anim. Ecol. 44: 719-730
- Morgan, M.D. 1980. Grazing and predation of the grass shrimp Pelaemonetes pugio. Limnol. & Oceanogr. 25(5): 896-902.
- Muenschler, W.L. 1915. A study of the algal associations of San Juan Island. Puget Sound Biol. Stat. Publ. 1:59-83.
- National Weather Service Publications, Sea Surface thermal analysis. U.S. Dept of Commerce, National Oceanographic and Atmospheric Association.
- Ngan, Y. and I.R. Price. 1980. Seasonal growth and reproduction of intertidal algae in Townsville region (Queensland, Australia). Aquat. Bot. 9: 117-134.
- Norall, T.L., A.C. Mathieson, and J.S. Kilar. 1981. Reproductive ecology of four subtidal red algae. J. Exp. Mar. Biol. Ecol. 54: 119-136.
- North, W.J. 1954. Size distribution, erosive activities, and gross metabolic efficiency of the marine intertidal snails, Littorina planaxis and L. scutulata. Biol. Bull. 106: 185-197.
- Paine, R.T. 1966. Food web complexity and species diversity. Am. Nat. 100: 65-75.
- Paine, R.T. Controlled manipulations in the marine intertidal zone, and their contributions to ecological theory. The changing scenes in natural sciences, 245-270.
- Paine, R.T. and S. Levin. 1981. Intertidal landscapes: disturbance and the dynamics of pattern. Ecol. Monographs. 51: 145-178.
- Paine, R.T. and R. Vadas. 1969. The effects of grazing by sea urchins, Strongylocentrotus spp., on benthic algal populations. Limnol. Oceanogr. 14: 710-719.
- Phillips, D.W. and G.N. Towers. 1981. Bromophenols of Rhodomela larix: Chemotaxonomy of morphological forms. Biochem. Syst. Ecol. 9: 1-3.
- Phillips, D.W. and G.N. Towers. 1982. Chemical ecology of red algal bromophenols. I. Temporal, interpopulational and within-thallus measurements of lanosol levels in Rhodomela larix (Turner) C. Agardh. J. Exp. Mar. Biol. Ecol. 58: 285-293.
- Phillips, D.W. and G.N. Towers. 1982. Chemical ecology of red algal bromophenols. II. Exudation of bromophenols by Rhodomela larix (Turner) C. Agardh. J. Exp. Mar. Biol. Ecol. 58: 295-302.

- Phinney, H.K. 1977. The macrophytic marine algae of Oregon. in The Marine Plant Biomass of the Pacific Northwest Coast. R.W. Krauss (ed.) O.S. Univ. Press. p. 93-116.
- Platt, W.J. 1975. The colonization and formation of equilibrium plant species associations on badger disturbances in a tall grass prairie. *Ecol. Monogr.* 45: 285-305.
- Prince, J.S. 1971. An ecological study of the marine red alga Chondrus crispus in the waters off Plymouth, Mass. Ph.D. Thesis, Cornell Univ. Ithaca, N.Y. 193pp.
- Randall, J.E. 1964. Contributions to the biology of the queen conch, Strombus gigas. *Bull. Mar. Sci. Gulf & Carib.* 14(2): 246-295.
- Reyes-Vasquez, G. 1970. Studies on the diatom flora living on Thalassia testudinum König in Biscayne Bay, Florida. *Bull. Mar. Sci.* 20(1): 105-134.
- Runge, E.J. 1966. Continental shelf sediments, Columbia River to Cape Blanco, Oregon. Ph.D. Thesis. Oregon State University.
- Saito, Y. 1980. Suitable habitats for certain algae with respect to their growth on the vertical surface of breakwaters. *Jpn. J. Phycol.* 28(3): 171-176.
- Santelics, B. 1978. The morphological variation of Pterocladia caerulescens (Gelidiales, Rhodophyta) in Hawaii. *Phycologia* 17(1): 53-59.
- Searles, R.B. 1980. The strategy of the red algal life history. *Am. Nat.* 115: 113-120.
- Sieburth, J. M. and J.T. Conover. 1965. Sargassum tannin, an antibiotic which retards fouling. *Nature* 208(1-5): 52-53.
- Smith, G.M. 1944. Marine algae of the Monterey peninsula. Stanford University press, Stanford, California.
- Sousa, W. 1979a. Experimental investigations of disturbance and ecological succession in a rocky intertidal algal community. *Ecol. Monogr.* 49(3): 227-254.
- Sousa, W. 1979b. Disturbance in marine intertidal boulder fields: The nonequilibrium maintenance of species diversity. *Ecol.* 60(6): 1225-1239.
- Sousa, W., S. Schroder and S. Gaines. 1981. Latitudinal variation in intertidal algal community structure: The influence of grazing and vegetative propagation. *Oecologia* 48: 297-307

- Stearns, S. 1976. Life history tactics: A review of the ideas. Quart. Rev. Biol. 51: 3-47.
- Steward, J.G. 1968. Morphological variation in Pterocladia pyramidale. J. Phycol. 4: 76-84.
- Stephenson, T.A. and A. Stephenson. 1972. Life between tidemarks on rocky shores. W.H. Freeman and Co. San Francisco.
- Strong, D.R. 1977. Epiphyte loads, tree falls, and perennial forest disruption; a mechanism for maintaining higher tree species richness in the tropics without animals. J. Biogeogr. 4: 215-218.
- Sutherland, J. 1974. Multiple stable points in natural communities. Am. Nat. 108: 859-873.
- Sutherland, J.P. 1981. The fouling community at Beauford, North Carolina: a study in stability. Am. Nat. 118: 488-498.
- Taylor, A.R. and L. M. Chen. 1973. The biology of Chondrus crispus Stackhouse: Systematics, Morphology and life history. Proc. N.S. Inst. Sci 27:1-33.
- Taylor, P.R. and M.M. Littler. 1982. The roles of compensatory mortality, physical disturbance, and substrate retention in the development and organization of a sand-influenced, rocky-intertidal community. Ecology 63: 135-146.
- Thurmen, H.V. 1975. Introductory Oceanography. Merrill Publ. Co. Columbus, Ohio.
- Turner, T. 1982. Community organization and succession in rocky intertidal surfgrass beds. Ph.D. Thesis, Oregon State University.
- Weinstein, B.T. Rold, D.E. Harrell Jr., M. Burns III, and J.R. Waaland. 1975. Reexamination of the bromphenols in the red alga Rhodomela larix. Phytochemistry 14: 2667-2670.
- Whittick, A. and R. Hooper. 1977. The reproduction and phenology of Antithamnion cruciatum (Rhodophyta: Ceramiales) in insular Newfoundland. Can. J. Bot. 55: 520-524.
- Wilbur, H.M., D.W. Tinkle and J.P. Collins. 1974. Environmental certainty, trophic level, and resource availability in life history evolution. Am. Nat. 108: 805-817.
- Williams, G. 1975. Sex and evolution. Princeton Univ. Press, Princeton, N. J.

- Wing, B. and K. Clendenning. 1971. Kelp surfaces and associated invertebrates. In North, W.J. (Ed.). The Biology of Giant kelp beds (Macrocystis) in California. Nova Hedwigia 32: 319-341.
- Yates, K. 1981. A Limpet kelp interaction: Description and definition. Masters Thesis, Oregon State University.
- Young, D. and M. Young. 1978. Regulation of species densities of seagrass associated macrobenthos: Evidence from field experiments in the Indian River Estuary, Florida. J. Mar. Res. 36: 569-593.
- Zimmerman, R., R. Gibson and J. Harrington. 1979. Herbivory and detritivory among gammaridean amphipods from a Florida seagrass community. Mar. Biol. 54: 41-47.

Appendix 1. Herbivore species from beds of *R. larix*. Data presented as mean number/g dry weight of host; n=2 for each sample; standard errors in parentheses. M=mid zone, L=low zone. Sampling dates May 1981 to February 1982.

Taxon	May		June		July		August		October		December		February	
	M	L	M	L	M	L	M	L	M	L	M	L	M	L
GASTROPODA														
<u>Littorina</u> <u>scutulata</u>	15.78 (6.00)	0	29.00 (2.72)	0.47 (0.66)	23.80 (2.23)	0	43.39 (19.29)	0.43 (0.16)	17.73 (5.96)	0.58 (0.29)	10.17 (1.58)	0.52 (0.55)	10.08 (7.31)	0
<u>Lacuna</u> <u>marmorata</u>	2.65 (0.50)	3.00 (0.71)	4.51 (3.05)	6.81 (4.98)	0.51 (0.71)	1.60 (0.17)	2.69 (3.80)	2.20 (0.82)	9.50 (10.70)	2.87 (0.19)	4.38 (0.49)	25.36 (0.67)	1.72 (1.17)	34.69 (21.65)
INSECTA														
Diptera larvae	2.16 (0.19)	0	3.77 (1.33)	4.67 (6.02)	2.63 (3.57)	15.10 (3.80)	3.19 (2.17)	2.63 (0.66)	2.73 (0.45)	1.54 (0.59)	0	0.29 (0.23)	7.94 (5.55)	6.21 (3.00)
CRUSTACEA														
Amphipoda	1.00 (1.42)	9.66 (0.40)	0	11.92 (3.59)	2.53 (2.86)	93.57 (7.00)	1.40 (0.23)	155.21 (107.13)	5.48 (4.33)	25.00 (9.94)	5.98 (0.66)	80.63 (48.52)	2.14 (1.77)	16.78 (8.02)
Isopoda	2.77 (1.75)	1.83 (0.94)	8.07 (0.60)	0.47 (0.66)	2.27 (2.50)	0	0.83 (1.17)	0.56 (0.35)	0	0	0.20 (0.28)	0.29 (0.23)	0.65 (0.28)	5.19 (4.45)