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Factors restricting recruitment of Ascophyllum nodosum L (Le Jolis)

Paula K B Philbrick
University of New Hampshire, Durham

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FACTORS RESTRICTING RECRUITMENT OF *ASCOPHYLLUM NODOSUM* L. (LE JOLIS)

BY

PAULA K. B. PHILBRICK

B.A. University of California at Santa Barbara, 1975

DISSERTATION

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in Partial Fulfillment of

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Ph. D. DISSERTATION

This dissertation has been examined and approved.

arthur C. mathieson

Arthur C. Mathieson, Professor of Plant Biology

Garrett E. Crow, Professor of Plant Biology

Alan L. Baker, Associate Professor of Plant Biology

Thomas D. Lee, Associate Professor of Forest Ecology

Christopher D. Neefus, Associate Professor of Plant Biology
and Biometrics

Dec. 19, 2003
Date

DEDICATION

I dedicate this work to the memories of my father, Kenneth J. Busse, a man of great ability and incredible focus, and to Dr. Warren, an inspiring statistician and teacher at UNH. Completion is dedicated to the vision and support of Dr.'s Mathieson and Crow, and the understanding of Dean Richards.

ACKNOWLEDGEMENTS

The support of two Central University Research Fund grants (1982, 1983) and a Doctoral Dissertation Fellowship (1983-4) are gratefully acknowledged. Support, space and supplies through the Jackson Estuarine Laboratory (Dr. A. C. Mathieson) made a critical difference. The loving support of my mother and my family were true gifts. The many discussions and sage advice of my advisor, Dr. Arthur C. Mathieson, were invaluable. He has been a tremendous role model and valued friend. The time and effort of my committee is gratefully acknowledged. My earnest thanks are extended for Dr. Garrett Crow's many comments on several longer versions, Dr. Thomas D. Lee's willingness to discuss methods and results on the spot as well as his help in the field, and the careful explanations of appropriate analysis by Dr. Christopher Neefus. Much of the field work was accomplished with the help of C. Thomas Philbrick, then a fellow graduate student and now an authority on aquatic plants and my husband. Thank you all.

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ABSTRACT

FACTORS RESTRICTING RECRUITMENT OF *ASCOPHYLLUM NODOSUM* L. (LE JOLIS)

by

Paula K. B. Philbrick

University of New Hampshire, May, 2004

Ascophyllum nodosum dominates a wide zone on the shore. Juveniles occur high in the zone where canopy is continuous and grazing animals few. Settlement could account for the restricted range if it were enhanced under canopy or on the upper shore. Settlement was monitored under canopy and in the open at four shore levels during spring 1983. Propagules settled everywhere. Settlement does not restrict plant establishment. Germlings caged and not caged were placed under canopy and in the open through the zone to evaluate the effects of animals and the physical environment (shore level x frond cover) on survival and growth. Animal impact overwhelmed environmental effects both summers (1982, 1983). Impact increased down the shore. For caged germlings, survival was dependent upon canopy high in the zone. Survival was greatest (@ +2.0 m in the understory) where growth was slowest. Growth increased 5 to 10 times down the shore, doubling in the open. A size-based exclusion experiment indicated that larger animals were most effective. Individual snails were caged with germlings and only *Littorina littorea* had significant effects. Smaller snails (< 0.6 cm) removed fewer germlings. When impact was related to size, *Littorina obtusata* and *Acmaea testudinalis* were effective but of secondary importance. Winter may afford a seasonal lapse in impact on the upper shore. Animals were less abundant in winter (1983-4), though larger *L. littorea* did not decline significantly. Caging experiments demonstrated that animal impact was important during the winter. *Ascophyllum* shares key features with climax tree species. *Ascophyllum* germlings are at a selective advantage in the understory. Suppression of growth in *Fucus vesiculosus* and *Ascophyllum* was significantly different. *Ascophyllum* suppressed in the understory high on the shore were transplanted low on the shore. Growth increased significantly. Suppressed juveniles are critical in regenerating lost cover, a 'juvenile plant bank.' *Ascophyllum* juveniles of intermediate sizes grow under *Ascophyllum* canopy but were more numerous under *Fucus vesiculosus*, poised for replacement.

INTRODUCTION

The fucoid brown alga *Ascophyllum nodosum* dominates rocky shores throughout the North Atlantic. Despite regular reproduction, establishment of new plants is rare. In New England, juveniles occur in the upper portion of the *Ascophyllum* zone. The purpose of my dissertation research was to explain the limited range in terms of the critical factors. Chapter I characterizes settlement patterns, while germling survival and growth with and without animals and under a wide range of physical environments are outlined in Chapter II. Several grazing species are common in the *Ascophyllum* zone. The effectiveness of each species in removing *Ascophyllum* germlings (= impact) was tested and results are reported in Chapter III. A winter decline in animal impact is anticipated. Surviving recruits on the upper shore may have several months to reach a size discouraging removal by animals (= safe size). Chapter IV focuses on differential abundance and impact of animals through the year, as well as the importance of a 'safe size.' On land, self-replacement of climax trees is favored by seedlings that are adapted to understory conditions, by saplings that are able to capitalize on conditions in an opening (*i.e.,* a gap), and by plants of intermediate sizes in the understory and ready to regain canopy monopolization. By analogy, *Ascophyllum* is a climax species on the shore. Conditions on the upper shore should favor self-replacement. Differential suppression beneath *Ascophyllum* canopy, faster growth with improved conditions, and a 'juvenile bank' are explored in Chapter V.

CHAPTER I

SETTLEMENT PATTERNS

Introduction

Ascophyllum nodosum (L.) Le Jolis[1] is a brown seaweed characteristic of rocky shores throughout the North Atlantic (cf. Lewis 1964, Baardseth 1970). Plants are large, and individual fronds can reach almost 2 meters in length. *Ascophyllum* creates a dense canopy, deeply shading the understory. The vertical range spans most of the shore exposed on a low tide (intertidal zone). Plants grow from an upper limit coinciding with high, neap tides (cf. Baker 1909, Zaneveld 1937, David 1943, Baardseth 1970) to below the low tide mark (subtidal zone). Vegetation zones on the shore are identified by the predominant species, and this broad band is the *Ascophyllum* zone (cf. Lewis 1964).

On shores rimming the North Atlantic Ocean, *Ascophyllum nodosum* (hereafter *Ascophyllum*; it is the same species throughout) occurs in all but the most exposed localities (David 1943). It grows wherever rock surfaces are stable and growing conditions are suitable (Lewis 1964). The cover is dense and perennial. Plants are long-lived (Boney 1965, Åberg 1992a). One aspect of the biology of *Ascophyllum* is

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[1] According to Doty and Newhouse (1954), the correct designation is *Ascophylla nodosa*, a combination made by Le Jolis. The species *Ascophylla laevigata* was described by Stackhouse (1809) and considered synonymous with *Fucus nodosus* Linnaeus. In emending the binomial, Le Jolis retained the specific epithet of priority and published the new combination *Ascophyllum nodosum*. He later noted that *Ascophylla nodosa* would have been in keeping with the form of the genus published by Stackhouse (Le Jolis 1856, 1896). However, *Ascophyllum* is conserved (*nom. et orth. cons.*; *Index Nominum Genericorum*) and is the form in common usage.

enigmatic; recruitment is limited despite considerable yearly reproductive effort (Printz 1956a, Sundene 1973, Cousens 1986).

Plants are reproductive each spring, and gametes are released in large numbers (Blackler 1956, Printz 1956a, Baardseth 1970, Åberg and Pavia 1997). The tissue expended in reproduction accounts for about 50% of the fresh weight of a frond (Josselyn and Mathieson 1978, Cousens 1986, Mathieson and Guo 1992, Åberg 1996). Though *Ascophyllum* is regularly and prolifically reproductive, establishment of new plants in a population is rare (Printz 1956b).

Once cleared from a surface, re-establishment of *Ascophyllum* is tenuous. Denuded patches are colonized by a predictable progression of species, though recolonization by *Ascophyllum* has rarely been observed (Knight and Parke 1950, Hruby and Norton 1979, Boney 1965, Baardseth 1970, Vadas *et al.* 1992). In only one study was canopy dominance regained (Keser and Larson 1984). Knight and Parke (1950) reported no appreciable cover nearly a decade after clearing while Vadas (Vadas and Wright 1986) found no evidence of recruitment over a 20 year period. In both cases, fertile populations were in close proximity. Colonization of new surfaces (bare rock, brick, ceramic tile) may be entirely lacking (Hatton 1938, Moore and Sproston 1940).

Small plants (< 20 cm in length) are relatively scarce (David 1943, Printz 1956b, Moss 1970, Sundene 1973). The size distribution is skewed, with a preponderance of large plants (> 50 cm), and few plants either intermediate (20 – 50 cm) or small (< 20 cm) in size (see Burrows 1956, Boney 1965, Baardseth 1970, Åberg 1992a). The limited number of small plants contrasts sharply with yearly reproductive potential.

In New England, small plants occur high in the *Ascophyllum* zone, especially from +1.8 to +2.0 m above Mean Low Water (Figure I - 1 a). There, *Ascophyllum* canopy is continuous (Fig. I – 1 b), plants grow at maximum density (plants/m^2) and have the greatest range in length (Fig. I - 1 c). The observations suggest that plant establishment occurs most regularly high in the zone (see Busse 1983). Thus, I designated +2.0 m as the 'recruitment zone.'

Small plants growing beneath adult canopy have narrow, cylindrical fronds (Figure I - 2), in contrast with the broad, flattened fronds of adults. I consider them 'juveniles' as they are not yet reproductive, though the term also connotes youth. Slow growth of developing plants characterizes *Ascophyllum* (Sundene 1973) and small plants may be quite old (Burrows 1956, Chapters II and V). Plants reach reproductive maturity at this site at a length ≥ 20 cm. Thus, juveniles range in size up to 20 cm and range in age as well. The term 'juvenile' can now replace 'small plant.'

Settlement may restrict recruitment on the shore (see Underwood and Denley 1984). Settlement is passive. Gametes are exuded onto frond surfaces during the low tide, and washed into the water column with the returning tide. The resulting zygotes (hereafter referred to as propagules[2]) settle onto the rock surface. If settlement densities were enhanced high in the zone or under canopy, settlement patterns could account for the restricted distribution of juveniles. The test hypotheses were: 1) **Settlement is affected by shore level** (subsequent testing to evaluate 'settlement is greater in the recruitment zone'), and 2) **Settlement is affected by frond cover**.

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[2] Propagules may be single-celled zygotes or multicelled germlings when they settle onto rock surfaces.

Materials and Methods

Study Site

Fort Stark is on the southeastern shoreline of Newcastle Island, New Hampshire (Figure I - 3). It is located at the mouth of the Great Bay Estuary System. The study area (Fig. I - 3, short arrow; 43°03'33" N latitude, 70°42'42" W longitude) is in the lee of Jaffrey Point. The shore consists of granite ledges 30 - 50 m wide, gradually sloping to seaward. Ledges are separated by cobble. The *Ascophyllum* zone extends 80 - 100 m, from the upper to lower extremes. *Ascophyllum* canopy is dense and continuous in the upper portion of the zone and becomes discontinuous low on the shore (Figure I - 4).

Physical and hydrographic factors are typical of cold, north temperate shores. Tides are mixed semi-diurnal, with a mean amplitude of 2.6 m (N.O.A.A. 1982). Air temperatures reach an average summer maximum of 78° F or 25.5° C and an average winter minimum of 14° F or -10° C (Oklahoma Climatological Survey 1955-1983). Seawater temperature ranges from 61° F or 16° C, to 30° F or -1.0° C. Salinity is generally 30 - 33‰ (Emerich Penniman *et al.* 1984).

Experimental Areas

Experimental areas were located every 0.5 m of elevation through the zone, on 3 adjacent rock ledges. Areas at +2.0, +1.5, +1.0, and +0.5 m above Mean Low Water were designated using a stadia-transit system and sighting against low tide. Sightings were repeated on several dates. Several experimental areas at each shore level were established on the 3 rock ledges.

Half of the experimental areas at each shore level were to be open areas, and half frond-covered areas. Open areas were cleared of vegetation. Comparable frond-covered areas occur naturally on the upper shore and were established on the lower shore. Stainless steel bolts were cemented to the rock using quick-drying marine cement (Maricrete). *Ascophyllum* plants were secured on bolts with cable ties. Light environments were rendered similar to +2.0 m (the 'recruitment zone'). Ten readings of light beneath the canopy in the recruitment zone were taken. The maximum reading became the threshold for artificially vegetated areas. When several rearrangements (floppings) of the fronds yielded sufficient shading, cover was adequate. Bolts were affixed to the rock in each experimental area. The large number of experimental areas was to allow arbitrary use of areas and rock ledges.

Settlement Tiles and Counts

Light-colored ceramic tiles were used as artificial substrata. The unglazed surface allowed easy detection of propagules using low magnification (10 x - 30 x) of a dissecting microscope. Substratum roughness influences settlement (Hatton 1938, Moss 1975), and tile surfaces were made irregularly rough by chipping across the surface with a chisel. Tiles were 5.5 cm on a side. They were drilled with a central hole to secure them onto bolts in experimental areas.

Tiles used to monitor settlement were not caged. Cage screening slows water flow and can alter settlement (see Underwood and Denley 1984). Instead, time in the field was kept short (one or two high tides, up to 24 hr.) to minimize animal impact.

Exposure to one or two high tides varied, depending upon the time of the following low tides and trying to arrange retrieval during daylight whenever possible.

Eight experimental environments represented the range of conditions on the shore (4 shore levels x 2 frond cover situations, *i.e.*, frond-covered or open). Sampling bracketed the period of gamete release, spring 1982. During the first 7 collection times, 4 replicates were included (n = 32) and during the last 8 collection times, 3 replicates were included (n = 24). Tiles were kept moist during transport back to the laboratory for propagule counts.

Treatment of the Data and Statistical Analysis

Minitab software was used for graphics and statistics (Minitab Software Inc., PA, U.S.A.). Wherever possible, data were analyzed parametrically to evaluate interaction between the factors. The Ryan-Joiner test was used to flag significant departure from normality, and significant heterogeneity among group variances was detected using F or Bartlett's tests. Data sets used and transformations applied are stated in the appropriate figure and table legends.

Propagule counts were standardized for direct comparison. Counts reflecting 2 high tide exposures were halved to be comparable with counts for a single high tide. Count data were highly variable and replicated two-fold, as the 3 or 4 replicates in each environment (shore level x frond cover group) and over the 15 collection times. Settlement patterns varied among the collection times. Therefore, to analyze the importance of shore level and frond cover overall, counts (propagules/tile) were summed by environment to yield environmental totals. Environmental totals represented different surface areas (4 replicates or 121 cm^2 for collection times 1 – 7, and 3 replicates or 91 cm^2 for times 8 – 15) and were standardized to 1 dm^2 of surface. The standardized environmental totals were used in the analysis of settlement *vs.* environment.

The full set of environmental totals (15 collections x 8 totals = 120) departed significantly from normality, despite transformation. Exclusion of four collection times ($\leq$ 3 propagules collected) and ranking of the data (n = 88), allowed both assumptions to be met for an Analysis of Variance on settlement *vs.* environment (Shore Level, Frond Cover). In addition, the significance of shore level and frond cover were analyzed separately (n = 120) using non-parametric tests and yielded outcomes similar to ANOVA using ranks. The effect of collection time had to be analyzed using a Kruskal-Wallis test.

Results

Propagules settled at all shore levels (Table I - I). The grand total, summing the totals for all 15 tides sampled was 1550 propagules/dm^2.

The totals suggest settlement peaks on May 1 and on about May 14 (Table I - I). The second peak was not definitive as samples were not taken on May 13 or 15 (see times 10 - 12).

Settlement maxima occurred at different shore levels during the two peaks. The larger peak on May 1 was associated with maximum settlement on the upper shore at +1.5 m (Table I - I; value underlined). The later peak, about May 14, was due to heavier settlement on the low shore (+0.5 m).

Shore level did not have a significant effect on settlement (Table I - II a), so subsequent testing ('settlement is greater in the recruitment zone') was unnecessary.

Settlement densities were not greater at **+2.0 m** (recruitment zone) but **least** high in the zone where juveniles occur (Figure I - 5 a). On none of the collection times was settlement maximal at +2.0 m (Table I - I).

Frond cover effects were not significant (Table I - II a). Settlement was greater under frond cover overall (Figure I - 5 b and c). Differences between frond-covered and open areas were greatest at the extremes (+2.0 and +0.5 m; Figure I - 5 b). The overall mean for canopy-covered surfaces was 1.6 times that for open areas (Fig. I - 5 c).

The effect of **collection time** was highly **significant** (Table I - II b). On two of the collection times, no propagules were collected (times 7 and 15) and on three others (times 1, 10 and 14) the totals were < 15 (Table I - I, Figure I - 6). The average number *per* tile was 8.4 (26/dm^2) due to the large number of zeroes and a moderate number of counts in the hundreds. On three of the collection times totals were larger in the open (times 1, 2, and 5), while on nine of the times they were larger under frond cover (Fig. I - 6). During peak settlement (May 1, 14), totals were larger under frond cover.

Discussion

The observed settlement peaks were two weeks apart. While the second peak is about May 14, a two week separation suggests that similar conditions triggered peak gamete release. Tidal amplitudes rise and fall regularly on a lunar cycle, and tides at the same time of day and of a similar range occur two weeks apart. The two dates were coincident with full and new moons, when tidal range is greatest. Gamete release in *Fucus ceranoides* has a semilunar periodicity (Brawley 1992, Brawley and Johnson

1992) with peaks synchronized on the full and new moons. That possibility is suggested for *Ascophyllum*.

While the potential for peak gamete release may be entrained to an environmental cycle (lunar, semilunar, tidal), specific conditions serve as immediate triggers (Brawley and Johnson 1992, Brawley *et al.* 1999). Gamete release in *Ascophyllum* occurs in response to heat and drying (Baker 1910, Bacon 1983, Vadas *et al.* 1990). Low tide occurred mid-day with warm, sunny weather and no breeze on May 1 and May 14 (field notes) so peak settlement was noted on days when heating and drying of fronds were maximized. Water temperature at high tide has a significant effect (Bacon 1983, Bacon and Vadas 1991). Peak gamete release may be realized given conditions determined by a combination of factors, such as the temperature differential between the fronds and the water of the returning tide. Notably, gamete release in other fucoid species is stimulated by a decrease in the concentration of dissolved organic carbon (DIC) in the water (Pearson *et al.* 1998). If important for *Ascophyllum*, depletion of DIC in the water column on a preceding high tide may serve as a primary cue.

Settlement peaks shadowed known release patterns. Gamete release occurs earliest on the high shore and later down the shore (David 1943). The first peak was the largest, and settlement densities were greatest on the upper shore (+1.5 m). On the upper shore, plant density is greatest (Fig. I - 1 c). Reproductive biomass may be concentrated on the upper shore, as observations suggest though detailed comparison of reproductive output for the upper and lower shore is lacking (numbers of reproductive laterals, receptacle size and number vary). The later peak about May 14, reflected heaviest settlement on the low shore. The second peak was modest, and plant density decreases on the low shore.

Settlement patterns do not account for the limited range of juveniles. While small plants occur high in the zone, settlement was least at +2.0 m and propagule densities were reduced on the upper shore.

Settlement densities were greater beneath the canopy, the gamete source. Considering the 15 tides sampled, about 330 more propagules/dm^2 under canopy *vs.* in the open. The reproductive season is a month long (≈ 60 tides), so differential settlement could result in a thousand more recruits/dm^2 in the understory.

High in the zone, open areas are lacking; low on the shore, continuous canopy is lacking. Natural settlement high on the shore would be similar to frond-covered areas; low on the shore it would be similar to open areas. When cover was provided low on the shore, settlement was enhanced. Maximum settlement occurred at +0.5 m several times, particularly late in the season. If cover were more extensive, settlement might be as well.

Settlement showed no consistent pattern. Maximum densities most frequently occurred at +1.5 m, but maxima occurred at +1.0 and +0.5 m (Table I - I). Totals under frond cover were generally larger but 'open' totals were sometimes greater (Fig. I - 6).

Depending upon the tide sampled, the data supported heavier settlement in the open or in the understory. Lazo *et al.* (1994) reported heavier settlement where canopy had been cut to about 10 cm. In both studies (the present study, Lazo *et al.* 1994) settlement was directly assessed. In other studies, settlement patterns are inferred from the distribution of recruits. Bertness *et al.* (1999) documented larger numbers of recruits under canopy, high in the zone. As they noted, the recruitment pattern reflected differential survival. Survival patterns modify settlement. In light of differential survival, settlement patterns cannot be reliably judged long after settlement. In particular, settlement patterns cannot be inferred from the distribution of juveniles.

Jenkins, Hawkins and Norton (1999) observed that naturally recruited plants were more numerous in openings. They note that differential settlement could be the cause, but that recruitment from a cryptic plant bank is also possible. Micro-sized plants already present (microrecruits *sensu* Ang 1991) may respond to improved light with increased growth. The same explanation was invoked for an apparent surge in recruits where canopy had been cut (Ang *et al.* 1996).

Canopy cover did not preclude settlement. Vadas *et al.* (1992) and Jenkins, Hawkins and Norton (1999) suggest that *Ascophyllum* canopy is a barrier to settlement and observed that juveniles can be abundant in openings. In the present study, settlement densities under canopy were not significantly different than in open areas.

Attachment is a critical phase (Vadas and Wright 1986, Vadas *et al.* 1990) and was not addressed here. Most studies of attachment tenacity involve artificially settled zygotes. Adhesion of *Sargassum* intensifies after a period in the water column (Norton 1980, 1983). I missed an opportunity by not returning the 'settlement' tiles to the field to test the tenacity of naturally settled propagules. Lazo *et al.* (1994) did. Survival patterns using laboratory-settled, cultured germlings placed into the field (Ch. II) were similar to the patterns observed using naturally settled recruits.

Short-term observations offered a direct assessment of settlement though the data were extremely variable. Roughly 70% of the counts (by tile) were zeroes. In the same environment, one tile might have 200 propagules while others had none. I avoided the use of cages, concerned that mesh might affect water flow and deposition. Lazo *et al.* (1994) used exclusion cages, and assessed settlement at the end of the reproductive season. Both approaches were satisfactory; however, counts over a longer sampling period should be less variable.

Spatial variability in settlement is well known for marine organisms (Underwood and Denley 1984, Hoffman and Ugarte 1985). Abundance of seaweed propagules varies within the water column and over time (Hoffman 1987, Hruby and Norton 1979, Amsler and Searles 1980, Zechman and Mathieson 1985). *Ascophyllum* propagules are not motile. Random turbulence and flow affect their dispersal; sinking and turbulent vectors lead to their deposition (see Amsler *et al.* 1992, Norton 1992; for *Ascophyllum*, Åberg 2001, Dudgeon *et al.* 2001). Spatial variability is not due to limited dispersal (Dudgeon *et al.* 2001).

Surface characteristics may contribute to patchiness in recruitment. Attachment is strongest on rough surfaces (Norton and Fetter 1981, Norton 1983, Vadas *et al.* 1992) and on bare rock (Jenkins, Hawkins and Norton 1999), and is favored in pits and crevices (Vadas *et al.* 1990). Attachment can be adversely affected by sediment (Mshigeni 1978) and algal crust (Jenkins, Hawkins and Norton 1999). Surface characteristics vary over a small spatial scale, potentially leading to patchiness in attachment and in the distribution of recruits.

Firm attachment is favored beneath *Ascophyllum* canopy (see Vadas and Wright 1986, Vadas *et al.* 1992). Amidst buoyant fronds, current flow is reduced (Johnson 1991, Brawley and Johnson 1992, Norton 1992). Flow slows again close to the substratum due to disruption by the mosaic of understory plants and animals. Surfaces under canopy experience relative calm (Chapman 1995; anecdotal evidence). Vadas *et al.* (1992) showed that tenacity of newly attached *Ascophyllum* is dependent upon several hours without disturbance (or longer, see Chapman 1995). Further, attachment structures of *Ascophyllum* germlings (rhizoids) ramify to a greater degree in the shade (Sheader and Moss 1975). Reduced flow, shade and surface calm promote secure attachment and characterize the understory.

Gamete release in fucoid algae has been tied to calm conditions. The concentration of dissolved inorganic carbon (primarily HCO_3^-) varies directly with water motion. Reduction in DIC stimulates gamete release in *Fucus distichus* L., *F. vesiculosus* L., and *Pelvetia compressa* (J. Agardh) De Toni, synchronizing release with decreased water motion and maximizing fertilization success (Pearson *et al.* 1998). The importance of [DIC] for *Ascophyllum* should be evaluated since calm water conditions are critical for effective attachment, and attachment is a phase crucial to successful recruitment (Vadas *et al.* 1990, Vadas *et al.* 1992).

Settlement does not limit recruitment, and could account for full replacement. At +2.0 m, where settlement densities were least, the potential recruits exceeded numbers of adult plants. Propagule totals over the sampling period (184 d/m^2 or 18,400/m^2, see Table I - I for +2.0 m), represent about 25% of the reproductive season (15 of 60 tides). Tens of thousands would be projected. Adult plants number 100 – 300/m^2. Settlement exceeded full replacement. Lazo *et al.* (1994) reported averages of 14 to 1335 zygotes for sampled areas, approximating several hundred to over ten thousand/m^2 (mid-shore). Settlement more than accounted for full replacement in both studies. Restriction of juveniles to the upper shore must reflect post-settlement modification.

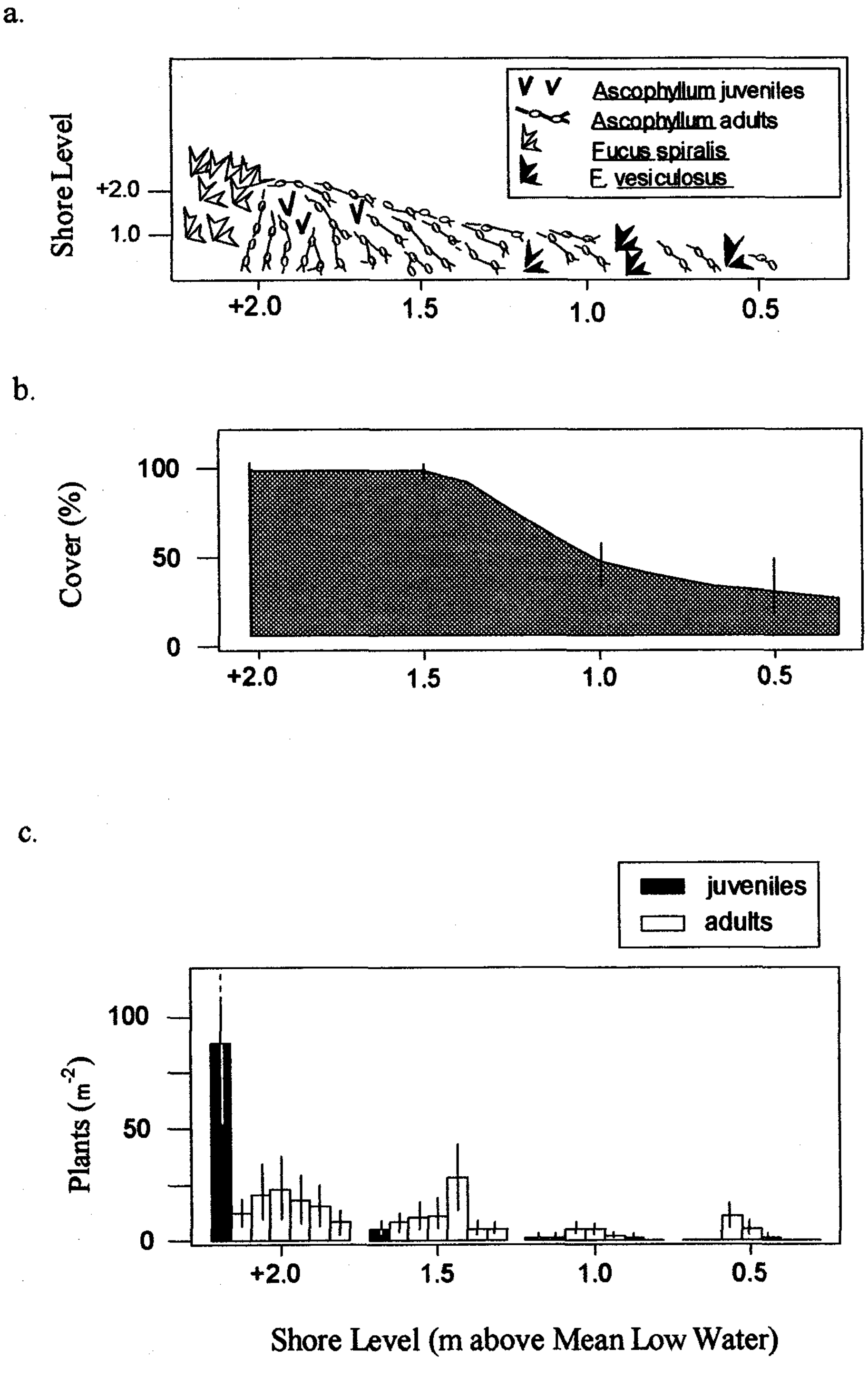

Figure I - 1. Initial Observations. Distribution of *Ascophyllum* (juveniles, adults) and *Fucus* species on the shore (a), *Ascophyllum* canopy cover (b) and size class distribution (c) by shore level. Means ± 1 S.E. are shown (b, c) using data from 6, 0.25 m^2 quadrats/shore level sampled at Ft. Stark in April 1982.

Figure I - 2. Small Plants. Ascophyllum from 1 – 6 cm in length, growing beneath adult frond cover high in the zone. The fronds are cylindrical initially, flattening with growth beyond several centimeters in length.

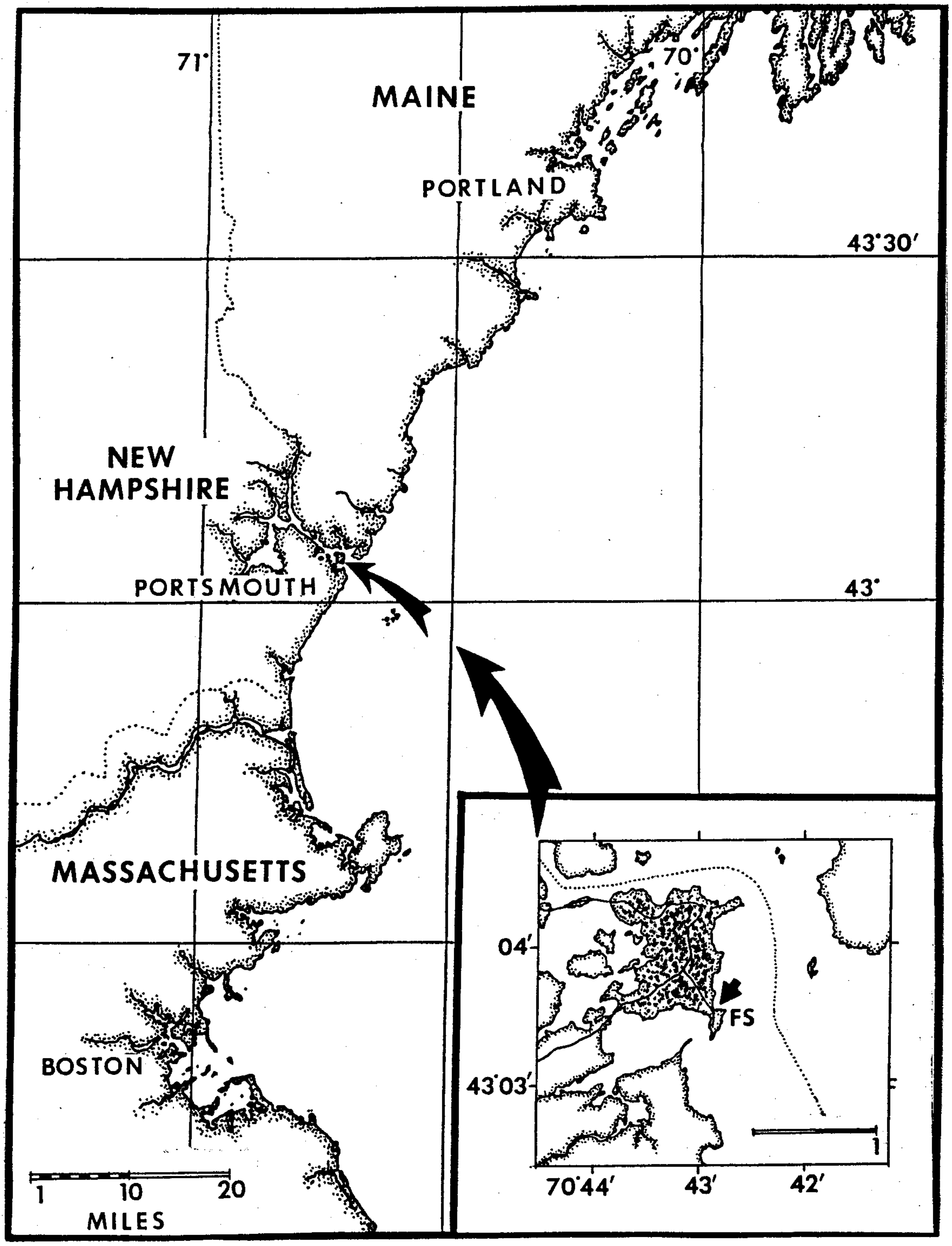

Figure I - 3. Location. Ft. Stark is on Newcastle Island, in New Hampshire.

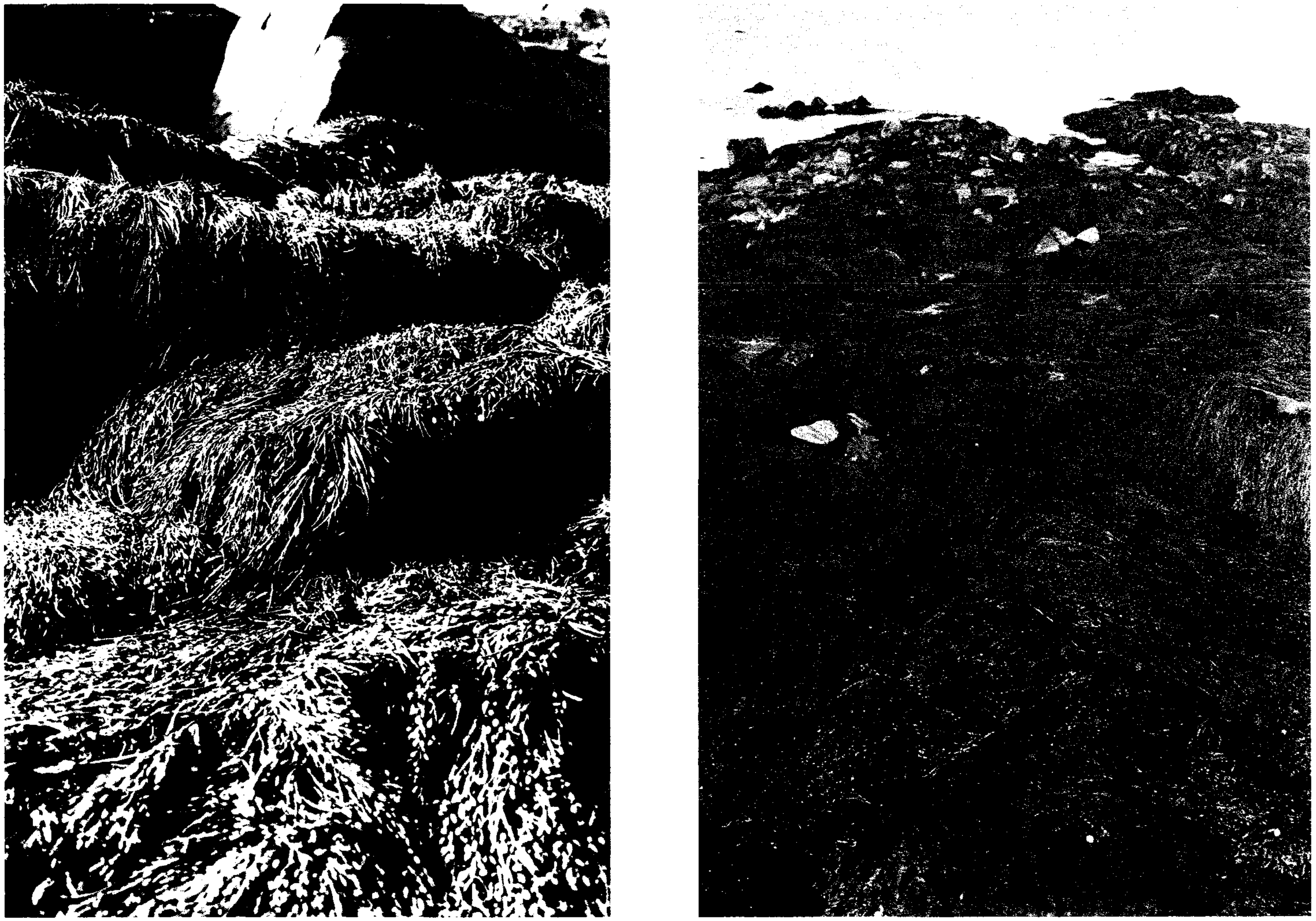

Figure I - 4. The Ascophyllum Zone. Cover is dense and continuous on the upper shore (a, from +1.5 m looking upshore) and and discontinuous on the lower shore (b, looking seaward). Zone extends 80 – 100 m.

Table I - I. Totals by Shore Level. Propagules (dm^2) by shore level, collection time ('time') and overall. Maximum values for each collection time are underlined. Shore level values were summed to give Totals by collection time (right column), shore level (at bottom) and overall (far right). Two collections were made on May 9 and 12 (a, b). Totals with 0 or 1 propagule/dm^2, indicated by ($^+$), were omitted from the analysis of settlement *vs.* environment.

		Shore Level (m)				
Time	Date	**+2.0**	**+1.5**	**+1.0**	**+0.5**	Total
1^+	April 28	0	1	0	0	1^+
2	April 30	3	0	8	8	**19**
3	May 1	121	214	167	115	**617**
4	May 2	15	113	19	90	**237**
5	May 3	11	84	65	39	**199**
6	May 6	2	1	29	1	**33**
7^+	May 9a	0	0	0	0	0^+
8	May 9b	0	0	0	22	**22**
9	May 12a	0	2	0	6	**8**
10^+	May 12b	0	1	0	0	1^+
11	May 14	28	98	26	169	**321**
12	May 17	2	7	4	27	**40**
13	May 18	1	22	13	10	**46**
14	May 19	1	3	1	1	**6**
15^+	May 28	0	0	0	0	0^+
		184	**546**	**332**	**488**	**1550**

Table I - II. Settlement Statistics. Results from analyses of settlement by environment (a) and by collection time (b). Environmental totals (frond cover x shore level groups) were standardized to 1 dm^2 of surface, and the standardized totals from eleven collection times were ranked and submitted to a 2-Way Analysis of Variance (a). Totals from all fifteen collection times were used without transformation for the Kruskal-Wallis test (b).

a.

Settlement *vs.* Environment

Source	df	SS	MS	F	p-value
Shore Level	3	1751.1	583.7	0.94	0.427
Frond Cover	1	2190.0	2190.0	3.52	0.064
SL x FC	3	933.6	311.2	0.50	0.683
Error	80	49812.3	622.7		
Total	87	54687.0			

Neither shore level nor frond cover had a significant effect on settlement. Further comparison (+2 m *vs.* other shore levels) was unnecessary.

b.

Settlement *vs.* Collection Time

Results from a Kruskal-Wallis test indicated that collection time had a highly **significant** effect on settlement (H = 73.20 adjusted for ties, df = 14, $p < 0.0001$***).

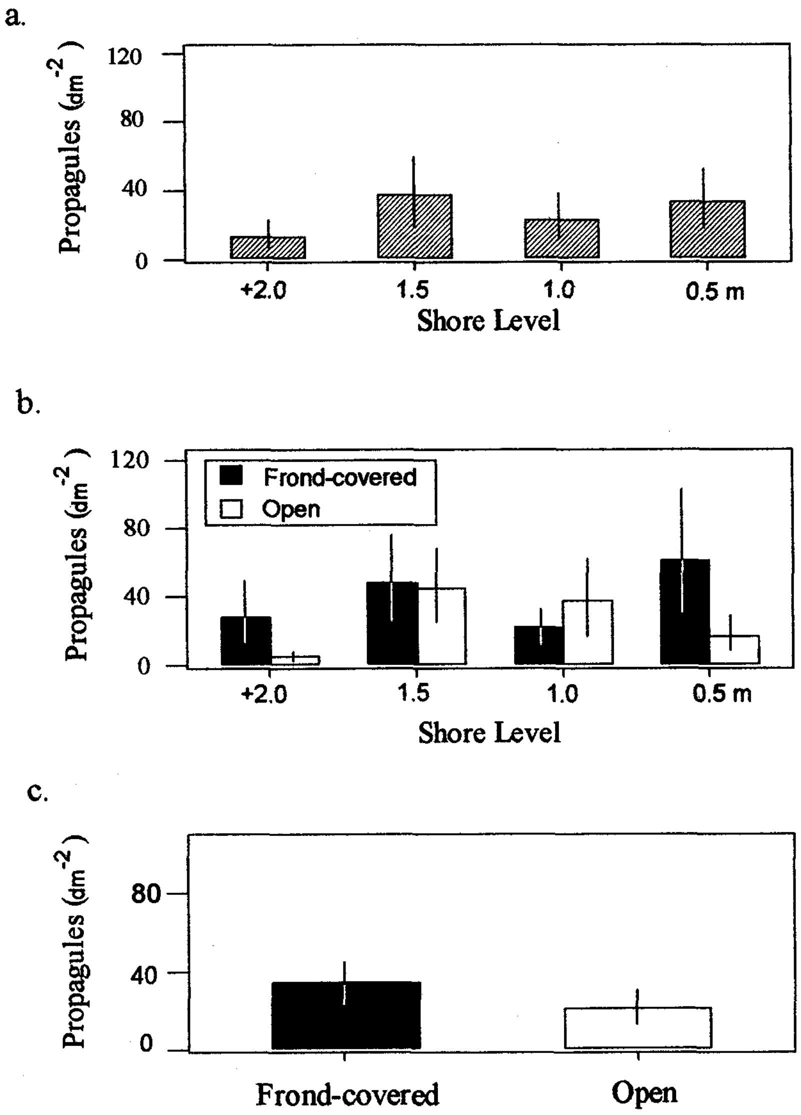

Figure I - 5. Settlement by Environment. Propagule densities by shore level (a), in frond-covered and open areas by shore level (b), and in frond-covered and open areas overall. Means ± 1 S.E. are shown.

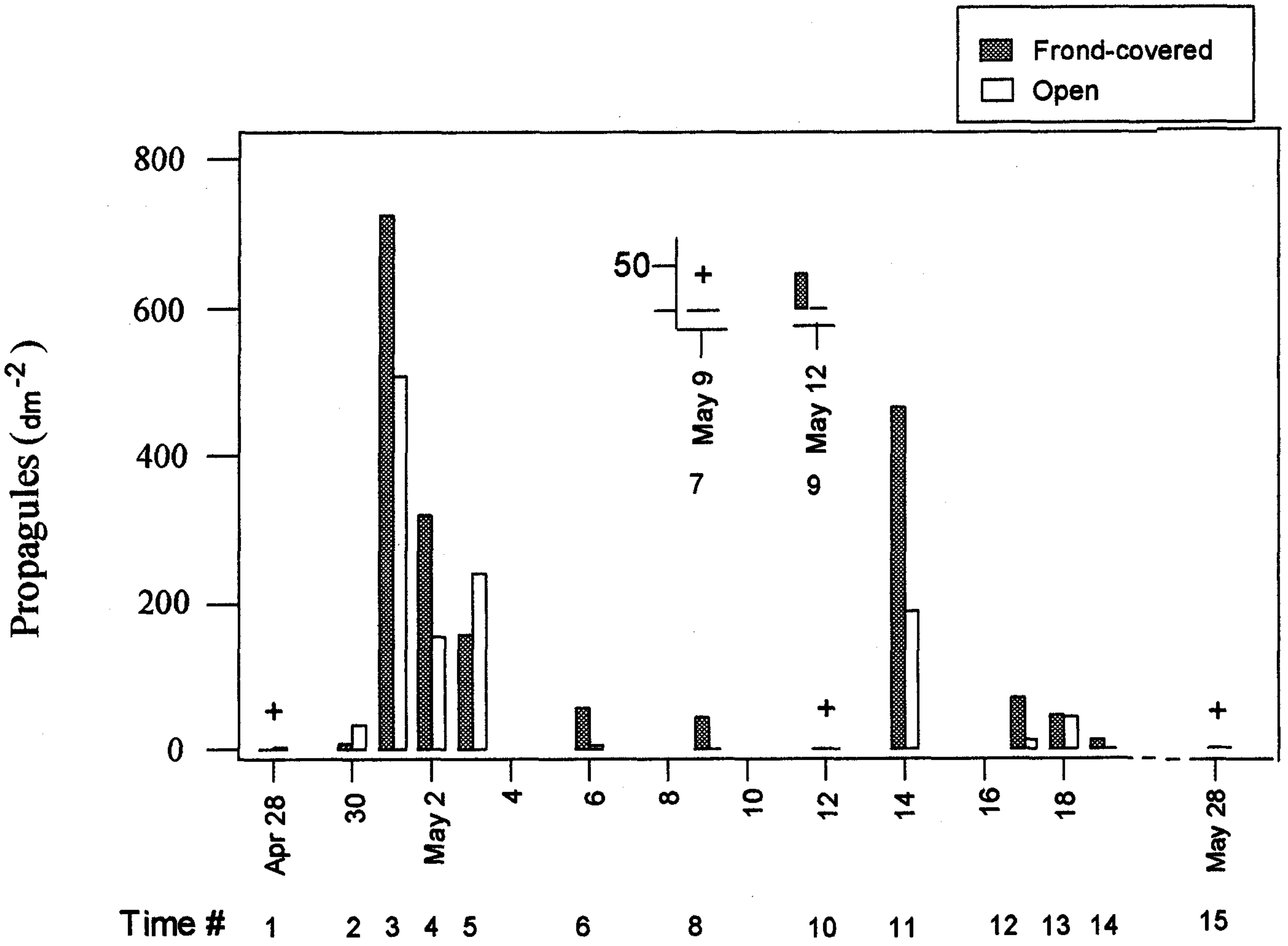

Figure I - 6. Totals by Situation. Propagule totals under frond-cover and in the open, by collection time. Earlier tides (May 9, 12) are inset above. Totals of 0, 1 are flagged (+). Final collection (May 28, #15) is later than its position suggests (break in axis).

CHAPTER II

SURVIVAL AND GROWTH OF DEVELOPING PLANTS

Introduction

In New England, *Ascophyllum* juveniles (plants < 20 cm long) are restricted to the upper portion of the *Ascophyllum* zone. The restricted range is not due to settlement, as propagules settle throughout the zone (Chapter I). Instead, it must reflect differential survival.

Historically, two explanations for limited recruitment have been proposed: a lack of sites favorable to development (David 1943), and loss of germlings to grazing animals (Boney 1965, Sundene 1973). Hatton (1938) and David (1943) suggested that surfaces beneath *Ascophyllum* canopy were too deeply shaded to support the growth of germlings. Hatton transplanted juveniles growing beneath the canopy to areas with 'improved conditions' and reported increased growth. Research concurrent with the present study evaluated the importance of grazing animals at mid-shore levels in New England (Miller and Vadas 1984). The present study assesses animal impact through the *Ascophyllum* zone (intertidal portion), and establishes the importance of animals and physical factors in light of the restricted distribution of juveniles.

Juvenile *Ascophyllum* are found in groups or in narrow bands, potentially delineating habitats favorable to their survival or growth (David 1943, Boney 1965). David (1943) observed that juveniles occur at the fringes of the *Ascophyllum* zone and suggested that conditions in the understory can not support germling development; I found that juveniles are most common in the understory, invoking a different explanation.

Juveniles occur high on the shore in New England (Figure II - 1 a), suggesting that **conditions** there **favor** the **survival or growth** of developing plants. On the upper shore, *Ascophyllum* canopy is continuous (Figure II - 1 b). The restricted distribution might be explained if survival of developing plants were dependent upon frond cover or if survival or growth were enhanced on the upper shore (physical factors). Alternatively, the range of survival may be limited by grazing animals (biological factor). Grazing snails are least abundant high in the zone and increase down the shore (Figure II – 1 c).

The working hypotheses concerning physical factors were that germling survival is dependent upon *Ascophyllum* canopy (**'survival is affected by frond cover'**), and that survival is enhanced on the upper shore (**'survival is affected by shore level'**). The idea that growth during early development is favored high in the zone was also evaluated (**'growth is affected by shore level'**). The importance of physical factors was assessed using caged germlings. The contention that grazing animals restrict the range of survival was evaluated by comparing survival of germlings not caged with the survival of caged germlings (**'animal impact varies with shore level'**). Where shore level effects were significant, differences in the means for the +2.0 m shore level ('recruitment zone') and the other shore levels were tested.

Exclusion cages are commonly used to determine the effects of grazing animals. Animals, however, may not graze (= consume) the plants. Watson and Norton (1985) cautioned that crawling, non-feeding snails dislodge *Ascophyllum* germlings. I refer to the effects of animals as animal impact, and not as grazing. Snails, and also limpets, are grazers but plant loss may not be due to grazing.

Materials and Methods

Germlings and Surveys

Germlings grown on tiles in the laboratory were transplanted into the field for the experiments. Fertile fronds were collected from at least 10 female and 10 male plants. During the first year (1982-3), collections were made in Long Cove, Maine and at the Isles of Shoals (Star Island), New Hampshire where gamete release was underway earlier. The second year (1983-4), reproductive material came from the study site at Ft. Stark, New Hampshire. In the laboratory, fronds were exposed to mild heat and desiccation to stimulate gamete release. Gametes from different sources were kept separate (*i.e.*, Long Cove and Isles of Shoals). Gametes rinsed from fronds were mixed, and the suspension was poured over submerged tiles. The resulting germlings were maintained in culture until onset of the experiments. Germlings two months old were placed into the field 1982-3, and germlings three months old were deployed in 1983-4.

Survival was assessed using germling counts. The counts involved sub-sampling of the tiles. Tiles were surveyed in a standard orientation with the identifying number to the bottom right. A grid of 1 cm^2 areas defined with colored string was placed over the tile, and germlings in 5 of the 1 cm^2 squares were counted and summed for a total. The 5 squares were the same for all tiles. They were randomly designated prior to the first census, considering only the squares not likely to be contacted during handling. Counts were taken before deployment, and at various intervals. The total before deployment was designated Initial Number and used as a covariate in statistical analyses.

Growth of the plants was evaluated using mean plant length. Length[1] of the 2 plants closest to the upper left corner of each square was measured and used to generate a mean (n = 46, generally). The ruler was a hypodermic needle inscribed in 0.5 mm increments. By the end of the first month, germlings had been cleared from all tiles not caged so growth studies were limited to caged tiles only. Due to gradual loss of plants from tiles, as well as tiles from environments, the number of observations decreased over time. To find growth rate for each replicate, growth in length over the period was divided by the number of months ([final length - initial length] / # months).

Differences in the tile surfaces, emerging communities, and in developing *Ascophyllum* plants were observed during the first year of experiments. The differences seemed to corroborate distinctness of the physical environments. Therefore, the degree of sedimentation, organisms present, numbers of snails settling onto the tiles (counted and removed), and numbers of branched and damaged *Ascophyllum* were assessed at survey times. Tiles were surveyed without knowledge of the assigned environment.

Design and Implementation

Placement of germlings into the field was delayed to be certain that natural settlement was negligible. As germling counts were used to assess survival, settlement would confound the counts. A lapse of at least 2 months was allowed. Experiments commenced July 24, 1982 and August 13, 1983.

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[1] Developing plants grow upward and their size could be called height or length. Length is used for adult fronds and will be used for the developing plants in this study for consistency.

Experimental areas cleared of macroalgae (open) and areas with equivalent *Ascophyllum* canopy (frond-covered) had been established at 4 shore levels (+2.0, +1.5, +1.0 and +0.5 m above Mean Low Water) and on three adjacent rock ledges during a previous study (Ch. I). *Ascophyllum* cover in frond-covered areas was comparable to that at +2.0 m. Light readings were taken under the canopy at +2.0 m, bolts were cemented onto the rock in experimental areas not sufficiently shady, and fronds were secured on the bolts until light levels were below the threshold understory reading (highest light value for +2.0 m). Bolts were affixed to the rock in all areas to accommodate tiles. Experimental areas were used opportunistically; however, replicates were spread among available areas.

A factorial design was employed to test the effects of shore level, frond cover and animal impact. Tiles, or germling populations, were placed in the open and under frond cover at each shore level. Half were caged to exclude animals, half were not caged. Cages were constructed of metal screen with mesh openings of 0.6 x 0.6 cm. Tiles were assigned randomly to treatment, with a restriction on the 1982-3 set that 2 of the 4 tiles in each treatment group come from Long Cove and 2 from Isles of Shoals parentage (equal representation). The first set of experiments (1982-3) included only the uppermost and lowermost shore levels (+2.0, +0.5 m) with 4 replicates, giving a total of 32 tiles; the second set (1983-4) included all 4 shore levels (+2.0, +1.5, +1.0 and +0.5 m) and 3 replicates, or 48 tiles (Table II - I).

Treatment of the Data and Statistical Analysis

Factorial analysis of the effects of animal impact, shore level and frond cover on survival was defeated by extreme differences in the intensity and speed of the responses. Animal impact was swift and definitive, while the effects of shore level and frond cover were gradual. Survival data was analyzed in parts; animal impact, and the physical environment.

Animal impact resulted in data with extreme heteroscedascity. Pairing of independent samples is suggested when variances are heterogeneous and yields unbiased results when the replicates are in random order (Snedecor and Cochran 1980). Thus, replicates were paired and the differences (survival, cage – survival, no cage) were arcsine transformed and submitted to an analysis of variance. The differences represent the increase in survival with animals excluded. As a precaution, all possible differences were tested and results were similar.

Importance of the physical environment on survival (shore level, frond cover effects) was assessed for all surveys. Plants were lost from tiles, as well as tiles from treatment groups, over the year. Results at month 1 were mirrored in the results for subsequent months with shifts in p-values but not in significance patterns. Therefore, results at one month and the significance values mid-way through the year (minimal losses and longer exposure) are reported. The first set of plants (1982-3) included germlings from Long Cove and Isles of Shoals parentage so Genetic Source was included as a factor in the analysis (month 1). For both sets, initial numbers of germlings varied and Initial Number was included as a covariate to adjust for an effect of plant density on survival. Results using arcsine transformed data for all four months (month 1 and 5 for

1982-3, month 1 and 6 for 1983-4) are reported. Notably, fit of the data for month 5 (1982-3) and month 1 (1983-4) to the assumption of normality was improved when survival percentages were ranked. Significance patterns were similar for ranked and arcsine transformed data sets.

Time to total demise (0% survival) was projected to compare the relative importance of animal impact, shore level and frond cover. Tiles exposed to animals (not caged) were cleared of germlings, so times were known ± 2 days. Tiles protected from animals retained plants and times had to be estimated. Initial plant densities were high relative to natural settlement densities. Thus, natural settlement densities determined in an earlier study (Ch. I) were used to estimate the number of recruits on a tile-sized surface over a reproductive season. Multiplying the number of recruits by the percentage of plants surviving at 12 months (present study) yielded the number of recruits at the end of a year. Time to total demise was projected using % loss in the final months.

Growth over the observation period was used to calculate growth rates (mm/mo.) by environment. Most records spanned 12 months but some growth rates had to be calculated using data for fewer months. Rates for tiles lost prior to February were not included in the analysis as growth differed in winter and spring/summer. Growth rates were submitted to ANOVA. Initial length varied among replicates and was included as a covariate in the analyses to adjust for the influence of initial size on growth.

Growth rate differences among survey times were analyzed for the second set of plants (1983-4). The effect of 'survey time' was tested using a 1-Way ANOVA and including means for all 8 environments (shore level x frond cover groups), all surveys.

Significant differences were then determined using a Student Newman Keuls Means Range Test.

Totals of damaged plants were analyzed statistically to determine whether incidence of damage was independent of environment. Data was transformed (y + 1 [$\log_{10}$(y + 1)]) and submitted to an analysis of frequencies (G test of Independence; Sokal and Rohlf 1969).

Results

Animal impact devastated germlings. Without the protection of a cage, germling populations were decimated within a month (Figure II - 2, Figure II - 3). Low on the shore, tile surfaces were cleared within days. Losses were more gradual up through the zone. Differences in **animal impact** with shore level were **significant** (Table II – II a), and impact was greater low on the shore (Table II – II b). During 1982-3, survival without a cage differed with frond cover (Fig. II – 2) as germlings were lost more rapidly under frond-cover at +2.0 m and more rapidly in the open at +0.5 m. Impact may have been affected by frond cover, but the first census was too late to record a meaningful difference (day 8, moved to day 2 for the second set of plants). Statistically, frond cover effects were not significant and neither was interaction of shore level and frond cover (SL x FC) for either 1982-3 or 1983-4 (Table II - II a). Differences between frond-covered and open areas were not observed during 1983-4 (Fig. II - 3).

Survival patterns for the caged treatments after one month (physical environment) differed with frond cover (Fig. II - 2, Fig. II - 3). During 1982-3 and 1983-4, survival in the open was reduced on the upper shore. The difference in survival between frond-covered and open areas decreased down the shore for the second set of plants (1983-4, Fig. II - 3). Considering both sets of plants, 10 – 30% of the original number remained after a month in the open (except +0.5 m, 1983-4) whereas 55 – 80% remained under canopy. Bleaching was common for germlings in the open, especially on the upper shore. At +2.0 m, and for both sets, many of the plants bleached within the first week. After a month, bleached plants had been lost. After 12 months, light-colored plants remained on one tile from each set (n = 8 in 1982-3, n = 35 in 1983-4) and none of them were in censused squares.

Survival over the year differed for the two sets of plants. During 1982-3, survival curves for frond-covered and open areas were distinctive while curves for the two shore levels were nearly identical (Figure II - 4). Germlings survived in large percentages under frond cover over the fall and winter, and declined rapidly in the open. Even low on the shore, survival in the open was limited. Under frond cover, populations waned through the spring and summer with 2 – 5% remaining at the end of a year. During 1983-4, germlings survived in larger percentages overall and trends associated with shore level were observed (Figure II - 5). Survival increased with shore level under canopy, and decreased with shore level in the open. Survival was greatest at the two extremes; at +2.0 m in the understory, and +0.5 m in the open. After a year, 40 - 60% of the original populations survived at these two extremes.

Frond cover was important both years; highly **significant** as an independent factor in 1982-3 and significant in its interaction with shore level 1983-4 (Table II - III). Neither genetic source nor initial number had significant effects (1982-3). Shore level was not significant 1982-3. However during 1983-4, survival depended upon shore level and particularly in the open. Survival in frond-covered environments as well as low on the shore in the open were not significantly different, though means for that group differed significantly from the means for the upper shore, open environments (Fig. II - 5).

The importance of factor interaction (Shore Level x Frond Cover) differed for the two sets of plants; SL x FC was not significant for 1982-3, though it was significant for 1983-4 (Table II - III, Figure II - 6). Significance of the interaction for the second set of plants reflects the opposite linear trends; survival increased with shore level in the understory, and decreased with shore level in the open.

The relative importance of all 3 factors (animal impact, shore level and frond cover) can be compared using projected survival times (Table II - IV). With impact by animals, *Ascophyllum* survived up to 2 weeks in the open. Frond cover made no difference low on the shore, but extended survival several months high on the shore. Without animals, survival up to several years was projected. Survival potential was greatest high in the zone, under canopy.

Growth was faster in the open and increased down the shore (Figure II - 7, Figure II - 8). The high shore was an exception as growth under frond-cover may have exceeded growth in the open; the few plants surviving in the open at +2.0 m grew little or not at all. A growth enhancement is evident in the spring/summer for the second set of plants (Fig. II - 8) but not for the first (Fig. II - 7). Loss of some of the longest plants is apparent low on the shore and in the open (1982-3, Fig. II - 7) so growth was calculated using length at 9 months for 2 of the tiles and may have been underestimated.

Mean plant lengths were used to calculate growth rates. Length increased gradually over time, and growth curves were best fit by a linear function rather than a logarithmic one (Fig. II - 7, Fig. II - 8).

Growth rates were submitted to ANOVA and the results indicated that both **shore level** and **frond cover** had **significant** effects (Table II - V). Initial length was included as a covariate and did not have a significant effect on growth for either set of plants. During 1982-3, interaction of shore level and frond cover was significant. During 1983-4, the factors were significant independently. Growth increased down the shore in frond-covered and open situations, and the magnitude was greater in the open (Fig. II - 8). Notably, growth at +1.5 m under frond-cover was apparently greater than growth at +1.0 m and the means fall out of a regular order. Statistically, mean growth rates were similar under canopy except at +0.5 m (Fig. II - 8) where growth was significantly greater. Growth increased at +0.5 m in the open, where plants averaged 1 cm more in length than their understory counterparts. Thus, growth was affected by shore level, however plants at **+2.0 m** grew at a rate significantly **slower** than on the lower shore.

Growth increased 4 to 5 times down the shore, and 1.2 to 2 times in the open except at +2.0 m (Table II – VI). Estimates of a year's growth suggest a 10-fold difference between plants in low, open situations and plants high on the shore in the understory. While plants averaged up to 2.4 cm/year (2.8 cm in length with initial length), a few attained 3.3 - 3.6 cm by the end of a year (4 cm after 15 months).

Environment affected plant size, development and pigmentation. Plants grown high on the shore were smaller, in length and **diameter**, than those grown low on the shore (Figure II - 9). Differences in size are apparent between the plants pictured, both populations grown beneath canopy. Plants grown in the open at +0.5 m were a centimeter longer. By 2 months' time, plants in the open were light to medium brown and those in the understory were dark. The first lateral branches were initiated after 2 months on open-grown plants, at 3 - 5 mm in length. Understory plants branched after 4 months, at 1 - 2 mm. Only a small percentage of the plants branched. In the spring, the fronds of **low shore plants** 2.5 – 3 cm long had begun to **flatten**.

Inspection of the growth rates for individual surveys suggests a spring/summer enhancement and greater variation in the open (Figure II - 10). Results from a 1-Way ANOVA indicated that growth rate differences over time were **significant** (n = 64, df = 7, F=3.23, p=0.06**). A Student Newman Keuls Mean Range Test established that mean growth rates in November/December differed significantly from April and August (q = 6.95, df = 65, # means = 6, p-value < 0.05*).

Canopy cover affected fouling. Tiles under frond cover developed a brown diatomaceous surface film within the first two months. Over the winter, a shifting mat of fine silt and diatom filaments covered the plants. Deposition was reduced in the open.

Community development differed with environment. The understory community was characterized by a **miniature** forest of *Fucus* germlings, red crusts, and small buttons of corallinaceous crusts; communities on tiles in the open included brown Ralfsioid crusts, *Fucus* and ulvoid green algae. Abundance increased down the shore.

Differences in abundance with shore level were particularly pronounced in the open; tiles place high in the zone were almost bare while those low on the shore developed lush, multi-tiered communities topped by a low canopy of *Fucus* and *Ulva* (to 15 cm). Snails settled everywhere, especially in the open and low on the shore.

Damaged *Ascophyllum* were noted in the second month (October). Damaged plants were localized on one part of the tile. Apical wounds (loss of the growing tip) and lateral wounds were observed. In some cases, only a stump remained. Healing was not evident. Apically damaged plants remained in place but did not grow. The exception was a stump that grew a branch from the edge of its blunted top the next spring.

The frequency of damage was not independent of environment. Incidence increased down the shore and was greater in the open (Table II - VII). Results from an analysis of frequencies indicated significance at $p < 0.01^*$ ($G = 15.2$, $df = 3$).

Discussion

Establishment is the weakest link in the colonization of new territories (Stebbins 1971). For late-successional plants, characterized by long lifespans and low recruitment (see Silvertown and Lovett Doust 1993), establishment of new plants in **existing** populations can be tenuous as well (cf. Hough and Forbes 1943, Whitney 1984; Ch. V). Developing plants are particularly susceptible to physical stress and animal consumers (for vascular plants see Harper 1977, Cook 1979; for algae see Vadas *et al.* 1992, Chapman 1995). They are small and sessile. Their tissues are soft and relatively undefended chemically (Watson and Norton 1985, Watson *et al.* 1990). Slow growth keeps them at risk for a protracted period.

Juveniles are restricted to the upper shore because animals restrict the range of survival. Impact varied significantly down the shore. Plant loss was most rapid where animals were most abundant. Vadas *et al.* (1982), Miller and Vadas (1984), and Lazo *et al.* (1994) demonstrated that, if germlings were not caged to exclude animals, survival was nil at mid-shore levels. Bertness *et al.* (1999) showed that animals limit the range of natural recruits at an estuarine site. Across the Atlantic, Åberg and Pavia (1997) found that juveniles are more abundant high in the *Ascophyllum* zone on the Isle of Man (U.K.).

Cages with mesh openings of 0.6 cm afforded effective protection. Likely removal agents include snails and limpets, possibly amphipods and isopods (see below). The impact of each of the common gastropods is evaluated elsewhere (Ch. III).

Numbers of larval snails settling on the tiles and the incidence of damaged *Ascophyllum* had similar distributions; most frequent low on the shore and in the open. Amphipods and isopods were observed occasionally. They consume *Ascophyllum* fronds and fucoid germlings (see Arrontes 1990, Lazo *et al.* 1994, Parker and Chapman 1994, Cervin and Aberg 1997), and are small enough to freely penetrate the cages.

Reproduction and early development of *Ascophyllum* take place in spring and summer when physical rigors are intense (Boney 1965) and animal activities peak (Kanwisher 1959, Menge 1975). On the shore, prevailing weather is superimposed on a wet/dry cycle. Physical conditions can be more extreme than in terrestrial situations (MacDonald *et al.* 1974). Elevated temperatures, light levels, and evaporative potentials typify spring and summer. Young stages are especially vulnerable to both physical stress (Baker 1910, Brawley and Johnson 1991) and removal (Vadas *et al.* 1992, Chapman 1995), yet are subjected to strong selective forces. Perhaps early culling of maladapted recruits carries an ecological premium.

Canopy provides an important refuge. Physical stress can be lethal on the upper shore (see Kanwisher 1966, Schonbeck and Norton 1978, Chock and Mathieson 1979, Schonbeck and Norton 1980, Brawley and Johnson 1991, Chapman 1995). Water loss high in the *Ascophyllum* zone is 3 - 5 times greater than low on the shore, and an order of magnitude less under canopy. As well, rock temperatures are 5 - 10° C lower (Bertness *et al.* 1999). Steep gradients in physical conditions exist down the shore and between frond-covered and open areas. Along the gradients, sensitivity determines survival.

Ascophyllum embryos are susceptible to the levels of desiccation and light typical of the upper shore, as demonstrated using methods highly sensitive to changes in photosynthetic performance (Lamote *et al.* 2001). In this study, nearly all the germlings in high, open areas bleached and were lost within a month. In another study, a third of the germlings in clearings at mid-shore levels bleached, died, and were lost within 23 days (Viejo *et al.* 1999). High light intensities, especially U.V. wavelengths, can lead to bleaching and death (see Biebl 1957, Hellebust 1970, Lüning 1981).

Germlings in the understory were darkly pigmented. Increased pigmentation with shading or increasing depth is well known for adult fronds (Ramus *et al.* 1977, Cousens 1982, Cousens 1985, Peckol *et al.* 1988).

Survival in the open differed between years. The disparity reflects timing. Germlings were deployed almost a month earlier in 1982 and endured more low tide exposures during hot summer weather (July and August). Natural recruits settling in late April or May would have additional exposure, but not when heat, light and desiccation are at their peak. Delay in deployment avoided natural settlement though 2+ months was too long a lapse. Perhaps it provided insight; that recruits may survive on the low shore in benign years.

Survival in the open may be more restricted than the results indicate. Different survival patterns for the 2 years suggest that physical stress dictates the extent of survival in the open, and weather varies year to year (see Gail 1918, Gunnill 1980, Little and Smith 1980, Leonard 2000). Experiments contemporary with natural settlement may indicate that survival is relegated to the understory. Further, survival patterns in the open may be conservative since cages have been shown to ameliorate physical stress (*i.e.*, McCook and Chapman 1993).

. Community development corroborated the gradient in physical stress down the shore for open situations. On the upper shore, tiles in the open were mostly bare. Only low on the shore did multi-tiered communities develop. A canopy of *Fucus* and *Ulva* grew to 15 cm, and suppressed growth of the *Fucus* recruited beneath.

Canopy cover did not preclude survival. Because light limits growth of adults, shade in the understory was purported to limit germling survival (Hatton 1938). The observation that juveniles grew at the fringes of the distribution provided further evidence (David 1943). Growth of developing plants was reduced under canopy, about half the rate of plants in the open, but it was continual. Plants survived in the understory, and in the largest percentages overall.

Canopy ameliorates heat and desiccation and may create a habitat stressful in terms of shade and fouling. The understory provides critical refuge from physical stress for organisms toleratant of the shade and siltation. Fleshy red crusts (alternate stages for *Chondrus crispus* Stackhouse and *Mastocarpus stellatus* (Stackhouse *in* Withering) Guiry) and corallinaceous crusts colonized tiles in the understory, and occur naturally under *Ascophyllum* canopy. They are sensitive to exposure at mid-shore levels, and bleach if overlying canopy is lost (Jenkins, Hawkins and Norton 1999; de O. Figueiredo *et al.* 2000). Growth of *Ascophyllum* was slower in the understory whilst growth of

Fucus was imperceptible. Enhanced sedimentation characterized understory surfaces. Deposition occurs when water flow slows, and sediment accumulates naturally beneath *Ascophyllum* canopy (Bertness *et al.* 1999). Cages enhance siltation (see Underwood and Denley 1984). In nature, grazing and crawling animals clear away sediment (Bertness 1984) and diatoms (Castenholz 1961). Cages excluded animals, and mats of silt and filaments (diatom and bacterial, see Sieburth and Tootle 1981) built-up. Under the mats, germlings remained healthy and responded to improved growing conditions in the spring.

Fronds can remove recruits. Fronds clear away barnacles (Hawkins 1983; Jenkins, Norton and Hawkins 1999, Leonard 1999), and dislodge *Ascophyllum* germlings (Miller and Vadas 1984, Vadas *et al.* 1992). The compliant fronds of *Ascophyllum* are less effective than those of other fucoids and may not contact the rock surface where plants are close-growing (see Jenkins, Hawkins and Norton 1999). Frond lashing and sweeping are important on exposed shores and in open areas within reach of adjacent plants. Sweeping effects were not evident in the present study. Germlings not caged were lost at similar rates in the open and under frond cover. Animal impact may have been too swift. Ironically, as originally described frond sweeping had positive effects on kelp recruitment by sweeping away grazers in a swath around an adult plant (Velimirov and Griffiths 1979).

Survival was greatest at +2.0 m, in the understory; where growth was slowest. Plants grew only 1-3 mm the first year high in the zone.

A rate of 1 mm/yr. for *Ascophyllum* germlings is widely cited and comes from Sundene's work (1973). It was an estimate, as he detected the plants during the second year. The rate is slower than rates herein and was determined from plants in the open, lower on the shore in Norway. Growth rates varied with environment at a single site, and have been shown to vary on a single plant (see Blackler 1956, Burrow's comments in the Discussion). Rates in published works must be carefully specified as to the particulars of geography, habitat and specific environment to facilitate meaningful comparison.

Growth increased down the shore, and doubled in the open. Though animals preclude survival low on the shore, growth can be 10 times faster there. Animals deny recruits the environments most favorable to growth. Further work must resolve whether recruits settling in low, open areas can survive the physical extremes over an entire summer. The growth rates observed suggest that plants might attain 3 or more cm in length, a size that may confer resistance to grazer removal (Lubchenco 1983, Ch. IV).

Seasonal differences in growth were significant during 1983-4. Plants grew faster in the spring/summer and slower in winter as described for adult *Ascophyllum* (MacFarlane 1932, David 1943, Printz 1956b, Mathieson *et al.* 1976, Peckol *et al.* 1988, Stengel and Dring 1997). Growth rates varied between surveys, suggesting that developing plants may be responsive to changing conditions on a shorter timescale. Indeed, monthly fluctuations characterize adult fronds (Peckol *et al.* 1988).

A few 'renegade' plants grew considerably taller than others. The fastest growth was about 0.3 cm/month **(3.6 cm/year)**. Exceptional growth during early development has been reported. Hatton (1938) reported **11 cm/yr.**, Sundene (1973) recorded **6 cm/yr.**, Keser and Larson (1984; 15 cm/16 months) observed **11 cm/yr.**, and Jenkins, Hawkins and Norton (1999; 20 and 42 cm/5yr) measured **4 - 8 cm/yr.** Yearly rates estimated from multi-year lengths are inaccurate because elongation potential increases with size. The estimates demonstrate potential variation. Stengel and Dring (1997) analyzed morphological variation in a population, and tied it to genetic differences. Genetic variation may belie extreme variation in growth. Strömgren (1977) reported that differences in growth among adult plants were genetically based.

Mean growth rates were calculated generally (plants measured were not the same survey to survey, mean length was derived from all measurements) and would not accurately capture the kind of individual variation discussed above. Genetic source was not a significant factor influencing growth among germling populations during 1982-3. Environment had a stronger influence, as germlings outplanted later (1983-4) started out smaller and grew taller the second year (Fig.'s II - 7, 8).

Plant morphology is sensitive to environment during initial development. Differences in size and branch production were noted. Understory plants were diminutive and branching was delayed. Open-grown plants were robust on the low shore. Interestingly, natural recruits high in the zone remain narrow and cylindrical until they surpass several centimeters in length. The growth form conjures up the elongation characteristic of etiolated seedlings. Low shore plants began to flatten beyond ~ 2.5 cm. Upper shore plants in the understory may have a growth form indicative of dense shade, and distinctive from the stunted ancients (thick, irregularly misshapen, blunted plants) in crevices and in dense groups above the main distribution. Juveniles are plants recruited over many years with growth suppressed in the understory (Cousens 1986, Vadas and Wright 1986), young only in a relative sense and growing exceedingly slowly.

In adults as well, light environment and shore level influence morphology (David 1943, Baardseth 1970, Cousens 1985, Peckol *et al.* 1988, Stengel and Dring 1997). Responses to shade and high density are similar, and density effects may be mediated by light (Viejo and Åberg 2001). Lazo (1992) summarized it succinctly; at high densities plants grow in length, at low densities they spread laterally. Upper and lower shore plants grow at different densities and have distinct habits. Upper shore plants are longer, have few major shoots, and are close-growing ($\leq$ 1.95 m long, 109 plants/m^2, Ft. Stark data). Lower shore plants are shorter, have many major shoots, and are widely spaced ($\leq$ 1 m, 21 plants/m^2). The two groups are so distinct that competition between them is predicted (Johnson *et al.* 1998).

Fucus, a fellow rockweed, is sensitive to crowding. At high densities, mean plant size and growth rate decrease (Ang and De Wreede 1992, Creed *et al.* 1996). It has been suggested that *Ascophyllum* germlings are density sensitive (Viejo *et al.* 1999). Plant densities in this study (50 -100/cm^2) correspond with high densities in other studies (Viejo *et al.* 1999, $\approx$ 53/cm^2; Vadas *et al.* 1990, $\approx$ 200/cm^2). At lower densities, mean size might increase. Creed *et al.* (1996) found that high densities led to greater size variability in *Fucus*, with more plants in the smaller size classes. However, maximum size was the same.

At high germling densities, self-thinning may occur (Lazo *et al.* 1994, Viejo and Åberg 2001). Self-thinning responses are best known for flowering plants. Loss of plants in the smallest size classes would be expected (*i.e.*, Silvertown and Lovett Doust 1993). Plant loss may result from purely physical effects (weakened attachment or displacement as neighbors expand). Absence of growth or decline in health prior to loss, signal a density-mediated response in a physiologically sensitive organism. Physiological responses to crowding, followed by loss, have been demonstrated for *Laminaria* and suggested for *Fucus* (Creed *et al.* 1998). *Ascophyllum* may be tolerant of crowding. Growth of adult fronds high in the zone may be **enhanced** by high density (Bertness and Leonard 1997). Density effects on growth are disproportionate as elongation of the longer shoots is undeterred while shorter shoots are suppressed (Lazo and Chapman 1998). The developing plants in this study remained healthy and grew measurably. At +2 m in the understory, plants grew at the highest densities yet were retained in the highest percentages. Initial number was not a significant factor in survival. Gradual losses continued over time. Rather than a physiological response, physical effects seem sufficient.

High density affords advantages. Dense packing may deter grazers (Hruby and Norton 1979, Hay 1981 and 1986), and ameliorate desiccation (Moss 1970, Schonbeck and Norton 1978; both Hatton 1938 and Viejo *et al.* 1999 note that low canopy is more effective). Even at the densities in this study, grazers were not deterred and survival in the open was limited.

The longest survival projection (several years) is an underestimate. A single tile, even a collection of tiles, represents too small a sampling area to accurately reflect processes that are spatially variable (settlement, survival). Survival data were derived from 5 squares. In some cases when 0% survival was recorded (no plants in the 5 sampled squares), plants remained in others. In the same way, a tile-sized area is but a small patch of surface relative to the extent of rock surface. Secondly, survival times had to be estimated for caged treatments. I assumed a constant rate of loss. Losses may decline as numbers dwindle, extending survival time.

The range in survival times was from 2 weeks to several years herein, 62 days for Maine sites (Miller and Vadas 1984, Vadas *et al.* 1990) and 2 years in Nova Scotia (Lazo *et al.* 1994). It would seem that plant establishment is doomed. The timeframe, however, is too limited for a long-lived species. One year of observation is too small a window to view a protracted and stochastic process.

Long-term variation is important. Survival patterns over longer time periods, including a larger sample of surface are needed. Scanning natural rock surfaces is difficult (see Lazo *et al.* 1994), but the best ceramic surface is only a substitute. Comparison of events on artificial substrata (for easy detection) with concurrent events on adjacent rock is indicated (see Chapman 1995).

Plant establishment is a series of interdependent steps. It represents a continual, gradual reduction in the number of survivors from an initial surplus in the number of propagules. Germling survival limits plant establishment in *Ascophyllum*. Animals restrict the range. Survival is most likely in the understory, high on the shore. Germlings in the open succumb to physical stress, and may be dislodged by waves and, possibly, sweeping fronds lower on the shore. In the sheltered understory, conditions suppress growth but favor survival. Nestled between adult holdfasts and interspersed within the patchwork of sessile animals and plants, some recruits persist.

Community complexity increases down the shore, mirrored in the tile biota. Numbers of potential spatial refuges, where plants might evade removal by animals, increase down the shore. If animal impact were reduced, then survival low on the shore might be realized. Growth is fastest there so plants would have the greatest probability of attaining a size large enough to evade removal the second year (Ch. IV).

Ascophyllum plants are remarkably resilient, have tremendous regenerative capacity, and live many decades (see Åberg 1992a). Recuperation of moribund, stunted plants suffering from thermal stress has been documented (Vadas *et al.* 1978). Regrowth after loss of 95% of the biomass has been reported (Åberg 1992b). Frond breakage and animal-inflicted wounds are common (see Mathieson *et al.* 1982, Åberg 1992b, Lazo *et al.* 1994, Stengel and Dring 1997). Wounding is a reality, and was evident on the developing plants in this study (the tiny wounds reflected access by small animals). *Ascophyllum*, at least as an adult, sustains damage and proliferates in spite of it.

Within a population, considerable morphological variation exists (David 1943, Baardseth 1970, Cousens 1982, Stengel and Dring 1997). Morphological and gender differences on plants in a common environment (Åberg 1989) bear evidence of reproductive success; the establishment of sexual recombinants in the population. Strömgren (1977) demonstrated that variation in apical growth rate is genetically based. Analysis of polymorphic gene loci provides biochemical evidence of reproductive success, with strong genetic differentiation within a population on a small spatial scale (Olsen and Stam 2000).

Plant establishment, though rare, is the source of new genetic combinations. Survival of a very few is reproductive success (Lazo *et al.* 1994). Each establishment event carries profound significance to the population. The new recombination is highly amplified (see Cheney and Mathieson 1978) as plants release massive numbers of gametes over decades of reproductive seasons. Unique combinations in the progeny start the process again in a rare establishment event.

Vegetative growth is more important in terms of biomass and perpetuation of a population than sexual reproduction (see Åberg 1992b, Lazo 1992, Chapman 1995).

Perenation seems the sole means of perpetuation on the low shore. Regrowth and vegetative spread serve a vital role; they maintain cover (see Ch. V) and afford the necessary time between successful recruitment episodes.

Ascophyllum canopy is pivotal to the success of a variety of organisms on the shore. *Ascophyllum* is a habitat architect, providing a range of habitats for the animals and plants whose survival hinges on its continued success. The canopy mediates processes in the understory (see Jenkins, Hawkins and Norton 1999). Frond cover was associated with distinct environments and communities on the tiles. Canopy suppresses development of some forms, extends feeding of surface browsers into the exposure period by retaining moisture, harbors animals and epiphytic plants, and shelters sensitive forms. Adult canopy may be critical for recruitment of *Ascophyllum* (Ch.V).

A common scenario emerges. Biological factors determine the lower limits of survival, and physical factors set the upper limits. In this case, adult canopy (a biological factor) adds another dimension. Animals restrict the range of recruitment, and physical conditions dictate the upper limits of survival outside the canopy. Adult canopy provides a critical refuge. Juvenile and adult plant distributions differ; one a subset within the other.

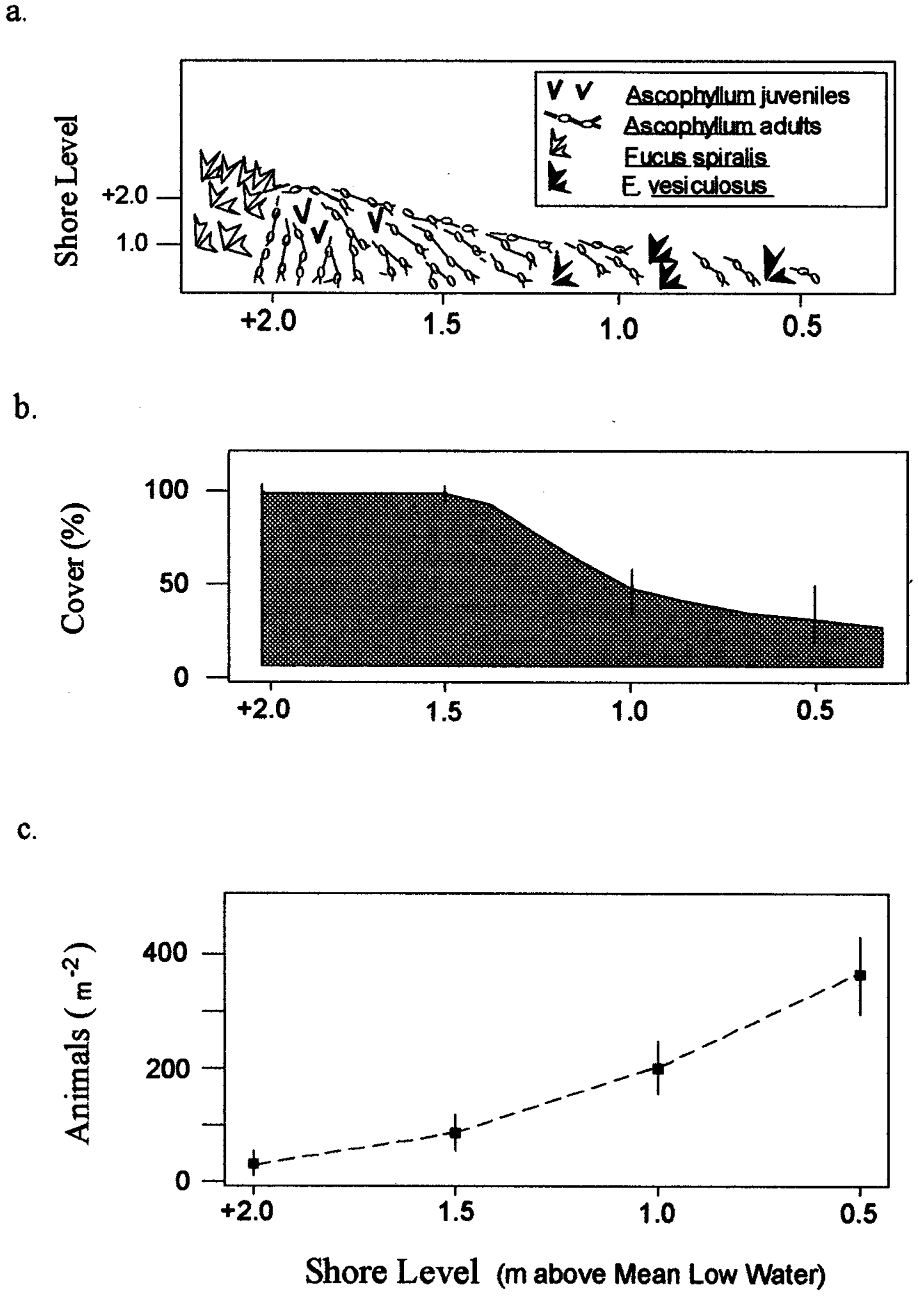


Figure II - 1. Initial Observations. Distribution of *Ascophyllum* (juveniles, adults) and *Fucus* species on the shore (a), *Ascophyllum* canopy cover (b) and abundance of grazing animals (c) by shore level. Means ± 1 S.E. are shown (b, c) using data from 6, 0.25 m^2 quadrats/shore level sampled at Ft. Stark in April, 1982.

Table II - I. Experimental Design. Allocation of replicates (germlings on tiles) to treatment groups for the experiments on survival and growth. Survival with and without animals, and in different physical environments (shore level x frond cover combinations) was evaluated. Caged replicates were used to assess growth.

	Frond-Covered		Open	
Shore Level	Animals (No Cage)	No Animals (Cage)	Animals (No Cage)	No Animals (Cage)
1982-3				
+2.0 m	n = 4	n = 4	n = 4	n = 4
+0.5 m	n = 4	n = 4	n = 4	n = 4
1983-4				
+2.0 m	n = 3	n = 3	n = 3	n = 3
+1.5 m	n = 3	n = 3	n = 3	n = 3
+1.0 m	n = 3	n = 3	n = 3	n = 3
+0.5 m	n = 3	n = 3	n = 3	n = 3

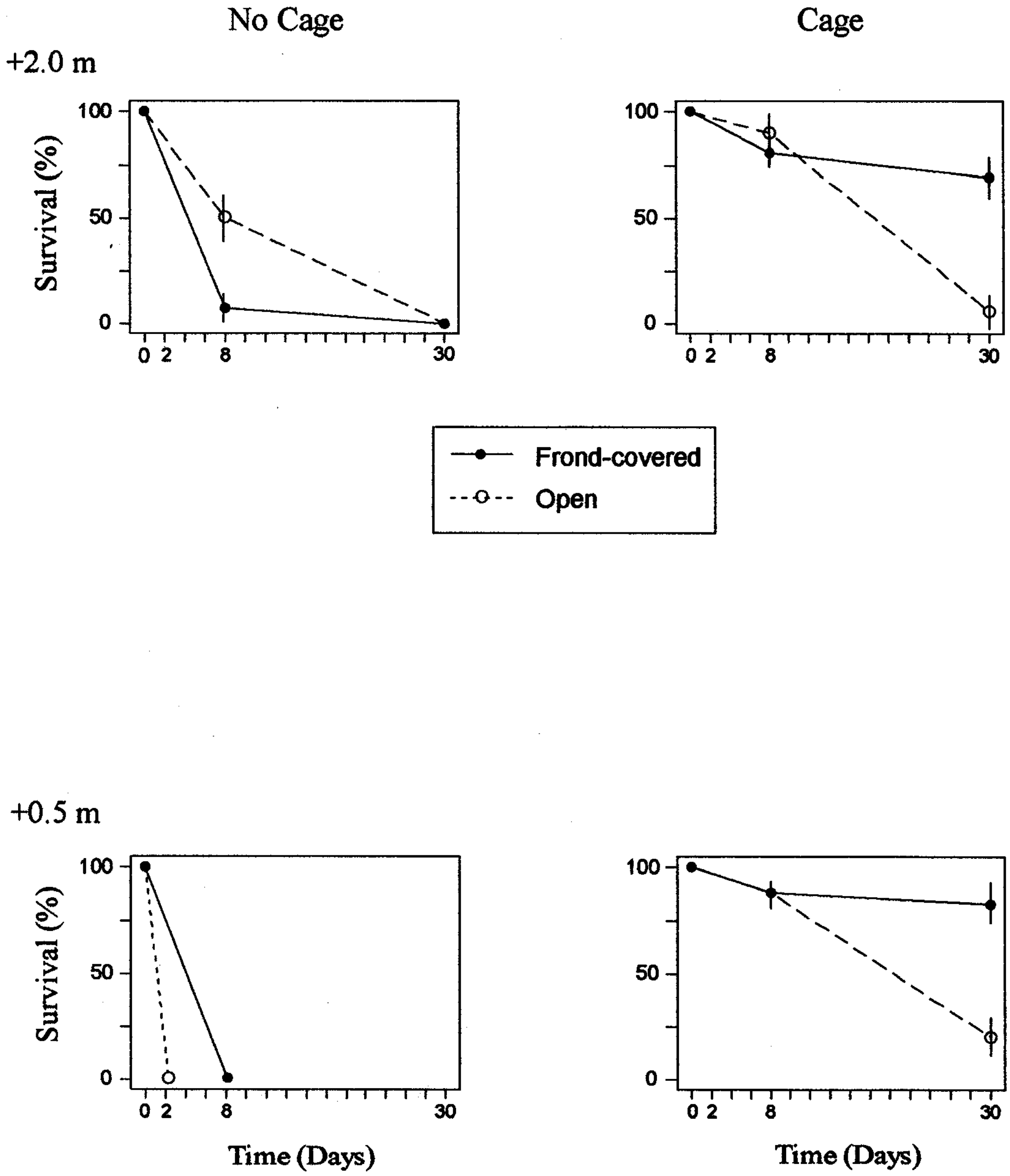


Figure II - 2. Short Term Survival, 1982-3. Survival the first month with and without animals, by environment. Means ± 1 S.E. are shown. Data for day 8 were used in the analysis of animal impact, and day 30 data (caged only) in the analysis of environment.

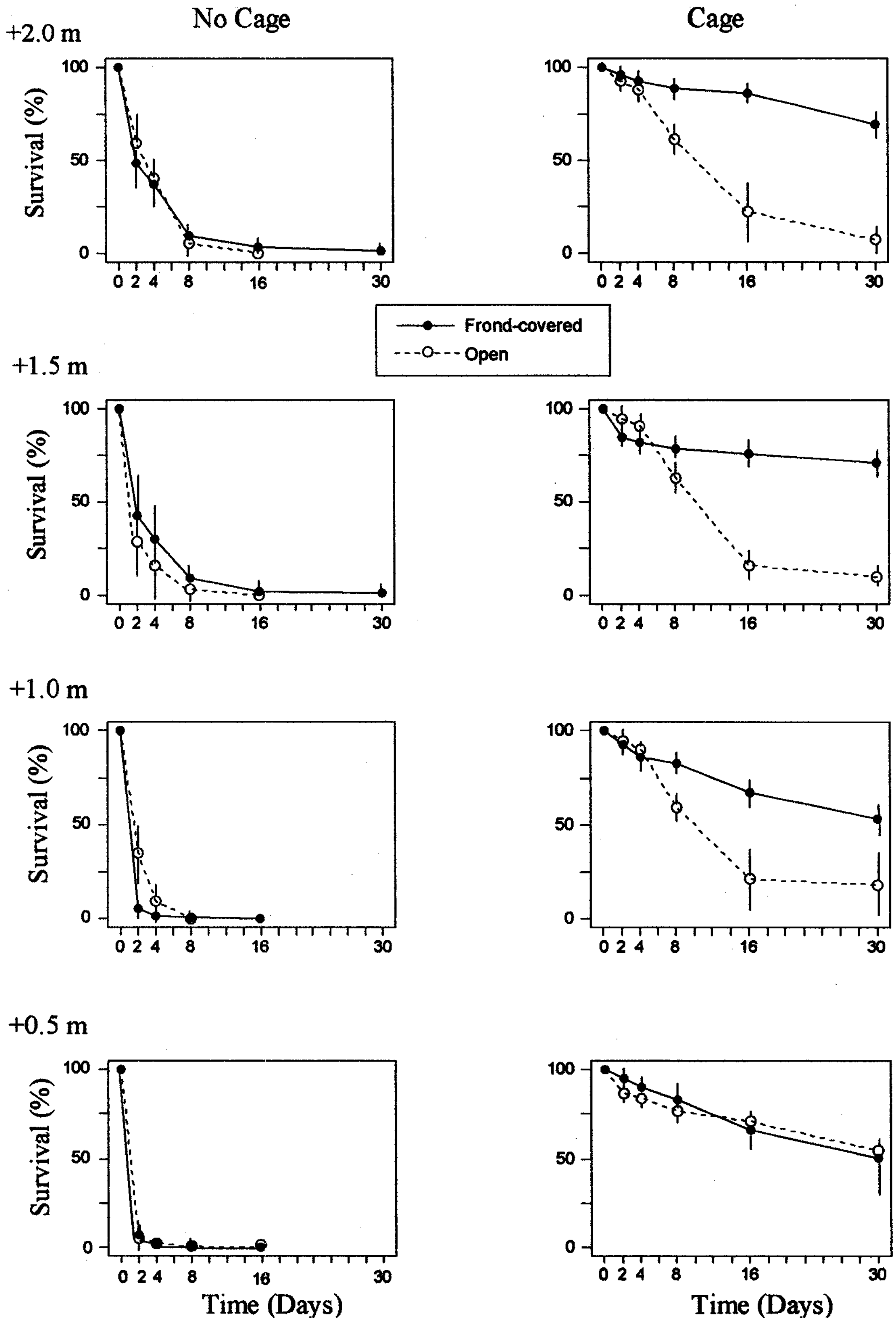


Figure II - 3. Short Term Survival, 1983-4. Survival the first month with and without animals, by environment. Means ± 1 S.E. shown. Data for day 4 (differences) were used in the analysis of animal impact, and day 30 data (caged) in the analysis of environment.

Table II - II. Animal Impact Statistics. Results from 2-Way ANOVA tests on the effect of environment on impact 1982-3 and 1983-4 (a), and mean survival differences (b). Data (a) are differences (survival, cage – survival, no cage) and represent the increase in survival with a cage. Differences on day 8 (1982-3) and day 4 (1983-4) were arcsine transformed and used in the analyses. Mean survival differences ±1 S.E. are listed by environment (b) and letters indicate means that differ significantly.

a. **Animal Impact *vs.* Environment**

1982-3

Source	df	SS	MS	F	p-value
Shore Level	1	1846	1846	8.61	0.013*
Frond Cover	1	442	442	2.06	0.177
SL x FC	1	569	569	2.65	0.129
Error	12	2574	214		
Total	15	5431			

1983-4

Source	df	SS	MS	F	p-value
Shore Level	3	2462.1	820.7	5.38	0.009**
Frond Cover	1	6.2	6.2	0.04	0.842
SL x FC	3	328.7	109.6	0.72	0.556
Error	16	2441.6	152.6		
Total	23	5238.6			

Tukey Pairwise Tests (1983-4) indicated that:

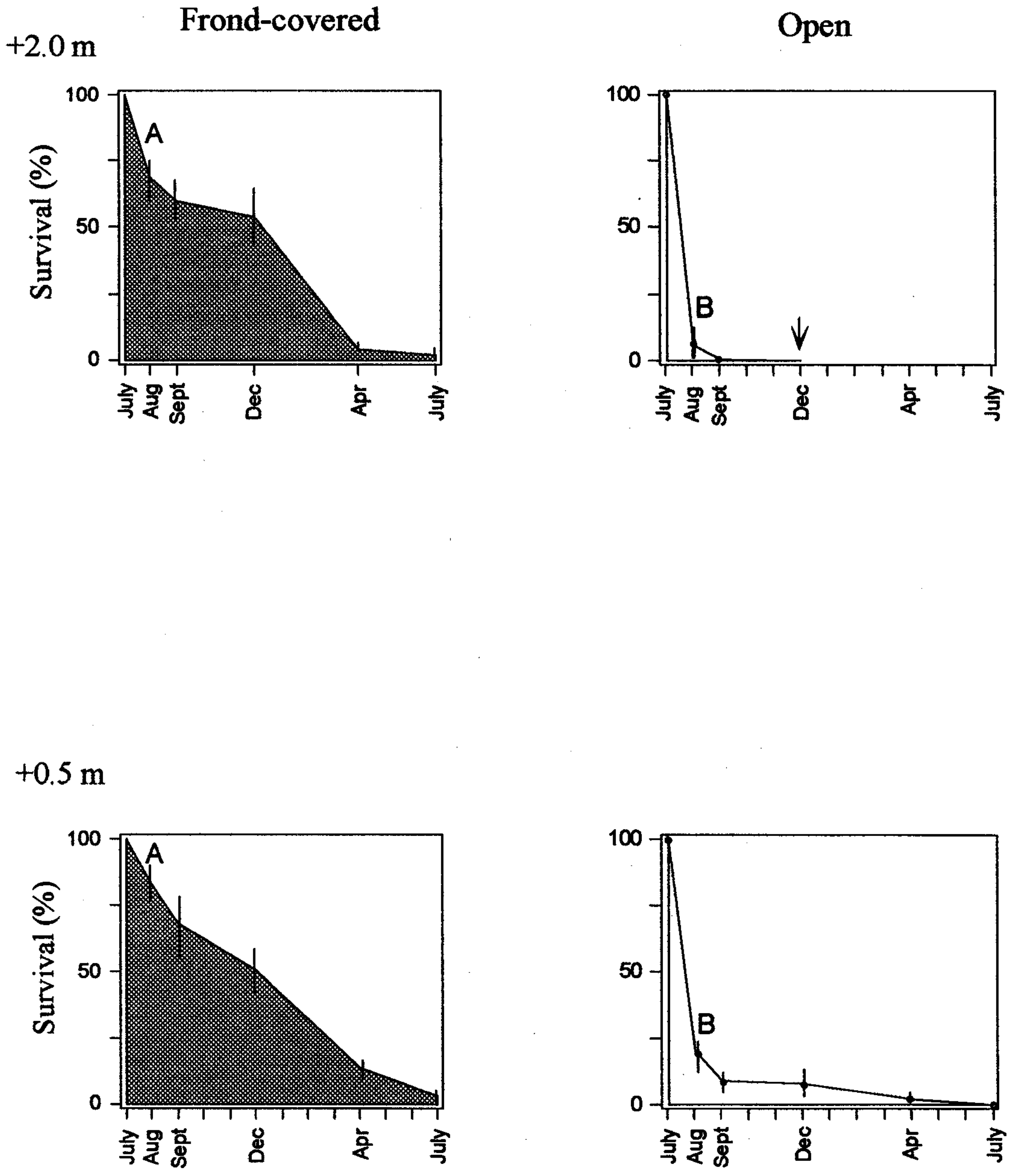
Pair Tested	T-Value	p-value (adj.)
+2.0 *vs.* +0.5 m	-2.952	0.042*
vs. +1.0 m	-2.736	0.063
vs. +1.5 m	-0.016	1.000

Shore level had a **significant** effect on animal impact both years. Impact at +2.0 m (recruitment zone) was significantly different than at +0.5 m.

b. **Mean Survival Differences**

(Increase in Survival with a Cage)

Shore Level	1982-3	1983-4
+2.0 m	57% ± 13.7 A	50% ± 11.3 AA
+1.5 m		54% ± 18.2 AA
+1.0 m		84% ± 5.5 AA
+0.5 m	88% ± 4.1 B	86% ± 2.7 BB



Frond-covered

Open

+2.0 m

+0.5 m

Figure II - 4. Long Term Survival, 1982-3. Survival by environment. Means ±1 S.E. are shown. Arrow indicates 0% survival (germlings in censused squares on all replicates decimated). Letters indicate means that differ significantly.

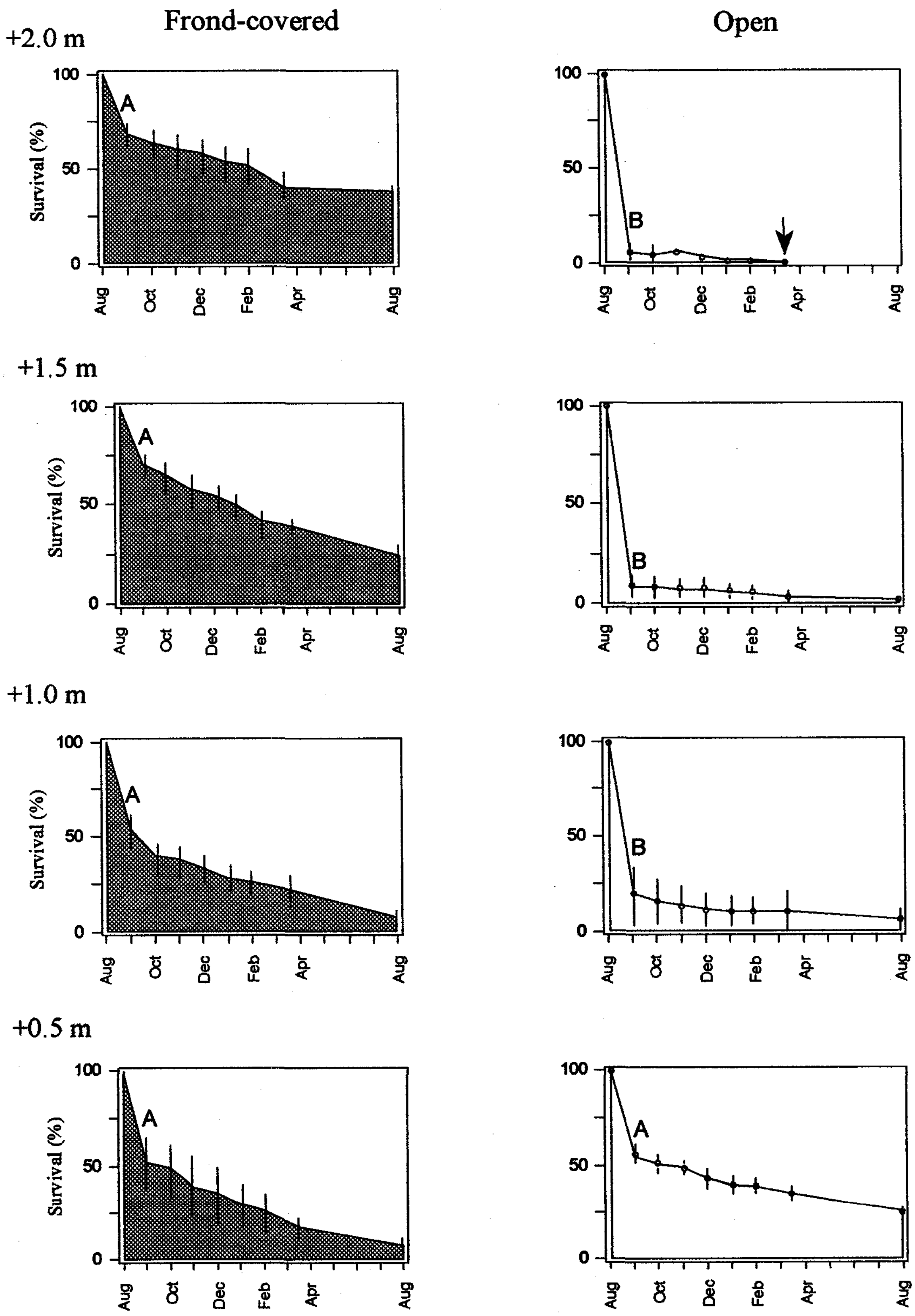


Figure II - 5. Long Term Survival, 1983-4. Survival by environment. Means ±1 S.E. are shown. Loss of all germlings is indicated (arrow). Letters indicate means that differ significantly.

Table II - III. Survival Statistics. Results from analyses of environment (shore level, frond cover) on survival. Results from ANOVA tests on survival at month 1 and at month 5 (1982-3) or 6 (1983-4). The percentages of plants surviving were arcsine transformed for the analyses. ANOVA tables for month 1 are shown as well as significance values for month 5 or 6. Genetic source was a factor included in the analysis 1982-3. Initial Number was included as a covariate in the analyses at 1 month. Results from pairwise tests of means (+2.0 m *vs.* other shore levels) are given below.

Survival *vs.* Environment

Source	df	SS	MS	F	p-value	
		1982-3			(1 mo.)	(5 mo.)
Initial Number	1	0.4	0.4	0.01	0.938	
Shore Level	1	349.7	349.7	5.41	0.053	0.582
Frond Cover	1	6981.2	6981.2	107.98	0.0001***	0.0001***
Genetic Source	1	59.7	59.7	0.92	0.369	0.101
SL x FC	1	3.6	3.6	0.06	0.820	0.402
FC x GS	1	9.9	9.9	0.15	0.707	0.276
SL x GS	1	2.4	2.4	0.04	0.854	0.946
SL x FC x GS	1	31.8	31.8	0.49	0.506	0.554
Error	7	452.6	64.7			
Total	15	7891.3				
		1983-4			(1 mo.)	(6 mo.)
Initial Number	1	2.5	2.5	0.02	0.891	
Shore Level	3	664.7	221.6	1.75	0.199	0.394
Frond Cover	1	4140.4	4140.4	32.78	0.0001	0.0001
SL x FC	3	1998.2	666.1	5.27	0.011*	0.012*
Error	15	1894.3	126.3			
Total	23	8700.1				

Frond cover had a **significant** effect on survival 1982-3, and a significant effect as it **interacted** with shore level 1983-4.

Tukey Pairwise tests (1983-4) indicated:

Pair Tested	T-Value	p-value (adj.)
+2.0 m Frond-covered *vs.* +2.0 m Open	4.83	0.004**
vs. +1.5 m Open	4.38	0.010*
vs. +1.0 m Open	3.70	0.034*
vs. +0.5 m Open	0.89	0.982

Frond-covered environments (all shore levels) and +0.5 m open were not significantly different. Open environments, except the lowest shore level, were significantly different from frond-covered ones.

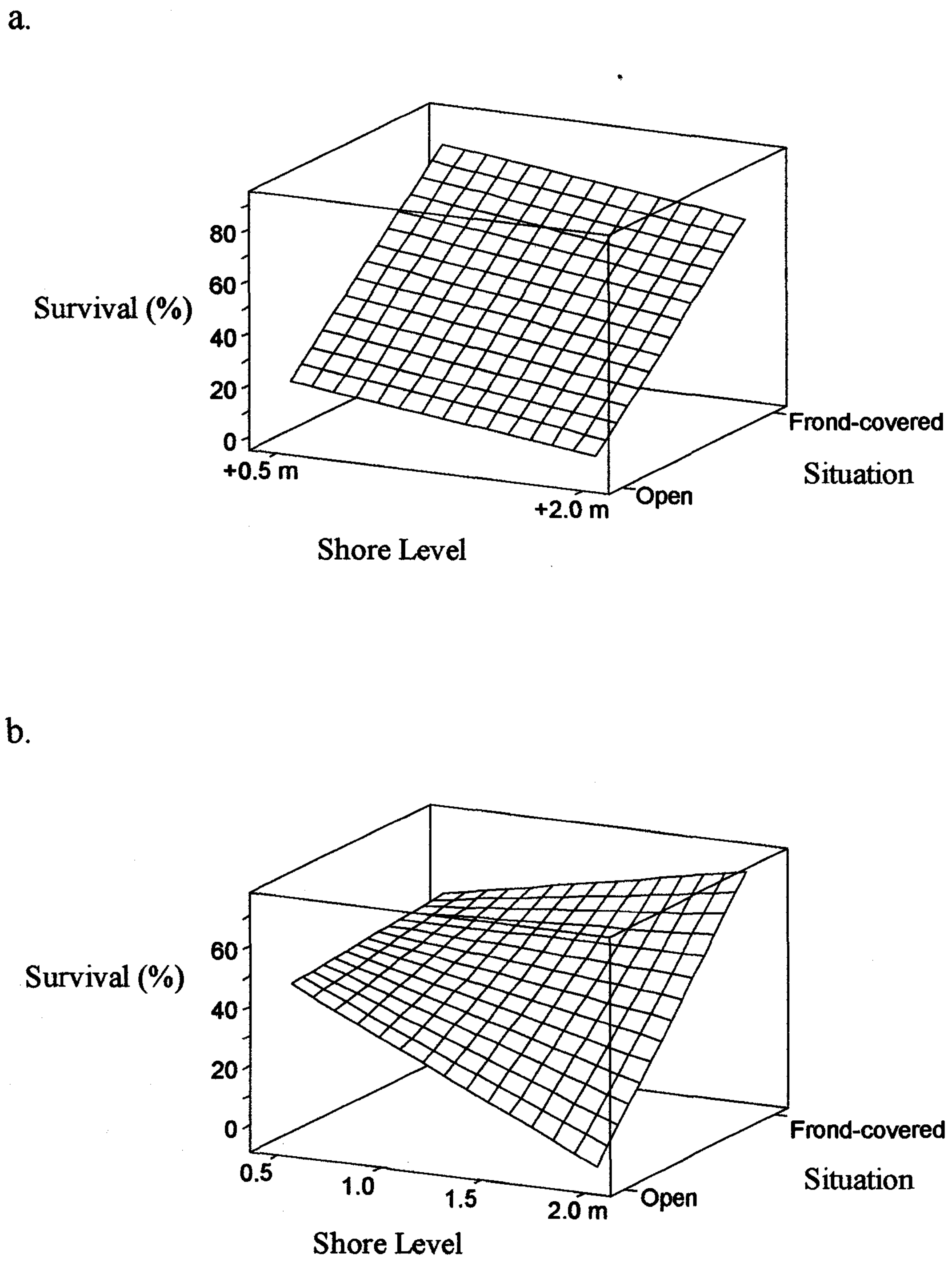


Figure II - 6. Factor Interaction. Response surfaces detailing germling survival after 1 month in the field during 1982-3 (a) and 1983-4 (b). Shore level increases left to right. Shore level x frond cover interaction was not significant 1982-3 (a), and was significant 1983-4 (b). Contour lines have been added to allow detection of curvature.

Table II – IV. Survival Projections. Survival times estimated from the 1983-4 experiments. Time to 0% survival (no plants remaining) is projected.

Animals		**No Animals**	
Open	Frond-covered	Open	Frond-covered
0.5 months **All Shore Levels**	0.5 – 4 mo. **Low Shore** **High Shore**	13 – 20 mo. **High** **Low**	18 – 60 mo. **Low** **High**

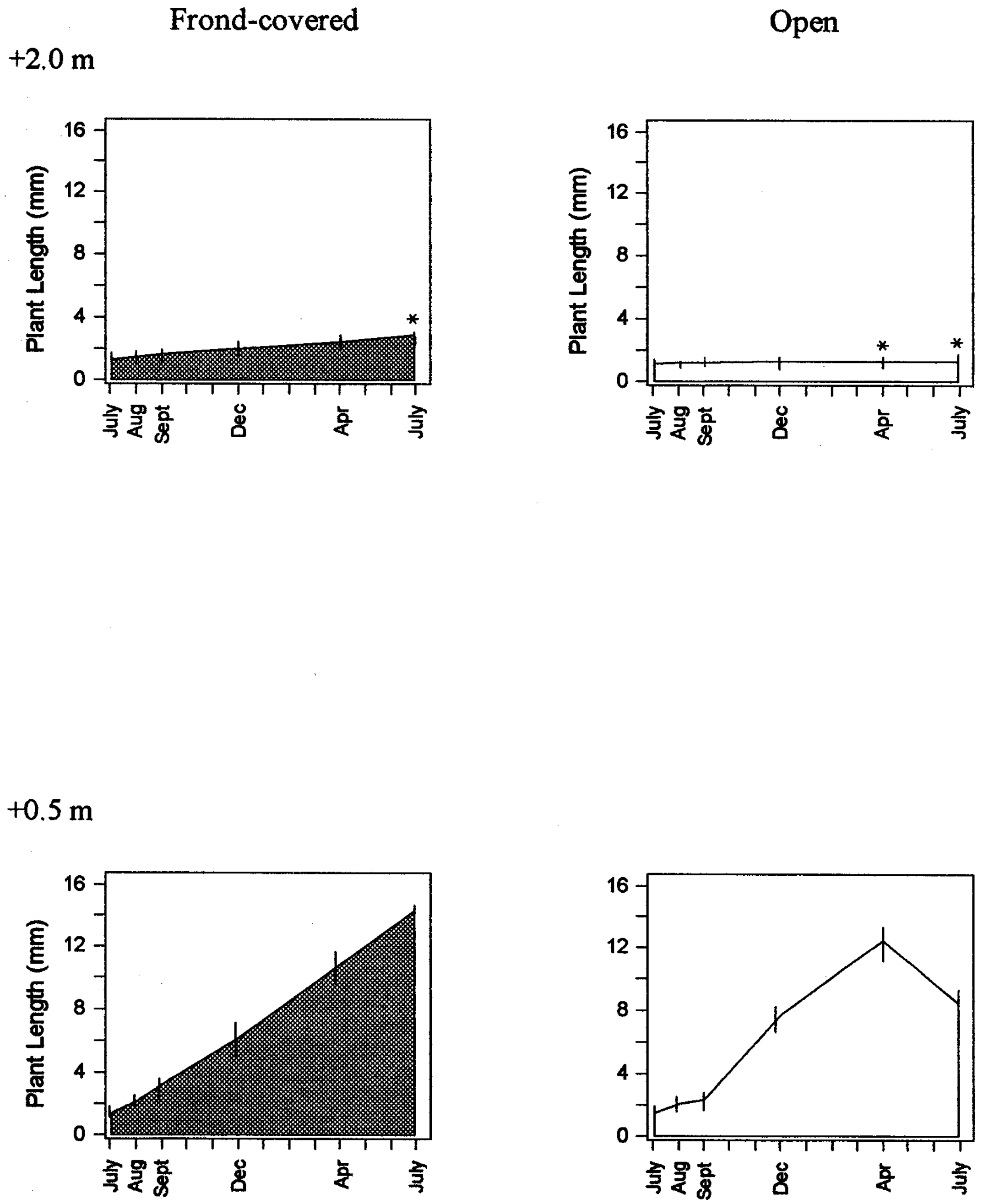


Figure II - 7. Growth, 1982-3. Plant length over the year, by environment. Means ± 1 S.E. are shown. Mean from one replicate only is indicated (*).

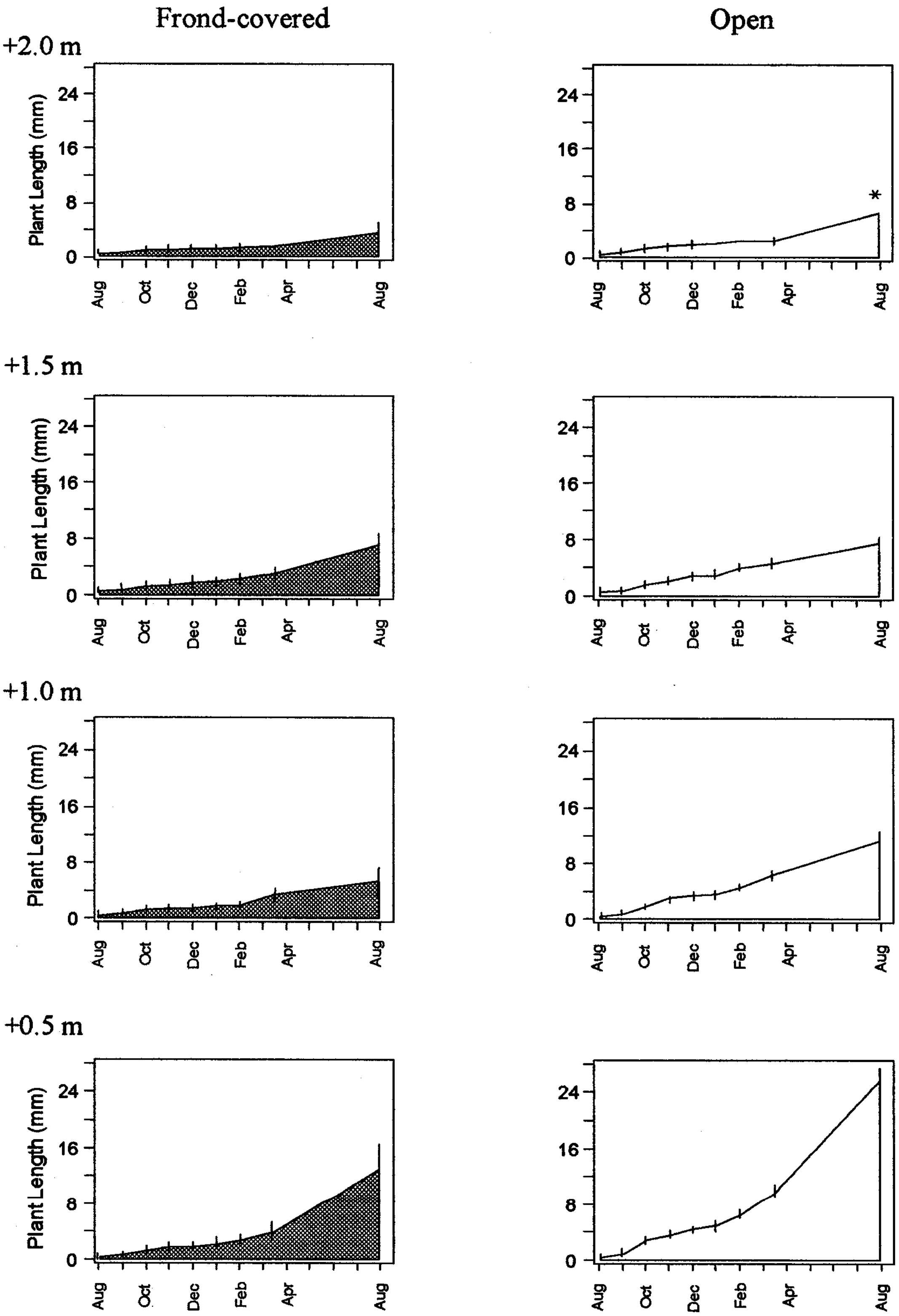


Figure II - 8. Growth, 1983-4. Plant length over the year, by environment. Means ±1 S.E. are shown. Mean from one replicate only is indicated (*).

Table II - V. Growth Statistics. Results from statistical tests on the effect of environment (shore level, frond cover) on growth. The 2-Way ANOVA tests included initial length as a covariate. Growth rates (mm/mo.) were ranked for the analyses. Results from pairwise tests (+2.0 m *vs.* the other shore levels) are given below.

Growth *vs.* Environment

Source	df	SS	MS	F	p-value
1982-3					
Initial Length	1	3.195	3.195	0.81	0.387
Shore Level	1	132.763	132.763	33.72	0.0001
Frond Cover	1	0.165	0.165	0.04	0.842
SL x FC	1	20.728	20.728	5.27	0.042*
Error	11	43.305	3.937		
Total	15	200.156			
1983-4					
Initial Length	1	0.727	0.727	0.08	0.787
Shore Level	3	385.566	128.522	13.60	0.001**
Frond Cover	1	99.496	99.496	10.53	0.008**
SL x FC	3	58.265	19.419	2.05	0.165
Error	11	103.981	9.453		
Total	19	648.035			

Shore Level and **Frond Cover** had **significant** effects on growth; as they interacted (1982-3) and as independent factors (1983-4).

Tukey Pairwise Tests indicated:

Pair Tested	T-Value	p-value (adj.)
---1982-3---		
+2.0 m Frond-covered *vs.* +2.0 m Open	1.701	0.368
vs. +0.5 m Open	-4.808	0.003**
vs. +0.5 m Frond-covered	-3.326	0.028*
---1983-4---		
+2.0 m *vs.* +1.5 m	-2.922	0.058
vs. +1.0 m	-3.109	0.042*
vs. +0.5 m	-6.327	0.0003***

Growth high on the shore differed significantly from growth low on the shore both years. Growth low on the shore differed between open and frond-covered situations.

Figure II - 9. Size Differences. The distinct sizes and morphologies of Ascophyllum plants grown low on the shore (left) and high in the zone (right), after 10 months in the field. Low shore plants are 2 – 3.5 cm compared to 2 – 3 mm for high shore. Plants on both tiles were grown under frond cover. The fronds of low shore plants have begun to flatten.

Table II - VI. Growth Rates. Mean growth rates (mm/mo. ± 1 standard deviation) by environment for both sets of plants with an estimate for growth in one year (cm). Means include 4 replicates for 1982-3 (except +2.0 m open, n = 2) and 3 replicates 1983-4 (except +2.0 m frond-covered and open, +0.5 m open; all with n = 2).

Growth Rate *vs.* Environment

	Frond-covered		Open	
Shore Level	Month (mm)	Year (cm)	Month (mm)	Year (cm)
---1982-3---				
+2.0 m	0.21 ± 0.12	< 0.3	0.03 ± 0.03	< 0.4
+0.5 m	1.01 ± 0.22	1.2	1.23 ± 0.19	1.5
---1983-4---				
+2.0 m	0.25 ± 0.18	0.3	0.40 ± 0.18	0.5
+1.5 m	0.55 ± 0.14	0.7	0.60 ± 0.13	0.7
+1.0 m	0.40 ± 0.12	0.5	0.93 ± 0.25	1.1
+0.5 m	1.00 ± 0.53	1.2	2.10 ± 0.31	2.5

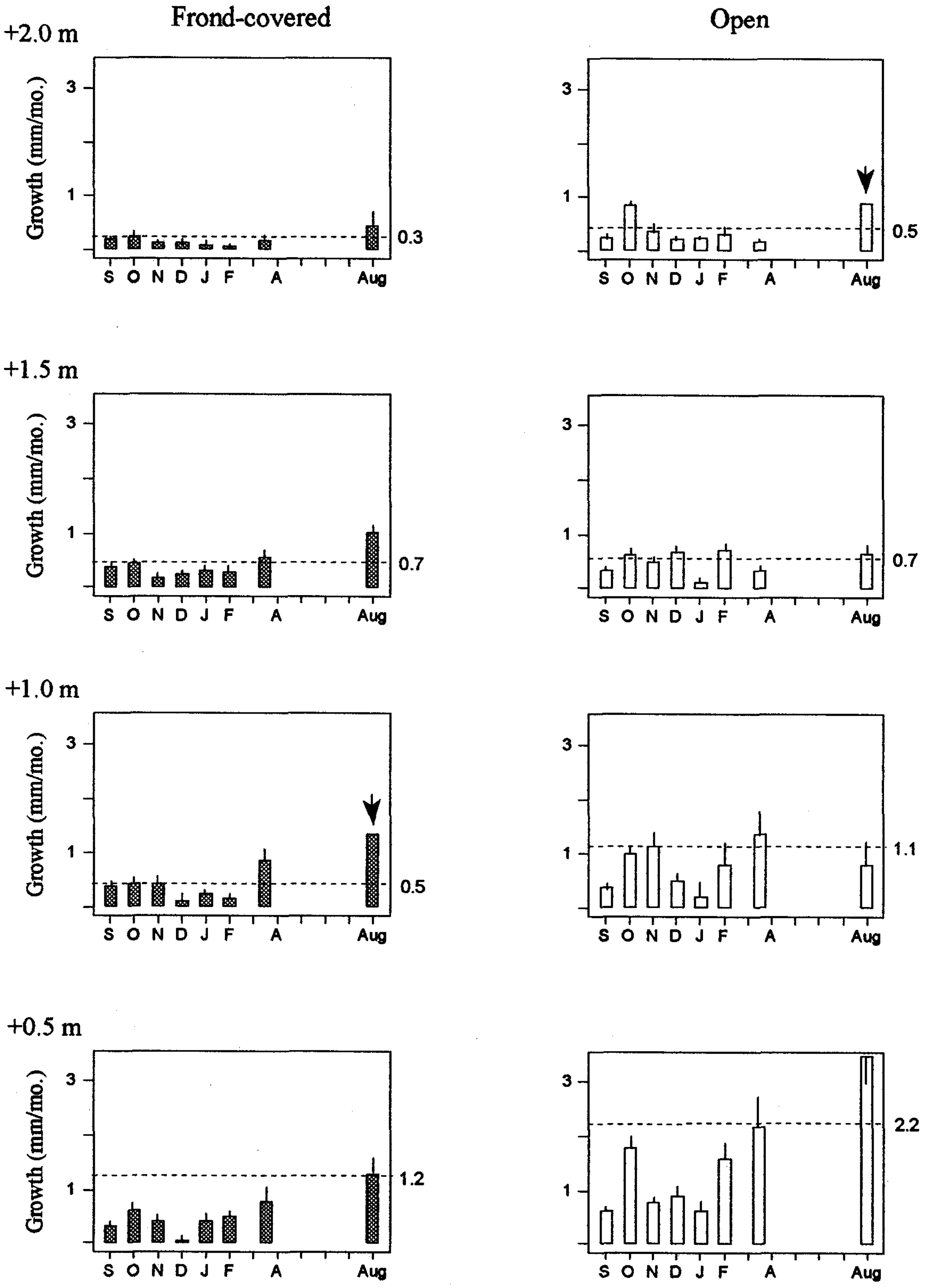


Figure II - 10. Growth Variation. Growth rates (mm/mo. ± 1 S.E.) by environment for all surveys. Rates for March/April (1.5 mo.) and August (4.5 mo.) were weighted in the yearly average (reference line). Mean based on 1 replicate is indicated (arrow)

Table II - VII. Damaged Plants. Numbers of damaged *Ascophyllum* observed during 1983-4, by environment. Counts by type of wound and totals are shown.

	Frond-Covered			Open			
Shore Level	**Apical**	**Lateral**	**Both**	**Apical**	**Lateral**	**Both**	**Total**
+2.0 m	0	1	1	1	0	1	2
+1.5 m	3	0	3	2	1	3	6
+1.0 m	0	0	0	26	12	38	38
+0.5 m	8	4	12	23	47	70	82
	11	5	16	52	60	112	128

CHAPTER III

ANIMAL IMPACT DIFFERS WITH SPECIES AND SIZE

Introduction

Grazing animals devastate yearly recruitment of *Ascophyllum nodosum* in the western Atlantic (Chapter II). Animals remove germlings from surfaces within days or weeks, as shown using exclusion cages. The importance of grazing animals at mid-shore levels has been demonstrated experimentally in Maine (Vadas *et al.* 1982, Miller and Vadas 1984) and in Nova Scotia, Canada (Lazo *et al.* 1994). A study in New Hampshire determined that animal impact is important throughout the *Ascophyllum* zone and becomes more intense down the shore (Ch. II).

In New England, grazers in the *Ascophyllum* zone include snails and limpets. Cages effective in protecting germlings have mesh openings that exclude animals larger than half a centimeter in width or height (*i.e.*, 0.6 cm; Ch. II). Adults of all species are excluded, except for *Lacuna vincta* (Montagu) which is small enough to penetrate the mesh. Caging studies demonstrate the importance of grazing animals but provide no direct evidence for the importance of any one.

The periwinkle snail, *Littorina littorea* (L.), has been implicated in the removal of *Ascophyllum* germlings (Knight and Parke 1950, Sundene 1973, Vadas *et al.* 1982, Keser and Larson 1984, Miller and Vadas 1984, Vadas and Wright 1986). It is the largest and most abundant of the grazers. The evidence is correlative. A relationship has been noted between a lack of recolonization by *Ascophyllum* and the abundance of *L. littorea* (Knight and Parke 1950, Sundene 1973). Extended along a salinity gradient, Keser and Larson (1984) found negligible recruitment in coastal sites where snails were abundant and documented successful recolonization in estuarine sites where snails were less numerous. A gradient in animal impact down the shore (Ch. II) correlates with the abundance of *L. littorea*. At the time of this study, direct evidence of impact by *L. littorea* was lacking. Further, an assessment of the relative importance of the common species was needed.

The role of *Littorina littorea* is controversial. Feeding studies indicate that periwinkle snails prefer soft-tissued seaweeds to *Ascophyllum* (see Menge 1975, Lubchenco 1986). Snails avoid *Ascophyllum*, even at the germling stage (Watson and Norton 1985). Geiselman (1980, Geiselman and McConnell 1981) concluded that phenolic compounds determine feeding selectivity of *L. littorea*. Concentrations of phenolics, particularly tannins, parallel the preference ranks; the least preferred foods have the highest tannin concentrations (*i.e.*, *Ascophyllum*).

While it is clear that animal impact results in germling loss, it is not clear that animals consume *Ascophyllum* germlings. Germling attachment is critical. *Ascophyllum* germlings are dislodged by waves and water motion (Vadas and Wright 1986; see also Vadas *et al.* 1990). Watson and Norton (1985) suggest that crawling snails dislodge plants. Developing plants may be undercut as snails graze along rock surfaces. Germlings are small, < 2 mm tall, and may be consumed incidentally.

The impact of the other species is potentially important. The snail second in abundance at the Ft. Stark study site, *Littorina obtusata* (L.), has a strong association with fucoid algae. Snails crawl toward *Fucus* and *Ascophyllum* preferentially, locating the plants initially by scent (Barkmann 1955, van Dongen 1956). Barkmann (1955) found that although *L. obtusata* consumed several seaweeds, it would lay eggs only on fucoids. Watson and Norton (1985, 1987) noted that *L. obtusata* is not deterred by the astringency of tannins in algal tissues, and they observed snails consuming *Ascophyllum* germlings. Thus, evidence points to a probable role of *L. obtusata*. *Littorina saxatilis* (Olivi) is primarily a detritivore but consumes germlings of filamentous forms (Sacchi *et al.* 1977) and ephemeral algae (see Lotze and Worm 2000). A possible role for limpets is suggested by studies in Europe, where limpets dominate the intertidal zone and profoundly affect recruitment dynamics of intertidal seaweeds (Lodge 1948, Lewis 1964, Hawkins and Hartnoll 1983).

The focus of the present study was to assess the impact of each of the common species on *Ascophyllum* germlings. Germling survival was used to assess this impact, and cages were used to exclude or include animals.

Size differences suggested that cages with appropriate mesh openings could roughly separate the effects of *Littorina obtusata* and *L. littorea*. Preliminary work, detailed below, determined the appropriate mesh size. The test hypotheses for the exclusion experiments were: 1) **impact is affected by mesh opening size** (specifically that impact increases with openings > 0.6 cm), and 2) **impact is reduced when *L. littorea* is excluded**. The exclusion experiments were followed by single-species inclusion studies. Individual snails were enclosed in cages with germlings, and each of the species was tested. The importance of size was tested for the 2 most abundant species (*Littorina littorea* and *L. obtusata*) by including small individuals in cages with germlings. The test hypothesis for all inclusion experiments was that **impact of a species differs significantly from the results when no animal was included** in the cage ('no impact').

In New England, grazers common in the *Ascophyllum* zone (see Figure III - 1) include *Littorina saxatilis* (Olivi), *L. obtusata* (L.), *L. littorea* (L.), and the limpet *Acmaea* (= *Collisella*) *testudinalis* (Müller). Other species are present but rare (see Croker 1972, Gosner 1978). The snail, *Lacuna vincta* (Montagu), is abundant low on the shore in spring or early summer (Smith 1973, Lubchenco 1980, Thomas and Page 1980, Worm and Chapman 1998). A few *Lacuna* were counted during surveys in April (1983) but specimens were hard to locate by June, when the experiments commenced. *Lacuna* can be abundant on *Ascophyllum* (Croker 1972). Snails cause extensive damage to *Fucus serratus* (Smith 1973, Thomas and Page 1980) and kelp (Fralick *et al.* 1974, Johnson and Mann 1986). Dense aggregations can be devastating (see Fralick *et al.* 1974). If snails were abundant on the low shore, impact by *Lacuna* could be important.

The animals have different ranges within the zone (Fig. III - 2), and their behavior dictates preferred grazing locations. *Littorina saxatilis* is found above *Ascophyllum*, and ranges into the *Ascophyllum* zone. Snails feed on the microflora, consume germlings and sporelings, ingest macroalgae, and feed on plant material in the detrital pool (Sacchi *et al.* 1977). *Littorina obtusata* ranges through the *Ascophyllum* zone with maximum abundance on the mid-shore (Barkmann 1955). Snails are found on *Fucus* and *Ascophyllum* plants, and prefer to graze on their fronds. *Littorina littorea* ranges through the *Ascophyllum* zone and into the subtidal. The snails graze along the rock surface (Gendron 1977), and consume surface growths, diatoms, microalgae and, preferably, soft-tissued macroalgae (Watson and Norton 1985). *Littorina littorea* is an opportunistic feeder and consumes larval animals and developing plants (see Hawkins 1996). Limpets are found on the mid-shore and lower. They are most abundant subtidally and in tide pools (Steneck 1982). Limpets are territorial, regularly scouring encroaching material from their patch of surface.

Materials and Methods

Differences in the size of the animals suggested that cages with appropriate mesh openings could exclude most *Littorina littorea*, while allowing access to *L. obtusata*. Width or height of the animal was important (whichever was greater). Several types of hardware cloth were available. Animals were measured in length, width and height using metric vernier calipers. The importance of length will become clear later. Samples of 31 *Littorina saxatilis*, 8 limpets (all the specimens located), and 31 each of *L. obtusata* and *L. littorea* were collected. Specimens of *L. obtusata* and *L. littorea* were numbered. All specimens were measured, and the *L. obtusata* and *L. littorea* were transported to the laboratory for weight determinations. Width was generally greater than height for all species. The choices for an intermediate screening were 1.3 and 1.9 cm mesh, functionally 1.1 and 1.7 cm minimum openings. Width was related to length as $L = W \div 0.8$, a reasonable estimate for all species[1]. Using the relation, maximum lengths of animals with access were 1.4 and 2.1 cm. Size data for *L. obtusata* from the spring survey indicated that most animals were ≤ 1.4 cm. Mesh with a 1.3 cm opening was selected.

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[1] Regressions using L, W data did not provide a better estimate. Slope-intercepts were 0.7 and 0.8, too large for small animals. Slopes ranged from 0.75 – 8.2, suggesting use of 0.8.

Cages used in the exclusion experiment had openings of 0.1 cm (total exclusion), 0.6 cm (exclusion), 1.3 cm (intermediate exclusion) and 2.5 cm (2.5 cm width x 3.75 cm height, no exclusion). Screen with 0.6 cm mesh excluded the bulk of the grazers in a previous study (Ch. II), although larval snails settled within the cages. Therefore, a smaller mesh (0.1 cm) was used for total exclusion. Access was tested in the field by passing animals of the critical lengths through the mesh.

During an initial survey (April 1983), length of all animals within quadrat samples was measured. The maximum lengths of animals capable of penetrating each mesh opening were estimated using $L = W \div 0.8$, and the numbers of animals/m^2 with access were determined using length data from the April survey. To see how well the caging scheme fit the situation in the summer, a second size survey was taken during the exclusion experiments. The spring survey included data from 10 quadrat samples at +2.0 and +0.5 m, and the summer survey (July 12, 1983) included 20 samples at each shore level. Surveys of animal abundance, but not size, were taken on other dates to document variation in abundance.

A complete set of treatments was placed under frond cover both high (+2.0 m) and low (+0.5 m) on the shore. Animal impact varies with shore level, and is significantly different at the extremes (Ch. II). Treatments were placed beneath frond cover to minimize the effects of water motion and maximize similarity of the physical environment. The treatment set included 6 treatments: 4 types of cages (openings 0.1 cm, 0.6 cm, 1.3 cm, 2.5 cm), no cage (opening = ∞ cm), and a low top placed 0.6 cm above the tile to serve as a 0.6 cm exclusion without screened sides. To render environments within cages comparable, all cages had tops of fine mesh screen (0.1 cm). Low tops were also constructed of fine mesh screen.

Animal impact for both the exclusion and inclusion experiments was assessed using the percentage of *Ascophyllum* germlings remaining on experimental tiles. Germlings were obtained by mixing gametes rinsed from reproductive fronds and pouring the suspension over submerged ceramic tiles. The tiles were $(5.5 \text{ cm})^2$ and had a central hole. Germling counts included the whole tile. A goal of between 50 and 300 germlings kept census time reasonable. Some thinning was necessary and individuals were carefully removed using fine forceps. Counts were made before placement in the field, and after 2, 5, 10 and 20 days. Tiles (= germling populations) were randomly assigned to treatment with 3 replicates. They were secured at the appropriate shore level on June 28, 1983 when germlings were 1.5 months old.

Single species inclusion experiments were undertaken on October 6, 1983. Inclusions were performed at a shore level appropriate for the species. Animals used were of a common size. They were taken from as close to the experimental areas as possible because feeding behavior is sensitive to changes in location (*Littorina littorea*; Newell *et al.* 1971). Treatments were replicated 3 times. Inclusion periods were 2 days and repeated 4 times, giving a total of 8 days. Tiles were transported back to the laboratory and germlings were censused after each inclusion. At the start of each inclusion, a new animal was introduced. Limiting inclusion to 2 days was to ensure that germling loss did not reflect starvation. Use of several animals over the 8 day period was to minimize the influence of aberrant behavior in any one. At the start, animals were measured (length), blotted and weighed. Thereafter, only length was measured.

Adult snails were tested using standard mesh cages (0.6 cm). *Littorina saxatilis* was tested at +2.0 m, and *L. obtusata, L. littorea* and *Acmaea testudinalis* were tested at +0.5 m. At each shore level, treatments included animal in a cage with germlings, cages with no animal included, and tiles that were not caged (ambient impact).

Small snail inclusion experiments ran concurrently with the adult inclusions, and were located at +0.5 m. Small *Littorina obtusata* and *L. littorea* were included in cages of the finest mesh (0.1 cm). Adult *L. littorea* were included in fine meshed cages as well in order to test the effect of opening size on impact.

Common sizes of the species differed and so did their weights. Grazing impact mirrors body weight (weight of the animal apart from the shell) more closely than weight of whole animals (see Moore 1937, Grahame 1973a, b). Fresh weights (whole animals) were assessed for the *Littorina obtusata* and *L. littorea* used for size measurements (n = 31) and then transported to the laboratory. The animals were then boiled in seawater, and then their bodies were extracted, blotted and weighed. The relationship between body weight (the best indicator of size) and length (an easy and direct measure in the field) was evaluated.

Results

The exclusion scheme differentiated between impact of *Littorina obtusata* and *L. littorea*. It was based on spring size data (Figure III - 3). An intermediate mesh opening of 1.3 cm was chosen to allow access to *L. obtusata* (100%, April data) while excluding most *L. littorea* (27% with access at +2.0 m, 43% at +0.5 m). Size data collected in July showed a similar pattern (Fig. III - 3). All *L. obtusata* sampled could penetrate the 1.3

cm mesh. About 40% of the *L. littorea* were excluded (July data) compared with over half the population based on spring data.

The abundance of grazers increased in the summer as compared to the spring, despite variation between survey date (Table III - I). Numbers of *Littorina obtusata*, especially at +2.0 m, and limpets did not show much change comparing summer means with overall means. *Littorina littorea* increased ≈ 15/m^2 at +2.0 m and 90/m^2 at +0.5 m.

Animal impact increased with opening size and was greater low on the shore (Figure III - 4). The critical opening of 1.3 cm (intermediate access) was associated with intermediate impact. The exclusion treatments (0.1 and 0.6 cm mesh) retained the highest percentage of *Ascophyllum* germlings. Where all animals had access (2.5 cm, and No Cage), fewer than 10% of the germlings remained after 20 days high on the shore while tiles were bare within 5 or 10 days low on the shore. Differential impact was apparent when comparing impact for1.3 cm openings at both shore levels.

Low tops were not effective. They confounded the effects of frond-sweeping and animal impact. *Ascophyllum* fronds caught on the corners of the top and were constrained to sweep across the tiles. Tiles that escaped sweeping fronds retained > 80% of the germlings; replicates that did not (n = 1 at +2.0 m and n = 2 at +0.5 m) had part of their surfaces swept clean.

Statistical results indicated that both opening size and shore level were significant factors (Table III - II). The same general trends were evident at +2.0 and +0.5 m (no significant interaction). Exclusion of animals significantly affected impact. Means for mesh openings up to 1.3 cm are all significantly different from ambient impact (No

Cage). Impact was significantly reduced when the larger *Littorina littorea* were excluded.

Size of the animals varied with species (Table III - III). *Littorina saxatilis* and *Acmaea testudinalis* weighed least, a tenth the weight of *L. littorea* adults. In terms of length, *L. saxatilis* adults were the smallest and *L. littorea* were the largest.

Impact by *Littorina saxatilis* (Figure III - 5 a) was negligible and > 80% of the germlings remained after 8 days. Ambient impact at +2.0 m resulted in < 20% of the germlings remaining. Impact low on the shore (Fig. III - 5 b) was greater and some tiles were bare by the 6th day. Impact associated with *L. littorea* resulted in 1 - 5% of the germlings remaining. Impact by *L. obtusata* and by the limpet *Acmaea* was moderate. Limpet impact varied among replicates, with 25% of the germlings remaining on 2 of the tiles and 78% on the other.

The impact of *Littorina saxatilis* (+2.0 m) as well as of *L. obtusata* and *Acmaea* (+0.5 m) were not significant (Table III – IV). Impact by adult *L. littorea* was significant and was statistically indistinguishable from ambient impact at +0.5 m.

During germling censuses for the inclusion treatments, several critical observations were made. Faint trails along the tile surfaces could be detected with the inclusion of adult *Littorina littorea*. Also, six *Ascophyllum* germlings were reduced to stumps. With adult *Littorina obtusata*, five germlings were wounded; 2 lost a terminal apex, and 3 were reduced to stumps. Although very few plants were wounded, the wounds provided direct evidence of impact.

Small snails had less impact than adults, and the impact of small *Littorina obtusata* was less than *L. littorea* (Figure III - 5 c). Impact by small snails was not statistically significant (Table III – V a). Based upon the inclusions of *L. littorea* adults, screening material did not affect impact (Table III – V b).

Impact varied with species. When the animals tested were ranked by observed impact after 8 days, the ranks fell out of order with size (Table III - VI). *Littorina littorea* juveniles exerted greater impact than size would suggest. For example, if impact were purely a function of size (length, weight), then impact of *L. littorea* juveniles should be > *L. obtusata* juveniles (it was), < *L. saxatilis* adults (it was greater), and about half the impact of *L. obtusata* adults (it was about equal). Limpets also exerted greater impact than size alone would predict.

Regressions relating body weight to length revealed a close relationship between those two factors (Table III – VII). Using $\log_{10}$values for both variables, length accounted for 96-97% of the variation in body weight.

Discussion

The impact of one species, *Littorina littorea,* was statistically significant. Adult snails reduced survival of *Ascophyllum* germlings. Further, their impact was statistically indistinguishable from ambient impact (No Cage).

Results from exclusion and inclusion experiments highlighted differential effects associated with species and size. Openings of 1.3 cm excluded only **the larger *Littorina littorea*.** All other species as well as juveniles and some adult *L. littorea* (Fig. III - 3) had access, yet impact was significantly reduced. Inclusion experiments tied impact to size directly. Impact by small *L. littorea* was not significant. Juvenile snails were < ⅓ the size of adults (0.5 cm *vs.* 1.9 cm long, Table III - III), and their impact was about ⅓ of an adult's impact (25 % *vs.* 75 %; Table III - VI, Rank Comparison). Impact will be considered in terms of size for all species later.

Observations made during the inclusion experiments provided insight beyond the statistics. Trails indicated that *Littorina littorea* crawled across the tiles. Germling loss showed that *L. littorea* was an efficient removal agent. While most germlings were removed, a few were wounded. The observations suggest that rasping was involved and undercutting was likely. *Littorina obtusata* also wounded germlings. Unique to *L. obtusata*, plant apices were lost. Thus, *L. obtusata* can impact *Ascophyllum* germlings. Limpet behavior was variable. Sometimes, there was no indication that the animals had moved and other times germlings were cleared from a portion of the tile. Limpet impact was localized. To gauge limpet impact, longer inclusion periods are indicated.

Germlings with tip loss and those reduced to stumps were observed in a previous study, and larval snails were removed from within the cages (Ch. II). Damage may have been due to *Littorina littorea* and *L. obtusata* small enough to penetrate the mesh. Small snails in the inclusion experiments did not wound germlings. Perhaps the 2 day inclusion period was too short. On the other hand, minute lateral wounds observed in a previous study (Ch. II) were not observed here. Lazo *et al.* (1994) offered plants to specific consumers and studied the wounds to be able to identify the animals involved (see also Norton *et al.* 1990). Inclusion experiments could be used to link wound types with specific animals, and to clarify the impact of larval, juvenile, and adult snails. The minute wounds may have been from isopod or amphipod grazers (see later).

Field-based experiments allowed assessments under natural conditions. Exclusion experiments provided a controlled moderation of ambient impact at both shore levels. Inclusion experiments afforded the chance to test each animal in its natural habitat and near its specific location. The experiments were run under ambient conditions of temperature, desiccation, and tidal exposure. Inclusion experiments offered no food choice (see Barker and Chapman 1990) but the aim was to determine potential impact and inclusion periods were kept short. Field-based inclusions could be used to determine whether germlings are dislodged or consumed. In fine-meshed cages, loose germlings collected along the edges of the cage.

Animal impact was greater low on the shore where animals, particularly *Littorina littorea* were 5 - 10 times as abundant (Table III – I). A gradient in animal impact down the shore has been reported (Ch. II). Bertness *et al.* (1999) reported natural recruitment of *Ascophyllum* high on the shore with few recruits low on the shore without protection from animals.

Procedural difficulties should be noted to improve future experiments and explain anomalies. In the exclusion experiment, impact was apparently less with an opening of 0.6 than 0.1 cm. In the inclusion experiment, *Littorina saxatilis* had less impact than 'no animal.' The anomalous observations were due to initial thinning of the germlings. Removal of some germlings led to the unexpected loss of others. Unattached germlings collected within fine-meshed cages in the 'no animal included' treatments, and provided insight. Alternative ways to reduce densities are to dilute gamete or zygote suspensions, or transfer individual zygotes to a suitable surface (see Viejo *et al.* 1999). Low tops used in the exclusion experiments excluded animals but trapped fronds. Others have used partial cages (*i.e.*,Worm and Chapman 1998), or fences and manual removal (Viejo *et al.* 1999, Lindegarth *et al.* 2001). Tops constructed of the same mesh rendered within-cage environments similar. The tops also decreased light. All treatments were placed under canopy. In cases where light is critical, clear screening is an alternative. Inclusion experiments were not initiated until October due to other on-going experiments. The late start did not seem to deter impact. Nevertheless, spring or summer would be optimal.

Littorina obtusata was of secondary importance in the removal of *Ascophyllum* germlings. Adult snails had modest impact, about the same as *L. littorea* juveniles half their size (Table III - VI). Barker and Chapman (1990) compared adult snails and found *L. obtusata* 2 to 3 times less effective than *L. littorea* in the removal of *Fucus* germlings. While *L. obtusata* was less effective at germling removal, the snails were 10 times more effective than *L. littorea* as consumers of adult fronds. In the field, about half the snails recorded during surveys were found on the rock where they might impact germlings. Norton *et al.* (1990) and Jenkins, Hawkins and Norton (1999) suggest that location (on fronds) limits the snail's impact on recruits.

The importance of *L. obtusata* should not be discounted. Snails are present in moderate abundance throughout the zone and consume frond tissue (Watson and Norton 1987, Chapman 1989, Barker and Chapman 1990). Snails may feed intensely, consuming inner tissues and leaving deep wounds (Pavia and Toth 2000, Amsler 2001). *Littorina obtusata* is not deterred by tannin concentrations that discourage *L. littorea* (Geiselman 1980, Watson and Norton 1985). Snails will not only brave a lawn of *Ascophyllum* germlings, which *L. littorea* avoids, but consume them (Watson and Norton 1987). Whereas *L. littorea* prefers *Ulva* to *Fucus/Ascophyllum*, *L. obtusata* prefers *Fucus* to *Ulva* (Norton *et al.* 1990). Snails did impact germlings, evinced by germling loss and wounding. Impact, minor for an individual, might be significant for half the *L. obtusata* population.

A feedback system between *Ascophyllum* (food) and *Littorina obtusata* (consumer) has been demonstrated. An inducible defense system was first described for *Fucus* and *Littorina sitkana* (Van Alstyne 1988). Grazing of fucoid fronds by *Littorina obtusata* leads to elevated tannin levels in injured plants (Yates and Peckol 1993, Peckol *et al.* 1996, Pavia and Brock 2000, Pavia and Toth 2000). Chemicals released into the water cause uninjured plants to concentrate tannins in their tissues (Toth and Pavia 2000, 2001). Snails prefer plants with lower tannin levels (Pavia, Toth and Åberg 1999). Frond tips and germlings naturally have lower concentrations and weaker chemical defenses (Norton *et al.* 1990). Tannin production increases with UV-B exposure (Pavia *et al.* 1997) and may be reduced in the shade, where germlings and juveniles develop. Tannin production incurs a metabolic cost, evident in decreased growth (Pavia, Toth and Åberg 1999).

Tannin levels may be associated with the presence of a fungal symbiont, *Mycosphearella ascophyllii*, present in *Ascophyllum* fronds. David (1943) questioned whether it is present at the germling stage. The question poses an intriguing ecological relationship, potentially a factor for successful recruitment of *Ascophyllum*.

Acmaea is not abundant in the *Ascophyllum* zone. The genus *Patella* in Europe, both larger and more abundant, regulates vegetation cycles on the shore (Hartnoll and Hawkins 1985). In New England, limited abundance, small size (see Worm and Chapman 1998) and localized effects downplay limpet impact on *Ascophyllum* recruitment.

Amphipods and isopods graze *Ascophyllum*. They are particularly abundant in spring and summer (Worm and Chapman 1998) and live in the *Ascophyllum* canopy, on *Ascophyllum* and its epiphytes. Amphipods at high densities impact *Fucus* germlings (Parker and Chapman 1994). Amphipods and isopods consume *Ascophyllum* germlings in the lab (Viejo *et al.* 1999) and were suspected in the loss of 13-day old *Ascophyllum* germlings placed in the field (Cervin and Åberg 1997). Feeding preferences differ with species and life stage (Pavia, Carr and Åberg 1999). Adult *Idotea granulosa*, an isopod, prefer *Ascophyllum* frond tips. Juvenile *Idotea* and juvenile *Gammarus locusta*, an amphipod, graze cut portions and meristematic tissues of *Ascophyllum* but prefer epiphytic plants. *Gammarus* adults prefer epiphytes. Amphipods and isopods are tolerant of tannins. *Idotea* species preferably consume plants with high tannin concentrations (Pavia, Toth and Åberg 1999, *I. granulosa*; Jormalainen *et al.* 2001, *I. baltica*). Preferred location of the animals, in the canopy layer, may focus feeding on adult tissues and epiphytic plants (Jormalainen *et al.* 2001) and away from recruits. Amphipods and isopods are highly mobile. The juveniles could freely penetrate standard cages yet survival within cages was high. Few were observed. Germling wounds (Ch. II) could be from isopods or amphipods. The animals are of limited importance relative to grazing snails.

Impact varied with species and was related to size. Impact of small *Littorina littorea* and *Acmaea* were disproportionate. Small *Littorina littorea* were half the weight of *L. obtusata* adults, though they had similar impact. *Littorina saxatilis* adults were slightly larger than the small *L. littorea* and had negligible impact. Notably, *L. saxatilis* was half the weight of the small *L. littorea.* Limpets were c. 1/7th the weight of adult *L.*

littorea and removed a third as many germlings. On a weight basis, small *L. littorea* had impact similar to adults, while limpets were more effective than adult *Littorina littorea*.

The regression of body weight on length indicated a strong relationship. Length alone was adopted as a reliable indicator of size without sacrifice of the animals, and was used in further studies (Ch. IV).

Densities of *Littorina littorea* in the western Atlantic are considerable (Barker and Chapman 1990, Norton *et al.* 1990, Vadas *et al.* 1992, Chapman 1995). Norton *et al.* (1990) categorized *L. littorea* densities > 250/m^2 as 'superabundant.' Cervin and Åberg (1997) experimentally determined that densities equivalent to 240/m^2 reduce survival of *Ascophyllum* germlings. Densities of *L. littorea* on our shores were > 240/m^2 low in the zone in the summer, and can exceed 400/m^2. Caging studies in Canada and in the New England have shown that grazing animals nullify recruitment (Miller and Vadas 1984, Vadas *et al.* 1992, Lazo *et al.* 1994). Densities may be artificially high (Vermeij 1978, Barker and Chapman 1990, Chapman 1995). As initially suggested by Knight and Parke (1950) and Sundene (1973), *L. littorea* has a major effect on recruitment of *Ascophyllum*. Impact is exacerbated by elevated densities.

Littorina littorea effectively removed *Ascophyllum* germlings, yet these young plants are a least-preferred food (Watson and Norton 1985). Least-preferred does not mean never eaten. High snail densities and limited food availability compel less discriminate feeding. *Littorina littorea* is, ultimately, an opportunisitic feeder (Hawkins 1996). Snails damage frond tips (MacFarlane 1932) and holdfasts (Fischer-Piette 1948), and they feed on ripe receptacles (MacFarlane 1932, David 1943, Hunter 1981). Also, germlings may be ingested incidentally along with other foods. Finally, snails preconditioned to particular fucoid algae, feed upon it (Imrie *et al.* 1990).

Watson and Norton (1985) suggested that crawling snails dislodge germlings. Attachment of germlings is relatively weak (Vadas *et al.* 1990, Vadas *et al.* 1992). Snails are effective bulldozers, clearing sediment (Bertness 1984) and probably dislodging germlings. However, wounds suggest that radular grinding is involved. As snails grind along surfaces, they may undercut germlings and sever rhizoidal connections. Germling losses due to thinning, showed that rhizoidal networks are easily disrupted.

The species impacting *Ascophyllum* change with geography (Norton *et al.* 1990, Chapman 1995, Lindegarth *et al.* 2001). In the western Atlantic, *L. littorea* is of overwhelming importance. In Europe, limpets regulate recruitment (Åberg and Pavia 1997; Johnson *et al.* 1997; Jenkins, Hawkins and Norton 1999). Snail densities on some European shores are > 250/m^2 and comparative studies have been suggested (Norton *et al.* 1990). When snails and limpets do not play major roles, isopod and amphipod grazers may be critical (Cervin and Åberg 1997).

Significant impact was associated with one species, *Littorina littorea*. Impact of *L. obtusata* and limpets was of secondary importance. Species and size were important factors. Given the number of large *L. littorea*/m^2, and that an adult snail can clear a surface 25 cm^2 in 8 days, snails low in the zone would impact all surfaces within a month. High in the zone, it could take 10 months. Regardless, all surfaces would be impacted within a year. Spatial and temporal variation in animal impact becomes critical (Ch. IV).

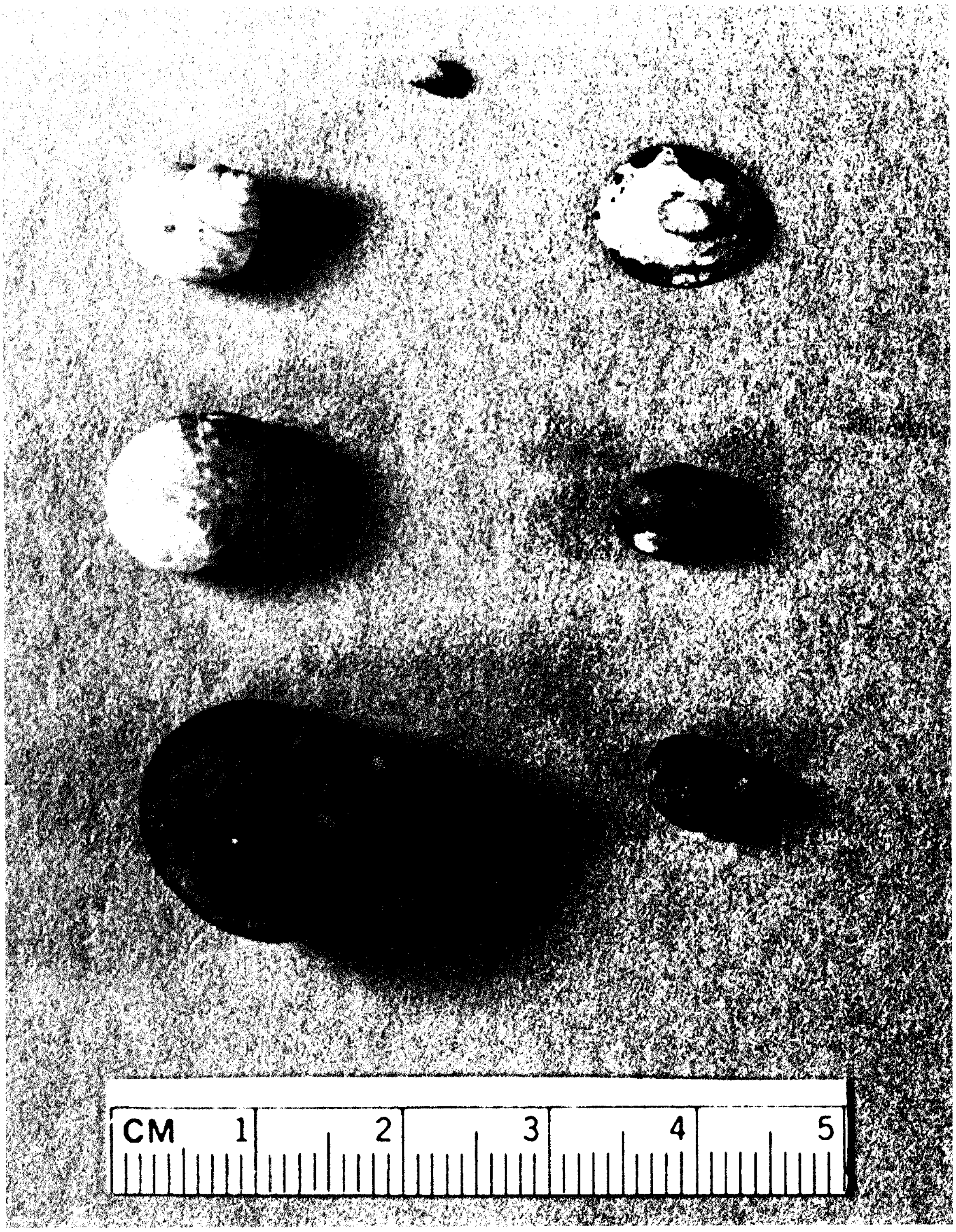


Figure III - 1. The Animals. The grazing animals common in the Ascophyllum zone and their relative sizes. Lacuna vincta (a), Littorina saxatilis (b), Acmaea testudinalis (c), Littorina obtusata of a common size (d) and a small individual (e), L. littorea of a common size (f) and a small individual (g).

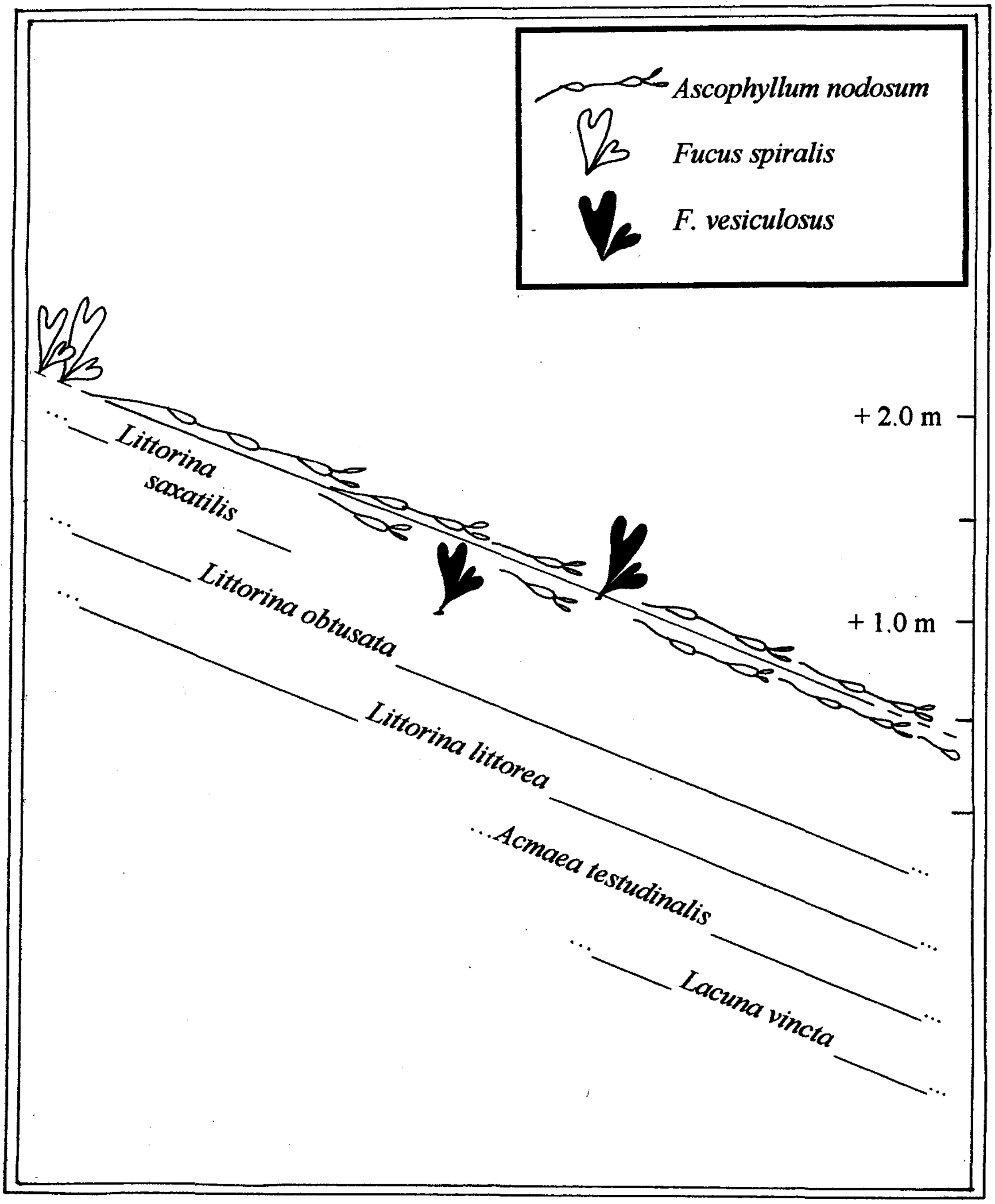


Figure III - 2. Animal Distribution. Range of the species on the shore relative to *Ascophyllum nodosum* and *Fucus* species.

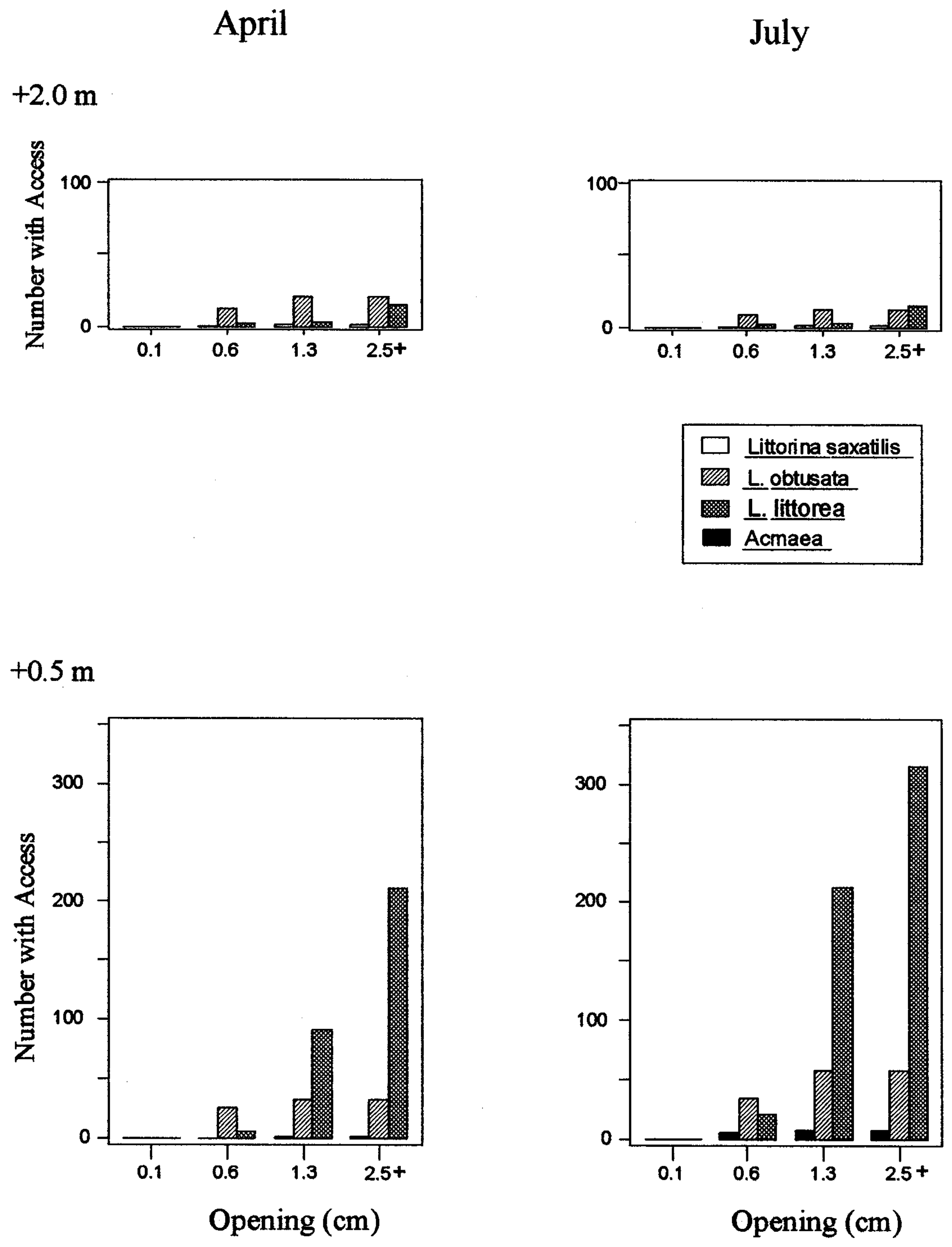


Figure III - 3. Exclusion Scheme. Numbers of animals (m^2) able to penetrate cages with different mesh opening sizes, by shore level. April (1983) survey data were used to select the hardware cloth for cage construction; July (1983) data indicate abundance during the exclusion experiment.

Table III - I. Abundance. Numbers of grazing animals (m^2) by shore level during the exclusion experiment. Values are means ± 1 standard deviation, rounded to whole integers except for *Littorina saxatilis* which was rare in the samples.

+2.0 m

Date	*Littorina obtusata*	*L. littorea*	*L. saxatilis*	All Grazers
June 29	21 ± 22	38 ± 29	0.1 ± 0.2	58 ± 40
June 30	16 ± 15	50 ± 61	0	64 ± 64
July 8	14 ± 21	48 ± 42	0	61 ± 51
July 12	13 ± 13	40 ± 42	0.2 ± 0.5	53 ± 43
July 27	6 ± 10	32 ± 30	0	38 ± 40
Summer Mean	13 ± 18	41 ± 42	0.2 ± 0.4	55 ± 47
Overall Mean	16 ± 6	25 ± 12	0.3 ± 0.8	40 ± 14

+0.5 m

Date	*Littorina obtusata*	*L. littorea*	*Acmaea testudinalis*	All Grazers
June 29	19 ± 24	562 ± 378	2 ± 6	584 ± 374
June 30	35 ± 48	467 ± 246	6 ± 10	509 ± 278
July 8	32 ± 42	323 ± 192	10 ± 14	365 ± 171
July 12	35 ± 38	334 ± 184	6 ± 10	374 ± 178
July 27	19 ± 21	227 ± 125	2 ± 5	248 ± 118
Summer Mean	28 ± 36	382 ± 264	5 ± 10	416 ± 265
Overall Mean	22 ± 12	296 ± 100	7 ± 6	325 ± 108

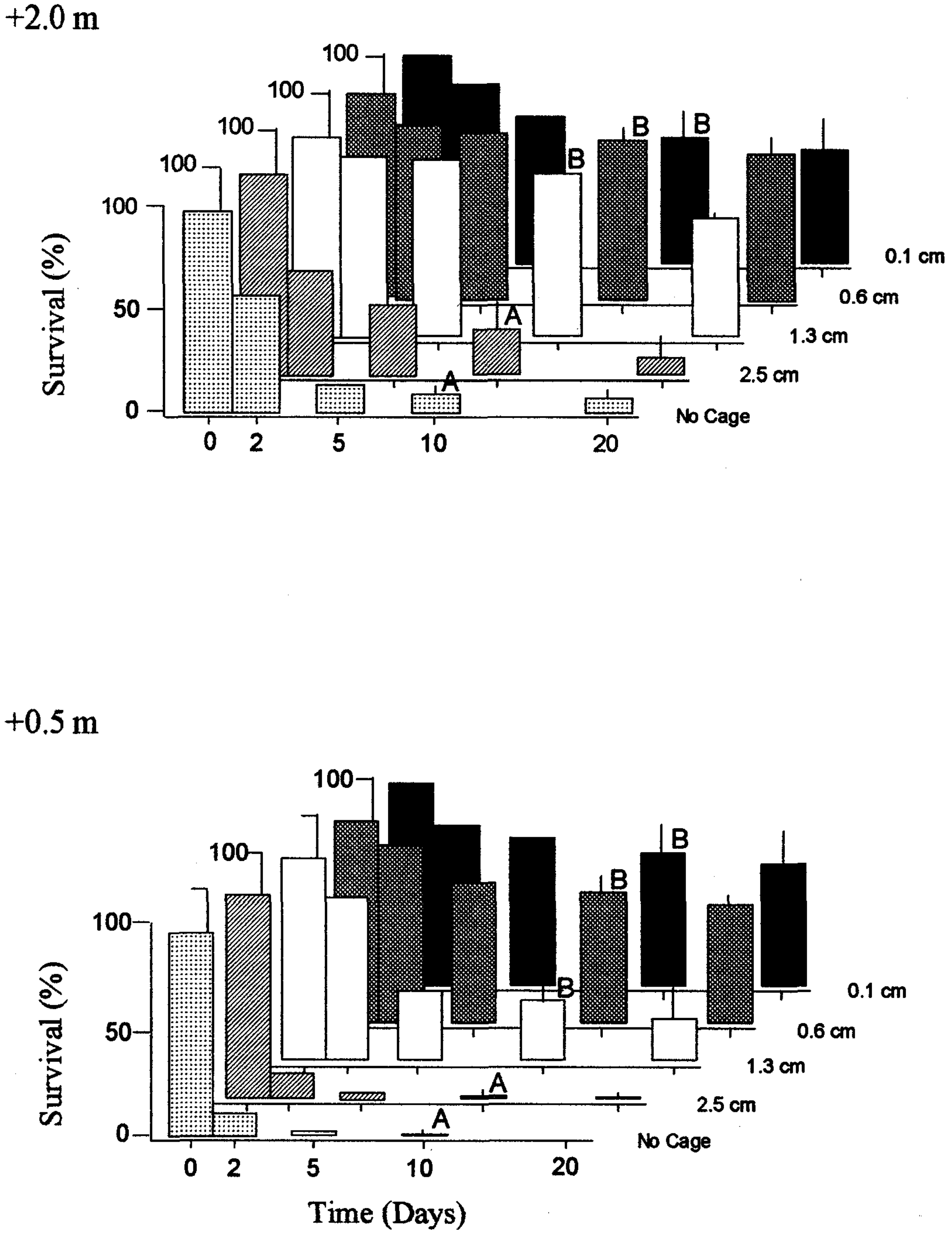


Figure III - 4. Exclusion. Survival when animal access was restricted based on size, by shore level. Mesh opening size or lack of protection (No Cage) indicated at right. Means are shown, ± 1 S.E. (day 10, 20). Letters indicate means that differ significantly for each shore level.

Table III - II. Exclusion Statistics. Results from an ANOVA test on the effect of mesh opening size on animal impact. Data are the percent of *Ascophyllum* germlings remaining after 10 days, rank transformed. Dunnett's test was used to compare means for the different opening sizes against a control (No Cage).

Exclusion

Source	df	SS	MS	F	p-value
Shore Level	1	513.78	513.78	15.35	0.001**
Opening Size	5	2300.00	460.00	13.74	0.0001***
SL x OS	5	265.89	53.18	1.59	0.201
Error	24	803.33	33.47		
Total	35	3883.00			

Opening Size	Description	T-value *versus* No Cage	p-value
0.1 cm	Total Exclusion	4.610	0.0001***
0.6 cm	Exclusion > 80 %	4.848	0.0001***
1.3 cm	Exclusion ≈ 50 %	3.815	0.001**
2.5 cm	Exclusion 0 %	0.477	0.657
0.6 cm = Low Top	Exclusion > 80 %	2.464	0.038*
∞ cm = No Cage	Total Access		

Impact differed **significantly** with **opening size** (ANOVA). Opening sizes excluding grazers (< 2.5 cm) resulted in impact that differed significantly from ambient impact (no cage) at both shore levels. Cages with the largest opening size (2.5 cm) did not significantly affect animal impact.

The critical opening size of **1.3 cm** was associated with **significantly** different levels of animal impact. Impact was significantly reduced with a 1.3 cm opening.

Table III - III. Size. Length (L) and weight (FW) of the animals used in the inclusion experiments. Fresh weight (FW) was measured for the initial inclusion period (Day 0 - 2). Dashed lines indicate that germlings were decimated during the previous inclusion period.

			Days			
			0 – 2	2 – 4	4 – 6	6 – 8
Species	Replicate	FW(gm)	------------Length (cm)----------			
			Adult Experiment			
Littorina saxatilis	1	0.2	0.7	0.7	0.7	0.7
	2	0.3	0.7	0.7	0.7	0.7
	3	0.2	0.7	0.7	0.7	0.8
L. obtusata	1	1.1	1.2	1.2	1.2	1.2
	2	1.1	1.2	1.1	1.2	1.3
	3	1.2	1.2	1.2	1.2	1.2
L. littorea	1	3.5	1.8	2.0	1.9	----
	2	3.7	1.8	1.9	1.9	----
	3	3.2	1.9	1.9	1.9	2.0
Acmaea testudinalis	1	0.5	1.1	1.2	1.2	1.2
	2	0.5	1.0	0.9	0.9	1.4
	3	0.6	1.1	1.2	1.2	1.4
			Small Animal Experiment			
L. obtusata	1	0.2	0.4	0.4	0.4	0.5
	2	0.3	0.4	0.4	0.4	0.5
	3	0.2	0.4	0.4	0.4	0.6
L. littorea	1	0.5	0.5	0.5	0.5	0.5
	2	0.5	0.4	0.5	0.5	0.6
	3	0.6	0.5	0.5	0.5	0.6
L. littorea, adult	1	4.5	2.0	2.0	2.0	2.1
	2	4.5	2.0	2.0	2.0	2.0
	3	4.7	2.0	2.0	2.0	----

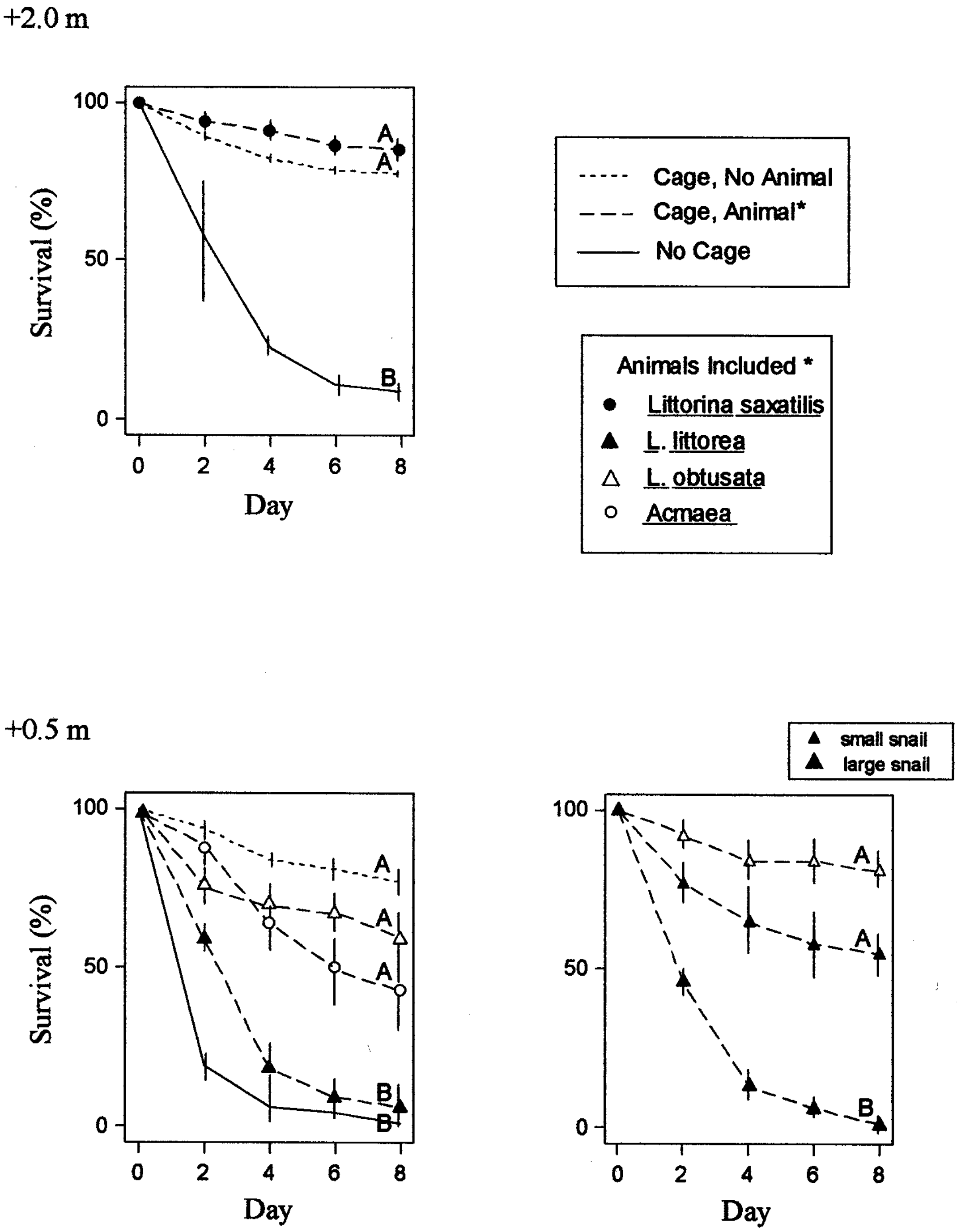


Figure III - 5. Inclusion. Impact of each species compared with no impact (no animal in the cage) and ambient impact (no cage). *Littorina saxatilis* was tested at +2 m, the others at +0.5 m. Impact by small *L. littorea*, *L. obtusata* and adult *L. littorea* was tested (lower right). Means ± 1 S.E. are shown. Letters indicate means that differ significantly.

Table III - IV. Adult Inclusion Statistics. Results from ANOVA tests on the effect of inclusion treatments, and the impact of adults of each species. Data are the percent of *Ascophyllum* germlings remaining after 6 days, arcsine transformed. Day 6 represented the last full set of observations as some tiles had been cleared of germlings. Cages were of standard mesh (0.6 cm). Dunnett's test was used to compare species means against a control.

Inclusion at +2.0 m

Source	df	SS	MS	F	p-value
Treatment	2	4714.1	2357.0	40.0	0.0001***
Error	6	353.5	58.9		
Total	8	5067.6			

Treatment	Description	T-value *versus* No Animal	p-value
1	No Animal in cage		
2	*Littorina saxatilis* included in cage	0.912	0.590
3	No Cage		

Inclusions at +0.5 m

Source	df	SS	MS	F	p-value
Treatment	4	8549.3	2137.3	17.0	0.0001***
Error	10	1257.3	215.7		
Total	14	9806.6			

Treatment	Description	T-value *versus* No Animal	p-value
1	No Animal in cage		
2	*Littorina obtusata* included in cage	-0.951	0.750
3	*L. littorea* included in cage	-6.153	0.000***
4	*Acmaea testudinalis* included in cage	-2.150	0.164
5	No Cage	-6.190	0.0001***

Note: One further comparison indicated that impact associated with *L. littorea* did not differ significantly from ambient impact (No Cage). The T-value was 0.4252 with a p-value of 0.978.

Impact associated with *Littorina littorea* differed significantly from no impact. Impact of *L. littorea* was not significantly different from ambient impact (No Cage).

Table III - V. Small Animal Inclusion Statistics. Results from ANOVA tests on the impact of small snails (a) and the effect of mesh size on impact of adult *Littorina littorea* (b). Data are the percentage of *Ascophyllum* germlings remaining after 6 days, arcsine transformed. Dunnett's test was used to compare species means against a control.

a.

Small Animal Inclusion at +0.5 m

Source	df	SS	MS	F	p-value
Treatment	4	10096.5	2524.1	19.4	0.0001***
Error	10	1300.0	130.0		
Total	14	11396.5			

Treatment	Description	T-value *versus* No Animal	p-value
1	No Animal in cage		
2	*Littorina obtusata* juvenile in cage	0.484	0.965
3	*L. littorea* juvenile in cage	- 1.541	0.393
4	*L. littorea* adult in cage	- 5.648	0.001***
5	No Cage	- 6.087	0.0001***

Impact by small snails of either species did not differ significantly from no impact.

b.

Mesh Size Effects

Impact by adult *L. littorea*, in a fine-meshed cage, was significant. A comparison of the results for adult *L. littorea* indicated that mesh size (0.6 cm *vs.* 0.1 cm) did not affect impact significantly (1-Way ANOVA, p = 0.93).

Table III – VI. Ranks. Impact compared with size (length, weight). Impact values for each species have been corrected by subtracting average germling loss when no animal was included. Impact is after 8 days of inclusion.

Rank Comparison

Impact (Least to Greatest)	Loss/8 days	Length (cm)	Weight (gm)
Littorina saxatilis	0 %	0.7	0.2
L. obtusata, juvenile	1 %	0.4	0.2
L. obtusata, adult	18 %	1.2	1.1
Acmaea testudinalis	24 %	1.1	0.5
L. littorea, juvenile	25 %	0.5	0.5
L. littorea, adult	75 %	1.9	3.5
	80%	2.0	4.5

Table III - VII. Size Predictors. Results from a regression of body weight (animal only) on length. Data are from samples of 31 snails for each species.

Regression Equation	$r^2_{adj.}$	$F_{reg.}$	p-value
Littorina obtusata			
$\mathrm{Log}_{10}\mathrm{BW} = -9.6 + 2.94\,(\mathrm{Log}_{10}\mathrm{L})$	97	1005.3	<0.03*
Littorina littorea			
$\mathrm{Log}_{10}\mathrm{BW} = -11.0 + 3.63\,(\mathrm{Log}_{10}\mathrm{L})$	96	776.6	<0.05*

CHAPTER IV

SAFE SIZE AND A TEMPORAL REFUGE

Introduction

Printz (1956a) surmised that 'special conditions' are required for establishment of *Ascophyllum nodosum* (L.) Le Jolis, and that they occur very infrequently. Based on the limited numbers of juveniles, recruitment of *Ascophyllum* is highly segregated over time (Printz 1956a, Boney 1965, Vadas and Wright 1986). Early survival is the bottleneck. Recruits are dislodged by waves and water motion (Vadas and Wright 1986, Vadas *et al.* 1990), sweeping fronds (Vadas *et al.* 1992), and crawling snails (Watson and Norton 1985, Chapter III). Germlings not dislodged, most likely those under *Ascophyllum* canopy (Vadas and Wright 1986, Vadas *et al.* 1992), are removed by grazing animals (Miller and Vadas 1984, Ch. II). Effective refuges, where germlings escape dislodgement and removal, might be the immediate product of 'special conditions.' Spatially, effective refuges are patches of surface sheltered from waves and sweeping fronds, as well as escaping animal impact. Temporally, winter conditions may reduce the impact of animals in the short term while severe weather cycles or multi-year predator abundance cycles could reduce animal impact over the long term.

Recruitment occurs most regularly high in the *Ascophyllum* zone (Ch. I, II). There, the canopy of adult plants provides shelter from waves and the close proximity of plants limits frond contact with the surface (Jenkins, Hawkins and Norton 1999).

Animals restrict the range of recruitment down the shore (Ch. II). The presence of juveniles attests to the fact that surfaces on the upper shore, at least sporadically, elude animal impact.

Animal impact is determined by the abundance, size and activity of the animals. Over the long term, variation in the factors that regulate animal impact (Southward 1956, Lewis and Bowman 1975, Hawkins and Hartnoll 1983), regulate recruitment of *Ascophyllum*. In the western Atlantic, densities of the primary removal agent, *Littorina littorea* (L.), are considerable. Even on the upper shore, where snails are least abundant, animals at summer densities remove all recruits within months (Ch. I, II). Potential refuges high in the zone become effective refuges only with a reduction in impact.

Winter affords a seasonal lapse in animal impact. Grazing and crawling of *Littorina littorea* decrease dramatically with the onset of colder temperatures and icy conditions (Newell 1958 a, b). Snails migrate down the shore as winter conditions become severe (Batchelder 1915, Gendron 1977). In New England, shifts to the low shore occur between November and March (Bertness *et al.* 1983, Bertness 1984). The prominence of a dark algal band high on the shore during the same period evinces a seasonal lapse in grazing (Menge 1975).

Fucus achieves some protection from grazing removal (cf. Jones 1946) with a size of 3 to 5 cm in length; a 'safe size' (Menge 1975, Lubchenco 1983). Assuming the same safe size for *Ascophyllum*, the time required could be 1 - 2 years for plants on the low shore and over a decade for those on the upper shore (Ch. II, IV).

The present study focused on a temporal refuge on the upper shore afforded by winter, and the effectiveness of a safe size ≥ 3 cm for *Ascophyllum*. Three gastropods

[*Littorina littorea* (L.), *L. obtusata* (L.), and *Acmaea testudinalis* (Müller)] were shown to remove *Ascophyllum* germlings in a previous study (Ch. III). Their numbers and sizes were assessed at various times, to evaluate abundance patterns over the year. A decline in the abundance of grazing animals on the upper shore is expected due to a downshore migration during winter. *Littorina littorea* is the primary removal agent (Ch. III) and larger *L. littorea* are particularly effective. Therefore, the abundance of *L. littorea*, particularly those ≥1.4 cm in length, was evaluated. Winter impact was assessed directly by placing germlings into the field with and without cages. Winter data were analyzed together with summer data from earlier experiments (Ch. II) to compare impact in winter *vs.* summer.

Materials and Methods

Abundance of grazing animals over the year was tracked using quadrat samples. Samples were taken at 4 shore levels (+2.0, +1.5 +1.0, +0.5 m above Mean Low Water) during most months, but were restricted to +2.0 and +0.5 m in June, July and February. Generally, 20 samples, $(25\ \text{cm})^2$ or $1/16^{\text{th}}\ \text{m}^2$ in area, were taken at each shore level. Sampling included three adjacent rock ledges at the Ft. Stark site, and the number of samples on any one ledge was a matter of convenience. The quadrat was tossed blindly at the appropriate shore level, and the animals within it were counted by species.

Counts/quadrat were used to generate mean abundance values for the 'whole shore' (data from the 2 or 4 shore levels sampled) and the upper shore by month. Count data for the 'whole shore' could not be successfully transformed to meet the assumptions of normality and homogeneity of variance so the effect of season on abundance was analyzed non-parametrically. The effect of season (summer *vs.* winter) on abundance at +2.0 m was analyzed using a 1-Way ANOVA.

In two summer months (June and July) and three winter months (November, January and February), the lengths of the animals were measured. Size data were used to evaluate a seasonal decline in the larger *Littorina littorea* high in the zone. Counts (number of larger snails/quadrat) were submitted to a 1-Way ANOVA to test the effect of season on the abundance of larger animals.

Animal impact in the winter was assessed in the field. Gametes rinsed from fertile fronds the preceding spring, when *Ascophyllum* was reproductive, were mixed and poured over tiles. The germlings were maintained in culture until the onset of experiments in February 1984. Germling counts were made with reference to an overlain grid, in the 20 squares least likely to be contacted during handling. Germlings were 9 months old when placed into the field. Tiles (= germling populations) were assigned randomly to treatment, with 3 replicates. The factors included shore level (+2, and +0.5 m), frond cover (present or absent), and access to grazing animals (none = cage, full = no cage, and intermediate = partial cage with five sides). Germling counts were taken before deployment and after 2, 8 and 16 days in the field. The percentage of germlings remaining provided an index of animal impact.

The caging scheme for winter experiments differed from the summer scheme as it included an additional treatment, the five-sided cage. The partial cage was an attempt to separate the confounded effects of water motion and animal impact. Water flow through full cages and five-sided cages (Figure IV – 1) would be similar. The cages were placed over the tiles with 2 cm clearance between the sides and the rock surface. Animals would gain access to germlings in the partial cages more slowly than tiles not caged. Thus, impact should be intermediate.

On three tiles from previous experiments, 2 and 3 year old *Ascophyllum* plants had attained lengths of 3 - 4 cm. The tiles had been maintained in the field in cages and supported a mixed biota. In order to determine whether a size of ≥ 3 cm confers safety from animal removal for *Ascophyllum*, the tiles (germling populations) were removed from their cages and placed in open areas on the low shore, where animals were abundant. The experiment took place in June, 1984.

Results

Abundance of grazing animals varied over the year, with a summer peak (Figure IV - 2 a). Numbers of grazers, and of *Littorina littorea* alone, peaked in June, declined in the fall and winter, and increased again in spring. A Kruskal-Wallis Test on the means for the eight months showed that differences between months were highly significant (H = 40.78, df = 8, p = 0.0001***). The mean for April 1983, not included in the analysis, and April 1984 did not differ significantly (Mann-Whitney Test, W = 5789.5, p = 530), suggesting a repeat of the observed spring increase.

Abundance of *Littorina littorea*, and of grazers as well, increased down the shore (Figure IV – 2 b). However, in November and March numbers at +1.5 m exceeded those at +2.0 m. Densities increased through the zone and were 5 to 10 times greater at +0.5 m.

Differences in the abundance of animals in the winter and summer were evaluated using the quadrat data for two summer months and three winter months (Fig. IV - 2 a).

Data were from the uppermost and lowermost shore levels, as summer data were only from those 2 shore levels (Fig. IV - 2 b).

Grazer abundance was reduced in winter, for the whole shore (estimated by the uppermost and lowermost shore levels) and the uppermost shore level alone (Figure IV – 2). Statistical results established a significant difference with season for the whole shore, and the upper shore (Table IV – I).

While abundance of *Littorina littorea* varied over the year and down the shore, size showed less change and no consistent pattern (Table IV - II). Mean length data indicated that large snails were present at all shore levels and during all months. Mean length did not increase in a regular way with shore level although the largest animals tended to occur lower on the shore.

Snails ≥1.4 cm in length (larger *Littorina littorea*) were present in statistically indistinguishable numbers during winter and summer. Both high and low on the shore, abundance did not differ significantly with season (Table IV - III). High in the zone, larger snails actually comprised a greater proportion of the *L. littorea* population in winter **(80%)** than in summer (40%).

Larger snails were especially abundant low on the shore (+1.0, +0.5 m) in April and at +1 m in August. April could represent an upshore shift with spring conditions and August a movement down the shore. Sampling was inadequate to resolve mid-shore movements or shifts between the intertidal and subtidal.

Caging experiments demonstrated that animal impact was important in the winter (Figure IV - 3). Germlings were lost in a matter of weeks, rather than days as in the summer. Impact was least with a full cage, moderate with a partial cage, and greatest without a cage. Differences in the loss rate, or intensity of impact, are apparent comparing curves from the upper and lower shore and winter *versus* summer.

Statistically, both shore level and caging treatment were significant factors affecting animal impact (Table IV - IV). The shore level x caging treatment interaction just escaped significance, echoing different impact in the open for the no cage treatments (Figure IV - 3). Five-sided cages mediated impact (Treatment Comparison) as the mean differed significantly from both 'No Cage' and 'Full Cage' (Table IV - IV).

Animal impact in the summer and winter differed in intensity (loss rate), but not in general pattern (Figure IV - 4). In both seasons, impact was greater low on the shore. Impact was more intense in the summer, however, season was not a significant factor (Table IV - V). Overall, frond cover was important; it was significant in its interaction with shore level (both summers included) and as an independent factor (summer 1984 data only). Without protection, germlings were lost from frond-covered and open areas alike **except** for the high shore in winter (Fig. IV – 4). With protection, losses were reduced **except** for open areas, high shore. Tukey pairwise tests indicated that +2.0 m, open areas were statistically distinct from the other groups (Table IV - V); impact in high, open areas was reduced during the winter and increased during the summer.

Discussion

Numbers of grazing animals, also *Littorina littorea* alone, were significantly reduced in winter as compared to summer (Fig. IV - 2, Table IV - I). A steep decline in the abundance of grazers occurred in the late summer and fall. Minimum densities were recorded in September. A downshore winter migration would be expected later; during

October or November. Instead, numbers declined in the fall and were reduced through the winter. The reduction spanned fall and winter, with the first sign of increased abundance in February. The pattern suggests that sampling should have included all months, with special interest in August.

Abundance on the low shore increased ≈ 90 animals/m^2 between September and November (Fig. IV – 1 b). Numbers on the whole shore and high in the zone decreased. Shifts could have been into the subtidal.

Evidence for a lapse in impact high in the zone was lacking. *Littorina littorea* ≥1.4 cm in length are most effective at germling removal (Ch. III). Abundance of snails on the high shore was reduced during the winter although the number of larger snails was not significantly different (Table IV – III). They were present throughout the year and mean lengths reflected their presence, being ≥1.0 cm in all cases. Larger snails merely made up a greater proportion of the grazing population during the winter.

The extent of a winter migration depends upon severity of the winter and size of the animals (Gendron 1977). In mild winters, migration can be wholly within the zone (Bertness 1984). The winter of 1983-4 was not severe. Sampling to accurately detect a downshore migration, involving mid-shore shifts, would be best served using an adequate number of permanent quadrats. *Littorina littorea* densities can vary greatly over a short distance and between rock outcrops. Random sampling of different ledges (populations isolated by gravel) may have missed subtle shifts.

Animal impact was evident in the winter. Caging experiments demonstrated that animals removed *Ascophyllum* germlings in both the summer and winter. Impact was less intense in the winter. Patterns of loss were similar for the two seasons, but proceeded at different rates.

Conditions in high, open areas in the winter were associated with a significant reduction in impact (Figure IV - 3). Open areas high in the zone are physically harsh, subjected to long exposure to freezing temperatures in the winter. Animals feed when submerged and continue as long as surfaces stay moist (Norton *et al.* 1990) and do not freeze (Newell 1958a, Newell *et al.* 1971). Surfaces in the open freeze first while those under canopy retain warmth and moisture (Leonard unpubl. in Bertness *et al.* 1999). Animal impact was reduced in the open and may have been extended under frond cover.

Germlings were lost from caged treatments high in the zone in the summer. Loss was not due to animal impact. Rather, it was an artifact of timing and the data used in the analysis. Animal impact in the summer was swift, detected within days even on the upper shore. Impact in winter was slower, taking weeks instead of days. Data used in the analysis were for day 8, a compromise. By that time, germlings high on the shore and in the open had bleached and most were lost within two weeks. Nevertheless, comparison of high, open areas in the two seasons brings out a critical contrast; rigorous physical conditions reduce survival in the summer while enhancing chances for continued survival through the winter since the harsh conditions reduce animal impact as well.

Winter experiments demonstrated the usefulness of a five-sided cage in separating the effects of water motion and animal impact. Full and partial cages had tops and sides so water flow across the tiles was similar. Differences in germling retention were, therefore, due to animals. Animal access was effectively mediated by the partial exclusion of the sides.

The caging experiments showed that animal impact was not as intense in the winter. Animal activities are responsive to temperature and grazing is most intense in the spring and summer when conditions are favorable (Norton *et al.* 1990). Feeding rates at 5° C are half those at 15° C (Barker and Chapman 1990). Migration of animals down the shore in winter may afford a lapse in animal impact high in the zone. Conversely, a massive movement of snails into the zone in spring as foraging aggregations (Vadas 1992 in Vadas *et al.* 1992) exacerbates impact at a time when animal activity is favored.

The safe size test indicated that plants 3 cm in length are not safe from animals. Tiles had to be retrieved after only 2 days in the field due to an impending storm. In that 2-day period, one of the tiles was cleared of plants and the other 2 remained unscathed. The results show the variability of animal impact and its intensity low on the shore in the summer.

The tiles used in the safe size test supported a mixed biota of *Ulva, Fucus*, micro-organisms, and *Ascophyllum* juveniles. *Ascophyllum* may have been removed or consumed as other algae were grazed and might have been avoided as a pure germling 'lawn' (Watson and Norton 1985). Petraitis (1983) found that a well-developed community including *Fucus* plants was cleared when the cage was removed. Safe size may be conditional; depending upon the associated biota, density of consumers, and the proximity of preferred foods.

Association can confer safety or increase risk. Grazing animals are loyal to a particular shore level (Smith and Newell 1955, Newell 1958a, b) and forage within a short range of 1.5 – 2 m (Norton *et al.* 1990). Movements are random (Petraitis 1982), although snails graze intensively where they encounter preferred foods and limit efforts where foods are less desirable (*i.e.*, Norton *et al.* 1990). Barnacle covered surfaces discourage grazing (Menge 1976, Lubchenco 1983). Some patches of surface are, in fact, consistently missed (Petriatis 1982, 1983). Spatial refuges may be defined by the associated biota. Where snails are not abundant, patches of surface may evade impact. Potential safe sites exist because of limited foraging range, shore level loyalty, and food cues.

Peckol *et al.* (1988) suggest that snail densities in excess of 100/m^2 limit recruitment of *Ascophyllum*. Cervin and Åberg (1997) determined experimentally that the equivalent of 240 snails/m^2 had a negative effect on germling survival. In the western Atlantic, densities > 200/m^2 are common on the mid and lower shore. Elevated snail densities result in more intensive and less selective foraging, jeopardizing the relative safety afforded by size. Potential safe sites may only become realized safe sites when animal densities are radically reduced.

Successive years with conditions resulting in lower fecundity, poor larval recruitment, or high snail mortality are implied for successful plant establishment on the upper shore. *Ascophyllum* develops slowly, requiring a number of years for a plant to reach a size conferring safety from animal removal. Moore (1937) and Dexter (1947) have documented fluctuation in the size of *Littorina littorea* populations reflecting extreme weather cycles.

Boney (1965) suggests that major recruitment episodes for *Ascophyllum* might occur every 10 - 15 years. His estimate presumed an average lifespan of 20 years (see Baardseth 1970). Åberg (1992a, b) determined that lifespans may be half a century or more. Thus, recruitment episodes may be more segregated over time. The lifespan of hemlock is hundreds of years and cyclical fluctuations in herbivore densities and recruitment peaks lag by several decades (see Hough and Forbes 1943, Whitney 1984). Longevity of *Ascophyllum* suggests that comparison with late successional tree species such as hemlock may be apt.

A tight ecological balance between *Fucus* and *Patella* has been detailed for European shores. At high limpet densities, grazing offsets algal recruitment. At low limpet densities, *Fucus* becomes established in large numbers and crowded conditions limit plant growth. The lifespans of the *Fucus* species involved are 2 to several years (Knight and Parke 1950, Boney 1966). With such a short lifespan, several successive years of low limpet recruitment can trigger a fucoid-limpet cycle (Lewis and Bowman 1975). Average times between cycles approximate 10 - 12 years (cf. Southward 1956). Cycling times for *Ascophyllum* could be many times longer.

Conditions resulting in plant establishment for *Ascophyllum* occur episodically (Printz 1956a, Boney 1965, Vadas and Wright 1984,Vadas *et al.* 1990) and by chance. Regular investment of energy in sexual reproduction is advantageous when conditions favoring recruitment and subsequent plant establishment are unpredictable over time. Notably, recruitment and plant establishment are far-removed temporally and imply a protracted favorable period. The apparent enigma of regular, costly investment in sexual reproduction and limited plant establishment may resolve to the stochastic nature of spatial and temporal refuges.

In most decades, few new plants become established. Establishment is restricted to the upper shore. Refuges, spatial and temporal, are critical. In a reproductive season when conditions are favorable, or 'special' (Printz 1956a), potential refuges become realized refuges. When conditions permit, the range of recruitment would extend further downshore. The vision adds a dynamic aspect to plant establishment patterns over the extreme long term.

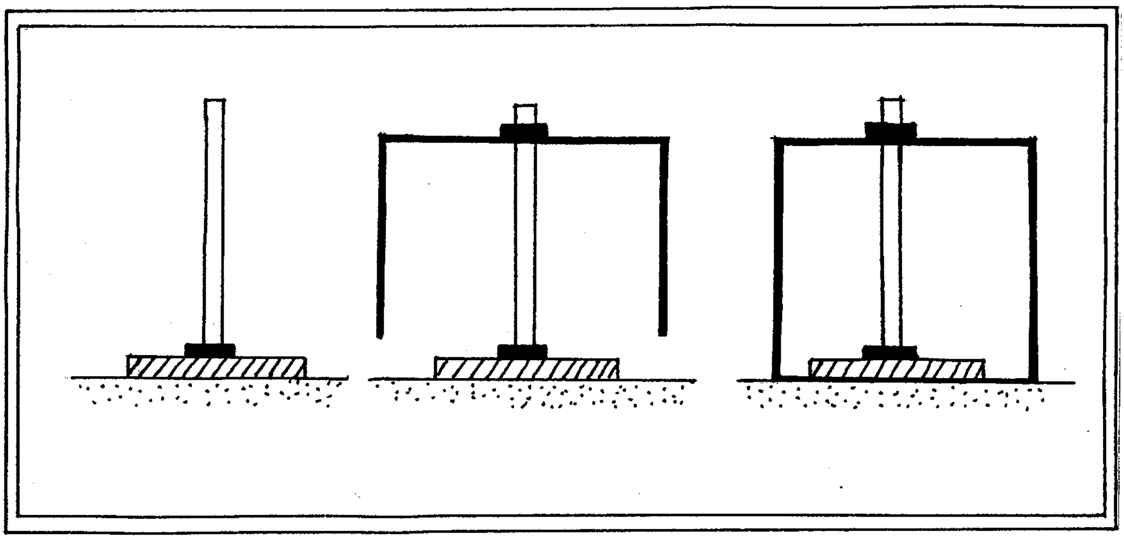


Figure IV - 1. Caging Treatments. A tile not caged, a tile within a partial cage (five-sided, or bottomless), and a tile within a full cage are shown. All treatments are viewed from the side.

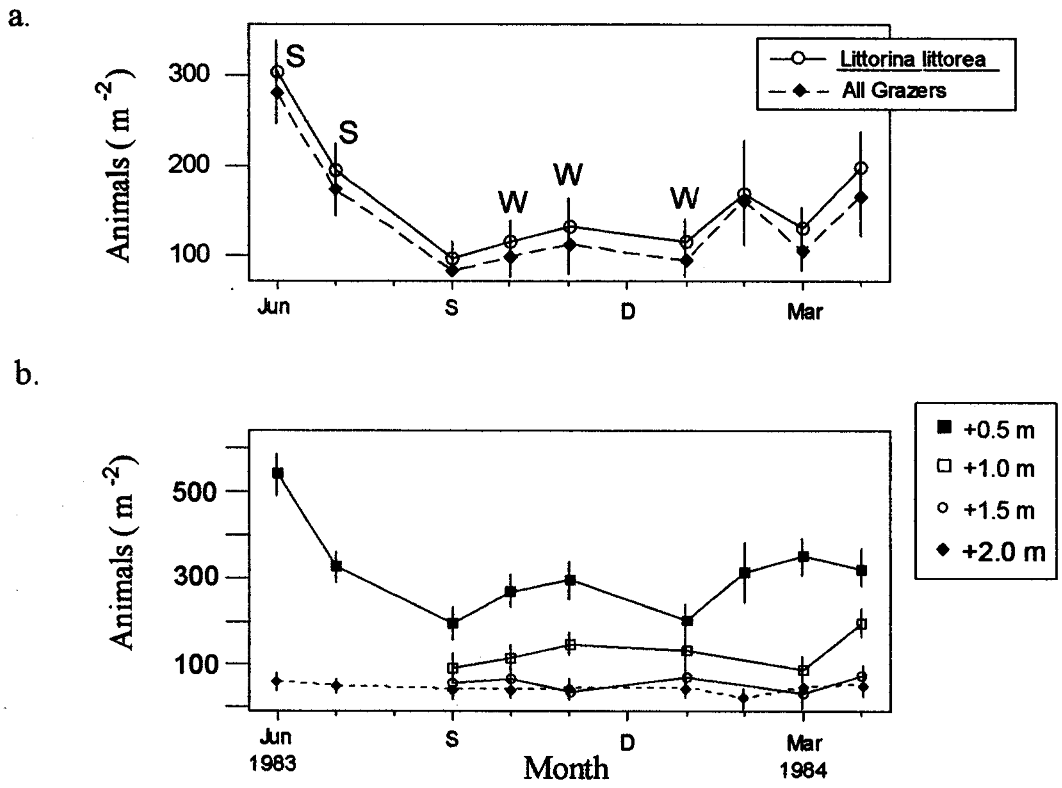


Figure IV - 2. Abundance. Grazing animals (m^2) over the year (a) and by shore level (b). Data are from quadrat samples taken at each shore level. Means ± 1 S.E. are shown. Letters indicate means that differ significantly.

Table IV – I. Abundance Statistics. Results from statistical analyses on the effect of season (winter, summer) on the abundance of grazing animals for the 'whole shore' (estimated by both shore levels) (a) and for +2.0 m (b). Data are the number of animals/quadrat with 120 quadrats (winter) and 172 quadrats (summer). For the +2.0 m analysis, data from 60 quadrats (winter) and 95 quadrats (summer) were included. b) Data were transformed as $\log_{10}(\text{count} + 1)$.

a.

Both Shore Levels

Results from a Mann-Whitney test indicated that abundance of grazing animals in winter was significantly different from the summer (W = 27976.5, p = 0.0001***).

b.

+2.0 m

Source	df	SS	MS	F	p-value
Season	1	0.8340	0.8340	8.38	0.004**
Error	154	15.3221	0.0995		
Total	155				

Season had a **significant** effect on the abundance of grazing animals on the shore. Season had a significant effect also on the abundance of *Littorina littorea* alone at +2.0 m (p = 0.029*).

Table IV - II. Size. Length of *Littorina littorea* (Mean ± 1 standard deviation) (a) and the abundance (number/m^2) of snails ≥ 1.4 cm in length by shore level and through the year (b).

a.

Length

	1983		1984			
	July	November	January	March	April	August
+2.0	1.2 ± 0.4	1.5 ± 0.4	1.1 ± 0.5	1.0 ± 0.6	1.2 ± 0.1	1.7 ± 0.2
+1.5		1.6 ± 0.5	1.0 ± 0.6	1.5 ± 0.1	1.4 ± 0.1	1.8 ± 0.2
+1.0		1.5 ± 0.5	1.1 ± 0.6	1.4 ± 0.1	1.6 ± 0.1	1.5 ± 0.3
+0.5	1.2 ± 0.2	1.6 ± 0.5	1.5 ± 0.5	1.3 ± 0.1	1.6 ± 0.1	1.7 ± 0.3

b.

Abundance of Larger Snails

	1983		1984			
	July	November	January	March	April	August
+2.0	12 ± 11	15 ± 19	9 ± 6	6 ± 13	13 ± 24	5 ± 12
+1.5		16 ± 12	11 ± 18	12 ± 10	30 ± 25	14 ± 21
+1.0		93 ± 100	47 ± 57	38 ± 38	123 ± 115	153 ± 134
+0.5	109 ± 71	200 ± 194	213 ± 258	196 ± 164	309 ± 205	189 ± 102

Table IV - III. Larger Snail Statistics. Results from statistical analyses of the effect of season on the abundance of larger *Littorina littorea*, by shore level. Data are from July (summer) and November and January (winter). Data for the +2.0 m shore level were transformed as $\log_{10}$ (count + 1) and used without transformation for the +0.5 m shore level analysis.

+2.0 m

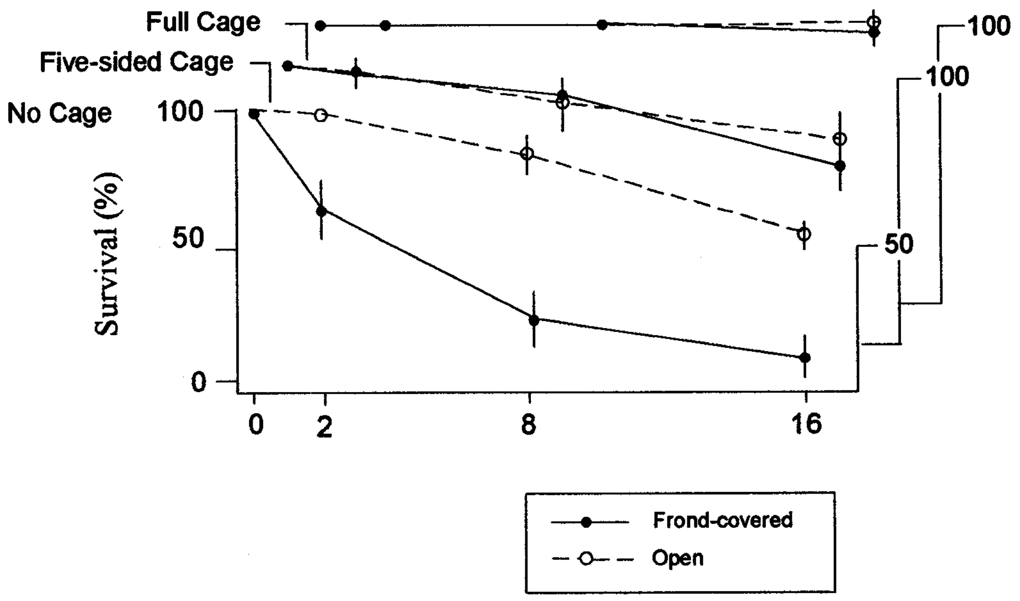
Source	df	SS	MS	F	p-value
Season	1	0.0127	0.0127	0.27	0.604
Error	54	2.5233	0.0467		
Total	55	2.536			

Season did not have a significant effect on the abundance of larger *Littorina littorea* high in the zone.

+0.5 m

Results from a Mann-Whitney U test (W = 416.5, p = 0.478) indicated that season did not have a significant effect on the abundance of larger *L. littorea* low on the shore

+2.0 m



+0.5 m

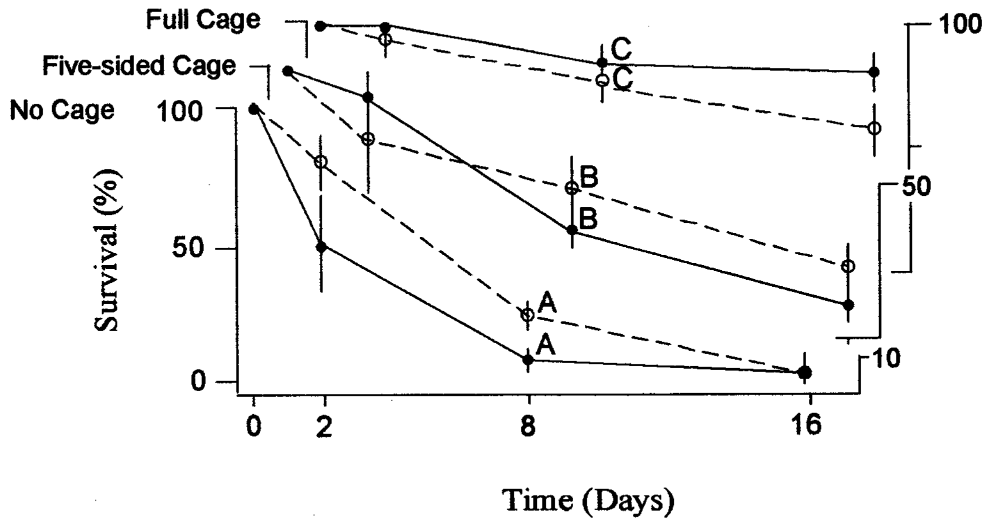


Figure IV - 3. Winter Impact. Survival over time with the protection of a full or incomplete (five-sided) cage *vs.* no cage, by shore level. Means ± 1 S.E. are shown. Letters indicate means that differ significantly.

Table IV - IV. Winter Statistics. Results from an ANOVA test on the effects of shore level, frond cover and caging treatment on animal impact in the winter. Data are the percentage of germlings surviving at day 8, rank transformed. Dunnett's tests were used to analyze differences associated with caging treatments.

Animal Impact in Winter

Source	df	SS	MS	F	p-value
Shore Level	1	1013.36	1013.36	26.26	0.0001***
Frond Cover	1	128.44	128.44	3.33	0.081
Treatment	2	1357.79	678.90	17.60	0.0001***
SL x FC	1	34.03	34.03	0.88	0.357
FC x Ttt	2	242.51	121.26	3.14	0.061
SL x Ttt	2	68.43	34.22	0.89	0.425
SL x FC x Ttt	2	71.43	35.72	0.93	0.410
Error	24	926.00	38.58		
Total	35	3842.00			

Caging Treatment	T-Value *vs.* No Cage	p-value
Five-sided Cage	2.90	0.014*
Full Cage	5.95	0.0001***
	T-Value *vs.* Full Cage	
Five-sided	3.04	0.017*

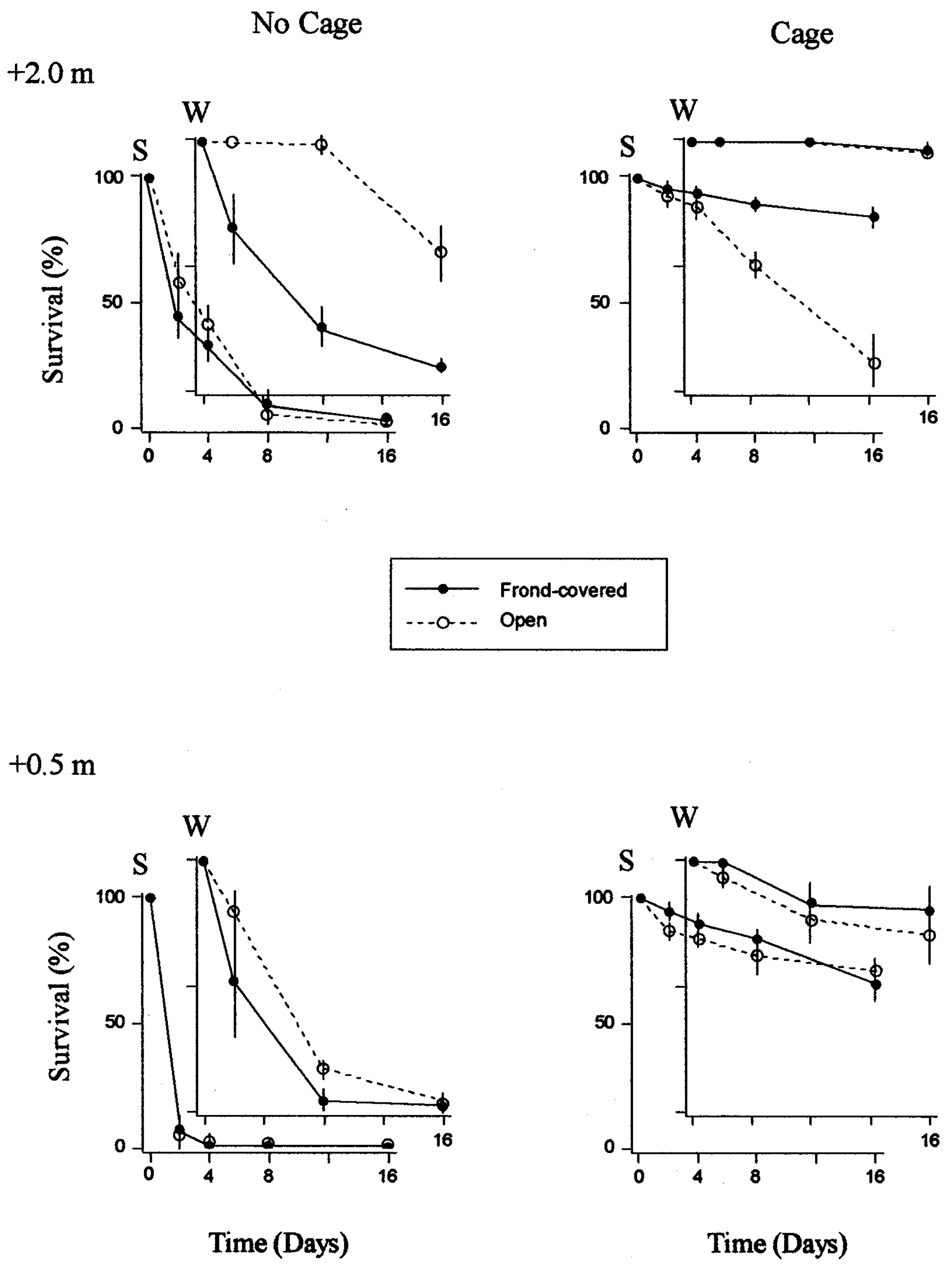


Figure IV - 4. Seasonal Impact. Animal impact in summer (S) and winter (W) by environment (shore level x frond cover groups). Means ± 1 S.E. are shown. Data for day 8 (as the difference in survival with a cage) were used in the analysis.

Table IV - V. Seasonal Statistics. Results from an ANOVA test on the effects of season, shore level and frond cover on animal impact, 1983-4. Data are the difference in survival (survival, cage – survival, no cage) on day 8, arcsine transformed.

Animal Impact Winter *vs.* Summer

Source	df	SS	MS	F	p-value
Shore Level	1	0.28517	0.28517	3.65	0.074
Frond Cover	1	0.99238	0.99238	12.70	0.003**
Season	1	0.22988	0.22988	2.94	0.106
SL x FC	1	0.12954	0.12954	1.66	0.216
FC x S	1	0.15843	0.15843	2.03	0.174
SL x FC x S	1	0.01766	0.01766	0.58	0.456
Error	16	1.24985	0.07812	0.23	0.641
Total	23	3.06291			

Frond cover had a **significant** effect on animal impact in both summer and winter.

CHAPTER V

CANOPY REGULATES RECRUITMENT OF *ASCOPHYLLUM*

Introduction

Ascophyllum nodosum (L.) Le Jolis is a climax species (Lewis 1964, Dring 1982, Archambault and Bourget 1983) and its extreme longevity is rare among seaweeds (Boney 1966). Features critical to the success of climax trees also characterize *Ascophyllum* (Cousens and Hutchings 1983, Cousens 1985 and 1986). Climax species are unique among forest trees (Harper 1977), and many of the same features distinguish *Ascophyllum* from other seaweeds on the shore.

Canopy determines the species composition in understory layers. Seeds of opportunistic flowering plants lie dormant in deep shade, accumulating in a seed bank. Shade-tolerant species comprise the understory vegetation. Seedlings and saplings of climax species are among them.

In the sheltered understory on the shore, moisture is retained and temperatures are moderated (Bertness *et al.* 1999). Canopy is a buffer against the effects of water motion and ice. When weather is extreme, storm surge can rip away fronds, tear out whole plants and propel objects (ice chunks, rocks) against the rocks, clearing surfaces of attached organisms (Dayton 1971). The understory can be a haven from physically rigorous conditions for those organisms adapted to the deep shade and tolerant of enhanced siltation (see Chapter II).

Reproductive success of climax trees depends upon their canopy, which creates and maintains an environment favorable to self-replacement (*i.e.* Marks 1974). Several key features must be in place: a shaded understory of long duration, adaptation of the juveniles to long term survival in dense shade (Grime 1979), shade sufficient to put other species at a selective disadvantage in the understory, retention of vigor, and a juvenile bank capable of regenerating lost cover in reduced time.

Ascophyllum canopy creates a shaded understory of considerable permanence. Plants provide extensive cover, continuous on the upper shore, and stable habitat that is an integral part of the shore community (*i.e.*, Lewis 1964). Plants live decades, with the potential to live over a century (Åberg 1992a, b). Thus, the shaded understory is an environment of long duration.

Beneath the canopy, light is limited. *Ascophyllum* juveniles are adapted for prolonged survival in deep shade, and are extremely shade-tolerant (Dring 1982). Germlings can survive 90 days in total darkness (Sheader and Moss 1975). Light levels beneath the canopy are 2 - 15 W/m^2, and compensating irradiances for *Ascophyllum* germlings are only 3 - 4 W/m^2 (Schonbeck and Norton 1978). Photosynthesis of newly settled germlings saturates at light levels as low as 6 W/m^2 (Sheader and Moss 1975).

Shade-tolerance is due to compensating changes in pigmentation and an adaptive physiology (Cousens and Hutchings 1983). *Ascophyllum* thalli conditioned to shade (Cousens 1985) or increased time underwater, have enhanced concentrations of chlorophylls a and c (Ramus *et al.* 1977; Peckol *et al.* 1988). Respiratory rates remain low over broad light and temperature regimes (Ramus *et al.*, 1977; Schonbeck and

Norton 1980, Huang and Boney 1983). Low respiratory rates limit growth and suppress vigor (Spurr and Barnes 1964; Grime 1965, 1966, Hutchinson 1967).

Baker (1910) associated slow growth with stress tolerance in fucoid algae. Dring (1982) singled out deep shade as a major stress for *Ascophyllum*. Slow growth and stress tolerance reflect physiological adaptation. Due to these adaptations, *Ascophyllum* juveniles are capable of long-term survival in the understory.

Juveniles of the canopy species are at a selective advantage in the understory, while less shade-tolerant species are at a disadvantage. Schonbeck and Norton (1978) compared the growth of *Ascophyllum* and *Fucus* germlings under low light and found that *Ascophyllum* outperformed *Fucus*. Respiration of *Fucus* also does not readily increase with light and temperature; however, photosynthetic efficiency of *Fucus* is more than double that of *Ascophyllum* (Ramus *et al.* 1977). Enhanced photosynthetic efficiency is adaptive in open conditions.

Juveniles accustomed to suppression, must be capable of faster growth when conditions improve. A 'release from suppression' has been reported for *Ascophyllum*. Burrows (1956) found that understory juveniles grew more rapidly in the open. Hatton (1938) transplanted upper shore juveniles to low shore sites and found that growth increased. The ages and specific histories of these transplants are unknown. Evidence for a release from suppression using plants of known histories will be re-examined here.

A build-up of juveniles in the forest understory ('advanced regeneration') is crucial to self-replacement in terrestrial systems (Marshall 1927, Hough and Forbes 1943). Seed banks are a ready source of recruits, and are important for opportunistic and mid-successional species. Under an intact canopy, seeds remain dormant. In an opening, increased light triggers germination. For climax tree species, seedlings and saplings are important reserves and have a height advantage. Saplings can recover canopy monopolization more quickly than newly germinated seedlings of the same species (Marks 1974). A head start is critical for slow-growing species.

On the shore, *Ascophyllum* juveniles grow under adult canopy near the upper limits of the distribution (Ch. I). They range in size. Field surveys in the present study documented their numbers and sizes.

Ascophyllum grows beneath other fucoid algae (Hatton 1938, Lewis 1964), in a position to ultimately replace them. Field surveys provided comparative data on *Ascophyllum* juveniles growing beneath *Fucus vesiculosus* L. and *F. spiralis* L. canopies.

The five features listed as key characteristics critical to the success of climax tree species are in evidence for *Ascophyllum*; a stable understory of long duration, extreme shade tolerance during development, understory conditions resulting in differential suppression, the capacity for faster growth in an opening, and a juvenile bank. The research cited was undertaken at a variety of geographical locations. A goal of the present study was to evaluate the features at a single location with similar genetic stock.

Canopy may be an effective barrier to settlement for potential competitors. In a forest, dense canopy may reduce the 'rain' of airborne seed from outside areas (*i.e.*, Harper 1977). In similar fashion in intertidal environments, frond cover may hinder settlement (Sousa 1979; Hawkins 1983; Jenkins, Hawkins and Norton 1999; Leonard 2000). *Ascophyllum* canopy has been shown to reduce recruitment of *Fucus*, serving as an effective barrier (Jenkins, Hawkins and Norton 1999). Canopy enhances settlement of *Ascophyllum* (Ch. I). Differential settlement of *Ascophyllum* and *Fucus* beneath

Ascophyllum canopy would favor self-replacement and could be a role that canopy plays in regulating recruitment. Therefore, the effects of ***Ascophyllum* canopy on *Fucus* recruitment** were evaluated.

Some of the material for the present study was derived from related experiments. *Fucus* recruitment and maximum growth of *Fucus* and *Ascophyllum* were assessed on the same tiles (artificial substrata) and during the same surveys described in Chapter II (1983-4). Young *Ascophyllum* plants acclimated to suppressive conditions in the field were available to investigate a release from suppression (Ch. II, 1982-3 set).

A number of hypotheses were tested. Regarding *Fucus*, the hypotheses were that 1) ***Fucus* colonization is reduced under an *Ascophyllum* canopy**, and developing ***Fucus* is at a selective disadvantage in the understory**. To test for a significant growth response given a release from suppression, plants acclimated to conditions high in the zone, where growth was slowest, were transplanted to the low shore sites, where growth was faster (see Ch. II). The hypothesis was that **growth increased with improved conditions** was tested by comparing growth of the transplants with growth of the plants maintained high in the zone.

The abundance and size of *Ascophyllum* juveniles under *Fucus spiralis* and *F. vesiculosus* canopies were assessed during field surveys taken as part of the present study to allow comparison with data collected earlier for *Ascophyllum*. The objective was to **evaluate the potential plant banks** for all three species. Juvenile sizes and growth rates (Ch. II) were then used to project the time for juveniles of different sizes to gain canopy dominance.

Materials and Methods

The study was conducted at Ft. Stark, New Hampshire, and utilized the experimental areas prepared for earlier investigations (Ch. I). Areas lacking *Ascophyllum* canopy ('open areas') and with equivalent canopy cover ('frond-covered areas') were established at shore elevations spanning the intertidal *Ascophyllum* zone, specifically +2.0, +1.5, +1.0, and +0.5 m above Mean Low Water. Bolts were cemented in each area. *Ascophyllum* germlings grown on ceramic tiles $(5.5\ \text{cm})^2$ were placed in cages to exclude grazing animals and secured in the areas on August 13, 1983. As shore level has a significant effect on growth of *Ascophyllum* (Ch. II, 1983-4), it was included as a factor in the experiments used to compare growth of *Fucus* with *Ascophyllum*.

Tiles were returned to the laboratory for counts and measurements. Surveys were made using low magnification of a dissecting scope. Lengths of the tallest *Fucus* and *Ascophyllum* on the tile were measured. A grid of 1 cm^2 areas was placed over the tile in a standard orientation. In 5 of the squares, randomly designated before the initial survey, *Fucus* recruits were counted.

Numbers of *Fucus* recruits fluctuated monthly among the censused squares and on the tiles. Therefore, all counts (all squares, all months) were averaged into a single grand mean for each tile. Grand means showed the same general pattern as monthly means. *Ascophyllum* germlings pre-empted space on the tiles so *Fucus* counts were tested for evidence of a negative correlation with *Ascophyllum* densities (Pearson Product Moment Correlation Coefficient). To analyze growth of *Ascophyllum* and *Fucus*, maximum length values (final – initial) were used to calculate growth over the period. The initial month was month 4, as that is when length measurements were first recorded.

Release from suppression was tested using plants placed in the field during July, 1982. Two tiles from high shore environments were transplanted to the low shore in May, 1983. One tile had been maintained in the open (n = 8 plants) and the other under frond cover (n = 35). First year data on growth of *Ascophyllum* suggested that frond cover was not a significant factor (Ch. II). Thus, the difference in conditioning (frond-covered *vs.* open) and the choice in transplanting (to +0.5 m, frond-covered or open) seemed arbitrary (see discussion). The two tiles were placed under the protection of frond-cover at +0.5 m, where tile loss was less likely. Length of all plants was measured at the time of transplant and three months later.

The numbers and sizes of juvenile *Ascophyllum* beneath *Fucus spiralis* and *F. vesiculosus* were sampled. *Fucus spiralis* grows immediately above *Ascophyllum* (+2.0 - +2.3 m), while *F. vesiculosus* is abundant in the open, mid-shore and lower. Of note, *F. vesiculosus* also occurs in openings on the upper shore, and atop *Ascophyllum* as an epiphyte. Within the quadrats, 25 x 25 cm (= 1/16th m^2), *Ascophyllum* juveniles were counted and measured. *Ascophyllum* juveniles can be distinguished from *Fucus* based on the degree of flattening, as well as the presence of a midrib and hairs. Ten samples were taken within each species. Juveniles under *Ascophyllum* were surveyed in April, 1983 and those under *Fucus* during September, 1983.

Frequencies, by size class, of *Ascophyllum* juveniles in the understories of the three species were analyzed statistically using a G-test of Independence (Sokal and Rohlf 1973). Evidence for a significant difference in the frequencies among size classes (5 cm intervals) was tested for *Ascophyllum* and *Fucus vesiculosus*. Frequencies under *F. spiralis* canopy could not be tested for size classes larger than the first interval (0 – 5 cm) as none of the juveniles was taller than 4 cm. Differences in the relative frequencies of plants < 5 cm tall were assessed in the same way using 1 cm intervals.

Time to regain dominance was projected using experimental data, measurements taken in the field, and observations from the literature. I used 0.05 cm for a newly settled individual. Plant length after 1 year was estimated using data for germlings grown in the field (see Ch. II, 1983-4). Growth in the understory was half that in the open, regardless of shore level; hence, length after 1 year was doubled for plants in the open (x 2), and multiplied by 1.5 for plants in the understory (half the increase) each successive year. The resulting lengths over time agree with data given in Sundene (1973). He recorded lengths of 1 – 15 cm attained over 10 – 14 months for plants in open situations (cf. Table I, Sundene 1973). Growth projections also agreed with laboratory-based measurements reported by Schonbeck and Norton (1980). At 12 – 20 cm, plant growth shifts and the first bladders and branches are produced. Comparing length against the number of bladders for plants measured at Ft. Stark, 10 cm/year seemed reasonable for the upper shore. The rate for plants under canopy was half that (5 cm). Stengel and Dring (1997), working in Ireland, reported that adult frond grew at rates of 10 cm/year on the high shore, 16 cm on the mid, and 12 cm on the lower shore. I adopted a rate of 15 cm/year for open, low shore populations. However, Peckol *et al.* (1988) recorded 25 cm/yr. for Rhode Island populations. As plants on the low shore are shorter (<1 m *vs.* 1.5 – 2 m) and highly branched, 15 cm seemed reasonable. Growth beneath the canopy was estimated at 7.5 cm/yr., half the open rate.

Some terms should be clarified. Recruitment and plant establishment differ in time. Plant establishment implies some permanence. The point at which a recruit (a plant derived from sexual reproduction and recruited to the population) becomes an established plant is not clear. Colonists are recruits, but naturally occurring juveniles are established plants. The first cm in length represents several years of growth, so juveniles (plants 1.5 – 20 cm) represent plants established in the population. Some may be lost, but they have become established over several years' time.

Results

Ascophyllum canopy was not an effective barrier for *Fucus vesiculosus*. *Fucus* colonized tiles in all environments (Figure V - 1). Colonization was greatest on the lower shore (+1.0, +0.5 m) and in the open (Fig. V – 1 a), with maximum densities at +1.0 m. Fewer *Fucus* recruited to surfaces under canopy but frond cover was not a significant factor (Table V - I).

The effect of shore level on *Fucus* densities was highly significant (Fig. V - 1, Table V - I). *Fucus* crowded surfaces on the lower shore, especially at +1.0 m. Densities approached 1000/cm^2. Recruitment was significantly greater on the lower shore than on the upper shore (Table V - I).

Fucus settled amidst a miniature forest of *Ascophyllum*. Open space on the tiles varied. Data (mean number of *Ascophyllum* pre-empting space, mean no. *Fucus* colonists) were analyzed for evidence of a significant negative correlation. Neither the individual survey data nor the grand means (averaged over all surveys) showed any significant correlation (Pearson correlation = - 0.073, p = 0.735, grand means). Colonization patterns were not influenced significantly by *Ascophyllum* germlings.

Fucus densities peaked at 2 different times over the year (Figure V - 1 b). Numbers of *Fucus* increased during the fall and peaked in November. Densities were greatest on the lower shore. The second peak was in August and was observed on the upper shore.

Growth of *Fucus* was enhanced on the lower shore and greatest in the open (Figure V - 2). Maximum growth occurred at +1.0 m. Shore level and frond cover had significant effects on *Fucus* growth (Table V - II a).

Ascophyllum canopy suppressed the growth of both *Ascophyllum* and *Fucus* germlings (Fig. V - 2). The contrast between growth in understory and in the open varied for the two seaweeds. Plants grew little during the winter, and maximally in spring. From the April survey (month 7.5) through the summer, *Fucus* grew 3.5 -12 cm in open situations but growth was arrested in the understory. *Ascophyllum* had minimal but measurable growth in the understory and faster growth in the open. Even so, potential growth of *Ascophyllum* (= growth in the open) was less than half that for *Fucus*.

Low shore dynamics were unique (Fig. V - 2). A spring growth increase was evident for plants in the **understory** as well as in the open. Understory plants attained about half the height of open-grown plants for both *Ascophyllum* and *Fucus*.

In the understory, growth of *Fucus* was compromised to a greater degree. Plants realized only a small percentage ($\leq$ 10%) of their potential growth on the upper shore and less than half at +0.5 m (Table V - II b). *Ascophyllum* realized half or more on the mid-shore. Suppression under the canopy differed significantly for the two species (Table V - II c). Relative suppression of *Ascophyllum* and *Fucus* differed significantly with shore level. Growth was suppressed to significantly different degrees, with strong suppression of *Fucus* on the upper shore where suppression of *Ascophyllum* was weak to moderate (Table V - II b, c; Shore Level x Species interaction).

Ascophyllum juveniles, suppressed high in the zone for 10 months, responded to improved conditions (Figure V - 3). The transplants grew 0.7 cm in three months, exceeding the rate for plants acclimated to the low shore. Low shore plants grew about 0.3 cm in the same period. Differences in growth were not significant between the transplants and low shore plants, and were significant between the transplants and their high shore counterparts (Fig. V – 3, Table V - III).

Juvenile *Ascophyllum* grew under the canopies of both species of *Fucus* as well as under *Ascophyllum* (Figure V - 4). Plants of a range of sizes were present under all three species. There were, however, **three times** as many under *F. vesiculosus* (with a canopy reaching ≈ 60 cm in length) as under *Ascophyllum* (reaching ≈ 160 cm). *F. vesiculosus* also had the largest number of intermediate-sized plants (5 - 20 cm). *F. spiralis*, the shortest of the canopy species (reaching 20 cm in the quadrats), had the fewest and none over 4 cm.

The frequencies of *Ascophyllum* juveniles among the 5 cm size classes did not differ significantly for *Ascophyllum* and *Fucus vesiculosus* canopies ($G = 2.38$, $X^2_{0.05,[3]} = 7.815$). Roughly 75% were 5 cm or less, 10% in the next two size classes (-10, -15cm) and 1 - 2% taller than 15 cm (2 and 4 plants). Likewise, the distribution of juveniles smaller than 5 cm was independent of species ($G = 11.76$, $X^2_{0.05,[8]} = 15.51$). Again, the smallest plants (up to 1 cm) were most abundant, with reduced numbers as size increased. All sizes were represented, except the 5 cm class under *F. spiralis* canopy.

The juvenile plant bank consisted mostly of small individuals. For all three species, about half were ≤1 cm in height. Plants up to 5 cm accounted for 75% of the 'advanced regeneration' available to fill a gap in the canopies of *Fucus vesiculosus* and *Ascophyllum nodosum*. While only a quarter of the juveniles were 10 – 20 cm, plants of intermediate sizes were present and would be most effective in regenerating lost cover.

Newly settled *Ascophyllum* in the understory might gain a height advantage over *Fucus vesiculosus* after 13 years of growth on the low shore and 20 years (+) on the high shore (Figure V – 5 a). No data was available for growth of 1 – 15 cm juveniles in the understory at +2.0 (see Schonbeck and Norton 1980 for rates in culture), and little for juveniles 3 – 15 cm on the low shore. The rates used were best estimates. Steady growth on a yearly basis and intact canopy cover were assumed.

In a gap, growth would be faster. Release from suppression was met with improved growth (transplant experiment). A germling (< 0.1 cm) could gain height advantage in 7 years on the low shore and 10 years on the high shore (Fig. V – 5 b). A juvenile c. 1.0 cm at the time of an opening could gain height superiority two years faster than a germling. A 20 cm juvenile would achieve height superiority in 3 - 4 years, less than half the time projected for a germling. The projections assume the maintenance of open conditions; quite unrealistic over periods longer than a year or two.

Discussion

Fucus vesiculosus and *Ascophyllum* vie for space in the spring, when space is at a premium. Both are reproductive in May (Niemeck and Mathieson 1976, Mathieson 1989; also Ch. I). Settlement of *Ascophyllum* lasts about a month (Ch. I) while settlement of *F. vesiculosus* lasts several months, continuing into the fall (Fig. V – 1 b, Knight and Parke 1950, Mathieson 1989). In the spring, an impressive variety of seaweed propagules is in the water column poised for settlement on the shore (Zechman and Mathieson 1985). *Fucus* and *Ascophyllum* are among them. Timing does not decrease potential competition for space.

During reproduction, *Fucus vesiculosus* has the advantage both in numbers and in length of the settlement period. Settlement densities of *Ascophyllum* during the reproductive season (Ch. I) are modest compared to the *Fucus* colonists counted (55 *vs.* > 900/cm^2, maximum densities). Prolonged settlement of *Fucus*, into the fall, increases the chance recruits will settle in favorable sites and replace those lost.

Ascophyllum canopy did not deter settlement of *Fucus*. Frond cover effects were not significant (Table V - 1). Reports that *Fucus* settlement is reduced by canopy (Jenkins, Hawkins and Norton 1999) were not substantiated for this site. Settlement was not evaluated directly. Large numbers of *Fucus* colonized surfaces on the lower shore regardless of an overlying *Ascophyllum* canopy. Notably, settlement of *Ascophyllum* is enhanced under its canopy (Ch. I.).

Conditions on the lower shore were favorable for both seaweeds. Maximum growth of *Fucus* occurred at +1.0 m, the same shore level as the densest recruitment. Maximum growth of *Ascophyllum* occurred lower on the shore; at +0.5 m. Growth of both seaweeds was greatest in the open. While maximal growth was segregated by shore level, both species had favorable recruitment and growth at +1.0 and at +0.5 m. Favored ranges during early development overlap.

Fucus vesiculosus was competent in the open. Growth of *Ascophyllum* germlings doubled in the open and plants grew c. 5 cm the first year under optimal conditions. *Fucus* grew 10 – 12 cm. Given open conditions, newly settled *F. vesiculosus* can grow to reproductive maturity in 2 - 3 years (1.8 cm/yr. in Niemeck and Mathieson 1976; Fig. V - 2). Plants would be > 20 cm and bushy, with well-developed branches. In 2 – 3 years, newly settled *Ascophyllum* might reach 10 cm. Plants would be linear and vegetative, with few branches. The more expansive *Fucus* would monopolize the canopy layer, leave a germling bank in the understory, and suppress growth of *Ascophyllum*. Further, *Ascophyllum* may only survive under canopy on the upper shore, where growth is suppressed. Growth is favored in the open, but survival in open situations may be restricted to the low shore (Ch. II).

Ascophyllum had a selective advantage over *Fucus vesiculosus* in the understory. Frond cover had a significant effect on the growth of both fucoids (Table V - II a). *Fucus* was compromised to a greater degree (Table V - II c) and plants remained ≤ 0.1 cm (Fig. V - 2). *Ascophyllum* in the understory grew 0.8 – 1 cm. *Fucus* was arrested in the deep shade, while *Ascophyllum* was not.

On the lower shore, *Ascophyllum* canopy had less of an effect on growth. At +0.5 m, plants in the understory achieved 2 cm (*Ascophyllum*) and 4 cm (*Fucus*) in length, the same sizes as upper shore plants grown in the open.

Both *Ascophyllum* and *Fucus* are tolerant of limiting conditions. They survive long periods in the dark (Sheader and Moss 1975, Vadas *et al.* 1992, Chapman 1995) and retain vigor. Plants in the understory remained dark and healthy even under a blanket of silt. The low shore plants, having endured this silt layer, had a spring surge in growth.

Fucus vesiculosus, maintained under low light and nutrients for a year in the laboratory, showed renewed growth with improved conditions (Creed *et al.* 1996).

Canopy species exert a controlling influence, regulating community development in the layers below (Jenkins, Hawkins and Norton 1999). As described by Marks (1974), this represents 'biotic regulation.' Light is critical for the germination and growth of opportunistic species, important to mid-successional species, and of less importance for the shade-adapted young of climax species. In a climax forest, species present in the seed bank are highly unrepresentative of the dominant vegetation (Silvertown and Lovett-Doust 1993) as their seed remains dormant under an intact canopy. On the shore, micro-sized germlings and sporelings or 'micro-recruits' (Ang 1991, see also Vadas *et al.* 1992, Creed *et al.* 1996) and spores in spore banks (Hoffman and Santelices 1991, Lotze *et al.* 1999, Lotze *et al.* 2000) lie in reserve awaiting higher light. Seed, spore and germling banks offer a second, but unequal, chance to monopolize space (Creed *et al.* 1996). Viability declines over time for vascular plants (Silvertown and Lovett-Doust 1993) and seaweeds (Creed *et al.* 1996, Lotze *et al.* 1999).

Fucus can settle in a gap and dominate the space before other species overgrow and suppress it. Its success hinges on good colonizing abilities coupled with rapid growth in open situations. *Fucus* also colonizes the understory where its germlings are in place, ready to respond to an opening and fill the gap. Gap size is not important, only gap presence (Worm and Chapman 1998).

Ascophyllum relies on slow growth, prolonged vigor, and a succession of openings. In a forest, a series of suppression/release cycles lead to ultimate domination by the climax tree species (Silvertown and Lovett-Doust 1993). Juveniles grow more rapidly in an opening, but are surpassed by faster-growing *Fucus* and suppressed under its canopy. Where grazing animals do not nullify recruitment, *Ascophyllum* may grow under a progression of canopies. Some seaweed canopies afford more light penetration and better growing conditions (see Hatton 1938 and *Enteromorpha*, Viejo *et al.* 1999).

Persistence over the long term in a suppressive environment or 'resistance to inanition' was described for grasses (Chippendale 1948), and later applied to trees (*i.e.*, Harper and White 1974). It is particularly descriptive of beech and hemlock seedlings that persist **hundreds** of years in the understory (Hough 1936), and retain vitality (Marshall 1927, Hough and Forbes 1943). Metabolic rates of the saplings are just above compensation, with little apparent growth (Silvertown and Lovett-Doust 1993).

Release from suppression is vital to successful self-replacement (Spurr and Barnes 1964, Grime 1966). *Ascophyllum* juveniles suppressed on the high shore responded to improved conditions on the low shore (Fig. V - 3). They grew more than twice the rate of low shore plants and significantly faster than plants maintained on the high shore (Table V - III c). Enhanced growth, beyond that of the plants acclimated to the low shore, is notable and was evident within a few months. While the results were clear, the experiment might be improved. The transplants came from different situations on the high shore; open and frond-covered. Growth experiments undertaken the year before transplantation suggested that canopy did not affect growth (1982-3; Ch. II). Later studies (1983-4; Ch. II) demonstrated that canopy significantly affected growth. Improvement in situation is greatest between high, understory (not high, open) and low, open environments. It is advised to transplant only *Ascophyllum* accustomed to the strongest suppression (+2.0 m, understory) to the most favorable sites (low, open).

Results from earlier work (Hatton 1938, Burrows 1956) and from the present study, show that juvenile plants can retain vitality in the understory. Hatton and Burrows transplanted naturally occurring juveniles into different environments. The juveniles had endured suppression for years or, possibly, decades. My plants had been under suppression for less than a year. Thus, by extension, *Ascophyllum* juveniles of a variety of ages retain vigor over extended periods. The results indicate that they are capable of responding to improved conditions (a gap) with a surge of growth.

A reserve of juveniles in the understory favors self-replacement of climax trees (Marshall 1927, Hough and Forbes 1943). For slow-growing, long-lived species, a juvenile bank affords a competitive edge (Marks 1974). Juveniles of intermediate sizes (*e.g.*, 5 to 20 cm) attain canopy superiority years sooner than a germling as they have a head start (Fig. V - 5).

The projections assume slow but continued growth in the understory, as observed in this study. Size class data and growth projections seem to agree. Observed frequencies (0 – 1 cm = 43 plants, to 2cm = 13 plants, to 3 cm = 10 plants, to 4 cm = 4 plants, to 5 cm = 3 plants) could reflect a build-up over 3 - 4 years in the first interval (it takes 3 - 4 years for plants to top 1 cm), 1½ yr. in the second interval, 1 yr. in the 3rd, and less than a year in the 4th and 5th. After 4 years of growth a plant would be about 1 cm, and after 8 years it would be about 5 cm.

Estimates for the low shore suggest that an *Ascophyllum* germling (< 0.1 cm) in the open would monopolize the canopy after 7 - 10 years (Fig. V - 5 b). Keser and Larson (1984) documented a return to canopy dominance in less time. *Ascophyllum* in clearings regained dominance in 3 years (mid-shore) and 5½ years (upper shore).

A ready reserve of *Ascophyllum* was present under both species of *Fucus*, available to replace them. Three times as many *Ascophyllum* juveniles grew under *Fucus vesiculosus* as beneath *Ascophyllum*. About twice as many of the juveniles under *F. vesiculosus* were of intermediate size (Fig. V - 4). The fewest *Ascophyllum* juveniles grew beneath *F. spiralis*, and they were all < 5cm.

Replacement of *Fucus vesiculosus* seems likely, but not *F. spiralis*. Survival of *Ascophyllum* is limited in the open, especially on the high shore (Ch. II). *Fucus spiralis* grows above *Ascophyllum*, where physical stress is more pronounced. All of the juveniles were considerably shorter than the *F. spiralis* canopy (4 *vs.* 15 cm). Juvenile *Ascophyllum* transplanted at the level of *F. spiralis* had lowered photosynthetic performance (Schonbeck and Norton 1978) or reduced growth (Hatton 1938). Some high shore transplants died (Hatton 1938). Juveniles in crevices above the *Ascophyllum* zone appear stunted at Ft. Stark which is characteristic of growth above the natural limits.

The story of *Ascophyllum* and *Fucus vesiculosus* is analogous to the tortoise and the hare. *Fucus* is quick; it grows rapidly in the open and quickly dominates gaps. *Ascophyllum* is slow and persistent. It makes gains during a series of openings. Unlike *Fucus*, with a lifespan of 2 - 3 years, *Ascophyllum* is in place for decades. The tortoise won the race because the hare stopped for a nap, giving the tortoise time to reach the finish line. A succession of openings (domination by a succession of *Fucus* canopies) gives *Ascophyllum* the time it needs to attain height superiority. Then, its canopy arrests growth of *Fucus* germlings left behind. Slow and steady wins the race (but see later).

The importance of a juvenile bank has not been appreciated. Suppressed plants in the understory are a resource and their role in replacement has been discussed in terms of a 'meristem bank' (Cousens 1986, Vadas and Wright 1986, Vadas *et al.* 1990). Because a juvenile bank is critical, clearing studies are not appropriate in determining the natural potential for recovery in a climax species. When surfaces are cleared, vital reserves are lost, including spore banks of opportunistic species (Lotze *et al.* 1999, Lotze and Worm 2000), germling banks of mid-successional species, and juvenile banks representing years of growth for late-successional species. Creed *et al.* (1996) stated that clearing represents the ultimate density manipulation (a negative density state, in fact). Loss of the juvenile plant bank, is a set-back to recovery and explains the long time lag in the re-establishment of a foundation species (Dayton 1972, Petraitis and Latham 1999). Controlled thinnings and experimental openings, combined with growth measurements of the juveniles beneath, are needed (Creed *et al.* 1996).

Canopy favors self-replacement, and Bertness *et al.* (1999) consider recruitment of *Ascophyllum* a case of facilitation. Research documents an increase in facilitative interactions where physical rigors increase. Stressful habitats associated with an increase in facilitative interactions include the upper shore (*i.e.*, Leonard 2000) and the alpine (Callaway 2002). Indeed, *Ascophyllum* canopy facilitates its own recruitment. The distinction is that facilitation enhances survival in the face of physical stress, while self-replacement goes a step further. Canopy creates an environment stressful in a different way (extreme shade) where its own recruits have a selective advantage.

Survival patterns were partially resolved in the present study. Weather conditions vary year to year and also cyclically. Due to slow growth, the period of heightened sensitivity for *Ascophyllum* may extend beyond the first year. Early development, as a physiologically sensitive period, is critical in determining the survival range (Brawley and Johnson 1992, Chapman 1995). Studies over several years, as well as repeated during different weather cycles, are needed to determine if recruitment (and in a larger context, plant establishment) is obligate to canopy cover.

Juveniles growing in the open may be lost, implying that canopy cover may be important in the longer term. Knight and Parke (1950) found that *Ascophyllum* colonized clearings, grew a few centimeters, and then disappeared. I lost some of the tallest plants during the final months of experiments in the present study. Neighboring plants or overlying canopy provide shelter critical for plants well into the juvenile phase. The drag of water flow on isolated individuals (in clearings, taller than surrounding plants) may overwhelm attachment strength after a critical length has been reached. Within the canopy, drag forces are reduced (Johnson 2000).

Burrows (1956) suggested that physiological tolerance of *Ascophyllum* broadens with age. The capacity for growth shows the same pattern. Saturating irradiances for newly settled germlings approximate 6 W/m^2 (Sheader and Moss 1975), while adult fronds are saturated between 30 - 50 W/m^2 (Strömgren 1977). Growth capacity in *Ascophyllum*, as well as for plants in general, is related to size (Silvertown and Lovett-Doust 1993). Germlings grew 0.2 – 5 cm/year. Adult fronds grow 9 - 25 cm/year. Thus, growth and photosynthetic capacity increase with size. An increasing capacity to utilize brighter light seems adaptive for effective survival of juveniles in the understory, and faster expansion through the canopy as an adult.

Cycles of openings and suppressions complicate aging of *Ascophyllum*. The number of air bladders along the longest axis has been used to age plants. It may be 2 or 3 years before the initial bladder is produced, so age has been estimated as the number of bladders + 1 or 2 (see Baardseth 1973, Cousens 1984, Åberg 1992a). Sundene (1973) found that it could take 5 or more years before production of the initial bladder. At Ft. Stark, bladders are not produced until plants are ≥12 cm. In the understory, this might be a dozen years.

For climax trees, understory juveniles have a recognizable stage structure (Silvertown and Lovett-Doust 1993). Saplings in the same general area are not a continuum of sizes but fall into groups of common size (recruit classes). The growth difference between recruit classes corresponds with gains made during gaps. Analysis of stage structure may provide insight into the aging of *Ascophyllum* juveniles.

Plants have the potential to live over a century (Åberg 1992a). Clonal plants are remarkable for their persistence, being potentially immortal (Silvertown and Lovett-Doust 1993). Modular growth of *Ascophyllum* allows for branch production in response to space, light and wounding (Cousens 1985, Lazo 1992, Lazo *et al.* 1994, Viejo and Åberg 2001). However, accumulated stress weakens plants and can result in eventual loss. Breakage due to ice (Mathieson *et al.* 1982, Åberg 1992) and wounding by animals (Lazo *et al.* 1994, Norton *et al.* 1990, Chapman 1995, Amsler 2001) are common. Growth slows in plants belonging to the 'oldest' size classes reflecting breakage and suggesting a natural decline with age (Åberg 1992b). Thus, potential longevity is cut short.

Juveniles of *Ascophyllum nodosum* have been reported in a number of geographies (Peckol *et al.* 1988; Åberg 1992b; Lazo 1992; Lazo *et al.* 1994; Åberg and Pavia 1997; Cervin and Åberg 1997; Jenkins, Hawkins and Norton 1999; Viejo and Åberg 2001). Reproductive success requires intermediary canopies on the upper shore and a lapse in animal impact on the lower shore (see Ch. II, III). Longevity of half a century includes a multitude of reproductive seasons. Natural recruitment events occur on a timescale beyond the typical focus of field studies (see Hruby and Norton 1979). Reproductive success of *Ascophyllum* must be considered in a different time context.

By its very nature, the cover of climax species is both extremely stable and fragile. Chapman (1979) concluded that stability is elusive; after disturbance, the process begins again. Rather than a stable end point, the climax is merely a long transitory phase (Spurr and Barnes 1964). Disturbance is an element of nature. Its frequency and intensity vary among habitats, sites and geographies. Once a climax vegetation is impacted beyond its resiliency, rebuilding through intermediate stages implies a long lapse before the climax species regains a foothold. The process may not be direct and may involve alternative states of varying duration (Petraitis and Latham 1999). Stability is at once exteme resistence to perturbation and, as a necessary compromise, extreme fragility once the threshold has been crossed (Horn 1974, 1975).

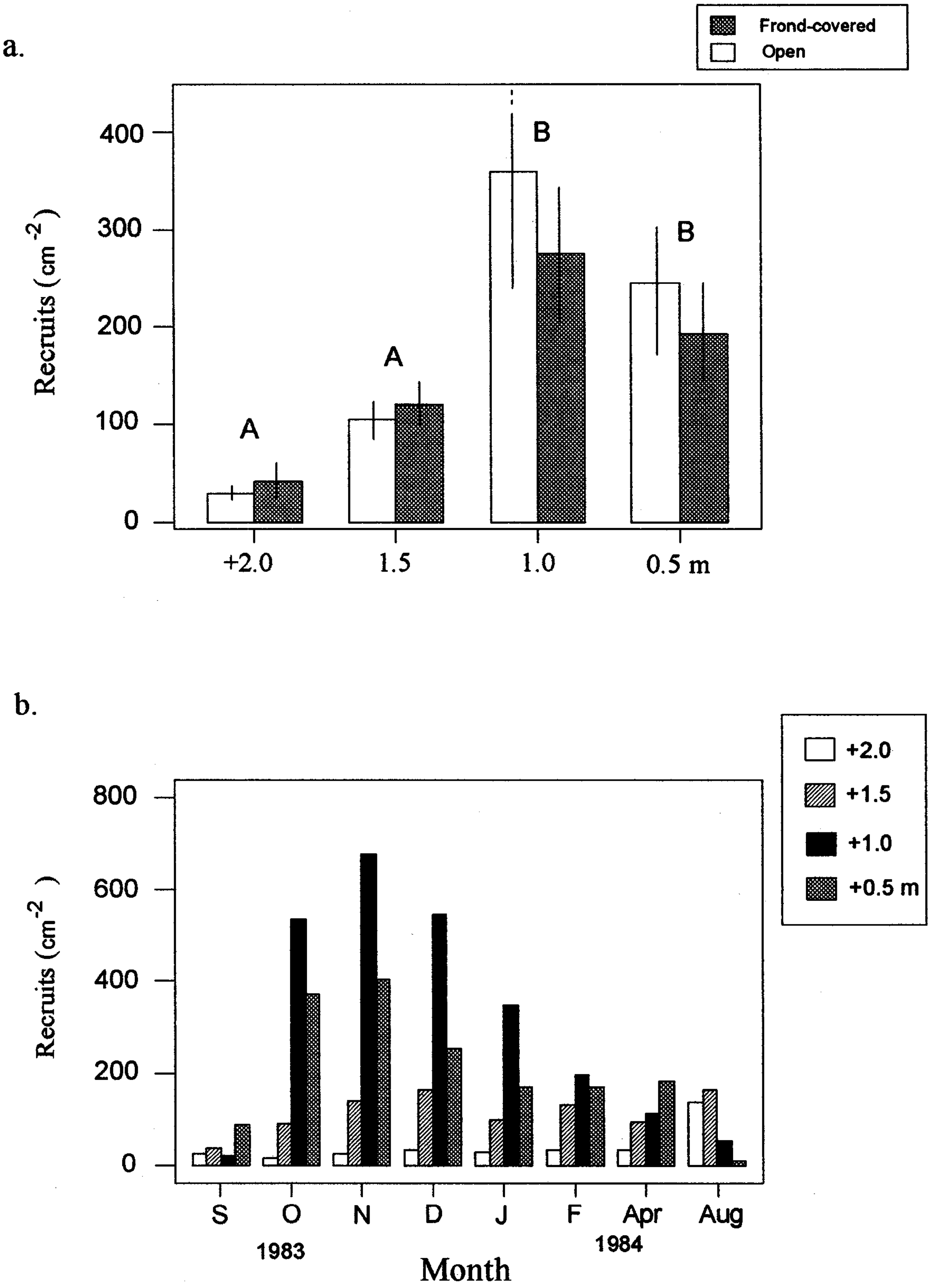


Figure V - 1. Fucus Colonization. *Fucus* recruits in frond-covered and open situations by shore level (a), and recruits by month at each shore level (b). Means ± 1 S.E. are shown (a), and means (b). Letters indicate means that differ significantly.

Table V - I. *Fucus* Colonization Statistics. Results from a 2-way ANOVA on the effects of environment shore level and frond cover on the number of *Fucus* recuits. Data are mean numbers of *Fucus* recruits/cm^2 averaged over all months to give a grand mean for each tile (n = 24).

Fucus Recruits

Source	df	SS	MS	F	p-value
Shore Level	3	271861	90620	23.39	0.0001***
Frond Cover	1	4499	4499	1.16	0.297
SL x FC	3	10903	3634	0.94	0.445
Error	16	61992	3875		
Total	23	349255			

Ascophyllum canopy did not have a significant effect on the number of *Fucus* recruits. **Shore level** did have a **significant** effect on the number of *Fucus* recruits.

Tukey Pairwise tests indicated :

Pair Tested	T-value	p-value
+2.0 m *vs.* +0.5 m	-5.100	0.0006***
+2.0 m *vs.* +1.0 m	-7.822	0.0001***
+1.5 m *vs.* +1.0 m	-5.690	0.0002***

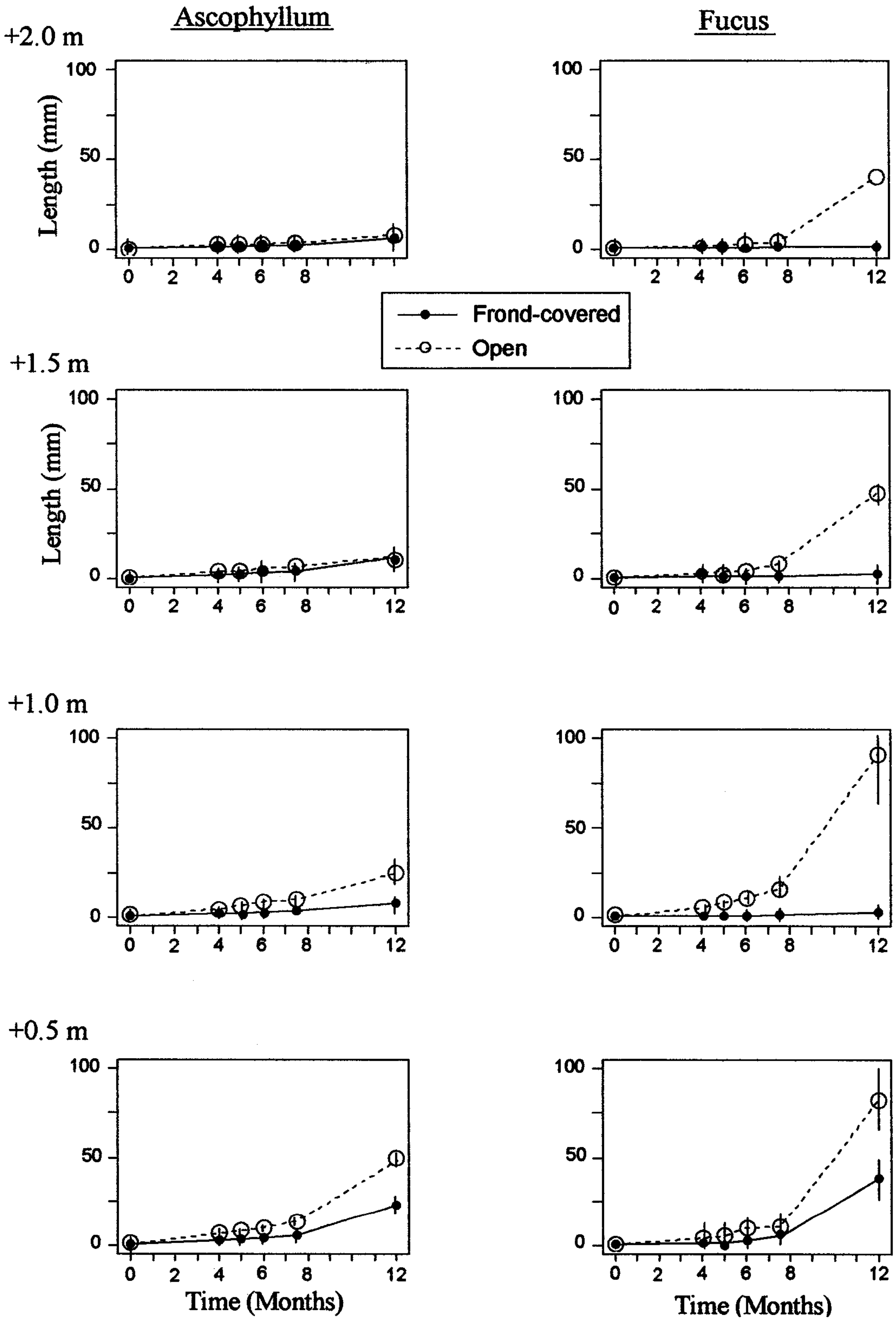


Figure V - 2. Differential Suppression. Mean maximum length of *Ascophyllum* and *Fucus* (tallest plant on the tile) by environment and over time. Means ±1 S.E. are shown.

Table V - II. Suppression Statistics. The effects of *Ascophyllum* canopy on the growth of developing *Fucus* and *Ascophyllum*. Results from a 2-Way ANOVA on the effects of shore level and frond cover on Fucus. Data are growth rates calculated from maximum length differences (month 12 – month 4) (a). Growth under the canopy as percentage of potential growth in the open (b). Results from a 2-Way ANOVA on suppression (% of growth in the open) by species and shore level. Data are the proportions (growth in the understory/growth in the open) ranked (c).

a. **Growth of *Fucus vs.* Environment**

Source	df	SS	MS	F	p-value
Shore Level	3	70.00	23.33	5.35	0.019*
Frond Cover	1	153.16	153.16	35.09	0.0001***
SL x FC	3	28.50	9.50	2.18	0.154
Error	10	43.64	4.36		
Total	17	295.30			

Shore level and **frond cover** had significant effects on the growth of developing *Fucus.*

b. **Growth in the Understory** (% of growth in the Open)

Shore Level	*Fucus*	*Ascophyllum*
+2.0	2% ± 2	80% ± 71
+1.5	6% ± 2	100% ± 44
+1.0	2% ± 2	48% ± 21
+0.5 m	40% ± 9	30% ± 22

c. **Suppression under *Ascophyllum* Canopy**

Source	df	SS	MS	F	p-value
Shore Level	3	36.500	12.167	1.99	0.195
Species	1	169.000	169.000	27.59	0.001
SL x Sp	3	85.500	28.500	4.65	0.036*
Error	8	49.000	6.125		
Total	15	340.000			

The degree of growth **suppression** differed **significantly** as in interacted with shore level for *Ascophyllum* and *Fucus.* Strong suppression of *Fucus* was observed on the upper and mid-shore (see 'b' above), while suppression of *Ascophyllum* was evident on the lower shore.

Tukey pairwise tests indicated:

Pair Tested	T-Value	p-value
+1.5 m *Ascophyllum vs.* +2.0 m Fucus	-5.051	0.013*
vs. +1.0 m *Fucus*	5.051	0.013*

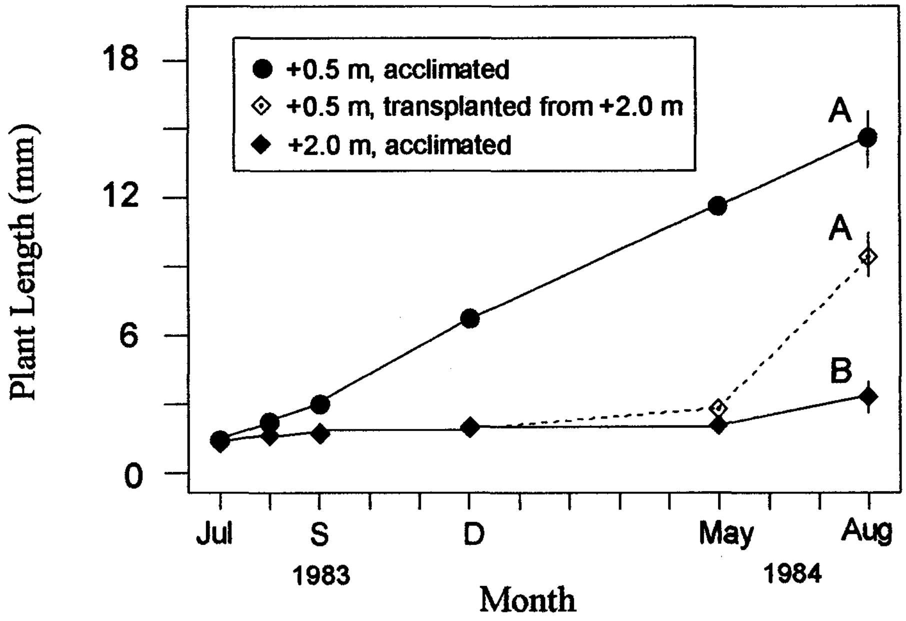


Figure V - 3. Release from Suppression. Growth of plants transplanted to the low shore compared with the growth of plants remaining at +2.0 m (+2.0 m, acclimated) and those acclimated to +0.5 m. Plants were transplanted in May and growth rates in the 3 months that followed were used in the analysis. Means are shown, ± 1 S.E. for the August values. Letters indicate groups that differ significantly.

Table V - III. Release from Suppression Statistics. Results from a 1-way ANOVA on the effect of condition (acclimated high, acclimated low, or transplanted) on the growth of developing *Ascophyllum*. The 3 groups are +2, acclimated; +0.5, acclimated, and +0.5, transplanted. Data are mean growth for the 3 month period (month 10-month 13).

Growth of Transplants *vs.* Acclimated Plants

Source	df	SS	MS	F	p-value
Condition	2	37.704	18.852	10.02	0.012*
Error	6	11.284	1.881		
Total	8	48.988			

Ascophyllum from the high shore showed a **significant** increase in growth with a change in **condition**; when transplanted to the low shore. Growth of the transplants was significantly different from growth of the plants maintained high in the zone (+2.0, acclimated) and was greater, but not significantly so, than growth of plants acclimated to the low shore (+0.5, acclimated).

Tukey Pairwise Tests indicated:

Pair Tested	T-Value	Adjusted p-value
+0.5 m, transplants *vs.* +0.5 m, acclimated	2.862	0.065
vs. +2, acclimated	4.477	0.010*

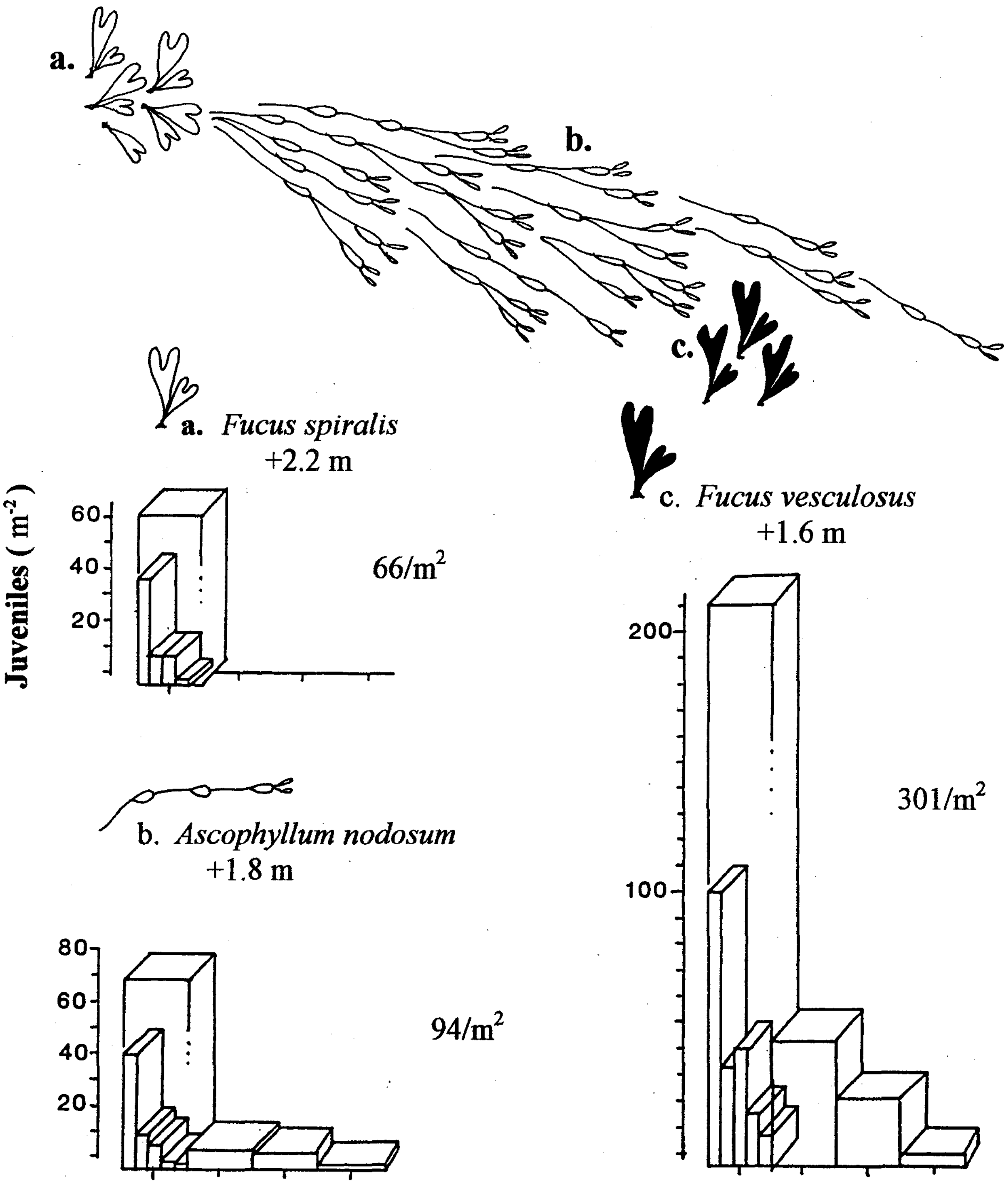


Figure V - 4. Juvenile Replacement. *Ascophyllum* plants growing under the canopies of *Fucus spiralis, F. vesiculosus* and *Ascophyllum nodosum* (5 cm intervals, 1 cm intervals).

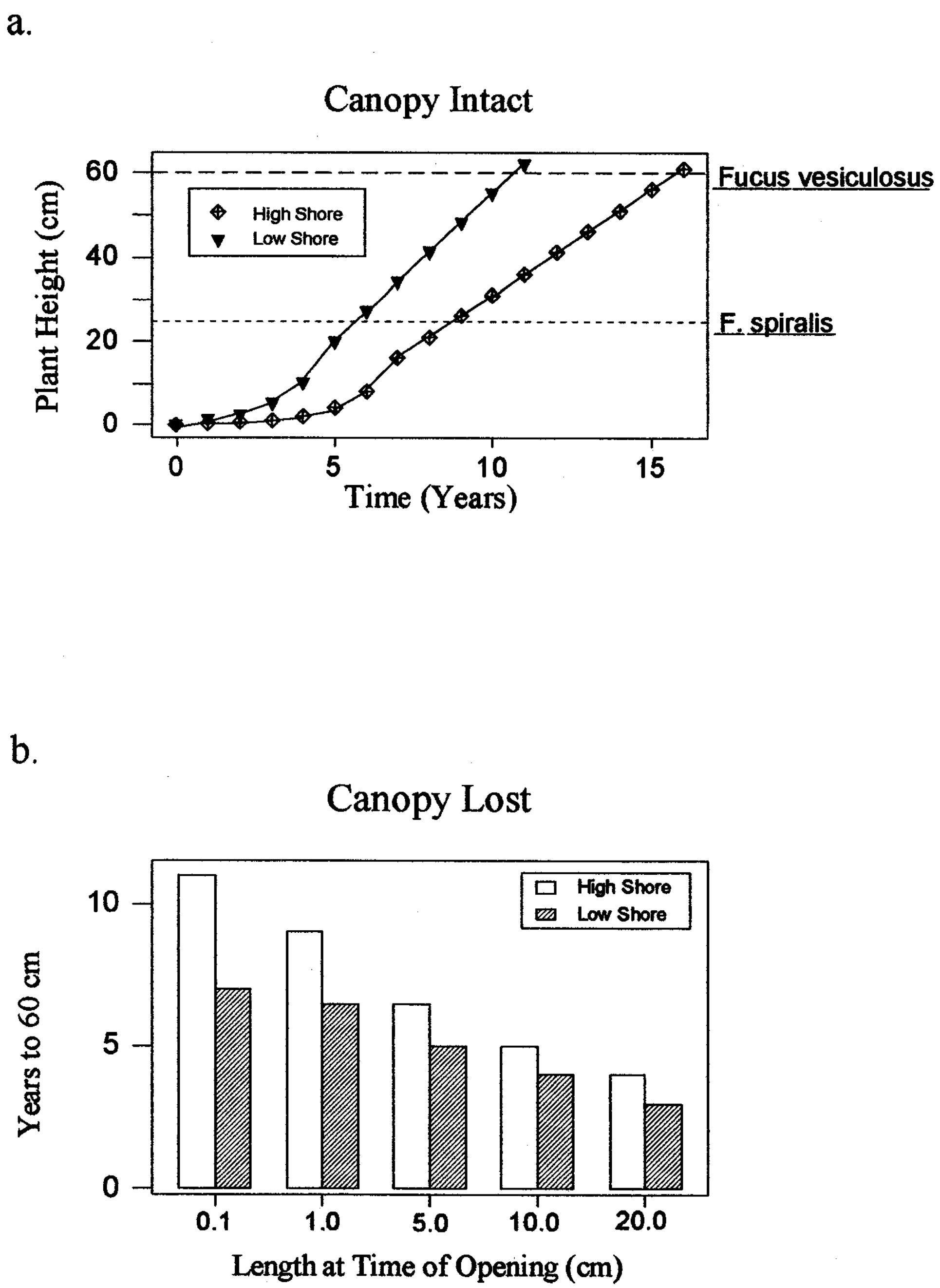


Figure V - 5. Dominance Projections. The time for a newly settled recruit to surpass 60 cm with the intact canopy intact (a), and for juveniles of various sizes to gain size superiority over *Fucus vesiculosus* in an opening (b). Estimates are given by shore level.

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