

JEM 561

FROND SIZE DISTRIBUTIONS AND THE EFFECTS OF THE ALGAL CANOPY ON THE BEHAVIOUR OF *ASCOPHYLLUM NODOSUM* (L.) Le Jolis

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(Received 1 April 1985; revision received 28 June 1985; accepted 8 July 1985)

Abstract: Stand sampling, field and laboratory experiments were conducted in order to examine the relationship between stand structure and individual frond behaviour in *Ascophyllum nodosum* (L.) Le Jolis. Size-frequency distributions were found to be extremely skewed, almost log-symmetrical. The majority of stand growth and reproduction was confined to a small number of dominant individuals. In exposed stands, fronds soon reached their maximum growth rate and produced numerous reproductive laterals. Vegetative laterals seldom survived for > 1 yr. In sheltered stands, fronds grew slowly at first and produced no laterals. As they increased in length, growth rate increased and vegetative laterals were produced; on emergence above the canopy growth rate reached a maximum and laterals became exclusively reproductive. The changes in frond behaviour in dense stands could be partially mimicked by moving sections of shoots within a canopy and by varying the light intensity. It is suggested that *A. nodosum* is extremely plastic in its behaviour, and many of the patterns of response found in natural populations can be explained by variations in availability of light.

Key words: population; behaviour; canopy; laterals; initiation; mortality; growth; light; *Ascophyllum*

INTRODUCTION

Much of seaweed ecological research has been concerned with the description and explanation of the distributions of species and communities in space (e.g. Lewis, 1964). Although there has been a small number of notable exceptions, few studies have been directed specifically at the population level of organization (Chapman, 1979). Part of this lack of attention may result from the extreme difficulty in many species of identifying individual plants, or genets (Russell & Fielding, 1981). It is usually possible in such cases, however, to recognize functional units equivalent to the ramets of higher plants, and populations can be studied in relation to these. The intention of the present study was to examine frond population structures of *Ascophyllum nodosum* (L.) Le Jolis and to relate the behaviour and fate of individual fronds to their positions within the algal canopy.

A. nodosum is widespread in the North Atlantic, where it may occur in dense, often monospecific stands of up to 8 kg dry wt · m⁻² (MacFarlane, 1952). It has been the

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subject of many laboratory studies (e.g. Ragan & Jensen, 1979; Terry & Moss, 1980), but usually without reference to the origin of the material, its size or its position within the natural populations. Because of its economic significance, the productivity of *A. nodosum* stands has received much recent attention (Keser, 1978; Niell, 1979; Sharp, 1981; Cousens, 1984). *A. nodosum* plants may be extremely long-lived and often the genetic individuals cannot be distinguished (Baardseth, 1970). They have, however, a distinct modular structure of sub-units having a much shorter turnover time (Cousens, 1984). Each holdfast produces a succession of shoot systems or fronds. These consist of a primary shoot, along the length of which are two rows of lateral pits. From the pits arise secondary laterals, which may be either vegetative or reproductive. Secondary vegetative laterals produce tertiary laterals which are usually reproductive. The reproductive laterals are referred to as receptacles and are shed each spring. Air bladders, or vesicles, are formed annually at the apices of vegetative shoots. The ages of unbroken shoots can be estimated from the number of vesicles, although care must be taken with primary shoots because the first vesicle may often not be formed until after a number of years (Cousens, 1981).

MATERIAL AND METHODS

The study was divided into three sections: (1) description of size-frequency distributions and the relationships between frond size and receptacle production; (2) examination of the development of fronds and the demography of their component parts; and (3) experiments to determine the extent to which frond development is affected by the algal canopy in general, and by availability of light in particular. A summary of all of the various aspects of the study is given in Table I. Five stands of *A. nodosum* were selected around an island at Polly Cove, Nova Scotia, Canada. All were at approximately mean tide level and established on granite bedrock. The stands could be ranked in degree of exposure to wave action according to their position relative to the open sea (Cousens, 1984, in press); Stand 1 was the most exposed and Stand 5 the most sheltered. Because of the large number of measurements made, not all aspects of frond behaviour could be examined in all stands. In some cases only the two extreme stands were studied. Although interpolation between extremes can lead to mistaken interpretations of behaviour over an entire gradient (Cousens, 1982), great care was taken in the consideration of the results thus obtained.

SIZE-FREQUENCY DISTRIBUTIONS AND ALLOMETRY

Samples of fronds were collected from each of Stands 1 to 5 in April 1979. In dense stands the task of collecting truly random samples of fronds is impractical since at low tide the largest fronds obscure all others. Instead, samples consisted of all the fronds within random collections of holdfasts. At each location a tape was stretched horizontally along the substratum. In order to avoid bias due to clumping the third

closest holdfasts to each of 20 to 25 random points along the tape were collected. The length of each frond was measured while still wet. Fronds were dried individually at 50 °C for 2 days. *Polysiphonia lanosa* (L.) Tandy and *Fucus vesiculosus* L. were both found epiphytically on some of the fronds, but their plants were small and few in number, and they were removed prior to measurement.

FROND DEVELOPMENT AND DEMOGRAPHY

Ascophyllum nodosum fronds are relatively slow growing and may survive for at least 15 yr before their primary shoot is first broken (David, 1943). The length of time required to follow the complete course of development for an individual frond would, therefore, be prohibitive. The ages of fronds usually cannot be determined from the number of vesicles since a high proportion of primary shoots are broken, and in any case the age at which the first vesicle forms may vary considerably (Baardseth, 1955; Sundene, 1973). The common practice of counting the maximum number of vesicles along any basipetal route and then adding one or two is likely to give very poor under-estimates of true frond age. Frond development, however, is, like the majority of processes in long-lived perennial plants, more likely to be size-specific than directly age-specific. For this reason it was decided to examine the relationships between various aspects of behaviour and frond length, rather than frond age. Every frond, as it develops, must grow up through the algal canopy; the conditions in which the upper regions of a frond find themselves will thus change as a frond increases in length, and frond behaviour will be expected to change accordingly. In all, five aspects of frond development were examined, special attention being paid to the behaviour of the youngest internode on the primary shoot and to the laterals attached directly to it.

Growth in length

At all sites fronds with unbroken primary shoots were marked by tying a short length of plastic tape about the basal internode, the loose ends being numbered using an indelible pen. Shoots were chosen such that the whole range of lengths found at each site was represented. The shortest primary shoots could not be marked directly by this method, so their labels were tied to an adjacent frond of markable size. The length from the holdfast to the furthest apex on the primary shoot was measured in July 1979 and again on the same date in July 1980.

Initiation of laterals

Laterals emerging from pits on primary shoots only were examined. Random samples of holdfasts were obtained from Stands 1 and 5 in late March 1980. For each frond with an unbroken primary shoot and at least two vesicles the length of the youngest complete internode and the distance from its base to the holdfast were measured. Numbers of lateral pits, vegetative laterals < 1 yr old and receptacles on the internode were counted.

Survival of vegetative laterals

In Stands 1 and 5, 50 fronds with intact primary shoots of a range of lengths were marked with plastic tape. The ages and locations of each lateral were recorded initially in April 1980 and at intervals thereafter.

Truncation of the primary shoot

A great proportion of primary shoots within natural populations of *A. nodosum* are broken. At what point does breakage take place and what effect does this have on lateral initiation? Some information on the rate of breakage of the primary shoot could be obtained from the frequency distributions of the number of vesicles on unbroken primary shoots. Within stands at Polly Cove the first vesicle was positioned consistently at approximately the same distance from the holdfast. Random samples of 20 holdfasts were collected, the required fronds selected and the number of vesicles along their primary shoot counted. Primary shoots without a vesicle were discarded. In order to examine the effects of the loss of the primary apex on lateral shoot initiation a sample of fronds with unbroken primary shoots were labelled with plastic tape at a location close to Stand 5. On 17 November 1979 the primary apices on half of the fronds were truncated immediately above the most recent vesicle. The numbers of receptacles and vegetative laterals on the youngest internode were counted 1 yr later.

FIELD AND LABORATORY EXPERIMENTS

Two field experiments were initiated to see if the patterns of development observed were fixed or whether they were plastic responses to changes in conditions. At a location close to Stand 5 apical portions of shoots were transferred from the top of the canopy to the bottom and vice versa. The top 5 cm of primary shoots were removed and tied to fronds at the required position with braided fishing line. Control shoots were cut and then tied at the same level from which they were removed. After 1 yr those remaining were measured and the number of receptacles and vegetative laterals counted. A 1-m² space a few metres away was cleared of all fronds longer than 15 cm. The growth and initiation of laterals by shoots that had at least two vesicles 1 yr later was recorded and compared with that of similar shoots beneath an adjacent intact canopy. The incident radiation at these two locations was measured on a sunny day in May at various depths when the canopy was just fully extended using a Lambda 192S underwater quantum irradiance sensor.

In order to examine the effects of shading on frond development an experiment was conducted under artificial conditions. Apical 10-cm portions from young, unbroken primary shoots with at least two vesicles were taken from beneath a dense canopy, as were similar portions from considerably older primary shoots with their apices in the upper regions of a canopy. These were both grown under a range of shading conditions at the Sandy Cove Marine Station, N.S.E.R.C. Atlantic Regional Laboratory, from

April 1980 to January 1981. Shoot sections were suspended from wooden frames in shallow plastic trays in a continuous flow of fresh sea water. Three of the trays were shaded with screens of black chiffon so as to reduce the relative irradiance to ≈ 50 , 25, and 12.5% of that in the fourth, unshaded tray. The trays were situated in a glasshouse under otherwise natural lighting. Growth rates and lateral initiation over this period were observed.

TABLE I
Summary of the measurements made in this study.

Aspect studied	Measurements made	Stands studied
Stand structure	Fronde length, total weight and weight of receptacles	1-5
Fronde development in natural stands	Growth in length of primary shoot	1-5
	Initiation of laterals on youngest internode of primary	1 and 5
	Survival of laterals	1 and 5
	"Age" at breakage of primary	1-5
Effect of breakage on lateral initiation by primary		Adjacent to 5
Position of shoot in canopy: shoots moved to different levels	Growth and lateral initiation by excised youngest internode of primary	Adjacent to 5
Canopy removal	Growth and lateral initiation by young primary shoots	Adjacent to 5
Effect of shading in laboratory	Growth and lateral initiation of excised primary shoot sections	-

RESULTS

SIZE-FREQUENCY DISTRIBUTIONS AND ALLOMETRY

Maximum frond lengths increased with shelter, reaching > 1 m in Stand 5 (Fig. 1); neither arithmetic nor geometric means reflected this trend (Table II). Frequency distributions of frond length were extremely skewed, some being almost log-symmetrical, although not log-normal (Fig. 2). Around 50% of fronds at each site were 5 cm or shorter. As a result only a small proportion of fronds reached into the upper regions of the canopy and provided most of the canopy biomass. The greatest frond biomass found was ≈ 25 g dry wt in Stand 4. Neither arithmetic nor geometric mean weights showed any clear trend along the exposure gradient (Table II). Frequency distributions

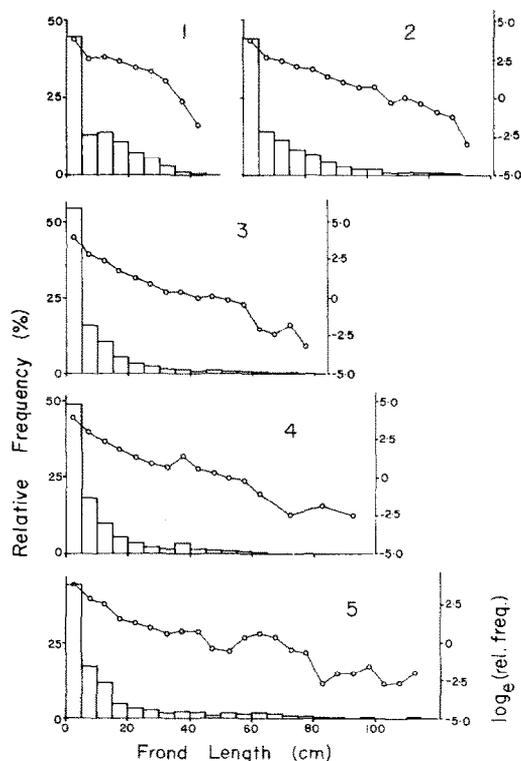


Fig. 1. Relative frequency histograms and \log_e (relative frequency) polygons of frond length for five stands along an exposure to wave action gradient: Stand 1, most exposed; Stand 5, most sheltered.

TABLE II

Fronid length, weight, and reproduction in five stands along a gradient of exposure to wave action.

Stand	Increasing shelter \longrightarrow				
	1	2	3	4	5
Sample size	1126	1676	2302	1256	1440
Fronid weight (g)					
Arithmetic mean	0.38	0.36	0.36	0.55	0.71
Geometric mean	0.038	0.065	0.030	0.053	0.041
Skewness	3.20	4.22	7.77	8.56	4.33
$C_{50}W$	10.47	4.99	2.18	3.86	2.48
Fronid length (cm)					
Arithmetic mean	9.87	11.73	9.05	10.74	14.20
Geometric mean	4.76	5.21	3.71	4.53	5.31
Skewness	0.89	1.63	2.28	1.94	2.19
Fronid reproduction (g)					
Arithmetic mean	0.046	0.192	0.091	0.116	0.125
Skewness	4.43	4.85	10.11	7.84	5.05
Maximum	1.24	8.30	12.33	8.80	4.82
% of fronds with no receptacles	71	77	90	88	85

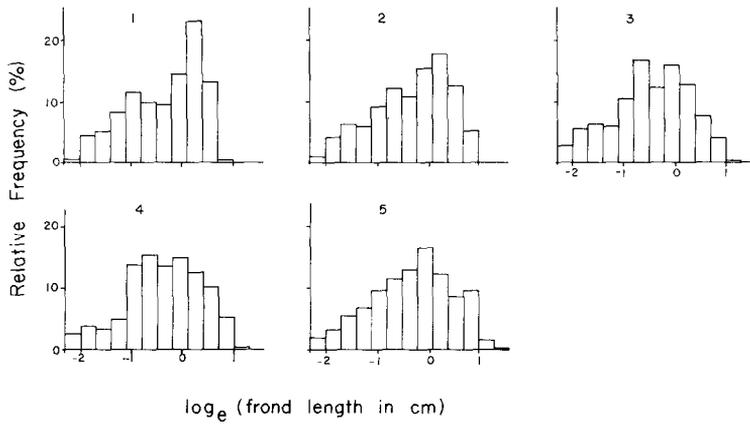


Fig. 2. Relative frequency histograms of \log_e (frond length) for five stands along an exposure to wave action gradient.

of the logarithm of frond weight were nearly symmetrical (Fig. 3). Table II also gives values for $C_{50}W$, the smallest percentage of fronds in a stand that together contribute 50% of the total stand biomass. $C_{50}W$ is greatest in extreme exposure, where the largest 10.47% of fronds contribute 50% of the standing crop, and least in Stand 3 where 50% of the standing crop is contributed by only the largest 2.18% of fronds.

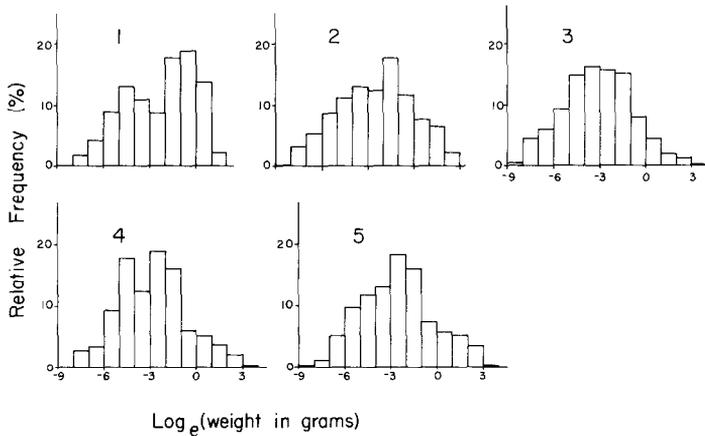


Fig. 3. Relative frequency histograms of \log_e (frond weight) for five stands along an exposure to wave action gradient.

Reproduction by individual fronds increased approximately linearly with frond weight. Regression lines for these relationships are as follows:

Stand 1	$R = 0.153w - 0.013;$	$r^2 = 0.61$
Stand 2	$R = 0.420w - 0.068;$	$r^2 = 0.88$
Stand 3	$R = 0.415w - 0.056;$	$r^2 = 0.93$
Stand 4	$R = 0.241w - 0.017;$	$r^2 = 0.91$
Stand 5	$R = 0.222w - 0.032;$	$r^2 = 0.87$

There was considerable overlap between data from Stands 4 and 5, and from Stands 2 and 3; there was virtually no overlap between data from these two pairs of stands. Although the nature of the data was such that tests of significance could not be used, it is clear that reproduction of individual fronds was greater for any given weight at the more exposed pair of stands (2 and 3). As a consequence of these reproduction-weight relationships, frequency distributions of reproduction were extremely skewed, with the majority of fronds at all sites having few or no receptacles (Table II).

FROND DEVELOPMENT

Growth in length

Increases in length over 1 yr by primary shoots are shown in Fig. 4. In all five stands growth increased with shoot length, apparently approaching some upper limit. This limit clearly increases from Stand 1 to Stand 3 and is perhaps lower at Stand 4 than at Stand 3. Although data for Stand 5 are limited due to mortality resulting from rotting beneath labels, growth rates of shoots < 15 cm in length are clearly very much less than shoots of similar sizes in Stand 4.

Initiation of laterals

The number of lateral pits per unit length of internode showed no significant correlation with distance from the substratum in either Stand 1 or Stand 5 ($r^2 = 0.174$ and 0.048 , respectively, $P > 0.05$). Increasing numbers of both vegetative and reproductive laterals with increasing length in Stand 5 (Fig. 5) must, therefore, result from an increase in the number of laterals per pit. Fig. 6 shows that in Stand 5 the type of lateral produced also changes with length. Short primary shoots produce few, if any, mainly vegetative laterals (note that no data are given for shoots < 10 cm since it is rare for any shoot of that length to have two vesicles); primary shoots > 50 cm produced large numbers of receptacles and only occasional vegetative laterals. Intermediate lengths reflected the change-over between these two behaviours, with increasing numbers of all laterals, of which the proportion that were reproductive also increased with length. In Stand 1 even the shortest fronds produced receptacles (Fig. 6). There was no obvious change-over of lateral type with increasing length, vegetative laterals were found in small numbers.

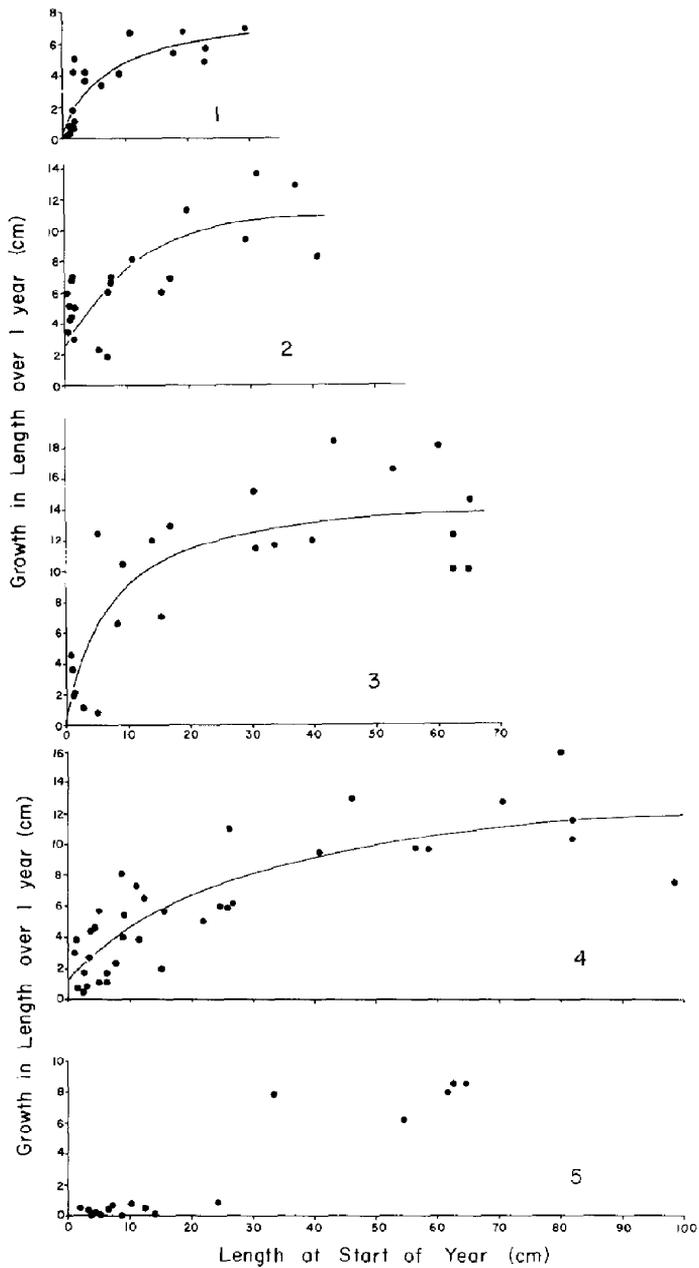


Fig. 4. Growth in length over 1 yr by unbroken primary shoots in five stands along an exposure to wave action gradient: fitted curves are of the form $y = a_1 + a_2 \exp[a_3/(a_3 + x)]$.

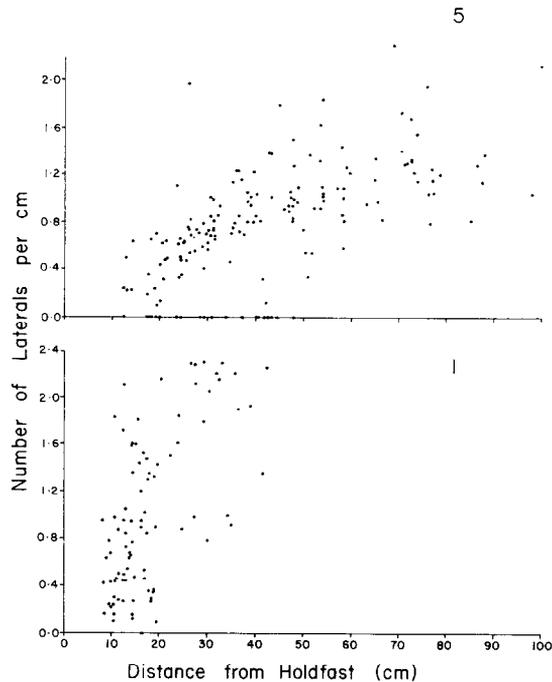


Fig. 5. Lateral initiation by the youngest complete internodes of unbroken primary shoots from extremes of an exposure to wave action gradient (Stands 1 and 5).

Survival of vegetative laterals

In Stand 5 losses of vegetative laterals increased with distance from the substratum and with lateral age (Fig. 7). Most of these were lost by the removal of a large portion of the frond, rather than by being individually removed at their lateral pits. Survival in Stand 1 was very much lower than in Stand 5; of the first-year laterals on labelled fronds only six remained after 1 yr (Fig. 8). In Stand 1 laterals in their second year were extremely uncommon.

Truncation of the primary shoot

Frequency distributions of numbers of vesicles on primary shoots are shown in Fig. 9. Since fronds can be aged only relative to the formation of the first vesicle, frequency is expressed relative to the number in the one-vesicle class. The equation $y = \exp[-(x/b)^c]$ (Pinder *et al.*, 1978) was fitted to the data by least squares linear regression of the transformed variables. This function has two parameters that allow survival curves to be compared, a "scale" parameter (b) and a "shape" parameter (c). If the probability of being broken increases with age c will be > 1.0 and if it decreases with age c will be < 1.0 . There is no clear trend in c with exposure to wave action. The

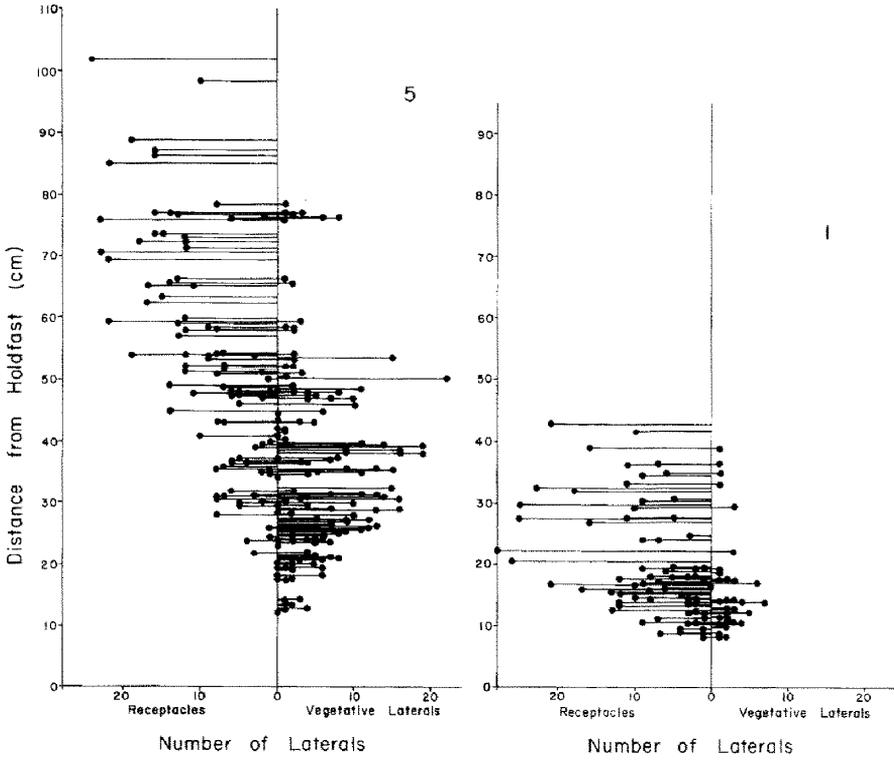


Fig. 6. Types of laterals produced by the youngest complete internodes of unbroken primary shoots from extremes of an exposure to wave action gradient (Stands 1 and 5).

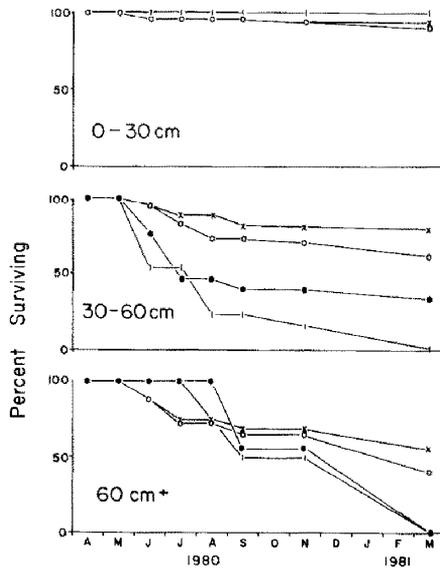


Fig. 7. Survival of vegetative lateral shoots of different ages, grouped according to distance from the holdfast in a sheltered stand: x, 1 yr old; o, 2 yr old; |, 3 yr old; ●, 4 yr old.

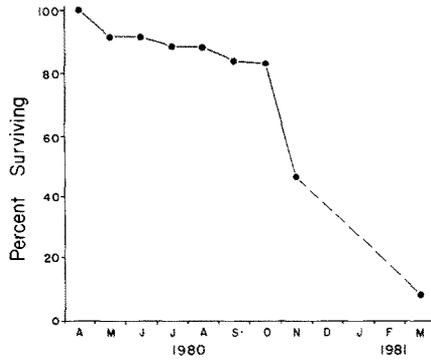


Fig. 8. Survival of 1-yr-old vegetative lateral shoots in an exposed stand.

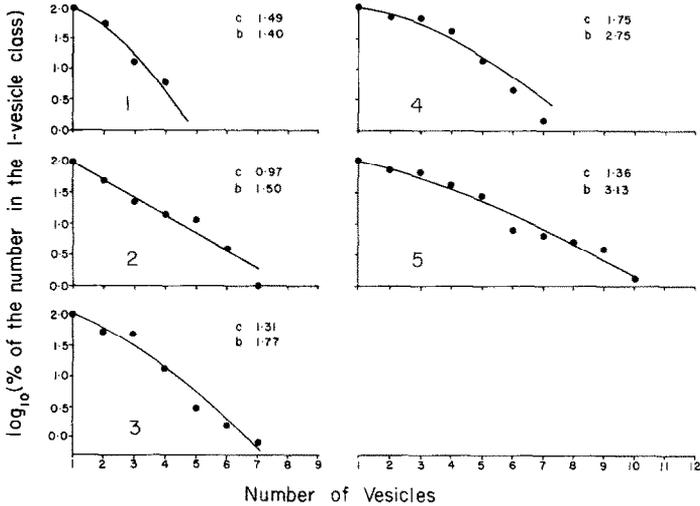


Fig. 9. Frequencies of unbroken primary shoots with a range of vesicle numbers along their lengths, standardized relative to the frequency of those with one vesicle: fitted curves are of the form $y = \exp[-(x/b)^c]$; estimated values of b and c are given.

scale parameter b , on the other hand, increased from Stand 1 to Stand 5, reflecting increasing longevity with increasing shelter.

Removal of the primary apex resulted in a slight increase in lateral initiation on the internode immediately proximal to the cut surface (Fig. 10). Small numbers of vegetative laterals were produced by most truncated shoots, whereas on controls very few vegetative laterals were initiated at all.

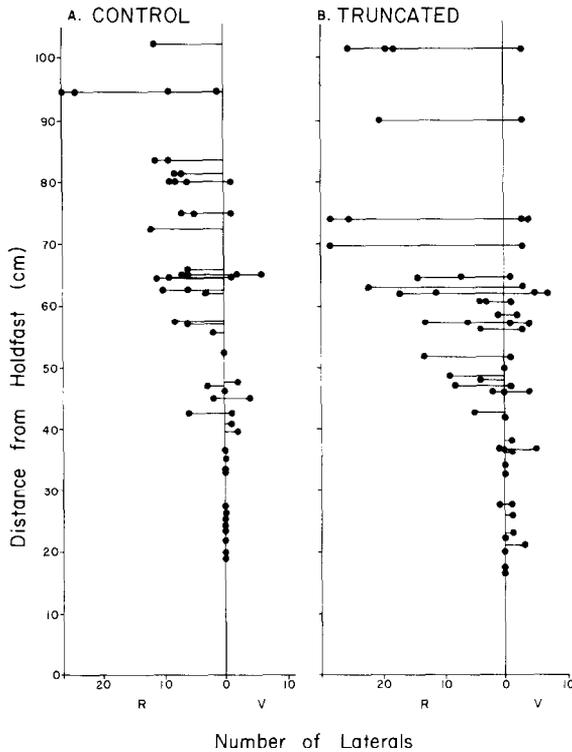


Fig. 10. Types of laterals produced by the youngest complete internodes of unbroken primary shoots which have either been left intact (A) or had their apices removed (B) in a dense, sheltered stand.

FIELD AND LABORATORY EXPERIMENTS

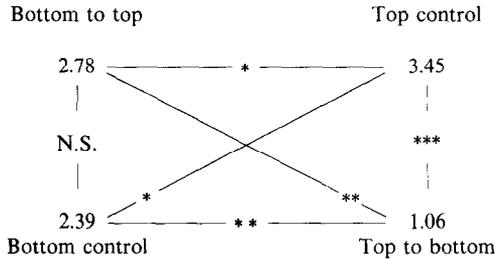
Growth of excised control sections of shoots was less beneath the algal canopy than on the canopy surface. Shoots moved to below the canopy from on top grew less than the controls at both levels (Table III). Growth of shoots moved in the opposite direction was slightly, but not significantly, greater than the below-canopy controls and significantly less than the above-canopy controls. In both cases the growth rates of transferred shoots were significantly lower than the growth rates of shoots normally growing at that level. The number of all laterals, vegetative and reproductive, per unit length of shoot was greatest for above-canopy controls. No laterals were produced by below-canopy controls. Movement of shoots to below the canopy significantly reduced the number of laterals, whereas movement to above the canopy resulted in lateral production, although significantly less than above-canopy controls. Shoots from the canopy surface produced similar proportions of receptacles at whichever level they were located. Shoots moved from below the canopy produced a much lower proportion of receptacles than above-canopy controls.

Clearance of the canopy resulted in a significant increase in growth rate and lateral

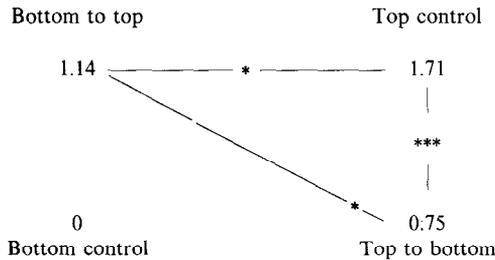
TABLE III

Growth and lateral initiation by excised sections of primary shoots tied at different levels in the canopy:
 *, $0.05 > P > 0.01$; **, $0.01 > P > 0.001$; ***, $P < 0.001$; N.S., not significant.

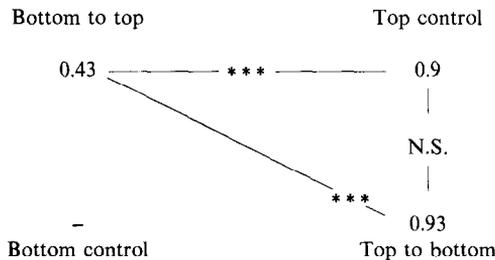
Mean lengths of apical tips (cm)



Mean number of laterals, vegetative and reproductive, per cm of internode



Percentage of reproductive laterals



initiation by young fronds (Table IV). The proportion of reproductive laterals decreased on canopy removal and was very much less than for excised shoot sections moved on to the canopy surface. It was also very noticeable that canopy removal caused a change in pigmentation of young fronds from very dark green to almost yellow. This was visually similar to the difference in colour between shoots on the canopy surface and those underneath. Irradiance within the canopy decreased greatly with depth, in contrast to where the canopy had been removed (Fig. 11).

TABLE IV

The effect of canopy removal on growth and lateral initiation by young fronds: **, $0.01 > P > 0.001$; ***, $P < 0.001$.

	Canopy removed (n = 26)		Control (n = 30)
Length of apical tip	7.06	***	4.12
Vegetative and reproductive laterals per cm of internode	0.67	**	0.23
Proportion of reproductive laterals	2.1	***	38.0

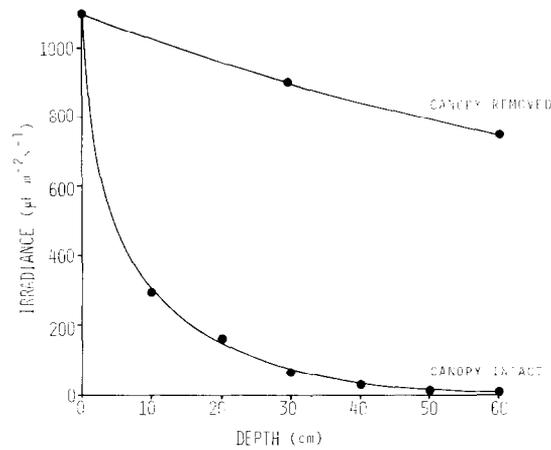


Fig. 11. Quantum irradiance in stands of *A. nodosum* on a sunny day in May, where either the canopy has been removed or left intact: curves are fitted by eye.

TABLE V

Growth and lateral initiation of shoot sections grown in shallow trays under a range of shading conditions: A, shoots from above the canopy; B, shoots from beneath the canopy; a similar superscript indicates no significant difference ($P > 0.05$).

Relative irradiance		100%	50%	25%	12.5%
Mean length of shoot apices (cm)	A	3.99 ^a	3.83 ^a	3.42 ^a	3.50 ^a
	B	3.76 ^b	4.29 ^b	4.27 ^b	2.82
Number of laterals (vegetative and reproductive) per cm of internode	A	2.49	1.84 ^c	1.33 ^c	0.41
	B	1.75	1.04	0.29 ^d	0.09 ^d
Percentage of reproductive laterals	A	0.96 ^e	0.99 ^e	1.00 ^e	1.00 ^e
	B	0.58 ^f	0.66 ^f	0.51 ^f	0.91

In the laboratory experiment only at 12.5% irradiance did shoot growth differ significantly ($P < 0.05$) from the other treatments (Table V), indicating that over most of the range of conditions light was not limiting to growth in length. Initiation of laterals was significantly reduced by increasing shade and was lower for frond sections originating from below the canopy than from those from the canopy surface. A larger proportion of laterals was reproductive on shoots derived from above the algal canopy than on those from below.

DISCUSSION

In a dense population, where light is an important limiting factor, there is a clear advantage to be gained by having light-collecting apparatus above that of neighbours. It is to be expected, therefore, that as populations develop and competition proceeds, the photosynthetic canopy will be raised higher and higher, and that the canopy will be raised furthest from the substratum under the most competitive conditions (Cousens, in press). In stands of marine algae mechanical removal of material by wave action will impose severe restrictions on canopy development. At sites of heavy wave action, fronds will be kept short and lateral branches will be quickly removed. This will restrict the canopy structure at such locations to being very low, with most biomass concentrated very close to the substratum. At sites sheltered from wave action, where mechanical restrictions are less important, canopy development will be able to proceed under competitive modification, and the biomass will become concentrated much further from the substratum.

The overwhelming picture that emerges from *A. nodosum* frond population structures is one of dominance by a small number of large fronds. In sheltered stands in particular, only a few, large individuals have their shoot systems on the canopy surface, contribute most of the stand growth and reproduction, and cause intense shade beneath them. The subordinate fronds experience little irradiance and as a result grow slowly and reproduce little, if at all. In terrestrial plant populations even-aged populations progress through time from symmetrical to log-symmetrical weight distributions (Obeid *et al.*, 1967) or even to bimodal (Rabinowitz, 1979). Recruitment, which must occur to maintain all-aged populations, will further tend to increase skewness of weight distributions. New recruits will be competitively inferior to the established individuals; as a result they may remain small for long periods and be subject to high mortality (Hett & Loucks, 1968). Extreme skewness of size-distributions is, therefore, expected to be usual for dense, all-aged populations of seaweeds as well as for higher plants. Most of the fronds can be considered as a "meristem bank" of potential recruits to the canopy surface. If they survive intact, any of these small fronds may become dominant. There is no evidence in the results of the present study to support Baardseth's (1970) contention that "once weak, always weak: once strong, always strong".

In exposed locations all *A. nodosum* fronds produce few vegetative laterals, but are prolific reproducers even at an early age. Such an allocation of resources is to be

expected in habitats where environmental severity is extreme and life expectancy of fronds is likely to be short. Also, in the absence of substantial competition, it is often observed that terrestrial plants reproduce more and at an earlier age and size than in dense stands (Matthews, 1963). In stands sheltered from wave action, where shading by the largest fronds is considerable, reproduction does not occur until they have reached a greater age and size. Young fronds produce almost no laterals at all and grow very slowly. Gradually, as they increase in size, vegetative laterals may be produced in great numbers, taking advantage of the increasingly favourable microclimate. When they reach the canopy surface, investment is, however, almost completely switched from vegetative growth to reproduction. Again, this pattern shares many similarities with the development of forest trees (Nanda, 1962). The indications from both the field and laboratory experiments reported here are that much of this change in behaviour is the result of phenotypic plasticity, rather than being a genetically fixed pattern of events. Changes in reproductive effort of other species of seaweeds with increasing competition (Russell, 1979) may not necessarily result from genetic differences through natural selection, but may be simply a phenotypic response to the environment in which they find themselves. There is clearly scope for considerable research on this topic. The development of *A. nodosum* fronds has been described in great detail by Baardseth (1955, 1970) and his results, particularly the age at which primary shoots form their first vesicle, have been used elsewhere (Seip, 1980). The fronds that he describes, however, were growing in a stand recovering from a recent harvest. Harvesting, by removing large portions of the canopy, can be expected to change drastically the conditions under which surviving fronds are growing. It is possible that many of the details of development described by Baardseth may be specific to harvested populations and may not apply to natural stands.

With such large and plastic changes in behaviour depending on both site and position within a population, it is clearly difficult to interpret many laboratory experiments in terms of field biology without knowing the exact origin of the material examined. It is likely that most pieces of fronds used in the laboratory are derived from mature fronds lying on the canopy surface at low tide; however, it would clearly be advantageous for this and other descriptive field data to be included in descriptions of laboratory experiments. Pieces of fronds may retain characteristics related to their origin for some considerable time. Growth studies of sporelings produced in the laboratory are rare for *A. nodosum*, largely because of a very slow growth rate. Such studies, however, would help to elucidate further some of the patterns of development described here. Within the present study the effects of light on receptacle initiation, pigmentation, and shoot growth would warrant more detailed investigation. For example, the reduced growth of shade-adapted shoots under low light but not of canopy-surface shoots is difficult to interpret and requires confirmation.

Several aspects of development in *A. nodosum* were found to be similar to patterns observed in terrestrial plants. Apart from reproduction, there were changes in pigmentation with both canopy position and light intensity resembling the difference between

“sun” and “shade” plants on land (Cousens, 1982; Boardman, 1977). Preliminary studies of photosynthetic rates support the similarity in sun and shade physiologies (Cousens, 1981). Elsewhere it has been reported that net annual production per unit area was similar to temperate forests (Cousens, 1984), and that density-weight relationships described for higher plants appeared to apply to seaweed stands (Cousens & Hutchings, 1983). For seaweed communities (Chapman, 1973) there also seem to be similarities in the factors determining zonation on the shore and zonation on mountains. Therefore, there appear to be fundamental similarities in behaviour at the biochemical, physiological, population, and community levels between at least some seaweeds and higher plants, despite basic differences in structure and function. A similar observation has been made by Knight & Parke (1950) for *Fucus* spp. This may, at first, appear surprising. All plant life is, however, dependent on many of the same, major, limiting resources. It is therefore likely that, regardless of taxonomy, there will only be a limited range of overall responses to changes in those resources. For example, where light is limiting, competition will result in some individuals obtaining a greater share than others, and this can only lead to a size hierarchy. Also, if the inferior competitors are to survive, they must increase their photosynthetic ability, such as by increasing their pigmentation or decreasing their compensation irradiance. In conclusion, it is likely that both higher and lower plants will be found to share many patterns of ecological and population biological responses.

ACKNOWLEDGEMENTS

The author would like to thank Drs E. C. Pielou and A. R. O. Chapman for their advice throughout this study. The study formed part of a Ph.D. thesis at Dalhousie University and was funded partly by a Canadian Commonwealth Scholarship and partly by a Natural Sciences and Engineering Research Council of Canada grant to Dr E. C. Pielou.

REFERENCES

- BAARDSETH, E., 1955. *Regrowth of Ascophyllum nodosum after harvesting*. Institute for Industrial Research and Standards, Dublin, 63 pp.
- BAARDSETH, E., 1970. Synopsis of biological data on knobbed wrack. *F.A.O. Fisheries Synopsis* 38, 46 pp.
- BOARDMAN, N. K., 1977. Comparative photosynthesis of sun and shade plants. *Annu. Rev. Plant Physiol.*, Vol. 28, pp. 355–377.
- CHAPMAN, A. R. O., 1973. A critique of prevailing attitudes towards the control of seaweed zonation on the sea shore. *Bot. Mar.*, Vol. 16, pp. 80–82.
- CHAPMAN, A. R. O., 1979. *Biology of seaweeds – levels of organisation*. University Park Press, Baltimore, 134 pp.
- COUSENS, R., 1981. Population biology of *Ascophyllum nodosum* (L.) Le Jolis. Ph.D. thesis, Dalhousie University, Halifax, Nova Scotia, 273 pp.
- COUSENS, R., 1982. The effect of exposure to wave action on the morphology and pigmentation of *Ascophyllum nodosum* (L.) Le Jolis in south-eastern Canada. *Bot. Mar.*, Vol. 25, pp. 191–195.

- COUSENS, R., 1984. Estimation of annual production by the intertidal brown alga *Ascophyllum nodosum* (L.) Le Jolis. *Bot. Mar.*, Vol. 27, pp. 217–227.
- COUSENS, in press. Quantitative reproduction and reproductive effort by stands of the brown alga *Ascophyllum nodosum* (L.) Le Jolis in south-eastern Canada. *Estuarine Coastal Self Sci.*
- COUSENS, R. & HUTCHINGS, M.J., 1983. The relationship between density and mean frond weight in monospecific seaweed stands. *Nature (London)*, Vol. 301, pp. 240–241.
- DAVID, H.M., 1943. Studies in the autecology of *Ascophyllum nodosum* Le Jol.. *J. Ecol.*, Vol. 31, pp. 178–198.
- HETT, J.M. & O.L. LOUCKS, 1968. Application of life-table analyses to tree seedlings in Quetico Provincial Park, Ontario. *For. Chron.*, Vol. 44, pp. 29–32.
- KESER, M., 1978. Ecological effects of harvesting on the growth of *Ascophyllum* and the growth dynamics of *Fucus*. Ph.D. thesis, University of Maine at Orono, 137 pp.
- KNIGHT, M. & M. PARKE, 1950. A biological study of *Fucus vesiculosus* and *F. serratus*. *J. Mar. Biol. Assoc. U.K.*, Vol. 29, pp. 439–514.
- LEWIS, J.R., 1964. *The ecology of rocky shores*. The English Universities Press Ltd., London, 323 pp.
- MACFARLANE, C., 1952. A survey of certain seaweeds of commercial importance in southwest Nova Scotia. *Can. J. Bot.*, Vol. 30, pp. 78–97.
- MATTHEWS, J.D., 1963. Factors affecting the production of seed by forest trees. *For. Abst.*, Vol. 24, pp. i–xiii.
- NANDA, K.K., 1962. Some observations on growth, branching behaviour and flowering of teak (*Tectona grandis* L.F.) in relation to light. *Ind. For.*, pp. 207–218.
- NIELL, F.X., 1979. Sobre la biología de *Ascophyllum nodosum* (L.) Le Jol. en Galicia. III. Biometría, crecimiento y producción. *Invest. Pesq.*, Vol. 43, pp. 505–518.
- OBEID, M., D. MACHIN & J.L. HARPER, 1967. Influence of density on plant variation in fibre flax. *Crop Sci.*, Vol. 7, pp. 471–473.
- PINDER, J.E., J.G. WIENER & M.H. SMITH, 1978. The Weibull distribution: a new method of summarizing survivorship data. *Ecology*, Vol. 59, pp. 175–179.
- RABINOWITZ, D., 1979. Bimodal distributions of seedling weight in relation to density of *Festuca paradoxa* Desv. *Nature (London)*, Vol. 277, pp. 297–298.
- RAGAN, M.A. & A. JENSEN, 1979. Quantitative studies on brown algal polyphenols. III. Light-mediated exudation of polyphenols from *Ascophyllum nodosum* (L.) Le Jol. *J. Exp. Mar. Biol. Ecol.*, Vol. 36, pp. 91–101.
- RUSSELL, G., 1979. Heavy receptacles in estuarine *Fucus vesiculosus* L. *Estuarine Coastal Mar. Sci.*, Vol. 9, pp. 659–661.
- RUSSELL, G. & A.J. FIELDING, 1981. Individuals, populations and communities. In *The biology of seaweeds*, edited by S.L. Lobban & M.J. Wynne, Blackwell Scientific Publishers, Oxford, pp. 393–420.
- SEIP, K.L., 1980. A computational model for growth and harvesting of the marine alga *Ascophyllum nodosum*. *Ecol. Model.*, Vol. 8, pp. 189–200.
- SHARP, G.J., 1981. An assessment of *Ascophyllum nodosum* harvesting methods in south-western Nova Scotia. *Can. Tech. Rep. Fish. Aquat. Sci.*, No. 1012, pp. 1–34.
- SUNDENE, O., 1973. Growth and reproduction in *Ascophyllum nodosum* (Phaeophyceae). *Norw. J. Bot.*, Vol. 20, pp. 249–255.
- TERRY, L.A. & B.L. MOSS, 1980. The effect of photoperiod on receptacle initiation in *Ascophyllum nodosum* (L.) Le Jol. *Br. Phycol. J.*, Vol. 15, pp. 291–301.