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DEMOGRAPHY OF HARVESTED
POPULATIONS OF
ASCOPHYLLUM NODOSUM

by

M. L. Lazo

Submitted in partial fulfillment of the
requirements for the degree of Ph.D. in Biology

at

Dalhousie University
Halifax, Nova Scotia
May 1992



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Abstract

The objectives were to determine the main factors that influence the growth of the seaweed *Ascophyllum nodosum* stands in southwestern Nova Scotia. A demographic approach was taken. Response variables were assessed at each life-cycle stage. A method to distinguish stages in the life cycle of modules was developed. Experimental studies were conducted to determine the effects of harvesting intensity and season, interference and herbivory on growth, reproduction, vegetative spread and survival.

The relationship between size and reproduction determined 4 life cycle stages. These were, class 1, below a minimum critical size needed for reproduction, class 2 and 3 within reproductive size, with class 2 being vegetative and class 3 reproductive, and class 4 the largest modules and almost always reproductive. This class also produced 10 times more eggs than modules in class 3.

Harvesting intensity and season did not appear to affect growth in size. The response of all classes (except class 4) was similar in that they all grew on average 10 cm in two years. Growth decreased with life cycle stage, with class 4 experiencing breakage rather than increases in size. As class 1 and 2 were the most numerous classes and of the fastest growth rates, the regrowth rate of a stand depends upon the numbers of modules in classes 1 and 2.

Interference influenced vegetative spread, growth in biomass and reproduction but effects were unusual. Low density promoted module natality but modules did not grow in size. High density inhibited vegetative spread but enhanced growth in size. More modules attained reproduction at high than at low densities. High density exerted a negative effect on the formation of class 1 modules but the effect on the other classes was positive or negative.

Herbivores consumed 99 % of the germlings in one year but did not affect modules. Vegetative spread emerged as a key factor of population growth. The present study suggested that the main factors that influence population growth are the growth rates of the smallest modules, interference and vegetative spread.

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Finally but very especially, I wish to thank my husband, John. He was the perfect companion and friend with who I shared fun times and support during the painful final stretch. Being aware that such a great companion is not so common, I consider myself very lucky.

Introduction

The fundamental objective of population ecology is to understand and describe the size and numbers of individuals in a population (Harper 1981, Chapman 1986a and ref. therein). A powerful way in which this can be thoroughly achieved for plant populations is by means of demographic assessment (Hutchings 1990). Statistics of births and deaths provide keys to predict future population trends. The basic equation that describes population dynamics is

$$N = N_0 + \text{births} - \text{deaths} + \text{immigrants} - \text{emigrants} \quad (1)$$

where N_0 is the number of individuals at time zero and N is the number of individuals at the next time interval considered.

Stand biomass has been more relevant to exploitation and consequently more widely studied than plant vital rates (growth, mortality, reproduction). This approach has limited predictive value. Knowledge of growth rates is important to maintaining sustainable harvest. Also, in the long term, yield depends on demographic parameters such as reproduction and mortality rates. For instance, a model of biomass recovery as a function of time in Norwegian stands of the seaweed *Ascophyllum nodosum* was used to determine the time interval between cuts (Seip 1980). As population parameters such as recruitment rates are not accounted for, detrimental effects on these are not readily detected. If harvesting reduces recruitment, the population will eventually decline but this

effect will not be detected by a model of biomass because individuals are long-lived and can regrow after harvesting.

Examination of population parameters provides a powerful tool to understand, describe and control populations of interest. While management may be possible with methods other than demographic assessments (i.e. assessments of counts or biomass), insights into future population trends are gained with statistics of vital rates. For instance, since the largest individuals can produce a disproportionate amount of offspring (Weiner 1988), selective cutting can severely reduce the number of individuals in the new generation. Assessment of the fecundity of individuals in different sizes can unravel the effect of cutting on future population size.

Simple counts of plants are not sufficient to assess changes through time because counts are not sensitive to alterations in population demography (Harper 1977, Hutchings 1990). For instance, *Ophrys sphegodes* in England is an endangered species of orchid. Counts of individuals carried over 10 years showed no particular change in the size of the population (Hutchings 1990). However, an analysis of demographic parameters showed that there was no new recruitment from seed and deaths of adults were being masked by sprouting from previously dormant tubers. Counts in the population did not give any logical reason to conclude that the size of the population was changing in any direction. Grazing animals were kept out of the area during flowering and settling time which resulted in increased seedling survival. The response of the population to the change in management would have not been clear without an analysis of recruitment and mortality rates.

The usefulness of demographic assessments is as follows: a) gain in information on the species' life cycles; b) detection of population deterioration and c) ability to determine how and why a population is changing (Hutchings 1990). Census techniques require more effort

and time than counts, but the insights obtained often make them well worth the effort.

Solbrig (1980), then adapted by Chapman (1986a), reported a list of minimum parameters needed to study plant populations. The list includes events of the life cycle correlated with age. As size is often a better predictor of those events (Chapman 1986b; Ebenman & Persson 1988) than age, I have adapted these parameters to size and expressed them in seaweed terminology. These are:

1. germling and adult mortality,
2. reproductive life and size span,
3. fertility (i.e. proportion of individuals reproducing at a particular time), and,
4. fecundity (i.e. number of spores or gametes produced by each size stage).

Although not included, vegetative spread (i.e. formation of new fronds) is an important component of fecundity in species that reproduce clonally (Taylor et al. 1981). In fact, vegetative spread can be the most important determinant of population growth in species with limited sexual recruitment (this study). Vegetative spread is also a significant factor of competitive relationships (Sackville-Hamilton et al. 1987). It is to be noted that vegetative spread is both the formation of new plants through a split-up process as well as the emergence of new fronds from meristematic tissue (see below in life cycle and morphology).

Studies where the above parameters have been looked at together are largely lacking despite the fact that they are the primary determinants of the size and abundance of plants (Chapman 1986a). The aim of the present study was to look at the above population parameters so as to understand the underlying mechanisms that regulate the growth of *Ascophyllum nodosum* populations. The information gained was, then, used to test basic assumptions of the

Lefkovitch matrix model that may be employed to determine the effect of harvesting on population growth.

Species

Ascophyllum nodosum is a species of seaweed within the division Phaeophyta and a member of the order Fucales. This species has two life forms, the attached form and the unattached form (Sharp 1987a). The former grows in the intertidal zone of rocky shores and is the object of this study. In southwestern Nova Scotia this species is found from the mean high water spring tide line to about 6 m in the subtidal. Its distribution extends from northern Norway and the White sea to Portugal in the Eastern Atlantic (Sharp 1987a). In the Western Atlantic, *A. nodosum* extends from Newfoundland and the St. Lawrence estuary (Sharp 1987a) to New Jersey (Baardseth 1970).

Ascophyllum nodosum is a dominant species of Western Atlantic shores but its abundance and size depends on the degree of exposure (Cousens 1985, Sharp 1987a). *Ascophyllum nodosum* does not withstand wave action and damage by ice. The greater the exposure to wave action and ice, the smaller the fronds (Cousens 1985). Plants are also broken and dislodged by ice (Åberg 1990a, b). The amount of biomass lost due to ice can make up a significant part of the annual crop (Mathieson et al. 1982).

The present study site is located in Woods Harbour, at 43° 32' lat. N and 65° 44' long. W, southwestern Nova Scotia. The site is mainly sheltered but at particular points exposure is greater. The experimental areas chosen extended horizontally from a distance of 1.5 m from the *Fucus* zone to 22 m below. The plant sizes increase with depth suggesting that conditions for growth improve with depth.

Life Cycle and Morphology

Ascophyllum has a monophasic life cycle with separate male and female gametophytes. The consistency of the dioecious trait has been used to identify genetic individuals (Åberg 1989). Fertilization takes place when sperm and eggs are released. Zygotes develop into an individual (genet) consisting primarily of a shoot with a holdfast. Reiteration (White 1979) of this unit results in a holdfast with from 1 to about 1000 shoots (unreported data collected in another study, Chapter 2). This type of construction is called modular (White 1979, Harper 1981, Begon et al. 1986). The shoots are called modules in terrestrial ecology and fronds in seaweed ecology. The term module will be used here to refer to primary fronds (Sharp 1987a) of an *A. nodosum* individual bearing in mind that the terms 'shoot', 'frond', and 'module' mean the same.

Module branching is typically dichotomous but lateral branches arising from lateral meristems are common as well. The reproductive structures, which arise from the same lateral meristems, are sac-like and are called receptacles. In the early stages of formation lateral branches and receptacles are morphologically similar. In a later stage the receptacles contain cavities or sacs called conceptacles where gametes are formed. When mature, gametes are released through a single pore in the conceptacle. More details on the morphology of this species are given elsewhere (Sharp 1987a).

New modules emerge clonally from the meristematic tissue of the holdfast or from the base of other modules and are called primary modules (to be distinguished from the lateral branches because these latter arise from lateral meristems). Each new module forms its own holdfast tissue with which the holdfast of the genet expands. The formation of new modules through clonal reproduction may be considered vegetative spread. Losses of holdfast tissue split the genet into separate clones (or 'plants') which can grow and split

again. Clones must be distinguished from the genet or 'individual' because the genets originate from a zygote. The occurrence of clonal reproduction in this species suggests that the genet may grow indefinitely and spread in time and space. Evidence from other species supports this view. Studies have shown that clones of a single genet may be spread over an area of 43 ha and that the genet may exceed 10,000 years old (Harberd 1962, 1967, see also Harper 1977, White 1979, Sackville-Hamilton et al. 1987).

The life span of an *A. nodosum* clone (or 'plant') is not known for certain but in theory it may be between 50 to 60 years (Åberg 1990b). Modules are also long-lived with a life span of up to 16 years (Peckol et al. 1988) or more, although rarely (pers. observ.).

The meaning of the terms used in the above section are below. As clones of different genets cannot be distinguished in this species, I refer to the clones throughout my thesis as 'plants' bearing in mind that these 'plants' may be clones of the same and/or different genets. I chose the term 'plant' because it is the most common term used by botanists.

Clone: Individuals derived by vegetative propagation from a single genet (White 1979, Begon et al. 1986).

Genet: The individual derived from a single embryo (Harper 1977, 1981, White 1979, Sackville-Hamilton et al. 1987, Begon et al. 1986).

Module: An axis. Multicellular unit of construction that is reiterated during the process of the genet's growth (Harper 1977, 1981, White 1979, Begon et al. 1986).

Ramet: A single module of a genet. Ramet is a particular type of module (Harper 1977, White 1979, Harper 1981). If it can survive on its own it is called ramet (Harper per. comm.). The modules of *A. nodosum* are ramets but I have used the term module in my thesis because it is a more general term and more widely known among zoologists and botanists.

Shoot: An axis with lateral appendages (i.e., branches and receptacles) and lateral meristems (White 1979).

Because modules are tightly packed, the morphology of an *A. nodosum* individual may be considered phalanx type (Harper 1981). This form grows as an advancing front, monospecific and occupying a zone of land and resources impenetrable to others. This growth form's disadvantage is self-shading and limited extent of spread.

The phenology of southwestern Nova Scotian stands is as follows (Sharp 1987a, pers. observ.). Fertilization takes place in early spring. Receptacles are shed approximately in May-June. A period of lateral growth follows during which lateral branches and receptacles are formed. Lateral branches and receptacles continue to grow until late fall. Thereafter only receptacles grow reaching maturity in winter and releasing gametes in spring. Maximum growth in module size takes place from spring to late fall. Growth rates and timing of maximum growth however, typically vary with locality (Mathieson et al. 1976).

Size

Since modular species grow as a result of the number and size of modules (see Harper 1977), the size of an *A. nodosum* genet is the summed biomass or numbers of all its modules of all plants originated clonally from a single zygote. Thus, the size of a genetic individual is potentially unlimited (Harper 1977, Hughes 1983, extracted from Schmid 1990). Plant and module sizes, instead, are easier to assess. The size of a plant is its biomass and number of modules. The size of a module is its biomass or an equivalent variable. The mean fresh weight of a plant in the studied stand is 162.2 g but can be as high as 9,850 g. On average, shoots are about 23-cm long but they can reach 170 cm, although rarely. The average fresh weight of a module is 3.6 g, with maximum of 1229.4 g. The data just given are from stands that had not been harvested for

approximately two years. Information on the distribution of biomass from the holdfast to the canopy is given elsewhere (Cousens 1985).

Ecology

Ascophyllum nodosum forms primarily monospecific stands. At the upper and lower limits of the *A. nodosum* zone are *Fucus* species and *Chondrus crispus*, respectively. The reason why *A. nodosum* apparently displaces these species may be a combination of successful sexual recruitment and life span. Experimentally scraped areas were colonized first by *Fucus* but later supplanted by *A. nodosum* (Keser & Larson 1984). Displacement and dominance was attributed to increased germling survival, longevity and resistance to mechanical removal. However, grazing significantly suppresses the recruitment of *A. nodosum* zygotes (Vadas et al. 1982 extracted from Chapman 1986a). There may be then a mechanism other than sexual recruitment that ensures space preemption. One such factor may be vegetative spread because species with a perennial holdfast and or extensive vegetative spread can prevent other species from invading their stands (Sousa et al. 1981). An evaluation of sexual recruitment relative to the role of vegetative spread would be useful to assess their relevance to population growth.

Demography

To be comprehensive, a demographic study of a modular species such as *A. nodosum* must include the statistics of births and deaths of the modules as well as that of the genets (Sackville-Hamilton et al. 1987). The equation that describes the population growth of modules is

$$n = n_0 + \text{module birth} + \text{module deaths} \quad (\text{Harper 1981}) \quad (2)$$

Where n_0 is the number of modules at time zero and n is the number of modules 1 time interval later.

Equation 2 describes the *growth* in size of genets, whereas equation 1 for N (above) describes the changes in *numbers* of genets. The population biology and demography of modules can be exemplified with the growth of a single zygote in culture (Harper 1981). A zygote gives rise to numerous modules that grow and then die. The set of modules may be considered a population of modules. The growth rate of this population is given by the births minus deaths of modules. The development of the population can consist of a phase of exponential growth followed by a linear phase where growth becomes resource-limited, to a phase where birth and death rates of modules are balanced. The sequence of phases is the growth of a single individual but it is, also, a population process at the module level. It is difficult to put this within a context of time because growth is density-dependent at some point (see Chapter 3). Light at ground level may be as low as 0.1 % of that of the surface (Cousens 1982a). Thus, zygotes and germlings may spend an indeterminate time without developing until conditions for growth improve. The lack of research suggests the relevance of the population dynamics of genets and modules to population theory has not been acknowledged in seaweed ecology.

Not distinguishing between genets and modules may have major implications in the formulation of population dynamics theory. The distinction between the two levels may be particularly important to understand the effects of interference upon seaweed stands. There is a small controversy in seaweed ecology concerning the effects of interference. One contention is that seaweeds grow and reproduce more at increased density than at low density (Schiel & Choat 1980, Schiel 1985a). The other contention is that there is a negative relationship between density and mean size. Density stress imposes a boundary condition for maximum mean size (Cousens & Hutchings

1983, Westoby & Howell 1986). A regression line with a -1.5 slope can be found for that boundary. Below that boundary condition any combination of density and size is possible. Cousens and Hutchings proposed that Schiel's & Choat's means were below such boundary and thus did not contradict general theory. This apparent contradiction may have arisen partly from the fact that Cousens & Hutchings and Schiel & Choat did not distinguish between plants and modules. Size and the way that plants and modules grow are not entirely comparable. The contention of the above authors may then appear contradictory because the responses of modules and plants are confounded. The two levels have to be distinguished to determine whether the responses of marine and terrestrial plants are comparable.

Harvesting

Harvesting of seaweeds is practised around the world (McHugh 1991). In Canada this industry is concentrated in the eastern provinces. The most profitable species are *Chondrus crispus*, *Laminaria* spp and *A. nodosum* (Pringle & Semple 1980, Sharp 1987a,b). Most research on harvesting populations has been concerned with the effects of harvesting intensity, frequency and cutting method on growth (Burns & Mathieson 1972, Sharp 1987a, Santelices et al. 1989, Sharp & Pringle 1990, Schiel & Nelson 1990, Vasquez & Santelices 1990). Responses other than growth (Burns & Mathieson 1972, Vasquez & Santelices 1990) have received little attention. However, assessment of the effect of harvesting on survivorship is essential to maintain long-term yield.

Research in the management of fisheries and forests includes a vast number of modelling studies, the majority of these being demographic (Getz & Haight 1989). Although harvesting of seaweeds has been practised for a long time and involves a multimillion dollar industry (Pringle & Semple 1980, Sharp 1987a), demographic modelling has not been recognized as a useful tool. Getz and Haight

(1989) summarized information on management of forests, fisheries and even rearing of insects for biological control but there was not one example of seaweed harvesting. There have also been very few attempts at all to manage the southwestern *A. nodosum* Nova Scotian stands (Sharp 1991, pers. com.). Size-based demographic models, such as the Leslie matrix models or modifications of it have been constructed to simulate the effects of harvesting in seaweeds (Ang 1987, Ang et al. 1990) or to achieve greater understanding of algal resources (Nyman et al. 1990, Chapman unpub.). However, studies using demographic models represent a marginal effort relative to the extent of exploitation.

Other problems with research in management of algal resources concern the methodology employed. Some empirical studies were unreplicated (Gendron 1989). The techniques employed were not the same as those used in commercial harvesting (Smith 1986, Gendron 1989), which result in more or less selective cuts or in cuts at heights different than incurred during commercial harvesting.

Management of *A. nodosum* in Nova Scotia is basically the result of personal experience. Stands are cut, left alone for a recovery period and cut again when the biomass seems to be at prior levels (anecdotal evidence). This scenario has worsened in recent times. With greater technology, the exploitation rate increased from about 60 to over 80% (Sharp 1991). The timing for a second harvest has also been adjusted to shorter time intervals between cuts. The present scenario suggests that the companies involved in the exploitation of this resource fail to address the issue of management and, what it is more, have moved towards uncontrolled exploitation.

Chapter 1

Identifying Size-Based Stages

Abstract

Size-based demographic studies have become common in recent times. It is important to classify size into appropriate categories or stages. The relationship between size, reproductive state and reproductive output in *Ascophyllum nodosum* modules was assessed. Findings were used to develop a method to classify modules into categories with biological meaning.

It was found that a minimum size was required for reproduction but attainment of the minimum size did not necessarily trigger formation of receptacles. The number of modules in reproductive state increased with size. Reproductive output increased with module size also. Using the relationship between size and number of reproductive modules and reproductive output, four size classes were identified. It is reasonable then to consider these classes as stages of the life cycle of *A. nodosum* modules

Introduction

Size-based demography studies have become more common in recent years in marine (Chapman 1986b, Ang 1987, Åberg 1990a,b; Ang & De Wreede 1990) and terrestrial ecology (Werner 1975, Werner & Caswell 1977, Bierzychudek 1982, Ebenman & Persson 1988). One of the reasons for the increasing popularity of size-based demographic studies is that plant size is generally a good predictor of stages of the life cycle. Reproduction under a certain size may not occur at all but its likelihood increases steadily thereafter with size (Werner 1975, Watkinson 1986, Caswell 1988, Lazo & McLachlan 1989). Fecundity in higher plants (Weiner 1984, Watkinson 1986, Caswell 1988) and seaweeds is often positively correlated with size (Chapman 1984). Also, reproductive output is believed to increase with biomass (Schiel 1985a, Ang 1987, Åberg 1990b,c,d). Whether reproductive biomass is *directly* proportional to fecundity, however, remains to be confirmed. The relationship between size and reproduction may then determine life cycle stages, for instance, differential mortality, reproductive performance and probability of flowering (Watkinson 1986).

Size-based demographic studies are possible without classifying individuals into life cycle stages. However, classification of individuals into classes that are associated with demographic processes (e.g. reproduction) for macrophytes are to be preferred because demographic assessments and particularly size-based transition matrix models are easier to interpret (Åberg 1990c). Classes correlated with demographic processes are those that identify stages of the life cycle, e.g. reproductively mature (Werner 1975, Caswell 1988). Size-based classes that comprise individuals in particular levels of reproductive maturity then can be considered to identify stages of the life-cycle.

Ascophyllum nodosum is a species of brown seaweed with modular construction. Plants are believed to be either male or female (Baardseth 1970, Åberg 1989). The reproductive structures, the receptacles, arise from lateral meristems. Personal observations suggested that reproductive modules tended to be more common among modules of large size and that large reproductive modules tended to have more receptacles than smaller ones. Reproductive state and fecundity then appeared to be size-dependent. Therefore this species offered an opportunity to develop a method to identify life cycle stages based on module size.

Materials and Methods

Hereafter life cycle stages are to be referred in the text as size classes. Assessments of size classes were conducted for modules, not plants. *Ascophyllum nodosum* in this and the following chapters (except in the introductions) was referred to as *Ascophyllum*.

Sampling

In January 1988 three rectangular plots (16 m X 21 m) were laid out from about 1.5 m distance from the *Fucus* belt with the long sides seawards. Because there were only few, small *Ascophyllum* plants immediately below the *Fucus* belt this zone was not included. As the size of the individuals increases with depth (unreported data collected from this study), and to ensure an even distribution of samples, a stratified random sampling procedure was employed. One horizontal transect at the top, middle (10.5 m from top) and bottom of the plot was run. All random sampling procedures employed in this study are as indicated elsewhere (Elliot 1971, Southwood 1966, Cochran 1977, Krebs 1989, Manly 1990).

Five 20-cm X 20-cm quadrats were placed along each transect using random numbers (15 quadrats/plot). All plants in these quadrats

were scraped from the substratum with a putty knife, bagged, brought back to the laboratory and processed within 24 h.

For each sample collected, the total wet weight of the sample and the wet weight and reproductive state of each module greater than 4 cm was recorded. Modules with receptacles were considered reproductive, otherwise they were vegetative.

Size Classes

A size frequency distribution of module weights showed that the number of reproductive modules increased with weight. Below 2.0 g modules were almost always vegetative. This set the limit for class 1 which included 85 % of the population. Of these 4 % were reproductive (obviously at the time of the year where reproduction takes place). Modules heavier than 42.0 g were almost always reproductive and this set the limit for another size class (class 4), comprising 1 % of the population. The remaining (2.0 - 42.0 g) modules were either vegetative or reproductive. Modules within this size interval were then divided into 2 more classes, class 2 being vegetative modules and class 3 being reproductive modules. The four classes can therefore be considered to be based on the relationship between weight and number of modules in reproductive state (i.e. reproductive frequencies). Note, however, that classes 2 and 3 are of same size but they will be referred to throughout my thesis as size classes for simplicity. The cut off point between the classes was, to an extent, subjective. However, I tested whether the number of modules in a reproductive state varied significantly among size classes. Results are in the text. The basis for this classification is supported by a study conducted by Mack & Harper (1977). These authors recognized that it is difficult to divide continuous data into unbiased size classes. Mack & Harper suggested that, where a close correlation between reproduction and weight exists, there is sound basis for size class divisions.

One objective of this study was to assess whether the relationship between size and reproductive state varied from one year to the next. To achieve this objective modules had to be assigned to a size class in the field to be monitored at regular intervals (see below). Because of this, modules could not be cut and thus biomass could not be estimated directly. The relationship between length and biomass was then assessed by means of regression analysis. The regression equation was:

$$\ln(\text{length}) = 3 + 0.44 \ln(\text{weight}) - 0.02 \ln(\text{weight}^2) \quad r^2 = 0.85$$

significant at 0.0001

Highly accurate predictions can be obtained from the correlation between length and stem diameter in terrestrial species (Hutchings 1975). However, as opposed to stem diameter, the measure of circumference of modules is a crude one (as used for plants, Cousens 1984, Åberg 1990c). High accuracy is desirable when the purpose is to estimate data which is subsequently used in statistical analysis. Here I only used the regression equation to identify the range of lengths of modules in each class.

Care was taken to meet the assumptions of the regression analysis as indicated in Neter et al. (1983). The distribution of the data was found to be normal (normal plot, $P > 0.01$) and variances were homogeneous (residual plot = random pattern). The samples used in the regression analysis were from harvested (Chapter 2, sampling) and control stands (see sampling, above). The lengths of each size class are below.

Class	Characteristics	Length (cm)
class 1	rarely reproductive	4.0 - 27.5
class 2	vegetative	27.6 - 78
class 3	reproductive	27.6 - 78
class 4	rarely vegetative	> 78

Classes 2 and 3 are of same size but were considered different because they are biologically different, one is vegetative and the other reproductive. I also distinguished these 2 classes because the fact that modules are large enough to reproduce does not mean they will become reproductive. It is known for several other species that individuals may spend their entire life within reproductive size and yet never become reproductive (Chapman 1984, see also Watkinson 1986, Braga 1990). Thus, it is possible that the physiological mechanisms operating in vegetative and reproductive modules are different. Since reproduction is, nevertheless, possible within this size interval, vegetative modules may be considered reproductively mature.

Contingency tables were used to test whether frequencies of reproduction depended on size class. Care was taken to meet assumptions of this analysis (Zar 1984).

Tagging

Plots were reduced to 14-m x 19-m and three permanent horizontal transects were laid out at the top, middle and bottom of the plot, marking the ends with steel rods partly buried in the substratum.

One point along each transect was selected every 3.5 m. The plant nearest to each of these points of the transect was chosen (5 plants/transect).

One module of each of four size classes (see above) in each plant was selected. The selection method consisted of picking a module from the base. The module chosen was the first I saw. Each selected module was tagged and the length and size class recorded. Tags, which were made of monofilament as used by Sharp & Tremblay (1985), were tied around the base of the module. A total of 180 modules were tagged. Tagged modules from another study (Chapter 2) were not used here because those stands were subjected to treatments whereas the present stands were not. The presence or absence, length and reproductive state of each module at the end of the study was assessed.

Fecundity

Computation of fecundity included only classes 3 and 4. Class 1 was not included because it was almost always vegetative and class 2 because it was vegetative. A random sample of 67 modules was collected in January 1990 from the three plots described above and from adjacent stands cut in 1988. Harvesting does not significantly affect the number of receptacles/module or the number of conceptacles/receptacle formed *after* the harvest (unreported analysis from another study, Chapter 2). At the time oogonia were not differentiated. The sample was then used to estimate the number of conceptacles/size class and sex ratio of the population. Five to ten receptacles/module were analyzed. The sex of each selected module was determined by visual examination of one or more conceptacles of two modules of the same plant. Data recorded for each module was length, mean receptacle weight, number of receptacles/module, number of conceptacles/receptacle and sex.

In April of 1990 a second sample of 41 modules was collected. Oogonia had then matured. Two receptacles were analyzed for each module. Data recorded for each module were length, mean receptacle weight, number of conceptacles/receptacle and sex. One conceptacle was split open and the number of oogonia counted. Since there are 4 eggs/oogonium, the number of oogonia/conceptacle was multiplied by 4 to obtain the total number of eggs produced in a single conceptacle.

The effect of module length on the production of eggs was tested to determine significant differences in fecundity between classes 3 and 4. The effect of the abundance of conceptacles/receptacle on the production of eggs of a conceptacle was determined to assess whether the mean egg/conceptacle depended on conceptacle abundance. The fecundities of classes 3 and 4 were estimated by computing the: 1) numbers of receptacles/module, 2) number of conceptacles/receptacle and 3) eggs/conceptacle. The egg production of a module was computed multiplying: mean number of eggs/conceptacle X mean number of conceptacles/receptacle X numbers of receptacles/module.

Data were analyzed with ANOVA. Care was taken to ensure assumptions of ANOVA were met (Underwood 1981). Normality was checked with normal plots and Kolmogorov-Smirnov (K-S) tests and homogeneity of variances with Cochran's test. Data on number of receptacles/module were transformed to \log_{10} to stabilize the variances. Error terms and degrees of freedom (d.f.) were estimated following the guidelines of Underwood (pers. com.) and Zar (1984). The power of the ANOVAs was also estimated (Zar 1984). Overall power ranged between 70% and 99%. Exceptions are given in text.

Results

Relationship between size and reproduction. The length of tagged modules in May 1989 and in April 1990 was divided in 10-cm intervals and the numbers and percentages of reproductive modules within each interval was estimated (Table 1). Table 1 shows that the percentage of modules attaining reproduction increases with length. Table 1 shows that this pattern was consistent in two consecutive years as well. Each year, the relationship between length and reproductive state was statistically significant. Only two modules smaller than 30 cm were reproductive in 1990.

A test was run to determine whether the number of reproductive modules differed among the size classes proposed here (see material and methods). Module lengths in May 1989 and April 1990 were then divided into 3 size classes and tested for differences in reproductive frequencies. Classes 2 and 3 were pooled because they differed by their reproductive state and not by their size. It was found that the size classes were significantly different (Table 2). Moreover, the relationship between size class and reproductive frequencies was statistically significant in the two consecutive years which suggests that the size-reproductive frequency relationship was not a sample artifact. The fact that class 2 is vegetative and class 3 reproductive enforces the distinctiveness of each class. The relationship between size and reproductive state can, then, be used to predict reproductive likelihood.

Assessment of the Fecundity of Classes 3 and 4. The mean number of receptacles per module did not depend on sex but on size class (Table 3). Class 4 modules produced on average five times (264) more receptacles than class 3 (50). Female modules bore an average of 32 receptacles/module in class 3 and 233 in class 4. The mean number of receptacles/module (pooling classes) was 124 in

the males and 164 in the females. This difference was not statistically significant but the power of the performed ANOVA was low (< 80%). However, power analysis also showed that the sample size should have been extremely large for the test to detect a significant difference with such small differences between male and female modules.

The average number of conceptacles in a receptacle depended on sex and size class but the interaction between these two was non-significant (Table 4). Averaging class 3 and class 4, male receptacles had significantly more conceptacles (102) than female receptacles (77). Pooling sexes, receptacles of class 4 modules bore 96 conceptacles whereas receptacles of class 3 modules bore 86. The conceptacle load for female receptacles in class 3 was 64 and 89 in class 4. Data were pooled to illustrate the differences in receptacle load in the classes and sexes. No statistical analysis was conducted with the pooled data.

The *mean* number of eggs in a single conceptacle was 459. The egg production of a conceptacle did not depend on the abundance of conceptacles in the receptacle ($P > 0.05$, Fig. 1). The coefficient of determination of receptacle weight vs number of eggs/conceptacle was 0.08. The coefficient of determination between receptacle mass and number of eggs/receptacle was even lower, 0.06. Although significant ($P = 0.001$), receptacle mass accounted for very little variance in egg production. The egg production of a conceptacle was then virtually the same in small and large receptacles. Thus, the fecundity of a module resulted from the number of receptacles and not from their biomass.

The reproductive output of a receptacle was equal to the mean number of eggs/conceptacle X the number of conceptacles/receptacle. Thus, the fecundity of a receptacle in a female class 3 module was,

459 X 64 = 29,376
 and of a female class 4 was
 459 X 89 = 40,851

The number of eggs produced by a female module (fecundity) in class 3 and 4 is equal to the reproductive output/receptacle X number of receptacles/module

no. egg/class 3 = 29,376 X 32 = 940,032 and,
 no. egg/class 4 = 40,851 X 233 = 9,518,283

Females in class 4 then produced 10.1 times more eggs than females in class 3 and thus potentially produced 10 times more offspring as well.

Sex Ratio. The sex ratio within each size class was 1:1. However, an anomalous gender distribution was found. The receptacles of a single module could be female or male. The conceptacles of a receptacle could be either female or male. Moreover, within a single conceptacle, there were sometimes oogonia and spermatangia. This meant then that the number of eggs produced by a module depends on whether it is monoecious or hermaphrodite and on how much male tissue there is in the conceptacles. It was also not clear how the amounts of female and male tissues in a receptacle should be assessed. I did not determine the number of anomalous individuals in my samples, and so I did not consider them in the estimation of the sex ratio. However, if their numbers were significant, the sex ratio might not be 1:1. It would depend on the overall amount of male and female tissues in the population. The male:female ratio might then affect the above estimates of fecundity.

Discussion

Life cycle stages

This study suggested that *Ascophyllum* modules can reasonably be viewed as growing into 4 stages correlated with events of their life cycle. These stages were determined by size, likelihood of reproduction and fecundity. A minimum size (27.5 cm) was required for reproduction. Below that minimum size modules (class 1) largely failed to become reproductive. Above that size, modules in reproductive state were noted suggesting that reproductive maturity was achieved. Between 27.5 cm and 78 cm, modules could be either vegetative or reproductive. Modules within this size interval that did not attain reproduction, were assigned to class 2 and those that were reproductive to class 3. The number of modules in reproductive state increased with size, modules in class 3 being generally larger in size than those in class 2. Class 4 included the largest modules. These were almost always reproductive and contributed ten times more offspring/module to the next generation than class 3. The fact that the relationship between size and reproductive state was statistically significant and that differences in fecundity due to size were so high suggested that size can be used to predict stages of the life cycle (i.e. reproduction, fecundity) and thus these size classes may be considered distinct stages of the life cycle of modules.

Fecundity cannot always be estimated accurately from reproductive weight. The correlation between reproductive mass and number of eggs was low and thus mass was not a good predictor of fecundity. There must then be other factors whose influence on egg production is more significant than receptacle mass. Another problem was hermaphroditism with conceptacles comprising sometimes both sexes. The fecundity of a size class in terms of eggs then might depend upon how much female and male tissue there is in that class.

In recent years, size-based classes have been used in ecological studies (Chapman 1986b, Werner & Caswell 1977, Caswell 1988) and in matrix models to project future population growth (Ang 1987,

Getz & Haight 1989, Åberg 1990a,b). There are two ways to choose size classes for transition matrix models. In one, size classes are biologically distinct, i.e. represent different stages (Crouse et al. 1987). This method is mostly limited to species where life cycle stages are morphologically distinguishable. In the other, size is divided relatively arbitrarily into intervals (Getz & Haight 1989, Åberg 1990c) and can be used when no differentiation into morphologically distinct stages exists. The disadvantage of this method is that it may produce too many size classes which are not biologically relevant (Åberg 1990c). My method might be viewed as a combination of both and can be used to construct demographic matrix models (Caswell 1989, and pers. com.). This method uses size as an indicator of stages but the stages are correlated with demographic processes. The main advantage of my method is that models may provide more information on future population trends (Åberg 1990a,b, also Caswell 1988, 1989). However, my classification has to be compared with other classifications of the same individuals to determine which one provides the most information about demographic fate. As far as I know this was the first time this method was used for a plant species. In species where size-based stages do not exist the alternative might be to use an algorithm including information on the life-cycle where possible. Åberg (1990c) used this approach to model populations of *Ascophyllum* plants where several categories were produced. Only one (the smallest) was biologically distinct.

Table 1. Percentage of reproductive modules along a range of 10-cm length intervals. Numbers of reproductive modules in each length interval are indicated between parentheses. The total number (N) of modules (vegetative and reproductive pooled) in each interval is also indicated.

Length	1989	N	1990	N
0-10	0 (0)	11	1 (1)	14
10-20	0 (0)	17	0 (0)	6
20-30	0 (0)	21	1 (1)	16
30-40	32 (6)	19	31 (4)	13
40-50	44 (7)	16	37 (6)	16
50-60	75 (15)	20	67 (10)	15
60-70	85 (11)	13	64 (7)	11
70-80	94 (15)	16	100 (3)	3
80-90	100 (17)	17	92 (12)	13
>90	100 (9)	9	92 (11)	12

1989 $X^2= 101.307$ $P>0.0001$;

1990 $X^2= 54.214$ $P= >0.0001$

Table 2. Percentage of reproductive modules in the three lengths intervals (cm) corresponding to classes 1, 2 & 3, and 4. Numbers of reproductive modules within each interval are given within parenthesis.

Year	4-27	27.1-78	> 78
1989	0 (0)	51 (43)	100 (37)
1990	4 (1)	43 (29)	93 (25)

1989 $X^2= 75.044$ $P= >0.0001$; 1990 $X^2= 40.782$ $P= >0.0001$

Table 3. ANOVA table. Effects of class and sex on the mean number of receptacles/module. c X s= size class by sex interaction. N= 67

Source	df	S.S.	F	P
class	1	11.88	31.18	0.0001
sex	1	0.44	1.14	>0.05
c X s	1	0.02	0.06	>0.05
error	56	21.33		

Table 4. ANOVA table. Effects of class and sex on the mean number of conceptacles/receptacle in any given module. c x s= size class by sex interaction. N=67

Source	df	S.S.	F	P
class	1	3507.6	4.49	0.04
sex	1	9641.5	12.36	0.0009
c X s	1	1332.7	1.70	>0.05
error	54	42135.4		

Figure 1. Relationship between mean number of eggs/conceptacle and number of conceptacles in a receptacle.

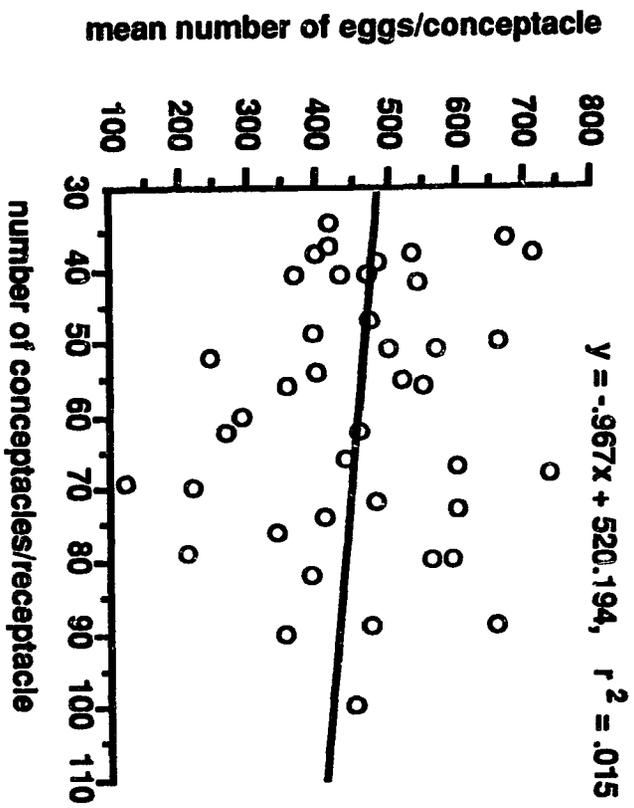


Figure 1

Chapter 2

Effects of Harvesting on *Ascophyllum nodosum*: a Life-Cycle Approach

Abstract

Southwestern Nova Scotian populations of *Ascophyllum nodosum* have a long history of being harvested but little or nothing is known of their vital rates (e.g. growth, survival) and the potential effects of harvesting on these rates. The vital rates of a population are the result of the combined vital rates of the life cycle stages. This study assessed the effects of harvesting on population vital rates using a life-cycle approach. Specifically, the effects of harvesting season and intensity on growth and mortality were assessed for each stage of the life cycle of the modules.

Harvesting enhanced growth as it was greater in harvested compared to uncut stands, although this finding needs statistical confirmation for most size classes. Differences among treatments, however, appeared largely non-significant. The effect of harvesting season accounted for less variation than the effect of harvesting intensity (needs statistical confirmation). Growth rates declined with increased size class, class 4 exhibiting more breakage than increases in size. Despite the differences in growth rates, the response to harvesting intensity of classes 1 to 3 was similar in that they all grew approximately 10 cm in two years. The small size

classes attained maximum growth in all treatments. Class 3 achieved maximum growth only in intensely cut plots.

Introduction

"How many of us would fly in an airplane built in someone's backyard without any blueprints? This airplane may look like others we have seen fly but that is not enough to ensure that it will fly...Should we demand any less of ourselves than to manage resources according to policies designed by resource scientists?... The absence of theory in resource management is just as likely to lead to a disaster, as is the absence of theory in aviation" (Getz & Haight 1989).

Through its long history of exploitation (Sharp 1987a) the southwestern Nova Scotian population of *Ascophyllum nodosum* has been harvested without blueprints (Sharp 1991). Management is rudimentary. Typically, this population is cut, left alone for 1 to 3 years and reharvested again (Sharp 1987a). The stand is harvested again if it has approximately same standing crop of biomass that it had before the previous harvest. There are little or no assessments of vital rates (growth, mortality) of this stand. Understanding the impact of harvesting on the vital rates is key to ensuring the long-term use and conservation of this natural resource.

In populations where different stages of the life cycle co-exist, population vital rates result from the combined vital rates of each life cycle stage. The population of modules of *A. nodosum* can be considered to grow into four life cycle stages (Chapter 1). The effect of harvesting may then depend on the responses of modules in each stage. Thus, the objective of my study was to assess the vital rates of each life cycle stage under various harvesting treatments.

Reviewing the literature, Sharp (1987a) reported growth rates for *A. nodosum* from several North Atlantic populations. Growth rates

varied from an average of 0.33-1.2 cm/month to 3.4 cm/month. Annual growth may be as high as 25 cm/year (Keser & Larson 1984, Peckol et al. 1988). The growth rate estimated for southwestern Nova Scotian stands was 1 cm/month (Sharp 1981). Discrepancies among populations are believed to result from geographic, vertical and temporal distribution of environmental factors (Mathieson et al. 1976, Sharp 1987a, Peckol et al. 1988). It is possible too, that variation also arises from differences in growth among life cycle stages. If growth rates change with life cycle stage, the overall mean growth will change with a change in the number of individuals in each stage. Assessing the variation due to life cycle stage may contribute to the accuracy of the estimates of population growth. Although the present study was not about methods to assess growth, methods other than the one used here are briefly discussed.

Since yield results from module growth minus mortality, mortality should be determined. The relevance to yield of losses through module breakage cannot be overlooked either. A significant part of the annual growth may be lost due to ice damage (Mathieson et al. 1982). If the degree of exposure to ice and desiccation increases in the stand after harvesting, breakage and mortality may increase. One might then expect that mortality and breakage are functions of harvesting intensity. Thus, growth may decline with harvesting intensity. Alternatively, since harvesting removes the canopy, growth of the understory modules may be enhanced and increased with the intensity of harvesting.

The effects of season and intensity of harvesting need to be investigated. If the effects of harvesting are detrimental, one may hypothesize that winter cuts may be worse than summer cuts due to increased exposure to ice and desiccation. The effects may also depend on the intensity of the cuts. The present study then had two objectives, to assess the effects of harvesting season and intensity on the growth, breakage and mortality of modules.

Materials and Methods

Study Site

The studied population is located at Woods Harbour, southwestern Nova Scotia, Canada. The site consists of a ledge extending horizontally seaward approximately 20 m to 100 m from the upper intertidal. The substratum is mainly composed of large granite boulders fixed in a mixture of sand, mud and cobbles. The *Ascophyllum* zone is limited above by a narrow band (approx. 0.50 m wide) of *Fucus* species, mainly *F. vesiculosus*. The studied stand is largely monospecific with *Fucus* spp occupying the tops of the highest rocks. Individuals are attached to boulders and thus cover is variable depending upon the interspersion of boulders. Almost all of the boulders are occupied by *Ascophyllum*. The stand is usually harvested. The last cutting was approximately two years prior to this study (anecdotal evidence). No formal records of the harvesting history for the stand prior to the study exist.

Experimental Design

A factorial design was used. One factor was harvesting season, with two levels, summer and winter. The other factor was harvesting intensity with four levels:

- a) high intensity (45 min.)
- b) medium intensity (30 min.),
- c) low intensity (15 min.),
- d) control (no harvest).

Plots were laid out in the field and one treatment was randomly assigned (i.e. using random numbers) to each of them.

Cuts at the above intensities were conducted in winter (February 1988) and summer (June 1988) to determine the effect of harvesting season and intensity. Each treatment was replicated 3 times. A

control consisting of 3 plots left intact was included. In total there were 21 plots. Treatments are referred to in the text as control, low winter, medium winter plots, etc. Harvesting was carried out with the Norwegian suction cutters of the type currently employed by a local contractor. Cuttings were as usual carted off. The cutters were operated by employees of the local harvesting company. A buoy was placed at each corner of the plot and the cutter harvested within those boundaries. It was not possible to determine the amount of biomass that should be removed in each level of harvesting intensity *prior* to the actual harvesting because there was no accurate way to determine how much biomass of the stand was being removed during the actual harvest. Therefore, harvesting intensity was measured here as effort (i.e. time harvesting) placed in the stand. The more time the worker spends in a stand the more thorough the cut (Fig. 2 shows that growth rates varied with harvesting intensity, suggesting that the method employed here resulted in three different levels of harvesting intensity). The amount of biomass removed was estimated as a *percentage* of the biomass in the stand *prior* to the harvest. The stands were sampled prior and after the harvest to estimate biomass (see below). Biomass sampling prior to and after harvesting indicated that the sensitivity of the sampling method employed was sometimes insufficient to assess the amount of biomass removed in plots cut at low intensity. Nevertheless, in those plots where a difference (i.e. between prior to and after harvest) was detected, an average of 18% (standard deviation, SD= 5) of the stand biomass was removed in the low-intensity harvest. In the medium-intensity harvesting treatment, on average, 60% (SD= 19) of the biomass was removed. As much biomass as possible was cut in the high intensity treatment, which amounted to an average of 70% (SD= 18). Bags were weighed after the harvest at the plant but unfortunately recording of weights was not properly conducted by the operators.

Sampling

Plots (16 m X 21 m), each comprising 3 transects, were laid out just as described in Chapter 1. The sampling procedure employed was also described in Chapter 1. Here additional information is given.

Each plot was sampled before and after harvesting to assess the amount of biomass removed by the harvest and the module size structure (see methods in Chapter 1). The total wet weight of each sample collected prior to and after harvesting was assessed. For all modules greater than 4 cm the wet weight and reproductive state were assessed. Modules bearing receptacles were considered reproductive; otherwise, modules were considered vegetative. The length of 2656 modules was also determined. When a sample (the content of a quadrat) was too large to be processed relatively readily, a subsample was randomly taken. To select the subsample all modules greater than 4 cm from the same sample, were mixed by hand in a container and then the sample was emptied on a 30 cm-wide surface divided into 30-cm x 30-cm squares. The surface comprised as many squares as needed to obtain an even cover of modules. One square was selected by means of random numbers. Its content was the subsample.

Tagging

Once harvesting was completed growth rates of individually marked modules were determined. Plots were reduced to 14-m x 19-m to avoid edge effects and modules were tagged. The tagging procedure employed was described in Chapter 1. A total of 1260 modules was tagged and monitored every three months for almost two years (see below). The presence or absence, length and reproductive state of the tagged modules was recorded at each census. Tag loss due to handling was extremely rare. Each module carried at least two tags (see below). Broken tags (not the modules) were replaced during censuses.

Some problems with the tags developed. A number of them deteriorated and were lost within the first six months of the survey. In November 1988, two more tags made of heavier, braided fishing line were tied around the module. Thus modules carried two to three tags. Where tag loss was evident, another identical module from the same plant was tagged, for that time only. Modules were *not* substituted again during the study. Due to the second tagging, each module had 3 tags. There was still uncertainty as to whether tag loss would continue and could be confounded with module mortality. Another problem was that the tag rubbed the module and might cut it. In order to determine whether tags caused mortality and whether tag loss was significant, a control for tags was conducted between July 1989 and June 1990. The control consisted essentially of modules that were selected but not tagged and their survivorship compared to the survivorship of the tagged modules. The experiment comprised three plots running between the experimental plots. Three transects were laid out and plants selected along these in the same fashion as in the experimental plots. All modules, except four of each size class, were cut off the holdfast. The number of modules selected in each size class was recorded for each plant, transect and plot. At the end of the study the total number of modules surviving one year was assessed. It was found that tag loss was not significant and that the loss of modules observed in experimental plots was due to natural mortality. Eleven percent of the selected modules in the control-for tag experiment had been naturally removed during that time. The number of tagged modules in experimental plots that could not be accounted for (i.e. presumably dead) was also assessed. The assessment was done for both 1988-1989 and 1989-1990. Eight and 13% of the modules initially tagged were missing at the end of the first and second year respectively (all treatments pooled). A G-test (Sokal & Rohlf 1981) showed that these percentages were statistically similar. Further, the average of these two years (10.5%) was practically identical to the module mortality in the control-for-tag experiment.

Size Classes

Intact modules were assigned to one of the 4 size classes described in Chapter 1. Modules truncated by the harvest were assigned to different categories. The literature suggests that if modules are cut too low, regrowth may be delayed or prevented (David 1943). The correlation between size and reproductive state (chapter 1) also suggests that reproductive modules may grow faster than vegetative modules. Treatment effects may then depend upon whether the module is cut and its reproductive state. Thus, if truncated during harvesting, modules were assigned to either class 'cut reproductive' or 'cut' depending on whether they had receptacles or not. The regression equation in Chapter 1 was *not* used to assign modules to these two classes).

The classification of each module into a particular size class was maintained throughout the study. For instance, modules that were class 2 at the beginning of the study were considered class 2 until the end and tested for treatment effects as such. However, modules could have moved to another class during this study. They were not reassigned to another class because the objective of the present study was to assess the effect of harvesting on a particular size class, one and two years after the harvest. This method is useful particularly for slow-growing species like *Ascophyllum* where responses may not be readily observable.

The response variables were:

Growth. It was measured as the difference between final length and initial length for the two periods, which ran from July 1988 to May 1989 and July 1988 to April 1990. The two periods comprised less than 12 or 24 months respectively but I refer to them as one- and two-year periods for simplicity. Growth thus estimated includes losses through breakage and is therefore net growth. Growth was negative if the fragment lost was greater than the increase in size. If modules broke but the increase in size was greater than the loss, growth was positive. Modules with positive

and negative growth cannot be completely separated. (Seasonal variation in growth is not presented here because this study aimed at determining yearly rather than seasonal growth. Differences in initial size between modules from winter and summer plots were analyzed with ANCOVA, with initial size being the covariate. See below).

Breakage. It was the percentage of modules with negative growth in each treatment. Since breakage can exert a significant effect on growth (Mathieson et al. 1982) and breakage can increase in a cut stand, two sets of statistical analyses were run to assess treatment effects on growth. One considered both positive and negative net growth values and the other only positive net growth values.

Survivorship. It was the proportion of modules in each size class that survived two years.

Statistical Analysis

The effects of harvesting season and intensity on module growth were tested for statistical significance. To account for differences in module size at the start of the experiment, initial module length was included in the analysis as a covariate (ANCOVA). However, the covariate was not significant and so the analysis was replaced with ANOVA. Data from individual plots were averaged for each size class and these averages were used in the statistical tests. The model was:

$$Y_{ijk} = \text{mean} + S_i + H_j + (S \times H)_{ij} + E_{k(ij)},$$

mean = Average growth of the entire population,

S = Effect of harvesting season,

H = Effect of harvesting intensity,

S X H = Effect of harvesting season by intensity interaction,

E = error in S and H

If the p values of the F test were > 0.05 , differences between means were considered non-significant. Error terms and degrees of freedom (df) were estimated following guidelines of Underwood (pers. com.) and Zar (1984). The power of the performed ANOVAs was estimated as well (Zar 1984). When the power was $< 80\%$ and the effects were non-significant, the results of ANOVAs were not reported. ANOVAs were reported when at least one main effect was significant. Variances were tested for homogeneity with Cochran's test (Underwood 1981). Significance values of 0.01 or smaller meant that the probability variances were heterogeneous was significant. ANOVA is robust to transgression of the assumption of normality (Underwood 1981). Data were nevertheless tested for normality with normal plots. If the significance value of the plot was 0.05 or smaller, data were normal. The assumption of normality was also checked with the Kolmogorov-Smirnov (K-S) test. If the result of this test was a P value greater than 0.05 the distribution of the data was consistent with a normal distribution. Below are the results of the tests of the assumptions of the ANOVA's in Table 5.

Size Class	Test	Results
1	K-S test normal plots Cochran's test	P > 0.05 P = 0.05 P > 0.05
Cut Repr.	K-S test normal plots Cochran's test	P > 0.05 P = 0.05 P > 0.05

Controls were not included in the above ANOVA model. However, upon detection of significant differences, comparisons with controls were conducted with Dunnett's test. Tukey's test test was employed for pairwise comparisons among the levels of a treatment. Dunnett and Tukey tests are recommended by Day & Quinn (1989). Figures were constructed using the data prior to averaging.

One separate ANOVA for each size class was performed to test for the effects of harvesting on the growth of each size class. Due to the tagging procedure employed, size classes were not independent (Hurlbert 1984). Because the modules of a plant are in tight clumps, they could influence each other's growth. Thus, size classes could not be compared for significant differences. Conclusions concerning growth differences among size classes were based on the visual examination of their standard errors.

Survivorship curves were estimated and tested using the Desu-Lee statistic (SPSS:X 1986).

Results

Population Growth

What follows is a description of the effect of harvesting on growth in each treatment given in Table 1. Note that no statistical tests were conducted on the data in Table 1. Tests for significant differences were carried out separately for each size class and are given below. Growth in cut plots appeared greater relative to control plots (Table 1). One year after the harvest, the growth in plots cut at medium intensity was lower than in plots cut at low or high intensity. Two years after the harvest, growth increased with the intensity of the cut (Table 1, Fig. 1). The average growth over the

two periods, at each harvesting intensity treatment, was slightly higher when plots were cut in winter than in summer. Exceptions were the high intensity plots where the winter averages were similar to or lower than those of summer. Overall, there was little difference between the growth in summer and winter plots over two years (pooling harvesting intensity treatments and classes, Fig. 2).

Pooling all size classes and treatments, modules grew on average 6 cm over 2 years. Variability in growth was very high (SD= 17.5), some modules growing 25 cm in one year and 35 cm in two years. The overall average was for the tagged modules. However, the number of modules in each size class that I tagged was different from that in the whole stand. The abundance of each size class may also vary, but not necessarily, with the intensity of the harvest. Sampling the stands after the harvest permitted an estimate of the number of modules in each size class, which is given in Table 2. Since the growth of cut and cut reproductive modules was roughly similar to the growth of the other classes (below), the two were added to each of classes 1 to 3, depending on their size. None was added to class 4 because all truncated modules were smaller than class 4. The mean growth of each size class estimated from tagged modules in each harvesting treatment is also given in Table 2. With the data in Table 2, the mean growth of harvested stands was estimated (Table 3). The actual increase in module length in cut stands, pooling all treatments and size classes, averaged 8.8 cm in two years for summer and winter plots. The average from harvested stands (Table 3) and from my sample of tagged modules (Table 1) were then roughly similar. The averages from summer plots were slightly higher than those from winter plots (Table 3) which was different from the tagged module response for the two-year period. The discrepancy is due to the fact that there were more class 1 modules in the plots cut in summer than in the plots cut in winter. The difference between seasons was nevertheless, negligible. Table 3 also shows that stand growth did not increase with harvesting intensity. Increase in module length in uncut stands over the two-

year period (4.2 cm) was nevertheless lower than in harvested stands. Again the difference between the estimates from the tagged modules and Table 3 was due to the fact that the proportions of modules/size class in the whole plots and in my sample were different.

Treatment Effects on Growth over the One-Year Period

The average growth in each treatment is given in Figure 3. Most treatments were statistically non-significant. The power of the ANOVAs of all the non-significant effects was less than 80%. The lack of significance might be then due to the low power of the ANOVA rather than to actual lack of treatment effect. ANOVA tables then were not worth reporting here. The statistical tests excluding negative values for the two studied periods, also lacked power and thus they were not reported here.

One cause of the low power of the tests might be that treatments did not appear to exert obvious effects. For example, the average growth of most classes in winter and summer plots was similar (Table 4). Class 4 experienced breakage rather than increases in size (Table 4, Figure 3). With some exceptions, in plots cut either in summer or winter, averages varied relatively little with the intensity of the cuts (Fig. 3). The sample size then would have to be very high for the ANOVAs to have power to detect significance between treatments. Another reason for the non-significance of the main effects might be that there was a significant interaction in two cases (below).

The only cases in which treatment effects were detected were classes 1 and cut reproductive (Table 5). Although differences were small, harvesting season influenced the growth of class 1, growth being greater in plots cut in winter (5.5 cm SD=1.7) than in summer (4 cm, SD 1.3) and in the controls (2.3 cm, SD= 0.9, Dunnett P= 0.05). Growth in summer and control plots was comparable (Dunnett P>

0.05). The effect of harvesting intensity on cut reproductive modules was significant. Growth in plots cut at medium intensity (0.95 cm SD= 4.2) was lower (Tukey, $P = 0.05$) than in plots cut at low (6.6 cm SD= 3.1) and high (5.4 cm SD= 1.9) intensity. The growth from low and high intensity cuts were statistically similar (Tukey, $P > 0.05$).

The interaction of harvesting season and intensity was significant ($F, P < 0.05$) for classes 2 and cut modules but no consistent pattern emerged. The growth of class 2 decreased with harvesting intensity in winter plots and increased with harvesting intensity in summer plots. The growth of cut modules varied little with harvesting season X intensity interaction except in plots harvested at medium intensity where growth in the summer plots was negligible.

Treatment Effects on Growth over the Two-Year Period

The response of each size class to treatments over a two-year period are given in Figure 4. The effects of harvesting season and intensity on growth were always statistically non-significant. The power of the tests was low ($< 80\%$), which may be the reason of the lack of statistical significance. However, Figure 4 shows no clear evidence of differences among treatments and that variability was high. As above, the sample size would have to be exceptionally high to find small differences statistically significant. The harvesting season by intensity interaction was significant in class 2 only. The interaction may explain the non-significance of the main effects because winter averages tended to decrease with harvesting intensity whereas the reverse was true for the summer averages. Tests excluding negative values also lacked power and thus they were not included here.

Size Classes

Growth decreased with size class (pooling all treatments). The growth of classes 1 and 2 were similar, averaging 10.6 cm (SD=10.7). Class 3 grew 3 cm (SD=19.5) and class 4 experienced losses (-14 SD=32.6). Cut and cut reproductive modules grew approximately the same (7.3 SD=13.6) as classes 1 and 2.

The response to harvesting of all size classes (except class 4), appeared similar, growth *on average* being about 10 cm in two years (Fig. 4). In classes 1 and 3 and to a lesser extent 2, growth was negative or lower in control plots relative to treatment plots (Figs. 3, 4). However, growth did not increase with the intensity of the cut.

Most of the population after harvest was in class 1 and 2 while only 4 % of the modules were reproductive (Table 2). Population regrowth then stems mainly from class 1 and, to a lesser extent, class 2 (Table 2).

Breakage

It was hypothesized that harvesting might result in increased module breakage due to exposure to ice and desiccation in the stand. Overall, however, only 13% (N= 169) of the tagged modules in my sample experienced breakage over two years. Moreover, the frequency of breakage slightly decreased with increased harvesting intensity (control= 20% (n=37), low= 13% (n=46), medium= 14% (n=52), high = 9% (n=34)). Since the number of modules that broke in each class and treatment was so low, treatments were not tested for significant differences in breakage. Decreasing percentages of breakages with harvesting intensity suggested nonetheless that harvesting may actually decrease the chances of breakage.

Survival

About 71% of the modules survived two years. Harvesting season did not appear to affect survival, this being similar in summer (76%), winter (75%) plots. Survivorship in summer plots was consistently highest in plots cut at medium intensity, being statistically significant in cut reproductive modules (Table 6). In winter plots, survivorship was consistently lowest in plots cut at medium intensity, differences among treatments being significant in classes 1 and 2 (Table 6). Pooling all treatments, the survivorship curves for classes 1 to 4 appeared similar (Fig. 5). Seventy percent of the modules in control plots survived two years, survivorship of classes 1 to 4 being similar (Table 6).

Discussion

Growth

Variation in growth rates among North Atlantic *Ascophyllum* populations has been attributed to spatial, temporal and geographical distribution (Mathieson et al. 1976, Keser & Larson 1984, Peckol et al. 1988). My study suggested that another source of variation is module size because growth decreased with module size class. Thus, the growth rate of a population will be affected by the number of modules in each size class, i.e. stand size structure. If the size structure of populations varies among sites, and within a site through time, variation among the above studies might be also due to differences among population size structures.

Methods other than the one employed here have been used before to measure growth, although addressing production issues rather than individual variation. One of those methods uses the age and weight of the internodes between vesicles. The age of an internode can be obtained counting downwards from the unbroken apical tip of the module. The present study was not concerned with annual total production in a stand but, it may be argued that the basic technique of the aging methods could be used to measure the annual growth of

an individual module. Therefore, a brief comment on the application of aging method to assess module growth follows.

Cousens (1981, 1984) devised two methods to estimate growth in *Ascophyllum*, both making use of the annual formation of a vesicle. The methods assume that internodes can be aged (relative to the first vesicle) and that growth from year to year is constant. Growth is then estimated from the differences in weight between successive years. The assumption that modules can be aged may not be realistic. Cousens (1982b) noted that aging methods were incorrect for most modules in most populations. He noted that age is extremely difficult to estimate due to the great longevity of many modules, their ability to withstand repeated breakages and problems aging young modules. It may not be always true that one vesicle is formed annually either. Growth rates vary enormously among modules in laboratory (Strömngren 1981) and field (Cousens 1985) conditions. Extreme variation was noted in my sample of tagged modules as well. Both, Cousens (1985) and I (i.e. in control stands) noted that small modules grew slowly. In my stands, 46% of the modules that did not grow measurably were in class 1. Variation in growth ranged from 0 to occasionally 25 cm in one year and 35 cm in two years in some modules. Since I never saw exceptionally long internodes, it is reasonable to think that fast growing modules may have produced more than one vesicle/year. Conversely, those modules that did not grow, could not have formed a vesicle. The age of an internode may then be anywhere from less than a year to several years old.

Another assumption that may not be realistic is that growth is constant through time. Growth depends on availability of light, temperature (Strömngren 1983), on interference (Chapter 3) and ice damage (Mathieson et al. 1982, Åberg 1990a,b). Module growth then may be expected to vary from year to year depending on the variation in the above factors.

Another method used to estimate growth is the Allen curve, although again for total stand production (Rice & Chapman 1982). Growth is calculated from the relationship between the numbers of survivors and the mean weight of survivors through the year. Growth can be obtained graphically by plotting a curve of survivorship against mean weight. The survivorship curve refers to a single cohort followed over a period. Losses of plant parts are not accounted for in the Allen curve and thus total production is underestimated. However, the amount lost has been considered negligible in other brown seaweeds (Rice & Chapman 1982). Even assuming that the set of tagged modules comprised in one size class in my study could be considered a 'cohort', the Allen curve method may not be applicable as it stands in my case. In *Ascophyllum*, losses may represent two or three years of growth (Mathieson et al. 1982) and in classes 3 and 4, losses can actually exceed mean increases in size. The Allen curve method then would not appear to accurately represent growth in *Ascophyllum*.

My method of subtracting initial length from final length permitted a direct estimate of annual growth. The technique was quick, simple and with small error range (pers. observ.). None of the methods devised by Cousens (1984) has an advantage in speed, each taking one person about five days to process a single sample. Size could also be obtained from the correlation between weight and the circumference of the module (as used for plants in Cousens 1984, Åberg 1990c). However, by contrast with length, the measure of circumference is a crude one. Nonetheless, my method should be compared with any others of the same individuals to assess which one is better. If the occurrence of modules that produce more or less than one vesicle per year is not significant, a minimum age at least relative to the first vesicles may be obtained and thus aging methods may be a useful tool.

The overall growth for harvested *Ascophyllum* southwestern Nova Scotia stands was about 4 cm a year. Should these stands not be

harvested again, the growth rates will probably decrease eventually to 2 cm/year as in the control plots. Assessment of the growth rates of individual size classes permitted an estimate of the average growth of the population. Knowledge of the growth rates of each size class and the numbers of individuals in each size class in a post-harvest stand can be used to predict future stand recovery. Methods other than this may be less accurate. Samples that comprise selected modules, for instance the largest modules, may underestimate growth. However, the advantage of my method over others need to be tested

Slight differences in growth due to harvesting season were noted but the differences were so small that they may not have biological meaning. Since the power of the ANOVAs was low, the effect of harvesting season needs confirmation. Studies for other seaweed species suggest that harvesting season may be important. It has been found in *Macrocystis pyrifera* (Westermeier & Moller 1990) and *Mastocarpus stellatus* (Burns & Mathieson 1972) that recovery depended significantly on cutting season, generally being better in summer cuts. Late spring harvests of *Porphyra* spp, known as karengo, resulted in greater yields than earlier harvests (Nelson & Conroy 1989). Although this latter study did not compare yields between seasons, it did show that within season harvest timing can be important, even if there are just a few months in between cuts. Recovery through sexual recruitment in areas cleared of *Durvillea antarctica* plants depended significantly on harvesting season (Hay & South 1979). Areas cleared in winter were successfully recolonized but when areas were cleared at other times, there was little, if any, recovery. Gomez & Westermeier (1991) reported that pruning season had no significant effect on the formation of modules in *Iridaea laminarioides*. Their experiments, however, were pseudoreplicated because treatments were not interspersed (Hurlbert 1984) and thus need confirmation.

Growth increased with harvesting intensity in my sample of tagged modules (Table 1, not tested statistically) but not the estimated growth for the entire harvested stands (Table 3). Growth in harvested stands was twice as great as in control stands nevertheless. Almost certainly, enhanced growth was due to the reduction of shading through the removal of the canopy. The fact that the growth of class 1 (that are in the understory) was enhanced by the harvesting and that growth in plots cut at low intensity was slower (Fig. 2) than in the other treatments, supports this view. Other studies for *Ascophyllum*, suggested the same. Plant growth in terms of biomass decreased in stands with increasing canopy (Chapter 3). Experimental manipulation of densities also showed that high density inhibited the abundance of modules in class 1 (Chapter 3). Apices from the bottom of the plant and of lateral branches in dense stands are light-limited (Cousens 1985). In agreement with my study, Sharp (1981) also suggested that biomass growth may be greater after cuts than in uncut stands. This evidence then suggests that the slow growth characteristic of *Ascophyllum* stands was partly due to self-shading. The enhancing effect of harvesting, however, may last for only a few years because as plant sizes in the stand increase (and so interference), growth rates may slow down.

Similar harvesting effects have been reported for other seaweed species. Removal of the canopy in *Laminaria longicruris* and *L. digitata* stands enhanced the growth of zygotes at least temporarily (Smith 1986) and of the stipe of small plants in the understory by a factor of 2 or more (Gendron 1989). Although this last experiment was not replicated, the fact that irradiance in the harvested site was 20 times higher than in uncut sites suggests that, indeed, plants in the understory were light-limited. The growth of recolonizing *Durvillea antarctica* plants in cleared and control areas as measured by stipe length has been compared. Stipes were significantly longer in cleared areas than in control areas (Hay & South 1979). The yield in the stand some time before and after the

clearing was also compared. It was found that the harvest in areas cleared of all plants and holdfasts, was 150% higher than the biomass removed originally. The recovery from areas where only the largest plants were removed, instead, was only 32% of the original stand biomass.

Another factor that may determine growth is the height of the cut. If the module is cut close to the holdfast, regeneration is poor, otherwise regeneration is relatively good (David 1943, MacFarlane 1952, Baardseth 1970, Sharp 1981, 1987a). This is so accepted that the Canadian government currently uses the cut height to regulate the commercial exploitation of this species. Minimum legal cut height is 12.7 cm (Sharp 1987a). In the present stands the mean cut height by mechanical harvesting was about 20 cm (SD= 21 cm), average for southwestern Nova Scotian stands (Sharp 1991 reported averages of cut modules between 10 cm and 30 cm). It is not known, why cut height determines regeneration potential. The reasons suggested by the literature are that there are no lateral meristems near the base to produce regeneration or that they are old (David 1943).

Regeneration from the holdfast is possible but may be extremely slow. Keser et al. (1981) harvested *Ascophyllum* from six sites in Maine. Plants were cut to the holdfast level (surface cut), and at 15 cm and 25 cm from it. Recalculating the means reported in this study, I found that after three years biomass recovery from surface cuts was several times lower than that from plants cut at 15 cm and 25 cm. It was only 8% of the initial harvest. The recovery at the other two heights averaged, was 62% of the original biomass.

The importance of preserving the holdfast and, or basal part of the modules, as a source of repopulation has been stressed for other species with similar growth forms (Lazo et al. 1989, Ang et al. 1990). In *Macrocystis pyrifera* pruning of modules had no effect on module formation but reduced the assimilation area of the thallus

causing a rapid onset of senility and death (Westermeier & Moller 1990). Cuts at the holdfast level, in *Iridaea laminarioides* plants, rendered a more profuse production of modules (Gomez & Westermeier 1991), but this study was pseudoreplicated and thus needs confirmation (above). Regeneration in *Porphyra* spp was enhanced if the holdfast was left intact (Nelson & Conroy 1989). Similarly growth in *Gymnogongrus furcellatus* was greatest when the harvest method left small modules intact (Santelices et al. 1989). Cuts where no apices were left or where whole plants were removed, yielded significantly lower crops or none at all.

Another factor affecting growth is harvesting frequency. Yearly harvest resulted in decreasing yields of *Ascophyllum* (Keser et al. 1981). Similar responses were observed in *Fucus vesiculosus* (Keser et al. 1981) and *Iridaea laminarioides* (Gomez & Westermeier 1991, this study remains to be confirmed). In contrast two cuts, 60 days apart, appeared to enhance the growth of *Porphyra* spp (Karengo) provided these left the holdfast intact (Nelson & Conroy 1989). The yield of this species, nevertheless, depended to an extent on site and harvest timing. The present stands are usually harvested every two or three years depending on the degree of regrowth. Occasionally in areas where recovery is exceptional, stands are harvested annually (Sharp 1987a). Regrowth depends on the amount of biomass remnant in the stand (Sharp 1991). Usually, the mechanical harvest leaves about 40% of remnant biomass. Recently, however, increased harvest pressure has resulted in remnant biomass of less than 40%. The time intervals between cuts then may have to be increased to four years or more to attain pre-harvest levels (Sharp 1991).

Size Classes

Growth decreased with module size, with class 4 experiencing negative growth. There was no clear evidence that the performance of cut and cut reproductive modules was different from that of classes 1 and 2. Size-dependent growth has been reported for other

species of brown seaweeds (Gonzales-Fragoso et al. 1991). Despite the differences in growth rates, the responses of the classes 1 to 3, cut and cut reproductive to the treatments were similar as they grew on average approximately 10 cm in two years. Growth was not a function of harvesting intensity. The small size classes and the cut and cut reproductive modules achieved maximum growth in plots harvested at low intensity. Class 3 achieved maximum growth in plots cut intensely. Inferences must be cautious as non-independence among sampling units may bias the results (Hurlbert 1984). So, results might change should this experiment be repeated with independent samples. Hopefully the bias, if any, was reduced by the fact that the estimated averages came from samples that included modules from the same plants (dependent sampling units) and from plants far apart (independent sampling units).

Breakage

Only a relatively small percentage of the tagged broke which suggested that breakage was not relevant to population growth. In contrast, a study in Maine reported that breakage was highly significant causing large losses. The average fragment of *Ascophyllum* removed by ice-rafting in those populations represented two to three years of growth (Mathieson et al. 1982).

Contrary to what was hypothesized, breakage tended to decrease with increased harvesting intensity. In fact, breakage over two years was more important in control, uncut, stands than in harvested stands. Increased exposure resulting from the cuts might have actually reduced chances of breakage. A study in Rhode Island also suggested that relative exposure did not induce breakage (Peckol et al. 1988). On the contrary, breakage was more common in subtidal populations than in intertidal populations where shelter was greater suggesting that crowding may increase breakage.

Survivorship

About 71% of the population of modules survived two years. This coincided with reports from Rhode Island where survivorship ranged from 67% to almost 90% per year (Peckol et al. 1988 and references therein). The proportion of surviving modules was higher in plots cut in the summer at medium intensity than at the other two intensities, whereas the reverse was true for the winter plots. There is no clear explanation for this.

The underlying causes of mortality were not evident. Harvesting intensity did not seem to have a negative effect on mortality. On the contrary, it may have even reduced the chances of lethal breakage. Grazing did not appear to result in module mortality either (Chapter 4).

Table 1. Mean growth (cm) in each harvesting treatment over one- and two-year periods. Size classes are pooled. SD= standard deviation, T. mean= treatment mean, N= numbers of modules.

Season	Harvesting Intensity 1988 - 1989			1988 - 1990		
	Low	Medium	High	Low	Medium	High
Summer	2.4	0.6	5.3	3.6	5.9	9.1
SD	12.1	9.6	9.8	25.0	12.3	16.3
N	169	161	169	129	155	141
Winter	4.0	2.4	3.7	5.2	6.8	8.8
SD	11.0	14.9	10.1	18.5	13.3	14.7
N	164	152	169	143	111	147
T. Mean	3.2	1.5	4.5	4.5	6.3	8.9
SD	11.6	12.5	10.0	21.7	12.7	15.5
N	333	313	338	272	266	288
control		1.1			1.0	
SD		10.8			19.0	
N		159			124	

Table 2. Numbers and percentages (%) of modules/size class in each treatment immediately after harvesting. The number of modules in uncut stands was estimated pooling samples from control plots and from uncut treatment plots prior to the harvest. Two-year mean growth of each size class is indicated. Cut and cut reproductive modules are added to size classes 1 to 3 depending on their size. Percentages are expressed as percentage of the overall population. Numbers are the total numbers of modules in the samples collected in the replicates of a treatment.

		Class 1	Class 2	Class 3	Class 4
Winter	Low	914	134	94	12
	%	79	12	8	1
	mean	7.9	12.7	(3.7)	(-18.5)
	Medium	782	91	50	10
	%	84	10	5	1
	mean	7.3	5.8	5.4	4.8
	High	486	75	36	6
	%	80	12	6	1
	mean	9.5	10.1	7.2	-5.7
Summer	Low	1,063	183	24	11
	%	83	14	2	0.8
	mean	10.5	12.1	2.6	-26.2
	Medium	1,481	150	19	3
	%	89	9	1	0.1
	mean	8.5	8.1	1.2	-18.1
	High	1,183	156	16	5
	%	87	11	1.1	0.3
	mean	9.6	12.3	10.3	-30.9
Uncut Stands		7,746	1,030	539	167
	%	82	11	6	2
	mean	4.1	10.6	-1.4	-10.7

Table 3. Estimated mean growth in length (cm) in uncut stands and stands harvested in winter and summer at low, medium and high intensity. Size classes were pooled.

Harvesting Intensity			
1988 - 1990			
Season	Low	Medium	High
Summer	10.3	8.3	9.8
Winter	7.8	7.2	9.3
Control		4.2	

Table 4. Mean growth (cm) of modules in classes 1 to 4, cut and cut reproductive in plots cut in summer and in winter. The averages for the one- and two-year periods were indicated. Harvesting intensity treatments were pooled. Cut repr.= cut reproductive. Numbers within parentheses are standard deviations.

Size Class	One-Year		Two-Year	
	Summer	Winter	Summer	Winter
1	9.6 (10.3)	10.7 (7.7)	9.6 (3.2)	10.3 (2.6)
2	11.2 (9.5)	10.7 (16.2)	12.6 (5.9)	9.8 (6.0)
3	5.2 (15.7)	4.1 (21.4)	6.4 (10.4)	4.3 (12.8)
4	-21.5 (39.1)	-8.0 (27.8)	-16.0 (13.8)	-7.0 (17.1)
cut	8.8 (13.3)	7.7 (8.4)	9.2 (5.0)	6.9 (3.1)
cut repr.	6.4 (14.2)	6.2 (16.7)	8.2 (7.0)	6.9 (6.2)

Table 5. ANOVA tables. Effects of harvesting (h.) season, intensity, and their interaction on growth over a one-year period. s X i = h. season by intensity interaction. Cut Rep.= cut reproductive.

Size Class	Source	df	S.S.	F	P
1	h. season	1	9.07	5.10	0.04
	h. intensity	2	10.03	2.82	>0.05
	s X i	2	21.35	0.85	>0.05
	error	10	3.01		
Cut Rep.	h. season	1	24.26	2.30	>0.05
	h. intensity	2	110.06	5.21	0.02
	s X i	2	4.80	0.23	>0.05
	error	10	126.68		

Table 6. Proportion of modules surviving two years in size classes 1-4, cut and cut reproductive (cut repr.) in each treatment. L= low intensity, M= medium intensity, H= high intensity. Significance levels (P) are indicated. Tested with Lee-Desu statistic. H.I.= harvesting intensity.

Size Class	Summer Harvest			Winter Harvest	
	H.I.	% Surviving	P	% Surviving	P
1	L	69	NS	73	0.03
	M	74		48	
	H	66		80	
2	L	73	NS	93	0.02
	M	83		57	
	H	72		92	
3	L	67	NS	76	NS
	M	83		63	
	H	62		92	
4	L	66	NS	65	NS
	M	89		55	
	H	71		100	
cut	L	83	NS	77	NS
	M	84		71	
	H	86		81	
cut repr.	L	64	0.01	79	NS
	M	100		64	
	H	71		85	

Control Plots

1	65
2	72
3	67
4	75

Figure 1. Two-year mean growth (cm) in control plots and plots harvested at low, medium and high intensity. Harvesting seasons and size classes are pooled. Bars are means with standard errors.

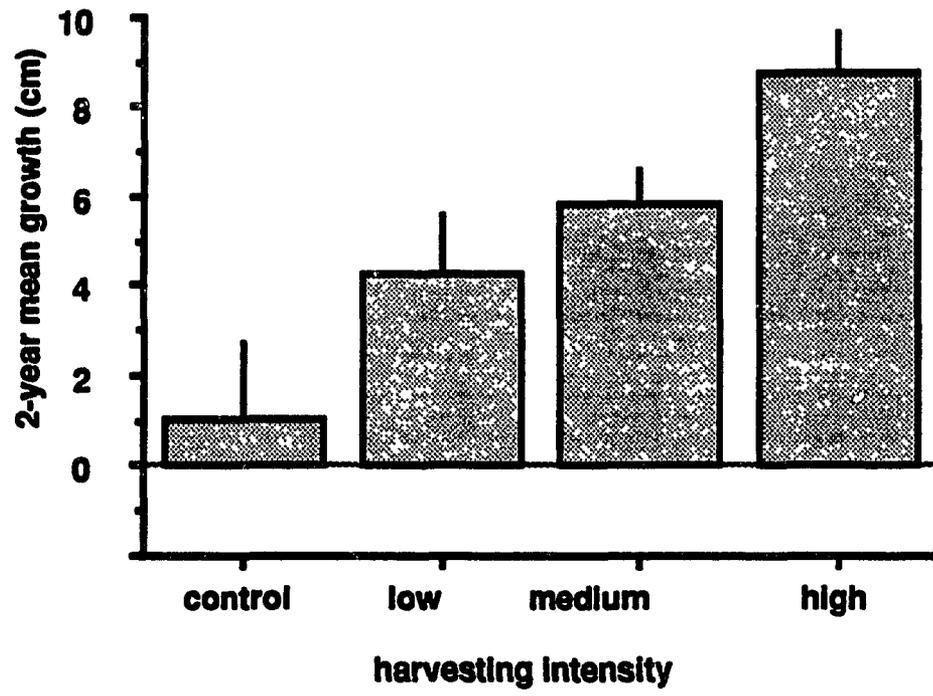


Figure 1

Figure 2. Two-year mean growth (cm) in control, winter and summer plots. Harvesting intensity treatments and size classes are pooled. Bars are means with standard errors.

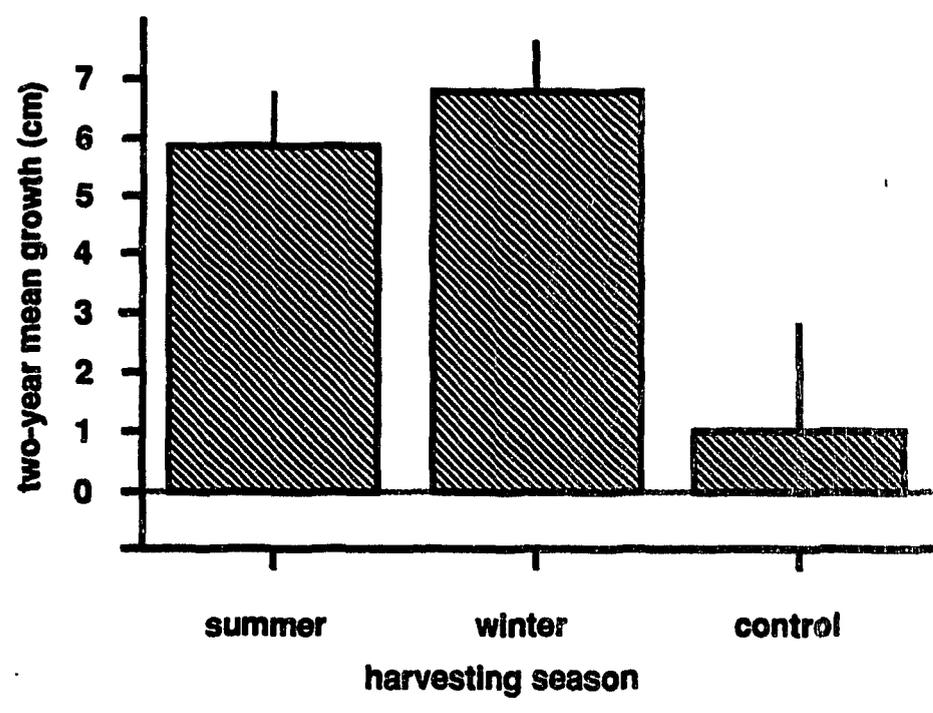


Figure 2

Figure 3. One-year mean growth (cm) of each size class in control and treatment plots. Averages for each harvesting season and intensity are given. Bars are means with standard errors.

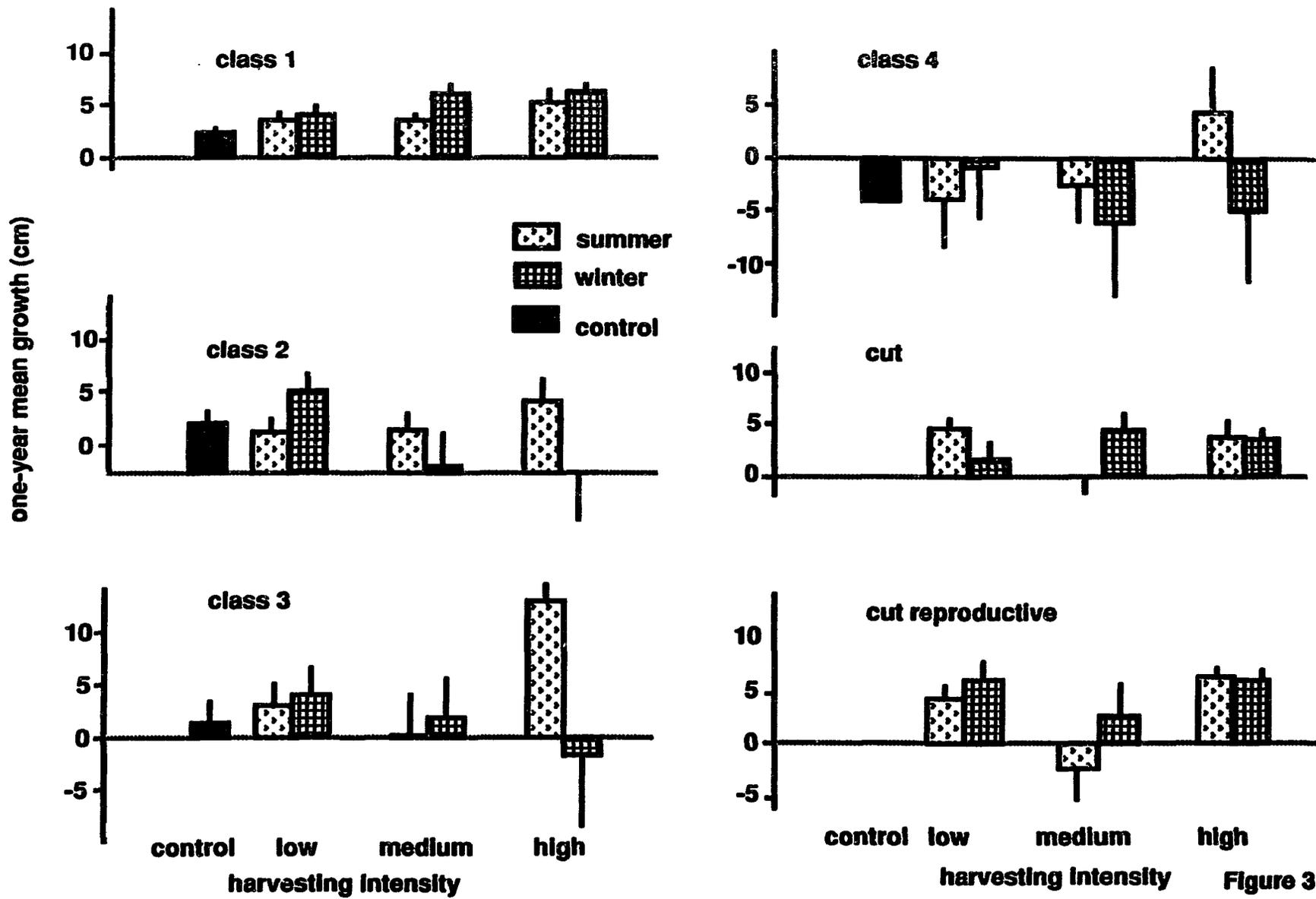
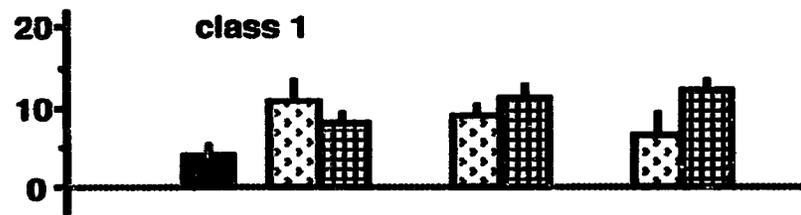


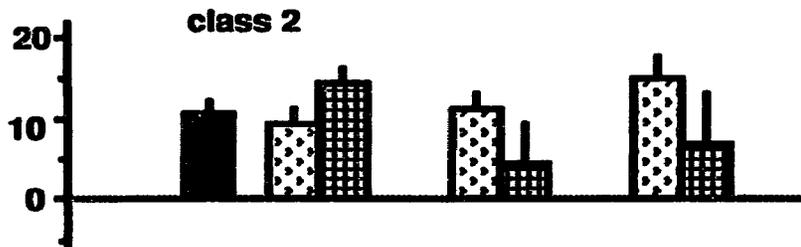
Figure 3 95

Figure 4. Two-year mean growth (cm) of each size class in control and treatment plots. Averages for each harvesting season and intensity are given. Bars are means with standard errors.

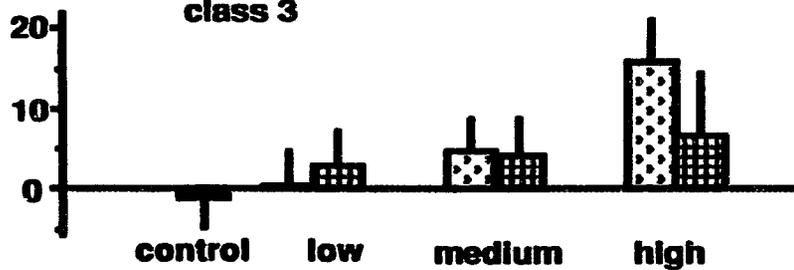
two-year mean growth (cm)



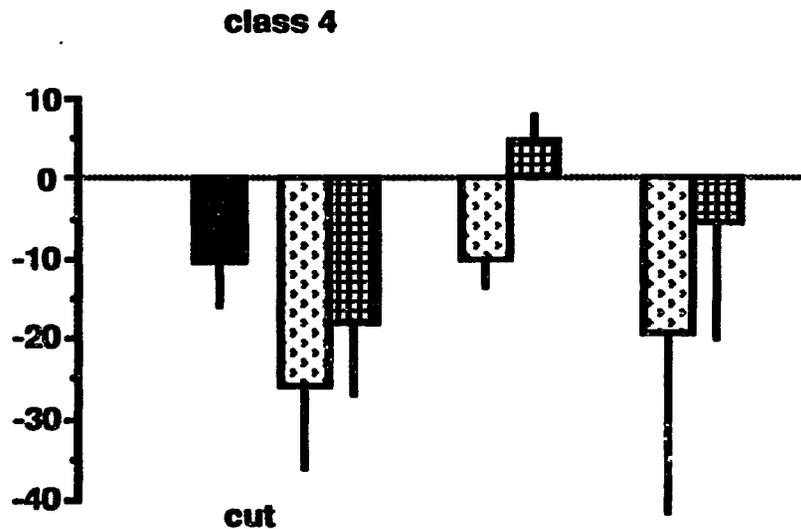
 summer
 winter
 control



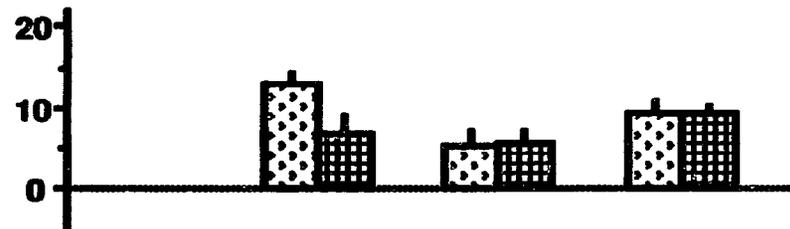
class 3



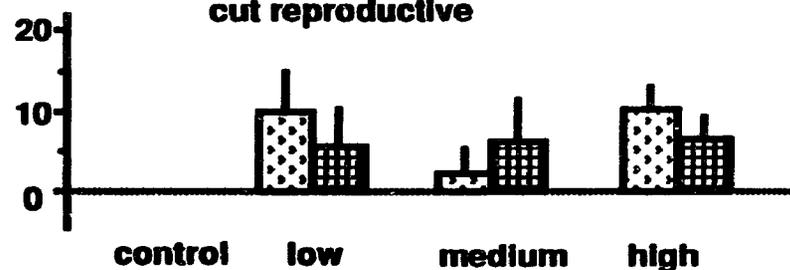
harvesting intensity



cut



cut reproductive



harvesting intensity

Figure 4

Figure 5. Survivorship curves of classes 1, 2, 3 and 4 over a two-year period. All treatments are pooled.



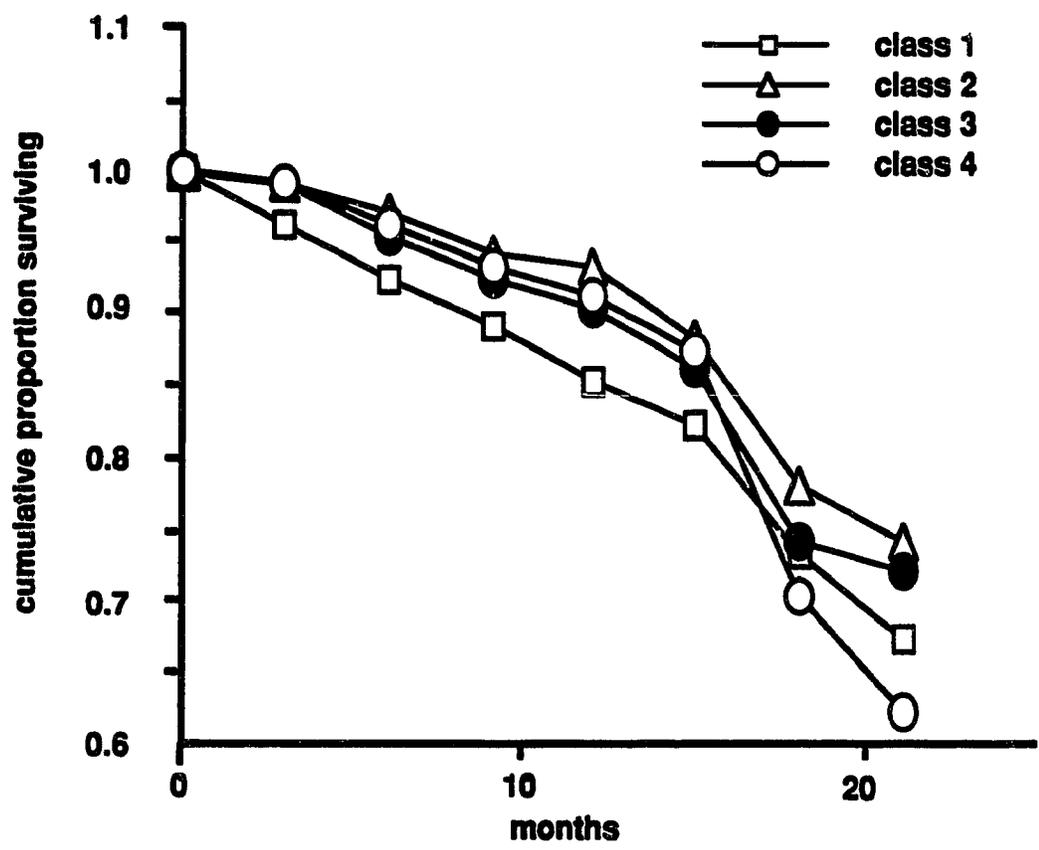


Figure 5

Chapter 3

Effects of Interference on Growth, Structural Organization and Reproduction: Sorting Through the Contradictions

Abstract

The effects of interference on seaweed demography are at present unclear. Some evidence suggests that, in contrast to terrestrial plants, seaweeds fare better at high density than at low density but this is only partly supported by the literature. One factor that may contribute to this confusion and that has not been investigated in seaweed ecology and that is that the responses of plants and modules to interference have not been distinguished. The present study assessed the responses of the plants and modules of *Ascophyllum nodosum* to interference in order to understand the effects of interference on seaweed demography.

Because crowding increases with the number and size of individuals, treatments included two levels of densities and various combinations of plant sizes. Density treatments were to test for the effect of number of individuals in a stand. Treatments of combination of plant sizes were to test for the effect of stand size structure. The effect of interference on the numbers of modules in 3 size-based life cycle stages (size classes) was also assessed.

Response variables were growth, abundances in each module life cycle stage, and reproduction. Growth was assessed in terms of biomass and module numbers. Responses were assessed at the plant and module level.

Interference had significant but unusual effects. At the plant level, low density promoted module birth but modules did not grow in size. High density limited production of modules but they increased in size. More modules achieved reproduction in a plant at high density than at low density. Growth in biomass in small and large plants tended to be lower in stands with increased numbers of plants of larger sizes (i.e. increased stand biomass). Stand size structure, however, did not appear to influence plant growth in numbers of modules. At the module level, the effect of density on the abundances of the three life cycle stages was positive or negative depending on the size class considered. The results suggested that plants and modules respond differently to density stress. Whether these effects agree with general theory for terrestrial plants also depended on what response variable was considered and how growth was assessed.

Introduction

Changes in the environment brought about by the proximity of individuals are called interference (Harper 1977). Most studies of terrestrial species conclude that that interference affects some aspects of population demography (Watkinson 1986) but there is no consensus regarding marine species (Schiel & Choat 1980, Cousens & Hutchings 1983, Schiel 1985a). The present study attempted to assess the effects of intraspecific interference on the population demography of *A. nodosum* and compared the findings with those for terrestrial plants.

The effects most commonly reported for terrestrial species are reduced mean size and differential mortality, reproductive output and allocation (White & Harper 1970, Harper 1977, Weiner 1988). The self-thinning rule describes changes in density due to growth with a straight regression line relating the \log_{10} of mean size with the \log_{10} of density, where a slope coefficient of -1.5 can be found. In crowded stands, some individuals cannot grow and, beyond certain critical levels of crowding, the smallest individuals eventually die. Stand thinning is more than compensated by the growth of the survivors. There is then a negative relationship between mean density and mean size, size increasing with declining density. Crowding can also influence reproductive likelihood and output (Weiner 1988). Other effects of crowding are greater size and reproductive inequality with large individuals growing and reproducing inordinately more than small individuals (Weiner 1988). Individual growth may also depend on the stand size structure, the growth of an individual decreasing with the number of neighbours bigger than itself (Hutchings 1986, Schiel & Foster 1986).

In seaweed stands the occurrence of interference has been shown but there is no consensus as to its effects on population demography (Dean et al. 1989, Reed et al. 1991). For instance, in contrast to terrestrial plants, plant weight and reproductive biomass in three seaweed species (*Sargassum sinclarii*, *Ecklonia radiata* and *Carpophyllum maschalocarpum*) were found to increase with density (Schiel & Choat 1980, Schiel 1985a). Schiel and Choat suggested then that the responses to crowding were different in marine and terrestrial environments. Since their stands were naturally-recruited, however, one can argue that crowding was low because thinning occurred during the early stages of stand development. Cousens & Hutchings (1983) proposed that Schiel's and Choat's (1980) findings did not contradict conventional theory. They proposed, instead, that the regression line of the self-thinning rule represents a boundary condition for the maximum size individuals can attain at given densities. Beyond that boundary mortality

occurs, but below that line all combinations of size and densities are possible. Thus, they suggested that the responses detected by Schiel & Choat were due to the fact that their stands had not reached such a limit.

There is also no consensus regarding mortality and recruitment in seaweeds. Distance to nearest neighbour in seaweed stands may or may not result in death (Chapman & Goudey 1983, Chapman 1984, Schiel 1985a). Density can result in mortality although not due to physiological stress but rather to mechanical effects (Schiel 1985a, Schiel & Foster 1986). Interference from adult individuals and among recruits has also been found to reduce recruitment of zygotes (Schiel & Foster 1986, Dean et al. 1989) but not in all cases (Chapman 1984).

Discrepancies among studies of interference may arise from the fact that potentially important sources of variation have not been addressed. For instance, most studies on terrestrial species use cohorts at various densities but stand size structures are generally not manipulated (except Westoby & Howell 1986). Empirical studies of seaweed ecology do not not manipulate stand size structures and often not even densities (although see Schiel & Choat 1980, Schiel 1985a). Because of logistic difficulties a common practice is to compare naturally recruited stands at low and high density (e.g. Schiel 1985a). If plants in the two 'treatments' differ in their sizes at the beginning of the study, comparisons may not be valid because in stands with larger plants crowding will be greater and will be reflected in the response variables. Thus, stress from density may be confounded with that due to plant sizes (or stand size structure). Controlling densities and stand size structures is then needed to accurately assess the effects of crowding.

Another problem is that modular species have two population levels, i.e. genets and modules. Genets and plants cannot be distinguished in *A. nodosum* (see Introduction of thesis) and so the purpose of this

study I regard plants and genets as "biological individuals" as defined by Urbanska (1990). A "biological individual is a structurally coherent, physiologically autonomous organism of sexual or asexual origin" and can be a genet or a single ramet (Urbanska 1990). Genets and plants are here then equivalent. It is important to distinguish between plant and module population levels because their responses to crowding are not the same. For instance, the thinning rule does not apply to modules but to genets (Kays & Harper 1974, Westoby 1984). In fact, module thinning may not occur at all because their natality may be density-regulated to avoid overpopulation (Thompson et al. 1990). The distinction between plants and modules has not been acknowledged in seaweed ecology as the lack of research in this area suggests. Åberg (1989) distinguished genets from clonally produced plants. However, his objective was to develop a method to identify genetic individuals, *not* to assess the effects of interference at different population levels. Distinguishing between the two is relevant to the understanding of the process that shape population structure. In species where module life cycle stages are size-dependent, interference is bound to have far-reaching effects on population demography. In suppressing growth, density can influence the abundances of modules in each life cycle stage and thus population size structure and fertility.

Another element of consideration is how growth is measured. In modular species, a plant grows both with the number and the biomass of its modules (Harper 1977). If the effects of interference on numerical abundances and biomass are not the same, one cannot draw general conclusions from using just one variable. Conclusions apply only to the variables considered.

Ascophyllum nodosum is a seaweed species with a modular construction and clonal reproduction (see Introduction of thesis). Stands can be extremely dense (pers. observ. and unreported data from this and another study, Chapter 1), and may result in irradiance

levels at the base of the plant of less than 0.1% of the surface as reported for other population (Cousens 1982a). Modules can be considered to grow into size-based life cycle stages (Chapter 1). Abundances of modules decrease with increasing life cycle stage (Chapter 2). Since interference may affect plant and module performance one can expect reduced plant and module growth and reproduction with increased interference. *Ascophyllum nodosum* offered an opportunity to look at the effects of interference in seaweed stands, distinguishing the responses of plants and modules. Attention was also paid to determining whether interference influences the abundances of modules in each life cycle stage.

The following questions were addressed:

- 1) What are the effects of interference on the population demography of *A. nodosum* plants and modules?
- 2) Are the effects of interference similar in terrestrial and marine plants ?

The present experiments included stands with mixtures of plants and modules in three life cycle stages in various combinations at low and high densities.

Materials and methods

This study was carried out between July 1988 and April 1990. Focus was on modules and plants (clones) not on genets (see Introduction of thesis).

Size Classes of Plants and Modules. Because of logistic difficulties, the delineation of module size classes in this study was a modification of that in Chapter 2. The principle underlying the present classification was the same, namely, that reproduction was size-dependent. The aim of Chapter 2 was to assess the vital rates of modules in different life cycle stages. Here, instead, the aim was to determine the effect of interference upon the abundances

of modules in successively larger size classes. That is, this study attempted to explain population size structure, *not* vital rates. The size classes were as follows:

Class 1: 4 to 27.5 cm,

Class 2: 27.5 to 40 cm and

Class 3: > 40 cm.

Class 1 is below minimum critical size for reproduction (Chapter 1). Modules in class 2 are either vegetative or reproductive. The two stages were pooled because at the time of setting this experiment, receptacles were not fully formed; thus, vegetative and reproductive modules could not be distinguished. Class 3 modules are only occasionally vegetative.

The plants were classified in 3 sizes:

Small plants (S): plants with only class 1 modules,

Medium plants (M): plants with 50 % modules in class 1 and 50 % in class 2,

Large plants (L): plants with 50 % modules in class 1 and 50 % in class 3.

Plants with the above module size structures or similar are very common, although wild plants occur in a wide array of module size structures (personal observations from this and another study, Chapter 2). The module size structure of plants had to be manipulated in order to test for the effects of stand size structure. That is, that the initial sizes of plants in low and high density stands were similar.

Treatments

Treatments included two module densities and five different stand size structures. Different stand size structures were made up with combinations of plant sizes. Each stand always comprised six plants. The two levels of stand densities resulted from the number

of modules/plant and not from the number of plants in the stand. The reason for this design was that plant density seemed to change little with time because mortality was low (pers. observ. from the study in Chapter 2, Åberg 1990a b). Module densities instead appeared to fluctuate more (pers. observ. from the study in Chapter 2). The amount of holdfast material as a potential source of new modules increases with the number of modules in the plant. Since the holdfast is basically the base of the module and was similar in all modules, the amount of holdfast material was essentially proportional to the number of modules in the plant (pers. observ., this study). Thus amount of holdfast tissue was accounted for in this experimental design. Treatments are given in Table 1a. High density is within maximum average natural densities (961 modules/0.25 m², data obtained from sampling in other study in Chapter 2). Each treatment was replicated up to six times and randomly assigned to a stand. During the course of this study losses of replicates occurred. The number of surviving replicates is given in Table 1a. A replicate was a 0.50-m x 0.50-m stand with six plants. The spatial arrangement of plant sizes in an individual stand is given below (Table 1b). I noted similar arrangements of plants in the study site (pers. observ., this study). Edge effect is discussed in text.

Table 1a. Densities and combinations of plant sizes (i.e. stand size structures). Number of surviving replicates are given. S= stands with only small plants, M= stands with only medium plants, L= stands with only large plants, SM= stands with small and medium plants, SML= stands with small, medium and large plants. m.= modules, pl.= plant.

density	no. plants & modules/stand	combination				
		S	M	L	SM	SML
low: 50 modules/plant	6 plants, 50 m./pl. X 6 pl. = 300 m./stand.	4	4	4	6	4
high: 150 modules/plant	6 plants, 150 m. X 6 = 900 m./stand.	4	4	2	2	4

Table 1b. Combination of plant sizes in a stand. Plants were placed approximately 15 cm from the right and left edges and 18 cm from the top and bottom of the grid.

stand S	M	L	SM	SML																														
<table style="width: 100%; text-align: center;"> <tr><td>S</td><td>S</td></tr> <tr><td>S</td><td>S</td></tr> <tr><td>S</td><td>S</td></tr> </table>	S	S	S	S	S	S	<table style="width: 100%; text-align: center;"> <tr><td>M</td><td>M</td></tr> <tr><td>M</td><td>M</td></tr> <tr><td>M</td><td>M</td></tr> </table>	M	M	M	M	M	M	<table style="width: 100%; text-align: center;"> <tr><td>L</td><td>L</td></tr> <tr><td>L</td><td>L</td></tr> <tr><td>L</td><td>L</td></tr> </table>	L	L	L	L	L	L	<table style="width: 100%; text-align: center;"> <tr><td>S</td><td>M</td></tr> <tr><td>M</td><td>S</td></tr> <tr><td>S</td><td>M</td></tr> </table>	S	M	M	S	S	M	<table style="width: 100%; text-align: center;"> <tr><td>S</td><td>L</td></tr> <tr><td>M</td><td>S</td></tr> <tr><td>L</td><td>M</td></tr> </table>	S	L	M	S	L	M
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Factors tested were density and stand size structure, i.e. combination of plant sizes. The levels of density were low and high (Table 1a) and the levels of stand size structure were S, M, L, SM, and SML (Table 1b). In order to determine the response of a plant to stands with increasing crowding (i.e. stands with plant of increasing sizes) but similar densities, comparisons between pure-size and mix-size stands were conducted. The comparisons were as follows:

plant size S in stands S vs SM vs SML,
 plant size M in stands M vs SM vs SML, and
 plant size L in stands L vs SML.

Response variables

Growth was measured in terms of number of modules and plant biomass. Biomass was determined by weighing each plant at the beginning (before placing in the stand) and the end of this study

(after removing from the stand). Only modules 4 cm or greater were considered in the assessment of numbers of modules. Absolute growth was the difference in the total number of modules, or biomass, between the beginning and end of this study (twenty one months). Growth as a proportion of initial size was estimated as well (proportional growth). Proportional growth was calculated by dividing absolute growth by initial module number, or the biomass of each individual plant. The individual values were then averaged for each plant size and stand. Proportional growth assessed the response of a plant in relation to its own size. Absolute growth was useful to determine the magnitude of the response in terms of numbers of modules or biomass. I estimated proportional and absolute growth to be able to compare my findings with general theory since most studies on interference assess responses in terms of relative and absolute growth (Hutchings 1986).

Change in Module abundance/size class (referred in text as change in numbers or abundance of modules) was the difference in number of modules/size class between the start and the end of the study. Thus, it is the *net* change in number of modules, which includes gains and losses due to mortality, breakage and growth. For instance, the change in number of modules in size class 2 was = no. growing from class 1 to class 2 - no. growing from class 2 to class 3 - no. which broke from class 2 to class 1 + no. which broke from class 3 to class 2 - mortality of class 2. It is emphasized that this study did not attempt to determine the transitions between classes (e.g. class 2 to 3, class 3 to 1, etc.). This study assessed the effect of interference upon the numerical abundance of a class, ultimately whether interference is responsible for the size structure of the population of modules.

In some cases there were fewer modules in a given class at the start than at the end of the study. Hence some abundance values were negative. For instance, if a plant had 50 modules in class 1 at the beginning of the study and 40 at the end, abundance was -10.

This negative value meant that the plant lost 10 class 1 modules, not that abundance was negative as clearly that is not possible. It is emphasized here that numerical abundances within a size class was the *net* change in numbers of modules/size class (during this study).

Reproduction was the difference in the number of reproductive modules between the beginning and the end of the study. In April 1989 and 1990 I counted the number of reproductive modules that attained reproduction in each plant and treatment. An increase or decrease in the number of reproductive modules would suggest that the effect of interference on reproduction was positive or negative respectively.

Experimental plants.

Because growth is slow (Chapter 2, 4), plants could not be grown from zygotes. Thus, the present study employed adult plants. Plants were collected from the field, scraping their holdfast off the substratum, and then taken to the laboratory. Each module of each plant was measured to determine the module size structure of the plant. If the number of modules/class exceeded the number needed (to make small, medium or large plants), extra modules were removed. When the number of modules in class 1 or class 2 in the plant was not enough, longer modules were cut to attain the desired length. The proportion of cut modules in each plant depended upon how many were needed. Modules cut by natural means or through harvesting are common in the present stands. Also, since Chapter 2 suggested that the performance of modules cut during harvesting was similar to that of intact modules, their response is unlikely to affect my analyses. If plants did not have enough modules, whole or parts of plants were assembled together until the desired density was obtained. The plants thus assembled were sewn on a square piece of synthetic material. Sewing needles and monofilament or braided fishing line were employed to attach the plants. These

plants can be compared with natural assemblages because plants from different genets can grow together resembling one individual (Åberg 1989).

Plants were sewn on a metallic, plastic-covered grid of the type used to make lobster traps. The distance between plants and their positions on the grid were identical in all treatments. The stands were then placed, interspaced, in the field adjacent to the area where they were collected; i.e. an area of mud consolidated with sand and small cobbles, devoid of vegetation.

Since the fishing line used for sewing could cut through modules or holdfast and cause mortality, a control for sewing effect was set up. Plants attached to small rocks were collected. The module structure of each was prepared as small, medium and large plants with 50 modules each. Plants were, then, placed in wooden boxes as stands SML, cemented and placed in the field along with the other treatments. The experiment ran between June 1989 to April 1990. At the end of this period the total number of modules in each size class was counted and tested with t-test against treatments SML low density with sewn plants. No significant differences ($P > 0.05$) were found.

Plant losses may occur due to natural removal. Because my plants were sewn to the substratum, this study could not account for natural plant mortality. However, since it is low (pers. observ. in another study (Chapter 2), Åberg 1990a,b) plant mortality may be considered negligible. Nevertheless, in one plant in my stands all modules rotted at the base and were lost. During this study I noticed that rotting at the base was a common cause of plant and module removal. From this view point my study did account for this type of mortality but survival was not analyzed statistically. Obviously growth and reproduction for this one plant could not be assessed and were treated as missing values in the statistical analyses.

Statistical Analysis.

The effects of density and combination of plant sizes on the response variables were analyzed by means of a two-crossed factor ANOVA. The power of the performed ANOVAs that yielded non-significant effects was estimated (Zar 1984). If the power was < 80% and all effects tested in the ANOVA were non-significant results were not reported. If at least one effect in the ANOVA table was significant, the table was included in the results section with the effects described as shown in the table, and a paragraph was included to comment on power analysis in the discussion section. Care was taken to meet all assumptions of this analysis (Underwood 1981). Heterogeneity of variances was tested with Cochran's test. When the probability of non-homogeneity was between 0.05 and 0.01 data were transformed to $\log_{10}(x)$. Some values of growth and change in abundances were negative and thus could not be transformed to \log_{10} . To obtain values greater than zero, the lowest negative value plus 10 was added to each. Data were then transformed to $\log_{10}(x)$. If the transformation did not stabilize the variances (Cochran's $P = 0.01$ or smaller), data were not included in text. Normality was checked with normal plots. If the result of this test was a significance value equal or smaller than 0.05 the distribution of the data were consistent with a normal distribution. Normality was also tested with Kolmogorov-Smirnov analysis. Significance values equal or smaller than 0.05 indicated that the data differed significantly from a normal distribution. The results of the tests for assumptions for each of the ANOVA tables in the Results section are shown below using the same number of table plus an a. For instance, Table 3 in Results is 3a here, Table 4 is 4a, etc.

Table	Plant Size	Test	Results
2a	small	K-S test normal plots Cochran's test	P > 0.05 P < 0.01 P > 0.05
	medium	K-S test normal plots Cochran's test	P > 0.05 P < 0.01 P > 0.05
	large	K-S test normal plots Cochran's test	P > 0.05 P < 0.01 P > 0.05
3a	small	K-S test normal plots Cochran's test	P > 0.05 P < 0.01 P > 0.05
	medium	K-S test normal plots Cochran's test	P > 0.05 P < 0.01 P > 0.05
	large	K-S test normal plots Cochran's test	P > 0.05 P < 0.01 P > 0.05
4a	small	K-S test normal plots Cochran's test	P > 0.05 P < 0.01 P > 0.05
	medium	K-S test normal plots Cochran's test	P > 0.05 P < 0.01 P > 0.05
	large	K-S test normal plots Cochran's test	P > 0.05 P < 0.01 P > 0.05

5a	small	K-S test normal plots Cochran's test	P > 0.05 P < 0.01 P > 0.05
	medium	K-S test normal plots Cochran's test	P > 0.05 P = 0.05 P > 0.05
6a	small	K-S test normal plots Cochran's test	P > 0.05 P < 0.01 P > 0.05
	medium	K-S test normal plots Cochran's test	P > 0.05 P = 0.05 P > 0.03
7a	small	K-S test normal plots Cochran's test	P > 0.05 P < 0.01 P > 0.05
	medium	K-S test normal plots Cochran's test	P > 0.05 P < 0.01 P > 0.05
	large	K-S test normal plots Cochran's test	P > 0.05 P < 0.01 P > 0.05

Data on growth (and abundance of modules/size class) was averaged for each plant size, (or module size class) and replicate. These averages were the data used in the ANOVAs. The model employed was:

$$Y_{ij} = \text{mean} + D_i + C_j + (D \times C)_{ij} + E_{(ij)}$$

mean= Grand mean for the entire population,

D= Effect due to density,

C= Effect due to combination of plant sizes,

D x C= Effect due to density by combination of plant sizes interaction,

E= Error.

Results

Stands

Growth: Number of Modules

The average number of new modules/plant in a stand formed in two years in each treatment is given in Figure 1. New modules were formed at low and high density treatments but significantly more were formed at low than at high densities (ANOVA, $P < 0.0001$). The effect of the combination of plant sizes on the number of new modules/plant was non-significant (ANOVA $P > 0.05$). At low density, module birth tended to be relatively lower in pure-size stands than in mix-size stands, suggesting that crowding was greater in stands with plants of similar sizes. A somewhat inverse pattern was noted at high density in S, SM and M stands, but as biomass and canopy in the stand increased, growth declined. No new modules were formed in L stands in two years. The ANOVA table was not included here because the values for individual plant sizes across treatments gave the same results (below).

Relative to the stand density, the increase in number of modules showed a pattern similar to the one described above. At high and at low densities the average increase was 0.2 and 1.4 times the initial number of modules respectively (Fig. 2).

Growth: Biomass

In contrast to the increase in module numbers, mean biomass increased considerably more at high than at low densities (ANOVA $P < 0.0001$, Fig. 3). From Figures 1 and 3 it is reasonable to think that few modules were born at high density but perhaps they and or the existing ones too, increased in biomass. At low density many new modules were formed but perhaps they and or the existing modules,

did not increase in size. Biomass increased from S to SM to M stands at high density and declined in SML and L stands. In contrast, at low density, growth tended to increase with increasing initial biomass and plant sizes in the stand, although averages in pure-size stands were comparatively lower than in mix-size stands. However, the effect of combination of plant sizes was non-significant (ANOVA, $P > 0.05$). The ANOVA table was not included here because analysis for individual plant sizes across treatments gave the same results (below).

Relative to the initial biomass growth was greater at low than at high densities (Fig. 4). The only exceptions were stands M and L where where growth in biomass for both densities were similar. At low density, growth was increasingly slower in stands with increased initial stand biomass and plant sizes except in SML stands where growth was relatively high. At high density, growth also decreased in stands with increased initial biomass and plant sizes, except in M stands where a small growth peak occurred.

Plants

Growth: Number of Modules

The birth of modules in a plant depended on density, being lower at high than at low densities (Fig. 5a-c, Table 2). Averaging the three plant sizes, about 25 modules were formed at high density and 63 at low density in 21 months. Combinations of sizes X density combination (d X c) interaction were always non-significant, despite the variability noted among treatments. The lack of significance of these two effects suggests that within a given density, stand size structure did not influence module birth.

Growth: Biomass

The increase in biomass was significantly lower at low density than at high densities in small and medium plants (Fig. 6a-b, Table 3). Density had no effect on large plants, treatment averages being similar (Fig. 6c). The effect of combination of sizes was significant in small and large plants. At high density, growth decreased significantly with increasing initial biomass and canopy in the stand, whereas at low density, the decline was comparatively less in small plants and high in large plants. Medium plants were not significantly affected by the combination of plant sizes, although their response at high density was similar to that of small and large plants. The density x combination of plant sizes (d X c) interaction was not significant for any plant size.

The increase relative to the initial plant biomass was slower at high density than at low density (Fig. 7a-c). The growth of small and medium plants changed little with combination of plant sizes in the stand (Fig. 7a,b). However, the response of large plants was different (Fig. 7c). At high density, large plants grew the same in mixed and pure-size stands. At low density growth declined dramatically with the increase in crowding in L stands.

Abundance of Modules within a Size Class

Figure 8 shows changes in numerical abundances in classes 1, 2 and 3 in each treatment and plant size. The significance of the statistical tests are in Tables 4 to 6. High density suppressed abundance of modules into class 1 in all plant sizes (Fig. 8a-c). The effect was particularly severe in small plants where module losses occurred (Fig. 8a, Table 4) with fewer modules at the end than at the beginning of this study. Changes in abundance of modules in class 1 in small, medium and large plants did not depend upon the combination of plant sizes in the stand or on the d X c interaction, although variation across stands was observed.

Density was a significant factor determining the abundance of modules in class 2 but the effect depended upon plant size (Fig. 8d-f, Table 5). The effect of high density was positive in small plants (Fig. 8d) and negative in medium ones (Fig. 8e) where module losses occurred. The combination of plant sizes in the stand or the $d \times c$ interaction did not influence the abundance of modules in these two plant sizes. Heterogeneity of variances in large plants did not allow statistical testing but Figure 8f suggests that high density enhanced the abundance of modules into class 2. Figure 8f also suggests that the effects of combination of plant sizes and its interaction with density were non-significant.

The effect of density on the abundance of modules into class 3 was non-significant on small plants (Table 6, Fig. 8g-i) presumably because few modules (5 to 10) in small plants grew to class 3 during 21 months (Fig. 8g). High density significantly enhanced the number of modules in class 3 in medium plants (Fig. 8h). Figure 8i suggests that density also influenced the numerical abundance of class 3 in large plants. Module losses occurred at both densities but particularly at high than at low densities. The combination of plant sizes or the $d \times c$ interaction did not appear significant in any plant size.

In summary, Figure 8 shows that the change in abundance of modules in each size class was regulated by density. The effect of high density was negative or positive depending upon module size class. Class 1 was the only one that was consistently suppressed by density in all plant sizes. Losses of modules in class 2 at high density occurred in plants with class 2 modules (i.e. medium plants, Fig. 8e), and the losses correlated with an increase in the abundance of class 3 (in the same plants, Fig. 8h). Since medium plants did not have class 3 modules at the beginning of the study, class 3 modules were modules in class 2 that grew to a larger stage. While module losses in class 2 were higher at high than at low densities (Fig. 8e)

the increase in class 3 was maximum at high density and relatively lower at low density (Fig. 8h). A similar pattern was also noted in classes 1 and 2 (figs. 8a vs 8d). So, as shown above, high density promoted growth in size while low density influenced the abundance of modules in a class. In large plants, however, high density appeared to promote breakage rather than growth. Losses of modules in class 3 at high density were noted (Fig. 8i) and were correlated with an increase in the abundance of modules in class 2 (Fig. 8f). Since there were no class 2 modules in large plants at the beginning of this study, probably some modules in class 2 were modules in class 3 that broke and became class 2. Modules growing from class 1 to class 2 probably also contributed to the increase in abundance in class 2. Figure 8 then suggests that the abundance of modules in a particular size class in a given plant depended upon the module size structure.

I emphasize that the purpose of the above paragraphs was to determine whether density and stand size structure influenced *changes* in the number of modules in a given size class. By comparing Figure 8, correlations can be established that allow to suggest the underlying processes of these changes.

Reproduction

Stands

The abundance of new modules attaining reproduction in a stand was enhanced at high density (Fig. 9, $P < 0.0001$). However, the combination of plant sizes and the $d \times c$ interaction exerted no influence. The abundance of new reproductive modules in treatments of maximum crowding (L stand) was similar at both densities. Tests are below.

Plants

Small, medium and large plants produced more reproductive modules at high than at low densities (Fig. 10a-c, Table 7). The only

exception was large plants in L stands where averages were similar at both densities. On average about 8 and 20 modules/plant attained reproduction at low and high densities respectively. Although fertility varied across treatments, the effects of combination of plant sizes and the d X c interaction were non-significant.

Discussion

Dean et al. (1989) note many parallels between the determinants of population dynamics and demography of terrestrial species. In terms of within-species interactions, a large body of literature shows that, in dense, terrestrial stands, plants usually exhibit reduced growth, reproduction and survival (Schiel & Foster 1986). However, there remains controversy over whether terrestrial models apply to seaweed stands. The basis of this controversy is outlined in the Introduction of this study and reviewed in detail by Schiel & Foster 1986. Methodological problems may have contributed to this controversy, the problems being insufficient manipulative experiments, a lack of distinction between plants and modules and the variable responses chosen (Introduction). The effects of density on biomass or numbers of modules/individual are not the same (this study). Moreover, assessments of biomass alone in plant stands may be meaningless because size classes are lumped together concealing their abundances (Schiel & Foster 1986). Schiel and Foster (1986) state that biomass measures alone cannot be used for any consideration of population biology or demography and thus have little use in assessing interactions. This viewpoint is particularly true when life cycle stages are size-based because interference will eventually determine the abundances of each size class and thus affect population structure, demography and fertility (this study). The present study was the first of its kind to examine the effects of crowding on plants and modules in order to understand the responses of marine species to interference. Also to understand the effects of interference and ultimately population structure, this study

considered alternative variable responses. Attention was paid to the effects of interference on the numerical abundances of each life cycle stage in order to understand the processes that shape module population structure.

This study suggested that interference exerted a significant influence on the population demography of *Ascophyllum*. However, the effects of interference were not entirely parallel to those observed in terrestrial plants, which is discussed below. Moreover, the responses detected may depend upon the population level (i.e. modules or plants) and the variable response considered as well as the type of question asked.

Two types of growth responses were found. The overall increase in number of modules/plant in a stand was three times higher at low than at high densities, while up to 8.7 times higher relative to initial densities. Despite the fact that module natality was low at high density (relative to low density stands) new modules were formed at high density, except in L stands where crowding was maximum. Absolute growth in biomass/plant was significantly lower at low than at high densities. The contrast between growth in numbers of modules and in biomass means that at low density numerous modules were born but modules grew little in size. At high density, natality was restricted but modules increased in size. Responses did not depend on the size of the plant. The growth responses in number of modules and biomass approximates Westoby's (1984) view of growth dynamics in modular species, where plants (genet in Westoby's terms) grow by multiplication of modules rather than by increasing the size of modules. If stands are not crowded, thinning is unlikely and the number of modules may in fact, increase. Under crowded conditions most species would grow one or a few modules to full size, thereafter plants expand by multiplication of modules. Reduced module birth may also occur to prevent overpopulation (Hutchings & Mogie 1990, Thompson et al. 1990, De Kroon & Kwant 1991). In the present study the increase in

module size and limited module natality at high density suggested that *Ascophyllum* may fit this model. The fact that the birth of class 1 modules was suppressed at high density suggested that the limited production of modules in high density stands was not due to thinning but to regulation of module birth, although some mortality may also have occurred. Increased growth in biomass at high density also agrees with Schiel & Choat's (1980) and Schiel's (1985a) findings for three other species of brown seaweeds. Hymanson et al. (1990) found that stipe length, but not stipe diameter, in *Pterygophora californica*, increased significantly more at high than at low densities in experimental stands. If this was related to size then, this species also fared better under crowded conditions, although it was evident from wild stands that other factors also influenced stipe dimensions. As far as I know, there are no parallels cited for terrestrial plants. It is noted that the effect of density on the growth in biomass in large plants was statistically non-significant (Fig. 6c, Table 3). The low power of the performed ANOVA (< 80%) may explain the lack of non-significance. However, Figure 6c showed that growth varied little with density, suggesting that to a degree density did not in fact influenced the growth of large plants.

The second striking finding concerned reproduction. The number of modules attaining reproduction was higher at high than at low densities. The response was consistent through all stand size-structures and the three plant sizes. The finding was in agreement with Schiel & Choat's (1980) and Schiel's (1985b) report that demonstrated that fertility was positively related to density. Furthermore, gametophytes in the field would not reproduce at very low densities (≤ 1 recruit/mm², Schiel 1985a). More reproductive modules in high than low density stands was also unusual because it is generally held that there are trade-offs between sexual and asexual reproduction (Weiner 1988). At low density, vegetative spread is favoured, with this advantage providing colonization of space and propagation of the genotype. At high density sexual

reproduction is promoted for the dispersal of novel genotypes that have a better chance of survival. This model, however, is only partly supported by empirical evidence. *Ascophyllum* may not fit this model. While vegetative spread was relatively suppressed in high density stands, growth in biomass and the number of new modules achieving reproduction both increased at high density. It must be noted, nonetheless, that the increase in reproduction found in my high density stands does not necessarily involve an increase in sexual recruitment. In fact, sexual recruitment and fertility in *Ascophyllum* were not correlated (Chapter 1 and 4).

The underlying mechanisms of the present responses may result from the combined effects of irradiance, temperature, translocation and abundance of modules. Translocation of hormones has been identified in *Ascophyllum* (Bradley 1991) and other brown seaweeds (Nys et al. 1990, 1991), although whether they really are hormones need confirmation (Evans & Trewavas 1991). In fact, it is known that in some brown seaweeds, transport takes place from relatively large areas into the apex where growth takes place (Diouris 1989). In the mechanism proposed here translocation would not be just within a module but among modules. Physiological integration may be particularly strong in phalanx species (Hutchings & Mogie 1990) like *Ascophyllum*. Translocation may be from modules in the canopy exposed to greater irradiance and temperature to understory apices arising from them. Since growth increases with irradiance and temperature (Strömberg 1983) it is reasonable to think that, at low density, high levels of irradiance and temperature promote module birth. However, as the number of existing large modules is low translocation from them to the newly formed modules may not be significant and thus they do not grow in size (immediately). By contrast, at high density the birth of modules may be inhibited by low-light availability near the holdfast (Deregibus & Trlica 1990, De Kroon & Kwant 1991) or apical dominance (Hutchings & Mogie 1990). However, as the number of existing large modules is relatively high

translocation may be significant and promote module growth in biomass.

Alternatively, growth in dense stands may be enhanced by other factors as well. During low tide, dense seaweed stands may be able to retain moisture and the photosynthetic capacity is probably better than in thinned stands (Paine 1990). Temperature can rise up to 30° C enhancing growth rate by more than 2000% during the first 2 hours (Strömberg 1981). Another explanation has to do with bacteria. *Ascophyllum* grows better in association with bacteria possibly because the bacteria, not the seaweed, produces growth-promoting substances (Evans & Trewavas 1991). If bacterial growth is favoured at high density and they generate growth-promoting substances, growth in biomass at high density is enhanced.

Another way in which crowding can affect reproduction is by influencing the gender allocation of a plant or the sex ratio in a stand (Weiner 1988, Ackerly & Jasien'ski 1990). In Chapter 1 I reported anomalies in the allocation of sex in *Ascophyllum*, anomalous modules being dioecious, monoecious and hermaphrodite. Supposedly this species is only dioecious (Baardseth 1970, Åberg 1989). In view of the influence of crowding on the present stands demography, it is possible to speculate that the anomalous distribution of gender results from crowding. In this sense the response of marine and terrestrial plants to crowding appears similar.

General theory states that plant growth decreases with the number of taller neighbours in terrestrial species (Hutchings 1986, Bonan 1988) and possibly in seaweeds as well (Reed & Foster 1986). The present study suggested this theory may be true, depending upon the variable response considered. For instance, plant growth in terms of biomass decreased with increasing initial biomass (i.e. combination of sizes) in the stand (although statistically non-significant for M plants). If the variable response chosen is module numbers, my

findings do not agree with general theory. Growth in terms of module numbers did not significantly decrease with increased initial stand biomass, although a slight negative trend was noticed in medium and large plants mostly at low density. In addition, even large plants exhibited reduced biomass increases. The decline was particularly dramatic in terms of proportional growth. At low density growth decreased eight times from SML stands to L stands (Fig. 7c), which was due to breakage. By comparison, the growth of small plants decreased only 1.2 from S to SML stands. In contrast to general theory then plants in the canopy may also be under stress from crowding.

The lack of significance of stand size structure on module natality in contrast to the significance of density is striking. Likely the reason was that large size does not matter because during low tide, modules lay in more or less random positions. Thus, large size does not necessarily ensure unequal capture of light and small modules are not necessarily shaded. In fact, laboratory evidence suggests that growth is enhanced during low tide due to exposure to heating by air and sun and short periods of desiccation (Strömgren 1981, 1983). Similar responses have been shown in other seaweeds. The photosynthesis of five species of brown seaweeds increased up to 25% during exposure, at least up to certain degree of desiccation tolerance (Dring & Brown 1982). Another factor that may minimize the effect of plant sizes on each other is morphology. Tall plants can intercept more light without shading than those with other morphologies (Carpenter 1990). Also, in theory, apical dominance reduces overlap by controlling the plant's shape (Callaghan et al. 1990).

One cannot rule out the possibility that stand size structure was non-significant because control for edge effect was not provided in the experimental stands. Plants growing in isolated patches in southwestern Nova Scotian stands are nevertheless common so that, the present findings apply at least to these plants. Westoby &

Howell (1986) found that edge effect is difficult to eliminate in experiments and that wild stands comprise gaps and thus, edges. The edge effect may then not be just an experimental inconvenience but a process with biological meaning. Also most species may be indifferent or respond similarly to gap environmental variables as suggested by a comparison of the survival, growth and recruitment of 300 species in canopy gaps vs shade sites (Welden & Hubbell 1992). Excluding the edge plants from the experiments does not always change the statistical significance of the findings either (Ackerly & Jasien'sky 1990).

A possible factor underlying the lack of statistical significance of stand size structure may be that the power of the tests was $< 80\%$. It is possible then that effects might have been significant, had the power being higher. However, Figures 5, 8 and 9 shows that, at low or high density treatments, responses varied relatively little with stand size structure. There is no obvious evidence that the combination of plant sizes in the stand influenced the response variables, at least for the experimental design used here. The sample size of the tests would then have to be extremely high to detect small differences among treatments.

Some studies suggest the responses of marine and terrestrial plants to crowding are different (Schiel & Choat 1980, Schiel 1985a, Carpenter 1990). Others hold that the maximum size a plant can attain is limited by crowding, regardless of whether they are marine or terrestrial (Watkinson 1986, Cousens & Hutchings 1983). My study may support both contentions. That is, overall, biomass growth measured in absolute terms increased in dense stands supporting Schiel and Choat's view but growth decreased with crowding (i.e. with numbers of large plants in the stand), which supported Cousens's and Hutchings's view. The decline in absolute or proportional growth with crowding, particularly of large plants (Figs. 6c and 7c), suggested indeed that density imposes a limit upon the plant's size. Module losses in class 3 in large plants at L stands

where crowding is maximum (Fig. 8i) also suggested that modules attained their maximum possible size. By contrast with terrestrial plants where the smallest individuals die (White & Harper 1970), in seaweeds the largest individuals broke, which coincided with Schiel's (1985b) report (Fig. 8i). The effect of density might have then not be mortality of small modules but breakage mostly of the largest modules (Fig. 8i) and reduced formation of small modules. Peckol et al. (1988) also noted that breakage in *Ascophyllum* was common for large modules characteristic of dense stands.

Therefore, whether marine and terrestrial stands respond similarly to density depends upon the question asked and on how growth is measured, i.e. biomass or numbers of modules. The literature also suggests that similarities with terrestrial systems depends upon how responses are measured. Reed et al. (1991) found that the responses to interference of kelp gametophytes depended enormously upon the experimental conditions. They grew gametophytes in still water and in aerated cultures as well as with various nutrient treatments. In still water, density stress had a negative effect upon growth and reproduction. In aerated cultures reproduction increased with density and growth increased with nutrient levels. Furthermore, gametophyte size in laboratory conditions was greater than in field conditions. There is evidence that the effects of interference are similar in marine and terrestrial plants (Dean et al. 1989). Survival of kelp juveniles was negatively correlated with the size and presence of canopy plants. Recruitment may also be inhibited by taller plants (see Schiel & Foster 1986). However, negative effects of interference may be restricted to populations of large canopy-forming kelps in deep waters where light levels are low and an extensive vertical structure exists (Dean et al. 1989). Thus, intertidal or shallow-water species with other morphologies are not likely to show the same responses as kelp (Reed & Foster 1986).

The fourth most striking finding concerned the change in numerical abundances in the three size classes. Again, the effect of density was significant but unexpected. According to conventional theory one could expect that growth into larger classes would be enhanced by low crowding conditions. Studies have shown that in the absence of a canopy, increases in number of modules in the canopy (Robertson 1987), growth and survival of zygotes and understory plants were enhanced (Dean et al. 1989, Hay & South 1979, Smith 1986, Reed & Foster 1984). In clonal perennial herbs module natality decreased with increasing density (De Kroon & Kwant 1991). In *Ascophyllum* high density suppressed the abundance of modules in class 1 (in all plant sizes) probably due to reduced light availability (Cousens 1982a, 1985), which agrees with theory. However, the effect of density on the other two classes was different. High density promoted growth in size from class 1 to 2 (Fig. 8a,d) and from class 2 to 3 (Fig. 8e,h) and possibly was responsible for breakage in class 3 (Fig. 8i). High density suppressed the abundances of class 1 (fig 8a) and 2 (fig. 8e) in small and medium plants but enhanced the abundances of classes 2 (fig. 8d) and 3 (Fig. 8h) in the same plants. Thus, the effect of density was positive or negative depending on the size class considered. The effect of density on the change in abundance of modules in class 3 in small plants was non-significant (Fig. 8g). The reason of the lack of significance may be that the power of the ANOVA was low. Figure 8g, however, showed that the difference between densities was small suggesting that density in fact did not influence the abundance of class 3 modules. In fact, very few modules (5 to 10) in class 1 grew to class 3 during this study.

The present study distinguished between modules and plants. Ideally, I should have considered genets instead of plants, but in *Ascophyllum* this is not possible because genets split producing identical plants. Plant responses to interference were similar regardless of their size. Abundances of modules in different life cycle stages (or size classes), instead, depended upon density, size

class and the module size structure of the plant. Growth patterns, may then be unique to plants (or genets) and modules.

Table 2. ANOVA table. Effects of density, combination of plant sizes and their interaction (d X c) upon the formation of new modules in each plant size. * Data transformed for the analysis.

Plant Size	Source	df	S.S.	F	P
Small	density	1	8185.73	8.46	<0.0001
	combination	2	386.79	0.20	>0.05
	d X c	2	1757.39	0.91	>0.05
	error	18	16334.59		
Medium *	density	1	0.67	15.63	<0.0001
	combination	2	0.03	0.39	>0.05
	d X c	2	0.09	0.01	>0.05
	error	18	0.78		
Large	density	1	7830.24	27.37	0.003
	combination	1	533.20	1.59	>0.05
	d X c	1	2.99	0.01	>0.05
	error	10	3350.06		

Table 3. ANOVA table. Effects of density, combination of plant sizes and their interaction (d X c) upon growth (g).

Plant Size	Source	df	S.S.	F	P
Small	density	1	120711.2	8.38	0.01
	combination	2	228846.3	7.94	0.003
	d X c	2	85276.3	2.96	>0.05
	error	18	259401.7		
Medium	density	1	1431850.7	15.64	0.001
	combination	2	320818.2	1.75	>0.05
	d X c	2	61992.5	0.34	>0.05
	error	18	1648342.7		
Large	density	1	1569.8	0.01	>0.05
	combination	1	639089.6	5.74	0.04
	d X c	1	41918.9	0.38	>0.05
	error	10	1113967.7		

Table 4. ANOVA table. Effects of density, combination and their interaction (d X c) upon the change in abundance of modules in class 1. *Data transformed for the analysis.

Plant Size	Source	df	S.S.	F	P
Small	density	1	28588.59	31.50	<0.0001
	combination	2	1745.20	0.96	>0.05
	d X c	2	2256.15	1.24	>0.05
	error	18	16334.59		
Medium	density	1	0.21	29.09	<0.0001
	combination	2	0.01	0.76	>0.05
	d X c	2	0.03	2.48	>0.05
	error	18	0.13		
Large	density	1	5980.0	15.94	0.003
	combination	1	119.2	0.32	>0.05
	d X c	1	93.2	0.25	>0.05
	error	10	3751.1		

Table 5. ANOVA table. Effects of density, combination of plant sizes and their interaction (d X c) upon the change in abundance of modules in class 2.

Plant Size	Source	df	S.S.	F	P
Small	density	1	5172.67	48.88	<0.0001
	combination	2	383.39	1.81	>0.05
	d X c	2	58.50	0.28	>0.05
	error	18	1904.79		
Medium	density	1	8114.25	646.53	<0.0001
	combination	2	63.76	2.54	>0.05
	d X c	2	73.85	2.94	>0.05
	error	18	225.91		

Table 6. ANOVA table. Effects of density, combination of plant sizes and their interaction (d X c) upon the change in abundance of modules in class 3. * transformation.

Plant Size	Source	df	S.S.	F	P
Small	density	1	44.69	1.37	>0.05
	combination	2	11.93	0.18	>0.05
	d X c	2	43.41	0.67	>0.05
	error	18	585.39		
Medium	density	1	7072.22	119.85	<0.0001
	combination	2	45.24	0.38	>0.05
	d X c	2	7.09	0.06	>0.05
	error	18	1062.22		

Table 7. ANOVA table. Effects of density, combination of plant sizes and their interaction (d X c) on the number of reproductive modules in small, medium and large plants. * Transformation.

Plant Size	Source	df	S.S.	F	P
Small	density	1	1759.88	48.69	<0.0001
	combination	2	4.46	0.06	>0.05
	d X c	2	43.36	0.60	>0.05
	error	18	650.63		
Medium	density	1	2722.51	154.98	<0.0001
	combination	2	26.32	0.75	>0.05
	d X c	2	6.02	0.17	>0.05
	error	18	316.20		
Large *	density	1	0.83	14.00	0.002
	combination	1	0.00	0.00	>0.05
	d X c	1	0.01	0.09	>0.05
	error	10	0.59		

Figures 1 to 4 encompass increments in size in terms of number of modules and biomass.

- 1) Absolute mean growth in number of new modules/plant produced in pure-size stands and mix-size stands at low and high density. Bars are means and standard errors. The three module size classes were pooled.
- 2) Growth in numbers of modules as a proportion of the initial module numbers across densities and size structures. The three module size classes were pooled.
- 3) Absolute mean growth/plant in biomass in pure-size and mix-size stands at low and high density. Bars are means and standard errors. The three module size classes were pooled.
- 4) Growth in biomass as a proportion of the initial stand biomass in pure-size and mix-size stands at low and high density. The three module size classes were pooled.

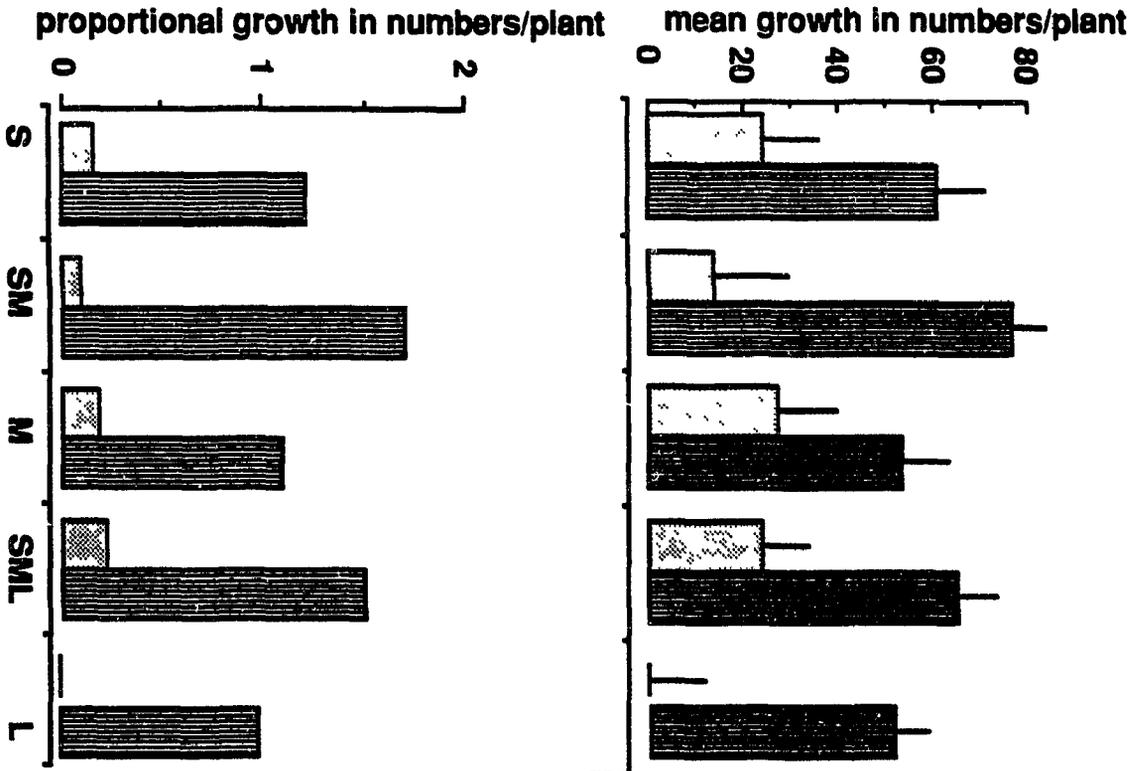


Fig. 1

Fig. 2

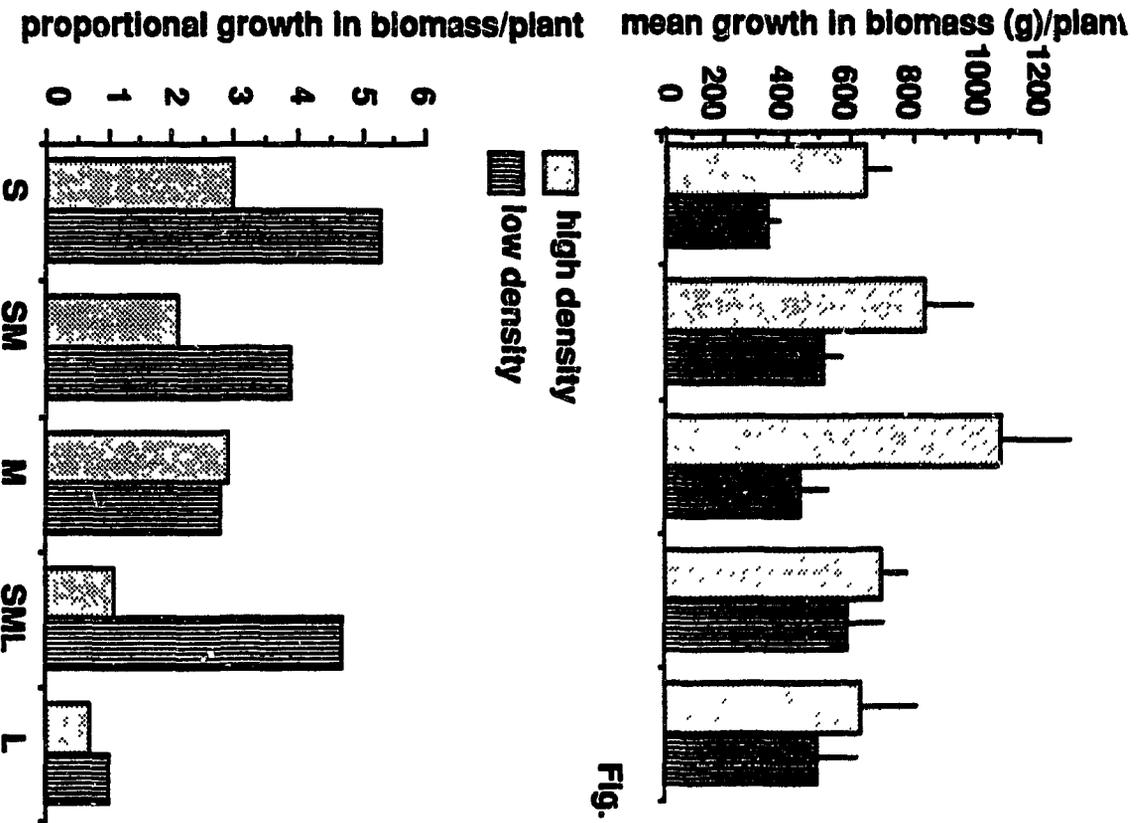


Fig. 3

Fig. 4

Figure 5. Absolute mean growth in numbers of modules/plant of a) small, b) medium and c) large plants in pure-size and mix-size stands at low and high density. Bars are means and standard errors.

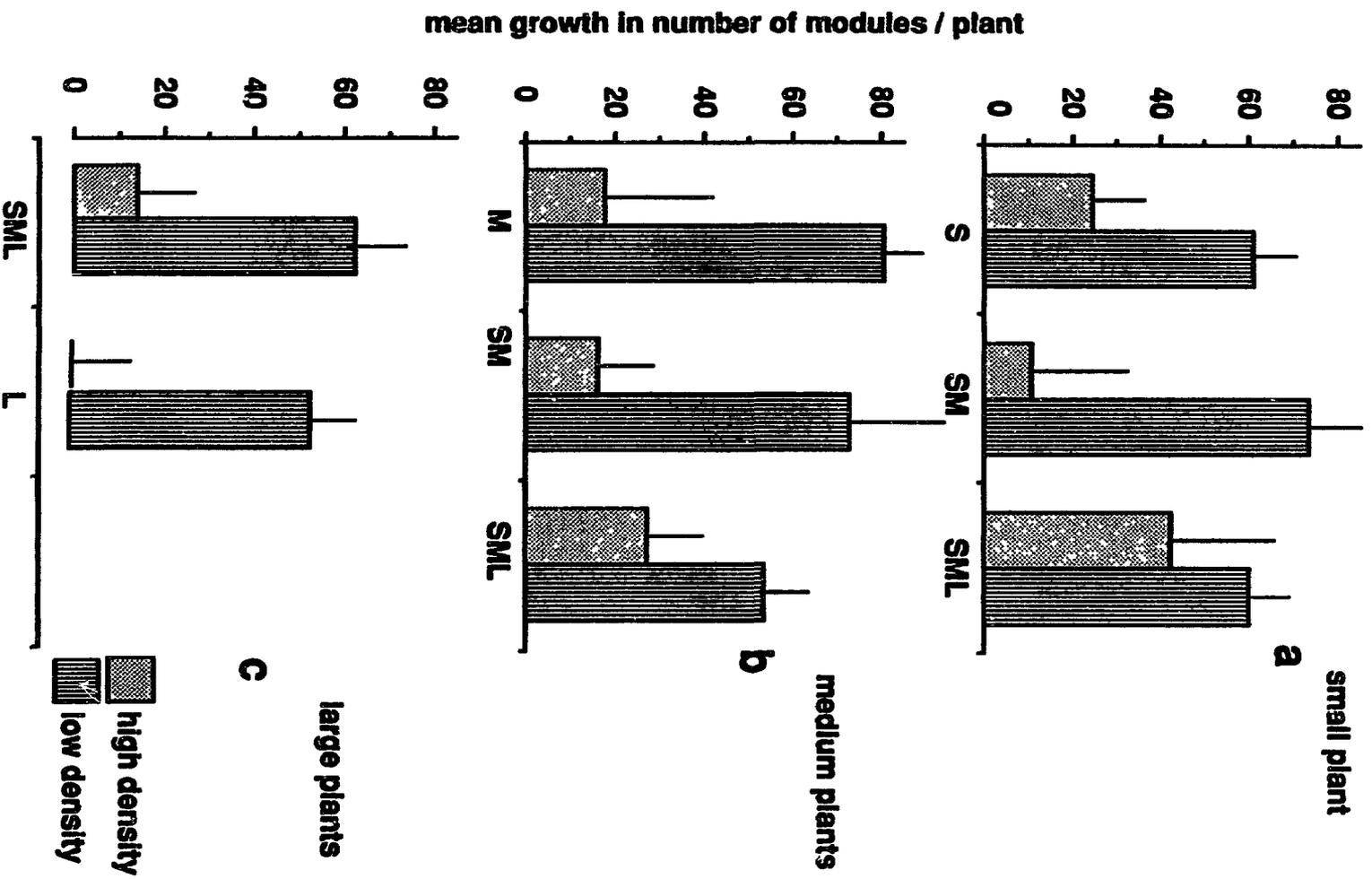


Figure 5

Figure 6. Absolute mean growth in biomass/plant of small, medium and large plants in pure-size and mix-size stands at low and high density. Bars are means and standard errors.

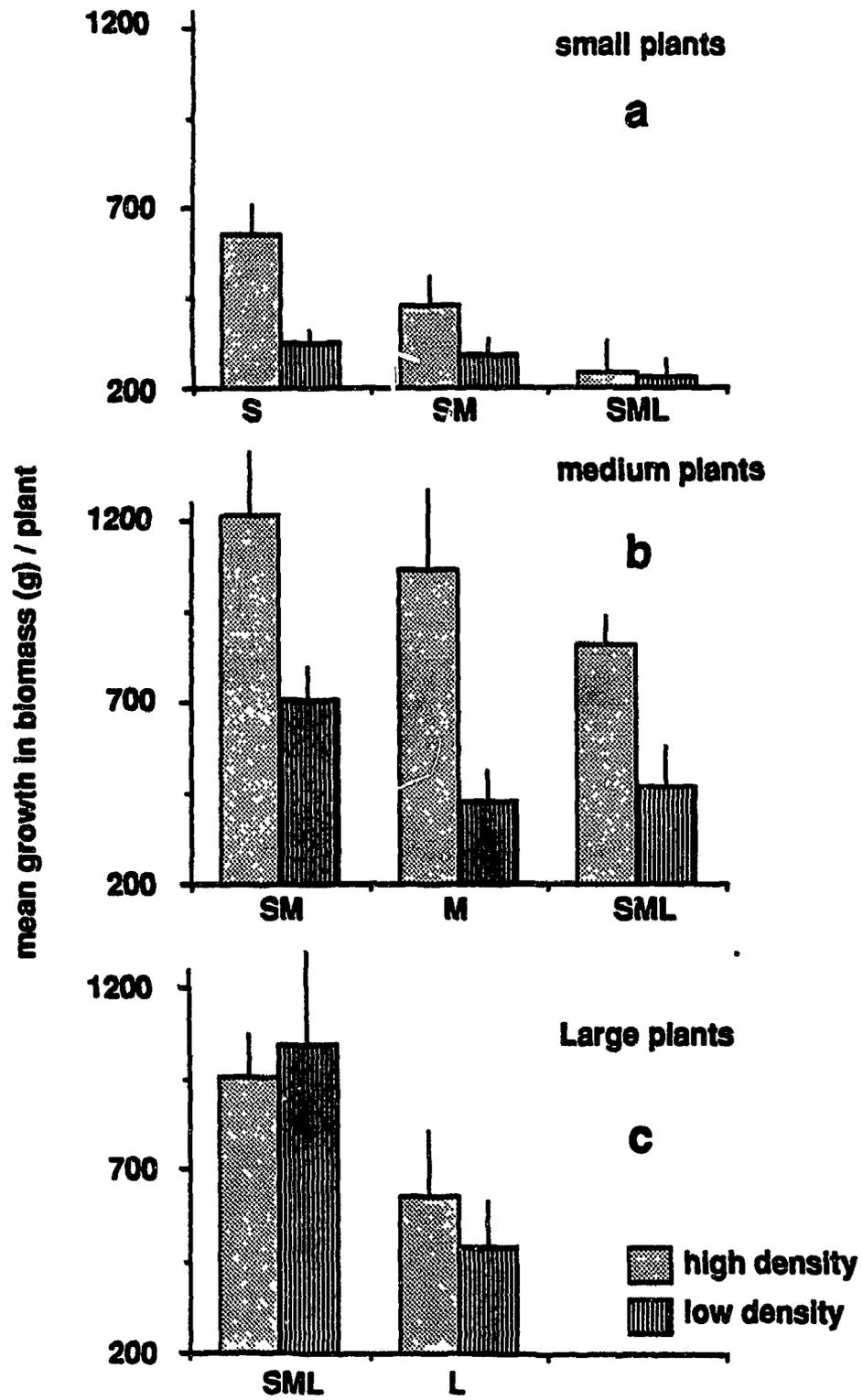


Figure 6

Figure 7. Proportional mean growth in biomass/plant of small, medium and large plants in pure-size and mix-size stands at low and high density.

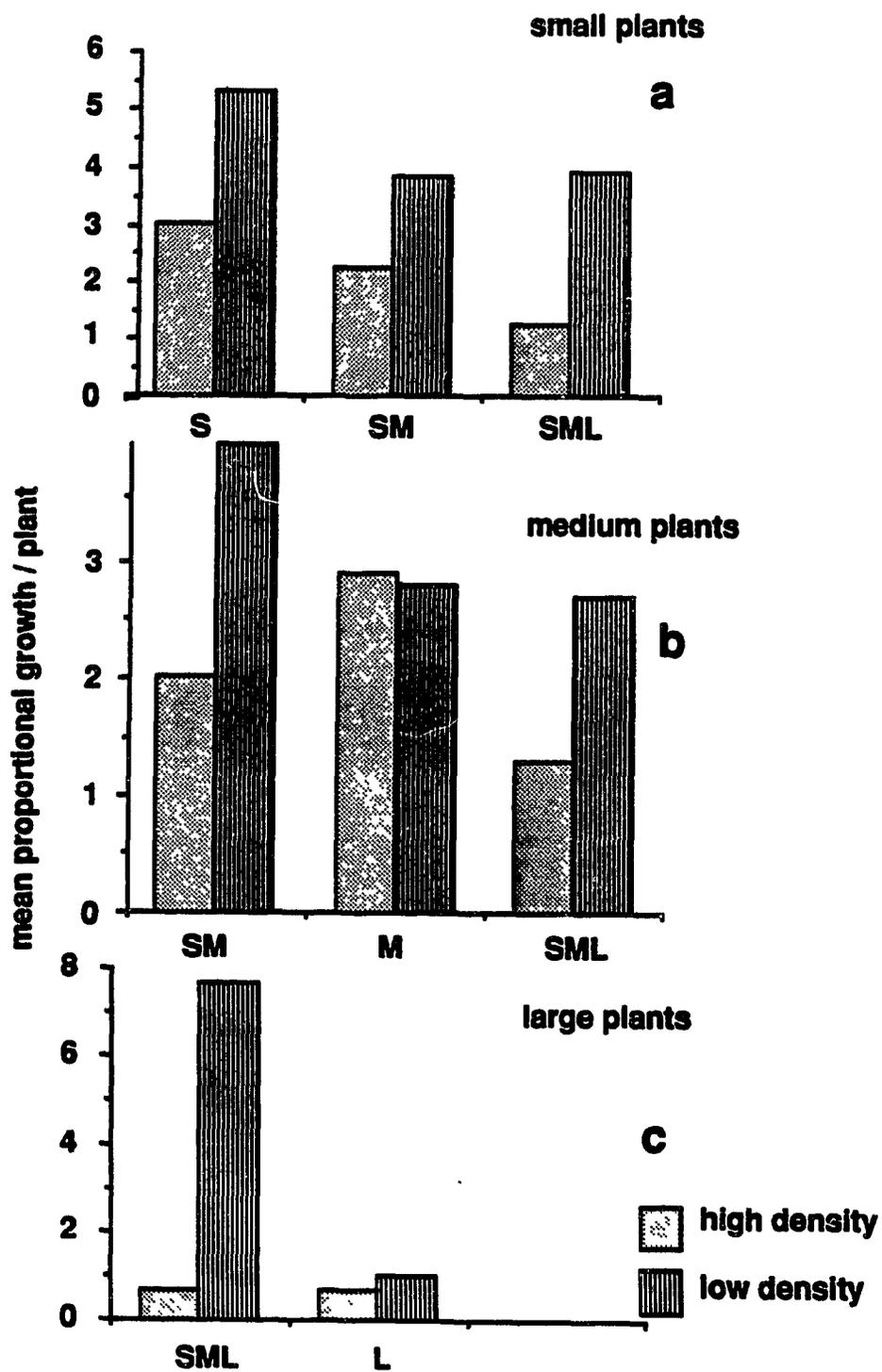


Figure 7

Figure 8. Change in the abundance of modules in classes 1 to 3 in small, medium and large plants in pure-size and mix-size stands at low and high density. Negative abundance values mean that at the end of the study there were fewer modules in a class than at the beginning (see materials and methods). Bars are means and standard errors.

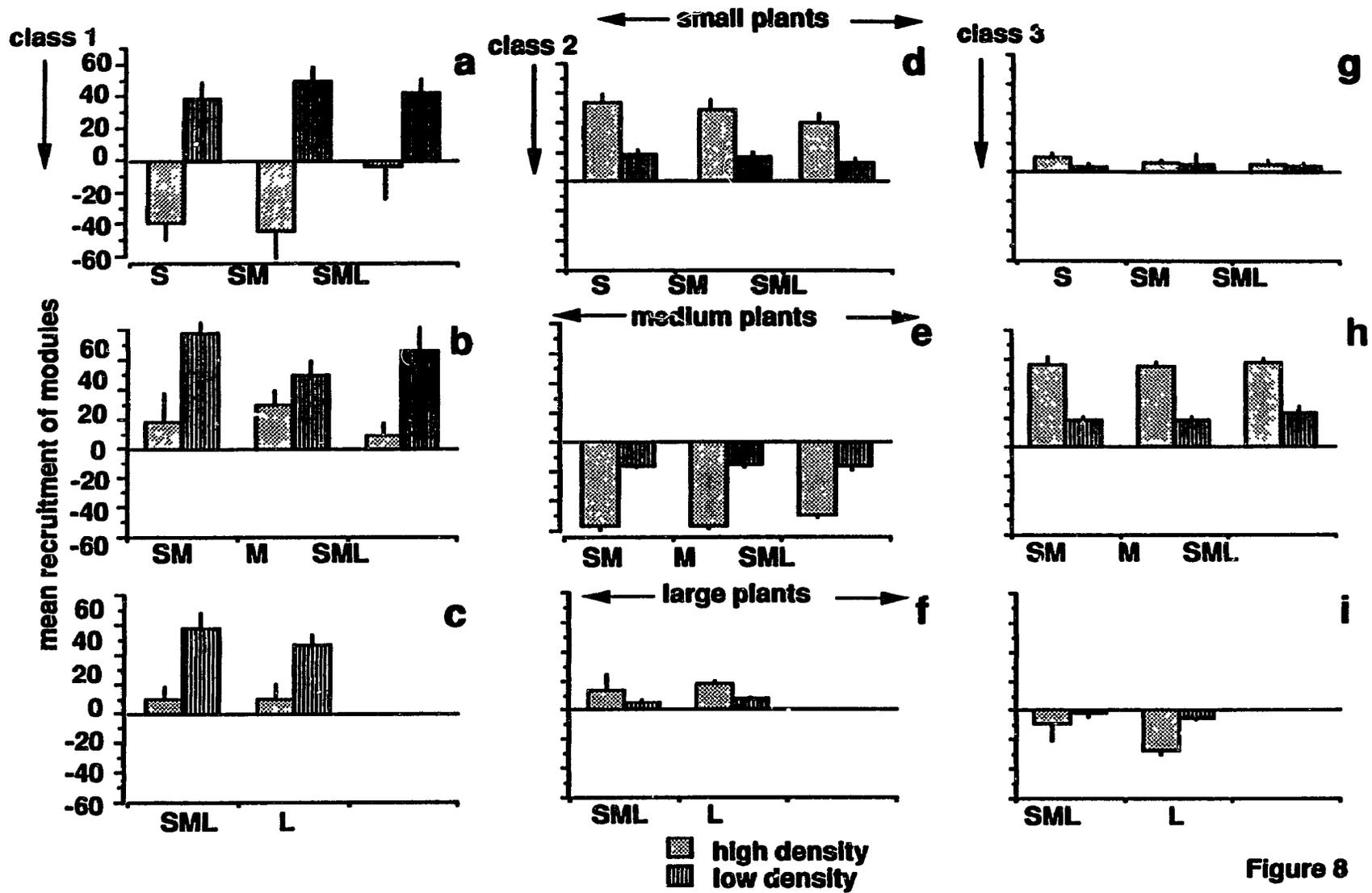


Figure 8

Figure 9. Absolute mean number of new reproductive modules/plant in pure-size stands and mix-size stands at low and high density. Bars are means with standard errors.

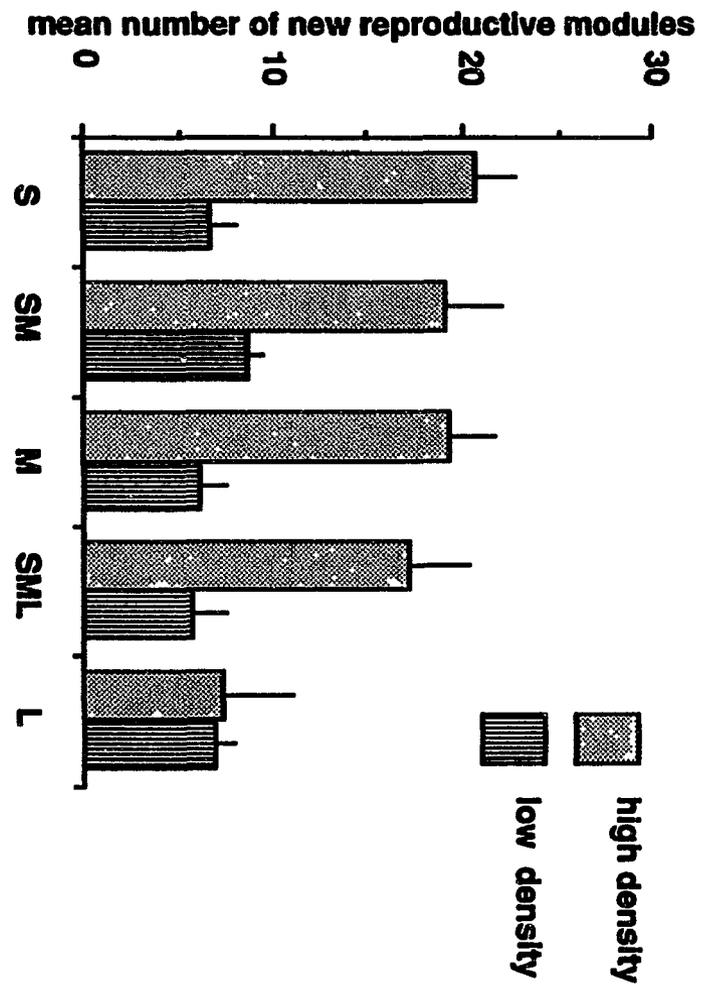


Figure 9

Figure 10. Absolute mean numbers of new reproductive of modules/plant in small, medium and large plants in pure-size and mix-size stands at low and high density. Bars are means with standard errors.

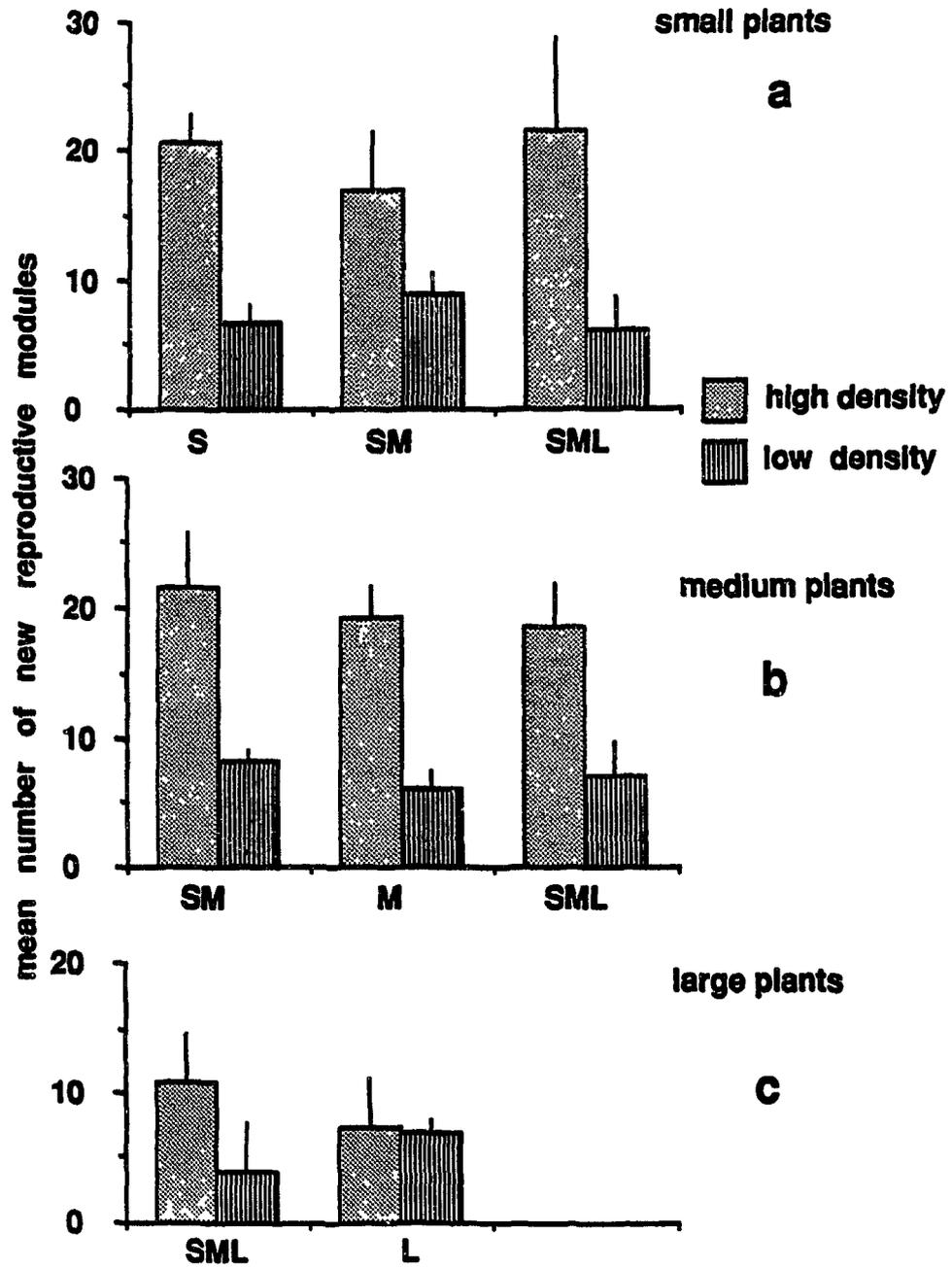


Figure 10

Chapter 4

Herbivores Consume Most *Ascophyllum nodosum* Recruits but do not Affect Modules.

Abstract

The mechanisms of growth of an *Ascophyllum nodosum* population in southwestern Nova Scotia are little understood. Grazing and harvesting are believed to have a detrimental effect on population size because they reduce sexual recruitment. However, it is possible that the present population grows through vegetative spread rather than sexual recruitment. Thus, this study assessed the effects of harvesting and grazing on sexual recruitment and compared its relevance to population growth with vegetative spread (Chapter 3). The effect of herbivory on module population structure was also evaluated. Attention was paid to determining whether grazing was differential, selecting for size and palatability.

It was found that by 1990 herbivores consumed 99% of the settled zygotes in 1989. Significant grazing pressure and slow growth suggested that the remaining germlings would not survive the subsequent years. Sexual recruitment appeared thus, ineffective. The potentially detrimental effect of harvesting on offspring numbers was apparently overridden by the effect of grazers. However, grazers did not affect module survival or breakage in a considerable degree. Size was thus, an escape from herbivory. Grazing pressure slightly increased with module size but was not

due to increased palatability. Vegetative spread emerged as a critical determinant of population growth.

Introduction

Numbers of births and deaths determine the growth of a population as well as its structure and demography. In species of modular structure, such as *Ascophyllum nodosum*, there are two sources of births and deaths, the genets and the modules (Harper 1981). To explain population growth and dynamics, it is important to determine mortality and natality at each of these two levels. Modules of this species can grow through four size-based stages of their life-cycle (Chapter 1) and losses and breakage in each of them must be assessed to understand what processes determine the demographic structure of the module population. This study assessed natality and mortality rates at the genet and module levels and the factors that influence these rates.

The *Ascophyllum nodosum* zone in southwestern Nova Scotia is luxurious and monospecific (pers. observ.) but the reason for this is difficult to explain. Undoubtedly, the physical characteristics of the area may account for much of the growth in biomass, but other factors must contribute to the structure and large size of this population. Implicit in the literature is that *A. nodosum* dominance is due to sexual recruitment (Keser & Larson 1984). However, most studies have consistently shown that sexual reproduction in this species is highly unsuccessful (David 1943, Printz 1956, Baardseth 1970, Peckol et al. 1988, Vadas et al. 1990). Almost 90% of the zygotes are dislodged by wave action alone before settlement (Vadas et al. 1990). Even after settlement, germlings may be removed by waves (Printz 1956). Grazing contributes significantly to mortality of settled zygotes as well (see Chapman 1986a). Almost 100% of the zygotes on Maine shores were consumed by grazers in a matter of two months (Vadas et al. 1982 in Chapman 1986a). In contrast to

sexual recruitment vegetative spread is highly successful (Chapter 3). This suggests that the monospecific character of southwestern Nova Scotian stands may result from vegetative spread instead of from sexual recruitment.

Another factor that may affect population size is commercial exploitation. Populations of *A. nodosum* in southwestern Nova Scotia have been harvested for 20 years (Sharp 1987a) but no serious attempts have been made to manage this resource (Sharp 1991). The long-term effects of harvesting are unknown in spite of the general belief that harvesting prior to the release of gametes may reduce the number of offspring (Burns & Mathieson 1972, Santelices et al. 1989, Ang et al. 1990). For management and conservation of this species the effects of harvesting upon the births and deaths in the population must be determined. If the effect of herbivory on zygote survival is significant, it must be compared to the relative effects of harvest.

Herbivores may also influence population structure and demography of brown seaweeds because they can consume adults or parts of adults (Watson & Norton 1985, 1987, Chapman 1989, Barker & Chapman 1990, Denton et al. 1990). *Ascophyllum nodosum* modules often appear badly wounded and broken apparently by herbivores. If wounds are near the base of the module and the module breaks at that point, grazing causes mortality. The largest modules of *A. nodosum* lose more biomass than the small ones (Chapter 2). If losses are caused by herbivores, vulnerability to grazing may depend upon module size and previous damage.

The objectives of this study were three-fold as follows,

- 1) to assess the relative importance of herbivory and harvesting on numbers of sexual offspring,
- 2) to evaluate the effect of herbivory on module breakage,
- 3) to assess whether some module life cycle stages are more vulnerable to herbivory than others.

Materials and methods

In southwestern Nova Scotian shores the most common herbivores were the snails *Littorina littorea* and *L. obtusata*. Grazer densities were not determined.

Grazing on zygotes

This experiment ran from March 1989 to April 1990. To estimate the number of zygotes in the population, traps were used. Traps (11-cm X 6-cm-clay tiles placed in wooden boxes bolted to rocks with 9-cm steel anchor bolts) were placed in the field prior to the release of gametes. To obtain surfaces somewhat similar to the rocks found in the study site, tiles were pressed against granite rocks while the clay was fresh, thus, obtaining a negative image. The tiles were then fired in a kiln. Granite rocks are the most common type of substratum in the study site.

After two months, when zygotes had settled (June 1989), tiles were brought back to the laboratory for counting. Tiles were divided in 8 columns and 4 rows. Four squares were randomly chosen and the zygotes counted under a stereoscopic microscope. On some tiles zygotes were too abundant to make accurate counts. Zygotes were removed with a razor blade, transferred to a Petri dish and then counted. Zygotes were counted before the release of new gametes a year later on squares not-previously scraped to estimate one-year survivorship.

Occasionally *Fucus* occurs on the tops of boulders within the *Ascophyllum* zone. Embryos of these two species are not distinguishable. Since traps were placed in the middle of the *Ascophyllum* zone which is basically monospecific, it was assumed that all zygotes belonged to this species. The few fucoid plants present in the plots were so much smaller than those of *Ascophyllum*, that they could not have contributed in a significant

degree to the zygote pool in my traps. Further, most traps were placed under an *Ascophyllum* plant because all rocks were occupied by this species, which also makes it most likely that, most if not all, were *A. nodosum* zygotes. Traps could not be fixed to the substratum in between rocks, as it consisted of mud consolidated with sand, shells and cobbles.

Treatments were designed to test for the effects of grazing and harvesting on zygote abundance. Two types of traps were employed, open boxes that allowed herbivory and exclusion boxes that did not. The exclusion boxes had a nitex screen placed on top and foam padding to seal the edges. Mesh size was 1 mm. The mesh size may have allowed small grazers in but a smaller mesh would have influenced the water flow and thus the zygote recruitment. Even then, the mesh size used may have altered the flow of water but there was no obvious solution to this problem. Open boxes had no screen. Two types of controls were established; one to control for box effect and the other for tile effect. To control for box effect tiles were bolted directly on the rock, without the box. To control for tile effect grids were placed on bare rock in the same study site. The grids were the same size as those on the tiles and the same sampling procedure for counting was employed (above). Counting on the bare rock was done 'in situ' with stereoscopic glasses and microscope. Because of the darkness of the rock and the fact that zygotes were often recruited in cracks and on the sides of barnacles counting was difficult.

The effect of harvesting on the number of sexual recruits was tested by placing the zygote traps in experimentally harvested and unharvested (control) plots. The design for this experiment was fully described elsewhere (Chapter 2). Here only a brief summary is given. Plots were harvested at three intensities, low, medium and high in the winter and summer. Each of these treatments was replicated three times. Controls were plots left unharvested. Three permanent horizontal transects were laid out at the top, middle

and bottom of each plot. Five plants along these transects were randomly selected and one module of each size class was tagged. If harvesting reduces the number of recruits, this effect would be strongest in intensely harvested plots. Recruitment in intensely harvested plots was then compared with the recruitment in the control plots. To test if cuts prior to the release of gametes reduced the number of offspring, I compared stands harvested intensely in the summer (after the release of gametes) vs stands cut intensely in the winter (prior to the release of gametes).

Two open and two exclusion boxes were placed in intensely-harvested and unharvested plots. The traps were positioned with alternating treatments, about 2 m from the middle transect and about 3 m from each other. Control boxes and tiles were placed along the middle transect in unharvested stands. In total this experiment involved 36 traps (18 open, 18 exclusion), 4 controls for boxes and 5 controls for tiles.

Factors tested were harvesting (cut, no cut) and herbivory (herbivores excluded, herbivores allowed). Treatment effects were tested for significant differences with ANOVA. Data (tables 1 and 3) were transformed to stabilize the variances with $\ln(x+1)$. Post-hoc pairwise comparisons of treatment means were done with Tukey-Kramer and Game-Howell tests.

Grazing on adults

The object of this experiment was to assess whether grazing is responsible for module mortality or breakage (*not* to compare grazed vs ungrazed modules). This study involved a survey of 152 tagged modules in harvested stands. The stands were three plots cut at medium intensity, two of them in summer and one in winter (Chapter 2). Medium intensity harvests are the average in the present population. Modules were examined for visible damage along the main axis. In case of bifurcation the longest branch was chosen. If the main axis was broken, measurements continued along a lateral

branch if it was < 0.5 cm from the end of the main axis. Damage was recorded as the number of herbivore marks. Only damage > 1 mm deep was recorded, including fresh wounds and wounds with scar tissue. Marks of this size are common and may be caused by amphipods rather than snails. There was also considerable damage < 1 mm, often as scraped surfaces. They were not considered here because they are unlikely to result in breakage. The tagged modules were censused once at the start of the study in June 1989 and at the end, in July 1990. By subtracting the initial number of excavations from the final count and standardizing for length, grazing pressure in one year can be estimated. By recording the position of the excavation in the first survey, it was possible to determine whether modules broke at the site of damage or not. There was no evidence that wounds could heal to the extent that one year later they could not be recognized again.

Results

Grazing on zygotes

In 1989, two months after settlement there were significant differences among treatments (Fig. 1). A first ANOVA showed that harvesting and its interaction with grazing had no effect on zygote density. The power of the ANOVA was low ($< 80\%$), which may be the reason of the lack of significance. However, Figure 1 shows that the average number of zygotes settled in open boxes was practically the same in control and harvested stands. The average from the exclusion boxes in control stands was lower than that in harvested stands but the standard errors are very large. It is reasonable to think then that harvesting did not greatly influence settlement. Harvesting treatments were pooled within herbivory treatments and tested again (ANOVA table is shown, Table 1). The effect of grazing on zygote density was highly significant. Mean zygote densities/tile are shown in Table 2. The highest abundance of zygotes in 1989

occurred in the herbivore exclusion boxes ($P = 0.05$). Densities in controls for boxes and open boxes were similar ($P > 0.05$), which means that there was no box effect. Bare rock (i.e. control for tiles) had significantly fewer zygotes ($P = 0.05$) than any other treatment. The difference between bare rock and control for box might have been due to the fact that counting was difficult (see materials and methods).

The number of zygotes decreased dramatically over one year (Table 2) particularly where herbivory was allowed (Fig. 1). Again a first ANOVA showed that harvesting intensity and its interaction with grazing had no significant effect. The power of the ANOVA was low but the means of harvested and control stands (Fig. 1) were almost identical suggesting that in fact harvesting did not influence settlement. Treatments were then pooled and tested (as above). ANOVA showed that grazing was highly significant (Table 3). Herbivore exclusion boxes had more zygotes ($P = 0.05$) than any other treatment (Table 2). There were no significant differences among the three other effects nor between bare rock and control for boxes ($P > 0.05$). The transition from egg to zygote was thus, strongly regulated by grazing. Although harvesting may have reduced offspring number, herbivory overrode any potential detrimental effects. The average number of recruits/tile for the two controls and open boxes was 13.1 (i.e. 0.07 m^2 , SD 9.7) over a one-year period. That is, there were 187 one-year old zygotes/ m^2 . Only 1% of the zygotes exposed to grazers survived one year. Even if mortality declines by 50% as zygotes grow in size, almost none will survive the next one or two years.

Grazing on modules

The number of excavations in a module slightly increased with module length (Fig. 2). The correlation coefficient was low, $r^2 = 0.09$, but significant ($p = 0.0001$). Fifty six percent of the modules

had one herbivory mark. Only rarely were modules heavily grazed. At the start of the study the average number of excavations/module was 2 and increased to 2.7 in a year. Excluding modules that broke, the relationship between damage in 1989 and new damage in the subsequent year was obtained. Broken modules were left out because damage between the first census and the date in which the module broke could not be determined. The correlation between the number of new excavations in 1990 vs the number of excavations in 1989 was low (0.06), although significant. This meant that past damage may slightly influence future grazing incidence.

Herbivory did not increase the probability of mortality. From the 152 modules in the sample only four (3%) were broken at the site where a herbivore bite existed. Breakage at sites other than the bites was twice as common. In total, thirteen (8.5%) modules broke and twenty (18%) were naturally removed.

Discussion

Herbivores consumed 99% of the recruits from zygotes in one year. The fact that the numbers of one-year old recruits in bare rocks and in my tiles were similar (see results) indicated that the recruitment estimate was not biased. This study suggests that if herbivory pressure does not vary radically from year to year, recruitment of *Ascophyllum* may be occasional. Additional evidence supports this view. I occasionally searched the study site between August 1987 and April 1990 and examined small rocks in the laboratory and never found recruits that could be seen either with magnifying glasses, with naked eye or microscope. Had they existed before 1987, recruits should have been at least several millimeters long and thus, visible by 1990. The lack of sexual recruitment agrees with numerous reports dating back many years and for different populations (David 1943, Printz 1956, Keser et al. 1981, Peckol et al. 1988, Vadas et al. 1990). Further, Watson and Norton (1987)

found that in laboratory conditions *Littorina obtusata* fed voraciously on *Ascophyllum* zygotes. However, the lack of recruitment observed in my study site may be restricted to the mid-intertidal zone where traps were placed, roughly at a distance of 11 m from the *Fucus* belt. In populations in Maine, recruitment may be more common higher in the shallow intertidal (Mathieson pers. com.)

The probability that a zygote survives grazing the next one or two years is almost zero. Their extremely slow growth (1 mm in a year) made them particularly vulnerable to grazers. Rare recruitment in Norwegian shores was also believed to result from slow growth and grazing (Baardseth 1970). In contrast, in laboratory, *Ascophyllum* growth rates were about 1.5 cm in 1 year (Baardseth 1970, Sideman & Mathieson 1983). In Rhode Island shores, growth rates were also about 1 cm in a year (Peckol et al. 1988). Although these growth rates are also low, they are nonetheless, ten times greater than in my study sites.

Low recruitment rates are in sharp contrast to Keser's & Larson's (1984). They found surprisingly high, although variable, recruitment numbers in scraped areas in Maine. On average there were 8,000 plants/m². Coverage by *Ascophyllum* in one site was as much as 52% in 16 months with individuals up to 15 cm high. After 66 months, this species had become dominant. In other sites the cover ranged from 50% to 1% over the same period, although it also depended upon the intertidal slope. Differences in cover between sites were attributed to the abundance and distribution of grazers. The reason for the discrepancy between their recruitment rates and mine is likely the difference in growth rates between our populations. As zygotes grow slower in my stand (1 mm in one year) than in theirs, recruits cannot escape herbivory.

Besides grazing there are other causes of zygote mortality. Before settlement most embryos are dislodged due to wave action (Vadas et al (1990). Availability of refuge is critical for the survival of

Ascophyllum (Keser & Larson 1984, Vadas et al. 1990) as well as for other related species such as *Fucus* (Lubchenco 1983) to escape exposure and grazing. Availability of substratum is equally important. Eggs can presumably germinate upon unconsolidated substratum (Keser & Larson 1984) but the lack of plants attached in the sand or mud in my stands indicates that stable substratum is required for further development. Substrata in the present stands may be limited because adult plants of *Ascophyllum* occupy most boulders. Another cause of mortality may be shading from adult plants. The fact that irradiance at ground level may be as little as less than 0.1% of that at the surface (Cousens 1982a) and that density suppresses the birth of modules (Chapter 3) suggest that zygotes may be negatively affected by the adults. David (1943) also believed that low recruitment in British populations was due to light limitation. The decline in recruitment numbers in the exclusion boxes, suggested that some self-thinning occurred. Vadas et al. (1990) reported similar findings from a laboratory study. He also found that survival of zygotes at high density was significantly lower than at medium and low densities. Survival of fucoid embryos can also depend on microhabitat temperatures and age (Brawley & Johnson 1991).

Despite the devastating effect of grazing, just a few sexual recruits may be all that is needed to ensure population growth. In *Laminaria* only 1 in 10^6 microbenthic stages grows to visible stage but it is sufficient to maintain population size (Chapman 1984). The fact that modules were invulnerable to grazers (below), indicated that survivorship increases with size and thus, size is an escape mechanism from grazers. Despite the poor sexual recruitment, the vegetative spread of the few survivors is successful (Chapter 3), which suggests that size-escape and vegetative spread are the mechanisms that ensure population size and dominance in the intertidal. Size-escape mechanisms and vegetative spread fit Lubchenco's and Gaines' (1981) model based on these two mechanisms as the significant factors responsible for plant

abundances within the intertidal. The relative importance of sexual and vegetative spread indeed suggested that the *Ascophyllum* zone is wide and monospecific because vegetative spread is high and appears to preclude invasion by other species. In fact, *Ascophyllum* may be considered a phalanx species (Sackville-Hamilton et al. 1987) as it consists of a holdfast and modules arranged in a tight clump (Introduction of thesis). Phalanx species may grow slowly but act as a 'front' defending the space occupied from other species (Harper 1981, Schmid & Harper 1985). With the formation of each new module, the holdfast increases in size, thus, securing physical space. The *Ascophyllum* habit seems to secure space for light and substratum. Relative to the volume of the upright part of the plant, the holdfast is small but a large area around it is denuded of vegetation (pers. observ.) except occasionally small *Ascophyllum* plants (pers. observ.). Shading plus the brushing effect of the modules against the substratum may discourage the growth of understory plants. Vegetative spread may then be a mechanism to ensure spatial dominance. Other studies of *Ascophyllum* may support this view. These studies report that when this species was removed, *Fucus* colonized rapidly because it grew faster (Baardseth 1970, Keser et al. 1981). *Fucus*, however, succeeded only in the short term. When *Ascophyllum* attained a large size, it excluded *Fucus* and became the dominant species (Keser & Larson 1984). Hence, the dominance observed by Keser & Larson, although initiated from sexual recruitment, must have resulted primarily from vegetative spread. Vegetative spread, not sexual recruitment, emerges from this discussion, as a key factor of population size.

Other seaweed species show similar mechanism of population growth. *Gigartina canaliculata*, *Laurencia pacifica* and *Gastroclonium coulterii* are known to recruit seasonally from spore but can rapidly colonize open space by means of vegetative spread (Sousa et al. 1981). Once turfs of these species are established further invasion is inhibited. *Chondrus* may also supplant *Fucus* by a similar mechanism (Lubchenco 1980). Vegetative propagation in

Gigartina teedii also appears to be the main mode of population maintenance (Braga 1990).

Harvesting did not appear to influence the recruitment of zygotes. Although the power of the test was low, the average recruitment in harvested and control plots were fairly similar. This study suggested that while harvesting might have limited the gamete pool, herbivory overrode this effect. Recruitment of new individuals then appeared to be controlled by natural factors, more than by human intervention. Transport of zygotes from harvested to unharvested stands might have been possible. However, it is unlikely that transport was significant because it is known for other species that most zygotes settle near the parent plant (Chapman 1986a, Schiel & Foster 1986). Previous authors concerned with the maintenance of harvestable seaweed resources (Burns & Mathieson 1972, Santelices et al. 1989, Ang et al. 1990) have suggested that harvesting prior to the release of gametes could have a detrimental effect upon the zygote pool. Theoretically this is true for *Sargassum* (Ang 1987). However, in the field this may not occur if there is no direct relationship between fecundity and recruitment. In *Ascophyllum* the production of eggs/module was high (Chapter 2) but most recruits did not survive grazing (this study). Correlation between fecundity and recruitment is difficult to predict even for related species. In *Laminaria longicuris* a close relationship between spore production and recruits was found but not so in *L. digitata* with which it occurs (Chapman 1984).

Nevertheless, harvesting can play a significant role in population growth and indirectly in benthic community structuring if it reduces the extent of vegetative spread. If the cut is too close to the holdfast the birth rate of modules may decrease (Chapter 2) resulting in population decline in the long-term. Thus, the lack of sexual recruitment enforces my view (Chapter 2) and that of other authors (Sharp 1981, 1987) that the regulation of cutting height is essential for population regrowth.

Herbivory did not appear to influence the transition rates between module size classes and was not a significant factor of module population size structure and demography. The number of modules that broke due to herbivore damage was negligible. Rather, breakage was twice as likely at places where there were no herbivore marks. However, it is possible that breakage by herbivory occurred in between censuses and was not noticed. The frequency recorded was then the minimum. Modules were two times more likely to be naturally removed than broken. Another study of *Ascophyllum* modules also suggested that the incidence of fracture was low (Chapter 2). Thus, even if damage by grazers was higher than recorded here, breakage was not an important determinant of transitions among size classes. The lack of correlation between breakage and herbivory did not coincide with a study for central Nova Scotian *Ascophyllum* populations which showed that up to 90% of the modules that broke, fractured occurred where the axis had been weakened by herbivore damage (Lowell et al. 1991). What is more, the probability of breakage in these damaged modules increased 3 to 16 times. Breakage occurred because of the accumulation of stress (*sensu* Lowell et al. 1991) at the site of damage. There is no obvious explanation for the discrepancy between the two studies, although the pulling force exerted by the wind and or water in my population may be different from that in Lowell's population.

Grazing pressure increased slightly but significantly with module size. However, this correlation may have not been not due to increased palatability. Over half of the tagged modules had only one bite and rarely more. The correlation between module size and herbivory may simply be due to chance. The longer the module the greater the probability a grazer will bite it. The correlation might have also arisen if grazing changed the palatability of the module. Lowell et al. (1991) found that past damage was positively correlated ($r^2 = 83\%$) with future incidence of grazing. The

correlation was due to a herbivore-induced reduction in production of polyphenols that resulted in increased edibility. However, in my study new grazing damage was only weakly related to previous damage, which suggested that grazing might not have influenced palatability. Also, this species may not be a food source at all for *L. littorea* as suggested by laboratory studies (Watson & Norton 1985). Although *L. obtusata* feeds on *Ascophyllum* adults, it ranks low in their preferences (Watson & Norton 1987).

Table 1. ANOVA table. Effect of grazing on zygote density/tile 2 months after settlement. Data was transformed to $\ln(x + 1)$ to stabilize variances. P= probability that means are significantly different.

source	df	S.S.	F	P
grazing	3	200.5	43.26	0.0001
error	40	61.8		

Table 2. Mean density of zygotes/tile in each treatment 2 months after settlement (1989) and a year later (1990). SD= standard deviation.

	1989	SD	1989	SD
exclusion boxes	14,531	12,476.2	3,602.7	3072.7
open boxes	1,335.5	1,750.1	22.7	50.0
control tile	424	272.1	13.3	12.2
bare rock	14.4	16	3.2	7.1

P= 0.0001

Table 3. ANOVA table. Effect of grazing on one-year old zygote density/tile. Data was transformed to $\ln(1+x)$ to stabilize variances. P= probability that means are significantly different.

source	df	S.S.	F	P
grazing	3	377.5	25.54	0.0001
error	41	202.0		

Figure 1. Mean zygote density in open and exclusion boxes in control and intensely harvested stands 2 months and 1 year after settlement. Plots harvested in summer and winter are pooled. Bars are means with standard errors. Numbers on top of bars are frequencies of zygotes in each treatment.

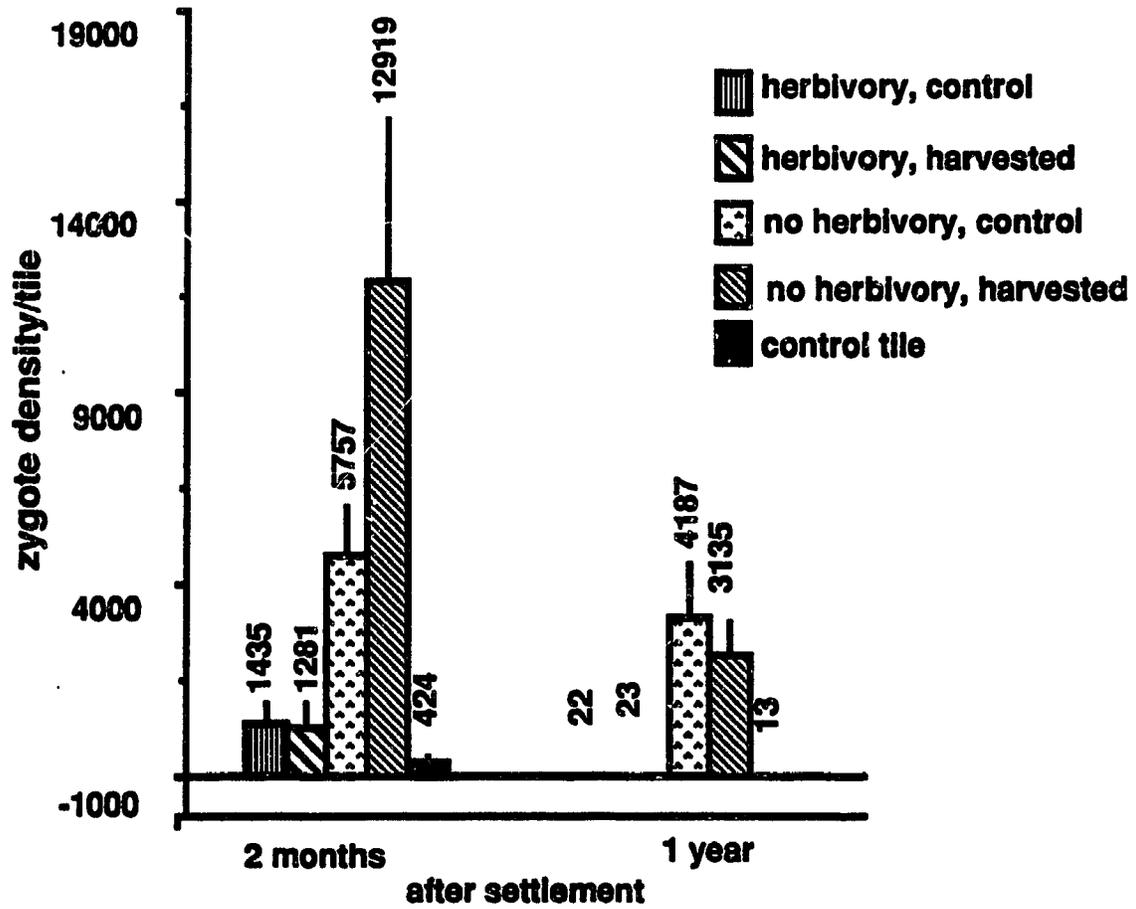


Figure 1

Figure 2. Relationship between number of herbivore excavations and module length. The length of modules in classes 1 to 4 is indicated. Classes 2 and 3 are same size.

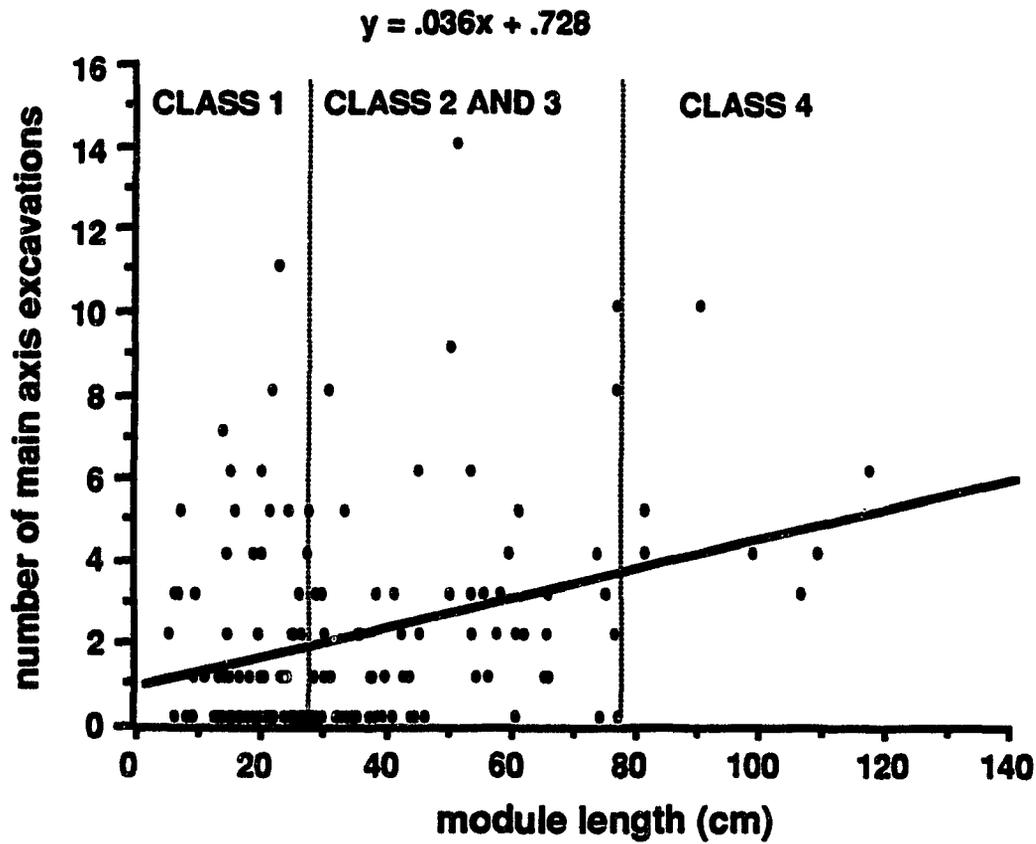


Figure 2

Discussion

Since the objectives of this research have been discussed within the context of each chapter, I thought it appropriate to end this study with a general discussion of one of the objectives not yet introduced. The objective was to gather the information necessary to construct a size-based Leslie matrix model. The discussion will, then, take place in the context of this model as used in ecological research and management. *Ascophyllum nodosum* will be referred from now on as *Ascophyllum*.

Studies of demography are a powerful way to analyze changes in a population through time (Hutchings 1990). Rates of birth and death can be used to project future population trends which provide a strong basis to make sensible decisions for the management of natural resources. Population projections are commonly done with transition matrix models, typically the Leslie matrix (Leslie 1945) and are commonly used to manage populations of plants and animals (Getz & Haight 1989). Transition matrix models are either based on age-classes (Leslie model) or size classes (e.g. Lefkovich matrix model). Size classes are preferred when size is a better predictor of life-cycle events (e.g. reproduction and mortality (Werner & Caswell 1977, also Watkinson 1986). Some extensions have been made to accommodate factors such as sex (Meagher 1982), interference (Solbrig et al. 1988) and alternation of life-cycle phases (Ang & De Wreede 1990, Ang et al. 1990). The history, construction, advantages and disadvantages of using age-based or size-based models have been discussed in many recent papers (Meagher 1982, Ang 1987, Getz & Haight 1989, Ang & De Wreede 1990, Åberg 1990a) and there is no need to repeat them. Instead the purpose of this discussion is to point out the flaws and

disadvantages of these matrix models which are rarely (Bierzychudek 1982, De Wreede 1986) or never acknowledged. Focus is on the Lefkovitch model since I considered size-based life cycle stages (or size classes). There are many variations of this model (Caswell 1989) but none seems appropriate for the present populations (below). I discuss the basic Lefkovitch matrix model because it is the simplest model and can be used as a general framework.

In recent years, size-based matrix models have been used for seaweed populations (Ang 1987, Ang & de Wreede 1990, Nyman et al. 1990, Åberg 1990a,b). The most common uses were to assess the stability of the population structure either for size classes (Ang & De Wreede 1990) or age classes (De Wreede 1986), to describe life-cycles (Ang et al. 1990, Ang & De Wreede 1990) and for management (Ang 1987, Ang et al. 1990). Matrix models are extremely useful in management of algal resources because they can project possible outcomes of exploitation (Ang 1987, Ang et al. 1990).

Three assumptions are commonly made when the model is applied and none of them is usually tested. The assumptions are, 1) that sexual recruitment or vegetative spread is relevant to population growth. This assumption concerns models for population of modules and *Ascophyllum* in particular. Often, the number of sexual offspring/individual can be estimated through some other variable, e.g. reproductive biomass (Åberg 1990a) which implies that there is a direct relationship between biomass and fecundity and between fecundity and offspring numbers. 2) Interference does not affect growth. Even when the model accounts for interference, it is assumed that interference exerts a negative effect on growth and survivorship (Getz & Haight 1989). Assuming a negative effect may be accurate for terrestrial populations (Harper 1977, Hutchings 1986) but not necessarily for marine plants because the effects of interference on these are not yet fully understood (reviewed in Chapter 3). 3) The sex ratio is known and it does not change with

time. However, sexual dimorphism in vital rates is well documented in many species (Caswell 1989). Asymmetric distributions of gender and life-cycle phases are common in seaweed (Edelstein & McLachlan 1967, Edwards 1973, Van der Meer 1981, Perez-Cirera 1982) and higher plant populations (Weiner 1988). Moreover, reproduction may be anomalous resulting in populations dominated by only one life-cycle phase (Destombe 1989). Some attempts to accommodate the effect of sexual dimorphism in demographic models are in Caswell (1989).

In general models of populations have been concerned with genets (Ang 1987, Åberg 1990a,b, Ang et al. 1990). However, models of module populations are needed to manage algal resources where modules are the main source of repopulation and hence yield. Populations of *Ascophyllum* may be an example. Biomass recovery in the stand after harvesting may result largely from vegetative spread rather than recolonization (Chapter 4). Because of the relevance of vegetative spread and the fact that growth (Chapter 2) and reproductive output (Chapter 1) depend upon module size, it seems reasonable to construct a Lefkovitch matrix model for the population of modules of this species. Moreover, *Ascophyllum* has a long history of being exploited but little is known of the long-term effects of harvesting on the population growth rate. Thus, the aim of this study was to assess whether the above three assumptions are met before using the Lefkovitch matrix to model the population of modules of this species. Results, methods and conclusions drawn here are based on empirical data obtained from other experiments conducted on this population (Chapters 1 to 4).

Lefkovitch matrix

The top row of the Lefkovitch matrix model comprises the number of offspring (sexual, asexual) produced by each size class at each time interval. The offspring may be sexual recruits, or in *Ascophyllum*, the number of new modules arising from the base of others. The

elements of the main diagonal are the probabilities of modules in any given size class staying in the same size class during a particular time interval. The elements below the diagonal are the probabilities of passing to a larger size class and the elements above the diagonal are the probabilities of passing to smaller size classes by breakage.

Assumptions

Sexual recruitment, vegetative spread. Number of offspring/size class. In the present populations the number of sexual offspring/size class was almost zero (Chapter 4). There were about 187 one-year old recruits/m² but it is unlikely that any of them would survive the next two years. Grazing and low growth rate were the cause of high mortality. In fact, 99% of the zygotes were eliminated from the time of settlement to the end of the first year. Even if only half of the survivors were eliminated in the two subsequent years, clearly sexual recruitment was occasional. The elements of the top row would then be zeroes.

The elements of the first row cannot be the number of new modules emerging from the base of each module size class. Most modules arise from the holdfast rather than from the base of other modules. The elements of the first row are then zero entries, or almost zero, despite the fact that clonal propagation is so successful that (Chapter 3) occasional survival of zygotes may be all that is needed to sustain population growth.

The inclusion of the number of sexual recruits/module in a matrix model for populations of modules is inappropriate. One zygote produced by a single module gives rise to a genetic individual, which is not equivalent to a module. The fecundities of modules and genets are not comparable. The fecundity of a genet is the sum of the fecundities of all its reproductive modules, including all modules of all plants that originated clonally.

Therefore, the size-based matrix model cannot be reliably constructed for modules, at least for the present populations. However, size-based matrix models for module populations have been constructed for other species of seaweeds. In *Macrocystis pyrifera*, vegetative recruits instead of sexual recruits were included in the model (Nyman et al. 1990). The aim of that study was to understand plant growth, viewing a single plant as a population of modules.

Given the difficulties in obtaining the fecundity of each size class, the Lefkovich matrix of the present populations should be constructed considering plants rather than modules. Plants would be classified into size classes according to the number and size of their modules. The model should include both sexual recruitment and vegetative spread. The latter is the number of new modules and plants formed clonally (by split-up process) from a plant in a given size class. The study most similar study to this, is one for Swedish populations of *Ascophyllum* (Åberg 1990a,b). A matrix for plant size classes was constructed but did not include vegetative spread. Probably the reason was that conventionally only zygotes are to be considered offspring. A model similar to the one proposed here was constructed for Jack-in-the-pulpit (*Arisaema triphylum*). The species is a perennial herb that reproduces sexually and clonally (Bierzychudek 1982). The model included two rows, one for seeds and the other for plants produced clonally.

Receptacle weight accounted for only 6% of the variability in egg production (per receptacle, Chapter 1). There is then little direct relationship between reproductive biomass and fecundity. Reproductive biomass, then, cannot yield accurate estimates of fecundity. For instance, if two modules have same number of receptacles, but one of them has larger receptacles than the other, one will conclude that the two modules have different fecundities.

This is wrong because fecundity in *Ascophyllum* increased directly with the number of receptacles, not with their biomass (Chapter 1). Therefore, the two modules have similar fecundities.

Where fecundity is assumed to be directly proportional to reproductive biomass, the results of the matrix model may be biased. There are at least two demographic studies where this method was applied, one for Swedish plants of *Ascophyllum* (Åberg 1990a,b) and the other for *Sargassum siliquosum* and *S. paniculatum* (Ang 1987). In the former, offspring numbers/size class were scaled to the reproductive biomass of each size class. Neither the number of eggs/size class nor zygote mortality were determined directly. If the number of eggs and biomass are not directly correlated, as in my population, the estimation of fecundity of each size class may be biased. In addition, if herbivory on zygotes is as effective as in my stands (Chapter 4), their recruitment is not correlated with the production of eggs, which would add further bias. Thus the reliability of the projections depends upon these foregoing conditions. In the second study (Ang 1987), the weights of all receptacles of individual plants were assessed (Ang per.com.), sexual recruitment was counted directly in field plots and the number of offspring per size class was estimated as a proportion of the reproductive biomass. This method has the advantage of skipping the determination of fecundity. However, if fecundity is not directly proportional to reproductive biomass, as in *Ascophyllum*, the number of offspring/size class may not be accurately estimated. Reproductive mass has also been used to relate fecundity to size in other studies (e.g. Schiel 1985a,b, Schiel & Choat 1980), although not necessarily for modelling purposes. The accuracy of the conclusions drawn concerning the relationship between size and fecundity may then also depend upon whether biomass and fecundity are directly correlated.

Mortality must be assessed directly. Had offspring of each size class been estimated from egg numbers in this study, the forecast of

the matrix model would have been that the population would grow through sexual recruitment by the millions which is wrong (Chapter 4). Mortality rates from related species cannot be used for the species of interest, even if they are from the same site. Chapman (1984) found a direct relationship between fecundity and recruitment in *Laminaria longicruris* but not so for the co-occurring *L. digitata*.

Errors in estimations of fecundity and mortality may have direct implications in management. It has been suggested that cuts prior to the release of gametes could reduce the number of offspring in the next generation (Burns & Mathieson 1972, Santelices et al. 1989, Ang et al. 1990). However, an assessment of recruitment in the field for *Ascophyllum* found that grazing may override any potential detrimental effect of harvesting (Chapter 4). Had recruitment been estimated with reproductive biomass instead of with direct counts in the field, one might have concluded that the above hypothesis was true when it was actually wrong. The relevance of herbivory to mortality would also go unnoticed.

Interference. As indicated in the introduction, the model does not consider the effect of interference and when it does, interference is expected to be detrimental to population growth. However, the effect of interference on *Ascophyllum* was negative on vegetative spread and positive on biomass increases. In addition, density effects on the abundance of each size class was also positive or negative depending on the size class considered. Projections of the Lefkovich matrix model may then not be accurate should the effects of interference not be considered. However, as the present field populations comprise patches with low and high densities, it is unclear whether the effect of density in high density patches is offset by that in low-density patches. If so, the overall effect of density on the transition rates may be non-significant. Thus, a Lefkovich matrix for *Ascophyllum* populations should be tested

empirically to determine whether density is relevant to population growth.

The effect of interference has been included in matrix models (Caswell 1989). The formulation of the models expresses the effect of density on a population parameter as being either negative or imposing a ceiling. Another possible formulation is one in which physiological or demographic processes possess an optimal density, with the response decreasing at either higher or lower densities. However, none of the three formulations can be used for the present population of *Ascophyllum*. As I said earlier (Chapter 3 and above), the effects of density may be positive or negative depending on the variable response chosen. In addition, at the module population level, the effect of density depends on the size class considered.

Incorporation of interference in the matrix model has been attempted successfully in terrestrial species because the effect of density is known to be negative. Population growth of *Viola fimbriatula* was simulated using a modified size-based matrix model (Solbrig et al. 1988). In this species seedling survival was function of adult density and adult survival was density-dependent. It was found that when the population of adults was below a certain critical value, the population of adults continued to increase. As new seedlings entered the adult stages, the population reached high densities at which point no seedlings survived. Seedling mortality then, reduced the number of adults below critical levels, but due to the lag in incorporating new seedlings the population was below critical density levels and the cycle was once more repeated.

Sex ratios. Modules of *Ascophyllum* populations in southwestern Nova Scotian are not strictly dioecious but may be monoecious and hermaphrodite (Chapter 1). Receptacles could comprise male and female conceptacles and conceptacles could include both sexes. Although the incidence of anomalous gender allocation was not determined, the possibility of such leads to questions concerning

whether the sex ratio estimated in Chapter 1 was correct as it was computed excluding anomalous modules. The fact that receptacles and conceptacles can contain the two genders further complicates the computation of the sex ratio (see Chapter 1). The exact gender allocation is needed to estimate fecundity.

Caswell (1989) says that if the life cycles of the sexes differ and the assumption that only female fertility matters fails (implicit in the basic Lefkovitch matrix model, Caswell 1989), then both sexes must be incorporated into demographic models. The models discussed by Caswell are for age classes and he considers important issues such as fertility as a function of the abundance of males and females, environmentally determined sex and effects of density.

As my study did not determine whether the life cycle of males and females in *Ascophyllum* are different, it cannot be suggested that the more modern models of Caswell (1989) can be used for my population. I did not consider age classes either. There are other basic problems that suggest that the models may not be applicable, although at this point there are too many unknowns (e.g. causes of sex determination and allocation) to draw strong conclusions concerning Caswell's models. The problems are that the Caswell's models are for two-sex populations. They do not take in account hermaphroditism. Moreover, hermaphroditism in *Ascophyllum* occurs at several levels. Because the fertility of a plant results from the fertility of all its modules, a model for the population of plants would probably have to incorporate fertility for plants that have all modules either male or female. Fertility should also be a function of hermaphroditism at the whole plant, module, receptacle and conceptacle levels. Another problem with Caswell's (1989) models is the assumption that high density has a negative effect on reproduction but in *Ascophyllum*, high density enhances reproduction (Chapter 3).

The relevance of sex ratios and breeding systems to population fertility cannot be ignored because they may influence the projections of the matrix model (Caswell 1989). Differences in reproductive schedules and reproductive output can, for instance, determine male bias that affects fecundity (Meagher 1982). Thus, a matrix model cannot ignore the male contribution. In addition, gender allocation can change in response to environmental factors (Weiner 1988). For instance, in the perennial herb, *Arisaema triphyllum*, the gender of its genet is determined by size (Bierzychudek 1982). Clonally produced plants can also change sex as they increase and decrease in size. In addition, this species responds to density by altering plant size. When transition matrices were constructed it was found that the matrix model did not account for the differential contribution of males and females and movement from one sex to another. Further, because the size structure and the transition probabilities were variable, the model's projections were not reliable.

This discussion raises the issue of the accuracy of the Lefkovich matrix model when the assumptions of the model are not met. If the assumptions of fecundity, interference and gender distribution are not tested projections may be equivocal. Alvarez-Buylla & Slatkin (1991) discuss additional problems concerning errors in the estimation of the confidence limits of the population growth rates predicted by the model.

The present findings illustrate the value of undertaking a demographic approach to provide data on which to base management decisions. Even if the results of demographic research are as expected, they provide a firm basis for decisions in management (Hutchings 1990). Without testing for the validity of basic assumptions, bias that results from the matrix model may be inevitable and may lead to serious consequences. Thus, demographic analyses are required, even though they may require extensive work and numerous experiments.

The Lefkovitch matrix model as it stands cannot be applied to the present populations. However, this study is a necessary lesson because it illustrates some possible pitfalls in applying this matrix model and it shows that the model may be misleading for management.

Conclusions

When applied to seaweed populations, the Lefkovitch matrix model makes three assumptions: 1) sexual recruitment and or vegetative spread are relevant to module populations and the number of offspring/size class can be estimated through some other variable, e.g. reproductive biomass, 2) interference does not affect growth and 3) the sex ratio is known and stable. The validity of the assumptions were investigated.

Vegetative spread was more relevant to population growth than sexual recruitment. Most zygotes do not survive to the adult stage and most modules arise from the holdfast. As a result the number of modules arising from other modules cannot be estimated with any degree of reliability. A model for the population of modules cannot be built because the number of new modules and sexual recruits/size class are very small. There is no direct relationship between sexual recruitment and reproductive biomass. Thus, the number of offspring/size class may not be accurately predicted using this variable. Interference affected growth in experimental populations but the effect could be either positive or negative. However, since populations comprise low- and high-density patches, it is uncertain whether overall interference significantly affects transition rates within field populations. The Lefkovitch matrix model should be tested empirically at least for projections of few years. In some modules the allocation of gender was anomalous. Unless the female:male tissue ratio can be accurately assessed, the estimation of fecundity/size class is unreliable. The findings suggest that

since the Lefkovitch matrix model does not account for the above three factors, it not only may not provide clues for management but also may be misleading.

Bibliography

- Åberg, P. 1989. Distinguishing between genetic individuals in *Ascophyllum nodosum* populations on the Swedish west coast. *British Phycology Journal* 24: 183-190.
- Åberg, P. 1990a. Size based transition matrix study in two populations of the seaweed *Ascophyllum nodosum*. Ph.D. dissertation. Dept. Marine Botany, Faculty of Natural Sciences, Goteborg University. Sweden.
- Åberg, P. 1990b. Size based demography of the seaweed *Ascophyllum nodosum* in stochastic environments. Ph. D. dissertation. Dept. Marine Botany, Faculty of Natural Sciences, University of Goteborg, Sweden.
- Åberg, P. 1990c. Measuring size and choosing category size for a transition matrix study of the seaweed *Ascophyllum nodosum*. *Marine Ecology Progress Series* 63, 281-287.
- Åberg, P. 1990d. Size-dependent reproductive effort in two populations of the seaweed *Ascophyllum nodosum*. In: Demography and reproductive effort in stochastic environments. Ph.D. dissertation. Dept. of Botanica Marina, Faculty of Natural Sciences, Univ. Goteborg, Sweden.
- Ackerly, D. and M. Jasien'ski, 1990. Size-dependent variation of gender in high density stands of the monoecious annual, *Ambrosia artemisiifolia* (Asteraceae). *Oecologia* 82, 474-477.
- Alvarez-Buylla, E. and M. Slatkin, 1991. Finding confidence limits on population growth rates. *Trends in Ecology and Evolution* 6, 221-224.
- Ang, P. 1987. Use of projection matrix models in the assessment of harvesting strategies. *Hydrobiologia* 151/152: 191-196, 335-339. Twelfth International Seaweed Symposium. M.A. Ragan and C.J. Bird (Eds.). Dr. W. Junk Publishers. Netherlands.

- Ang, P. and R. De Wreede, 1990. Matrix models for algal life history stages. *Marine Ecology Progress Series* 59, 171-181.
- Ang, P.; R. De Wreede, F. Shaughnessy and L. Dyck, 1990. A simulation model for an *Iridaea splendens* (Gigartinales, Rhodophyta) population in Vancouver, Canada. *Hydrobiologia* 204/205: 191-196. Thirteenth International Seaweed Symposium. S. Lindstrom and P. Gabrielson (Eds.). Kluwer Academic publishers. Belgium.
- Baardseth, E. 1970. A synopsis of biological data on knobbed wrack, *Ascophyllum nodosum* (Linnaeus) Le Jolis. *FAO Fisheries Synopsis* 38, 41 pp.
- Barker, K. and A. Chapman, 1990. Feeding preferences of periwinkles among four species of *Fucus*. *Marine Biology* 106, 113-118.
- Begon, M.; J. Harper and C. Townsend, 1986. *Ecology. Individuals, Populations and Communities*. Sinauer Ass.; Inc. Publishers. Sunderland. 876 pp.
- Bierzuchudek, P. 1982. The demography of Jack-in-the-pulpit. A forest perennial that changes sex. *Ecological monographs* 52, 335-351.
- Benan, G. 1988. The size structure of theoretical plant populations: spatial patterns and neighbourhood effects. *Ecology* 69, 1721-1730.
- Bradley, P. 1991. Plant hormones do have a role in controlling growth and development of algae. *Journal of Phycology* 27, 317-321.
- Braga, M. 1990. Reproductive characteristics of *Gigartina teedii* (Roth) Lamouroux (Rhodophyta, Gigartinales), a turf-forming species: field and laboratory culture studies. *Botanica Marina* 33, 401-409.
- Brawley, S. and L. Johnson, 1991. Survival of fucoid embryos in the intertidal zone depends upon developmental stage and microhabitat. *Journal of Phycology* 27, 179-186.
- Burns, R. and A. Mathieson, 1972. Ecological studies of economic red algae. III. Growth and reproduction of natural and harvested populations of *Gigartina stellata* (Stackhouse) Batters in New Hampshire. *Journal of Experimental Marine Biology and Ecology* 9, 77-95.
- Callaghan, T.; B. Svensson, H. Bowman, D. Lindley and B. Carlsson, 1990. Models of clonal plant growth based on population dynamics and architecture. *Oikos* 57, 257-269.

- Carpenter, R. 1990. Competition among marine macroalgae: a physiological perspective. *Journal of Phycology* 26, 6-12.
- Caswell, H. 1988. Approaching size and age in matrix population models, 85-105. In: *Size-Structured Populations*. B. Ebenman and L. Persson (Eds.). Springer-Verlag.
- Caswell, H. 1989. *Matrix Population Models. Construction, Analysis and Interpretation*. Sinauer Association, Inc. Publishers. Sunderland, 328 pp.
- Chapman, A. 1984. Reproduction, recruitment and mortality in two species of *Laminaria* in southwest Nova Scotia. *Journal of Experimental Marine Biology and Ecology* 78, 99-109.
- Chapman, A. 1986a. Age versus stage: an analysis of age- and size-specific mortality and reproduction in a population of *Laminaria longicuris* Pyl. *Journal of Experimental Marine Biology and Ecology*, 97: 113-122.
- Chapman, A. 1986a. Population and community ecology of seaweeds. *Advances in Marine Biology* 23, 1-161.
- Chapman, A. 1989. Abundance of *Fucus spiralis* and ephemeral seaweeds in a high eulittoral zone: effects of grazers, canopy and substratum type. *Marine Biology* 102, 565-572.
- Chapman, A. and C. Goudey, 1983. Demographic study of the macrothallus of *Leathesia difformis* (Phaeophyta) in Nova Scotia. *Canadian Journal of Botany* 61, 319-323.
- Cochran, W. 1977. *Sampling Techniques*. J. Wiley and Sons. New York, 428 pp.
- Cousens, R. 1981. Variation in annual production by *Ascophyllum nodosum* (L.) Le Jolis with degree of exposure to wave action, 251-258. In: *Xth International Seaweed Symposium*. T. Levring (Ed.). Walter de Gruyter. Berlin.
- Cousens, R. 1982a. The effect of exposure to wave action on the morphology and pigmentation of *Ascophyllum nodosum* (L.) Le Jolis in South-Eastern Canada. *Botanica Marina* 25, 191-195.
- Cousens, R. 1982b. Popular misconceptions about *Ascophyllum nodosum* and their effect on their interpretation of its population dynamics from existing data. *British Phycological Journal* 17, 231.
- Cousens, R. 1984. Estimation of annual production by the intertidal brown alga *Ascophyllum nodosum* (L.) Le Jolis. *Botanica Marina* 27, 217-227.

- Cousens, R., 1985. Module size distributions and the effects of the algal canopy on the behaviour of *Ascophyllum nodosum* (L.) Le Jolis. *Journal of Experimental Marine Biology and Ecology* 92, 231-249.
- Cousens, R. and M. Hutchings, 1983. The relationship between density and mean module weight in monospecific seaweed stands. *Nature* 310, 240-241.
- Critchley, A.; P. de Visscher and P. Nienhuis, 1990. Canopy characteristics of the brown alga *Sargassum muticum* (Fucales, Phaeophyta) in Lake Grevelingen, Southwest Netherlands. *Hydrobiologia* 204/205, 211-217. Thirteenth International Seaweed Symposium. S. C. Lindstrom and P. Gabrielson (Eds.). Kluwer Academic Publishers.
- Crouse, D.; L. Crowder and H. Caswell, 1987. A stage-based population model for loggerhead sea turtles and implications for conservation. *Ecology*, 68, 1412-1423.
- David, H. 1943. Studies in the autoecology of *Ascophyllum nodosum* Le Jol. *Journal of Ecology* 31, 178-199.
- Day, R. and G. Quinn, 1989. Comparison of treatments after an analysis of variance in ecology. *Ecological Monographs* 59, 433-463.
- De Kroon, H. and R. Kwant, 1991. Density-dependent growth responses in two clonal herbs: regulation of shoot density. *Oecologia* 86, 298-304.
- De Wreede, R. 1986. Demographic characteristics of *Pterygophora californica* (Laminariales, Phaeophyta). *Phycologia* 25, 11-17.
- Dean, T.; K. Thies and S. Lagos, 1989. Survival of juvenile giant kelp: the effects of demographic factors, competitors, and grazers. *Ecology* 70, 483-495.
- Denton, A.; A. Chapman and J. Markham, 1990. Size-specific concentrations of phlorotannins (anti-herbivore compounds) in three species of *Fucus*. *Marine Ecology Progress Series* 65, 103-104.
- Deregibus, V. and M. Trlica, 1990. Influence of defoliation upon tiller structure and demography in two warm-season grasses. *Acta Oecologica* 11, 693-699.
- Destombe, C. 1989. What controls haploid-diploid ratio in the red alga, *Gracilaria verrucosa*? *Journal of Evolutionary Biology*. 2, 317-338.

- Diouris, M. 1989. Long-distance transport of ^{14}C -labelled assimilates in the Fucales: nature of translocated substances in *Fucus serratus*. *Phycologia* 28, 504-511.
- Dring, M. and F. Brown, 1982. Photosynthesis of intertidal brown algae during and after periods of emersion: a renewed search for physiological causes of zonation. *Marine Ecology Progress Series* 8, 301-308.
- Ebenman, B. and L. Persson, 1988. Dynamics of size-structured populations: An overview, 3-9. In: *Size-structured populations*. B. Ebenman and L. Persson (Eds.) Springer-Verlag Berlin Heidelberg, 284 pp.
- Edelstein, T. and J. McLachlan, 1967. Cystocarps and tetrasporangia on the same thallus in *Membranoptera alata* and *Polysiphonia urceolata*. *British Phycological Bulletin* 3, 185-187.
- Edwards, P. 1973. Life history studies of selected british *Ceramium* species. *Journal of Phycology* 9, 181-184.
- Elliot, J. 1971. Some Methods for the Statistical Analysis of Samples of Benthic Invertebrates. *Freshwater Biological Association. Scientific Publication No. 25*, 144 pp.
- Evans, L. and A. Trewavas, 1991. Is algal development controlled by plant growth substances? *Journal of Phycology* 27, 322-326.
- Gendron, L. 1989. Seasonal growth of the kelp *Laminaria longicruris* in Baie des Chaleurs, Quebec, in relation to nutrient and light availability. *Botanica Marina* 32, 345-354.
- Getz, W. and R. Haight, 1989. *Population Harvesting. Demographic Models of fish, forest and animal resources.* Princeton University Press, 392 pp.
- Gomez, I. and R. Westermeier, 1991. Module regrowth from basal disc in *Iridaea laminarioides* (Rhodophyta, Gigartinales) at Mehuin, Southern Chile. *Marine Ecology Progress Series* 73, 83-91.
- Gonzalez-Fragoso, J. S.; Ibarra-Obando and W. North, 1991. Frond elongation rates of shallow water *Macrocystis pyrifera* (L.) Ag. in northern Baja California, Mexico. *Journal of Applied Phycology* 3, 311-318.
- Harberd, D. 1962. Some observations on natural clones in *Festuca ovina*. *New Phytologist*, 61, 85.
- Harberd, D. 1967. Observations on natural clones in *Holcus mollis*. *New Phytologist* 66, 401-408.

- Harper, J. 1977. *Population Biology of Plants*. Academic Press. London, 892 pp.
- Harper, J. 1981. The concept of population in modular organisms, 53-77. In: *Theoretical Ecology. Principles and Applications*. M. May (Ed.). Blackwell Scientific Publications, 489 pp.
- Hay, C. and G. South, 1979. Experimental ecology with particular reference to proposed commercial harvesting of *Durvillea* (Phaeophyta, Durvilleales) in New Zealand. *Botanica Marina* 22, 431-436.
- Hurlbert, S. 1984. Pseudoreplication and the design of ecological field experiments. *Ecological Monographs* 54, 187-211.
- Hutchings, M. 1975. Some statistical problems associated with determination of population parameters for herbaceous plants in the field. *New Phytologist* 74, 349-363.
- Hutchings, M. 1986. The structure of plant populations, 97-136. In: *Plant Ecology*. M. Crawley (Ed.). Blackwell Scientific Publications. Oxford.
- Hutchings, M. 1990. The role of demographic studies in plant conservation: the case of *Ophrys sphegodes* in chalk grassland, 106-111. In: *Calcareous Grasslands. Ecology and Management. Proceedings of a Joint British Ecological Society/Nature Conservancy Council Symposium*. S. Hillier, D. Walton and D. Wells (Eds.) Bluntisham Books. Bluntisham.
- Hutchings, M. and M. Mogie, 1990. The spatial structure of clonal plants: Control and consequences, 57-76. In: *Clonal Growth in Plants: Regeneration and Function*. J. van Groenendael and H. de Kroon (Eds.). SPB Academic Publishing. The Hague. The Netherlands.
- Hymanson, Z; D. Reed, M. Foster and J. Carter, 1990. The validity of using morphological characteristics as predictors of age in the kelp *Pterygophora californica* (Laminariales, Phaeophyta). *Marine Ecology Progress Series* 59, 295-304.
- Kays, S. and J. Harper, 1974. The regulation of plant and tiller density in a grass sward. *Journal of Ecology* 62, 97-105.
- Keser, M. and B. Larson, 1984. Colonization and growth of *Ascophyllum nodosum* (Phaeophyta) in Maine. *Journal of Phycology* 20, 83-87.
- Keser, M.; R. Vadas and B. Larson, 1981. Regrowth of *Ascophyllum nodosum* and *Fucus vesiculosus* under various harvesting regimes in Maine, U.S.A. *Botanica Marina* 24, 29-38.

- Krebs, C. 1989. *Ecological Methodology*. Harper and Row, Publishers. New York, 654 pp.
- Lazo, M. and J. McLachlan, 1989. Reproduction of *Chondrus crispus* Stackhouse (Rhodophyta, Gigartinales) in sublittoral Prince Edward Island, Canada. *Journal of Applied Phycology* 1, 359-365.
- Lazo, M.; M. Greenwell and J. McLachlan, 1989. Population structure of *Chondrus crispus* Stackhouse (Gigartinaceae, Rhodophyta) along the coast of Prince Edward Island, Canada: distribution of gametophytic and sporophytic modules. *Journal of Experimental Marine Biology and Ecology* 126, 45-58.
- Leslie, P. 1945. On the use of matrices in certain population mathematics. *Biometrika* 33, 183-212.
- Lowell, R.; J. Markham, J. and K. Mann, 1991. Herbivore-like damage induces increased strength and toughness in a seaweed. *Proceedings of the Royal Society of London, B* 243, 31-38.
- Lubchenco, J. 1980. Algal zonation in the New England rocky intertidal community: an experimental analysis. *Ecology* 61, 333-344.
- Lubchenco, J. 1983. *Littorina* and *Fucus*: effects of herbivores, substratum heterogeneity, and plant escapes during succession. *Ecology* 64, 1116-1123.
- Lubchenco, J. and S. Gaines, 1981. A unified approach to marine plant-herbivore interactions. I. Populations and communities. *Annual Review of Ecology and Systematics* 12, 405-437.
- MacFarlane, C. 1952. A survey of certain seaweeds of commercial importance in Southwest Nova Scotia. *Canadian Journal of Botany* 30, 78-97.
- Mack, R. and J. Harper, 1977. Interference in dense annuals: spatial pattern and neighbourhood effects. *Journal of Ecology* 65, 345-363.
- Manly, B. 1990. Stage-structured populations. Sampling, analysis and simulation. Chapman and Hall. New York,
- Mathieson, A.; C. Penniman, P. Busse and E. Tvetter-Gallagher, 1982. Effects of ice on *Ascophyllum nodosum* within the Great Bay estuary system of New Hampshire-Maine. *Journal of Phycology* 18, 331-336.
- Mathieson, A.; J. Shipman, J. O'Shea and R. Hasevlat, 1976. Seasonal growth and reproduction of estuarine fucoid algae in New

- England. *Journal of Marine Biology and Ecology* 25, 273-284.
- McHugh, D. 1991. Worldwide distribution of commercial resources of seaweeds including *Gelidium*. *Hydrobiologia* 221, 19-20.
- Meagher, T. 1982. The population biology of *Chamaelirium luteum*, a dioecious member of the Lily family: two-sex population projections and stable population structure. *Ecology* 63, 1701-1711.
- Nelson, W. and A. Conroy, 1989. Effect of harvest method and timing on yield and regeneration of karengo (*Porphyra* spp) (Bangiales, Rhodophyta) in New Zealand. *Journal of Applied Phycology* 1, 277-283.
- Neter, J.; W. Wasserman and M. Kutner, 1983. *Applied Linear Regression Models*. R. Irwin, Inc. Illinois, 547 pp.
- Niell, F.X. 1979. Sobre la biología de *Ascophyllum nodosum* (L.) Le Jol. en Galicia. III. Biometría, crecimiento y reproducción. *Investigaciones pesqueras* 43, 501-518.
- Nyman, M.; M. Brown, M. Neushul and J. Keogh, 1990. *Macrocystis pyrifera* in New Zealand: testing two mathematical models for whole plant growth. *Journal of Applied Phycology* 2, 249-257.
- Nys, R. de; P. Jameson, N. Chin, M. Brown and K. Sanderson, 1990. The cytokinins as endogenous growth regulators in *Macrocystis pyrifera* (L.) C. Ag. (Phaeophyceae). *Botanica Marina* 33, 467-475.
- Nys, R. de; P. Jameson and M. Brown, 1991. The influence of cytokinins on the growth of *Macrocystis pyrifera*. *Botanica Marina* 34, 465-467.
- Paine, R. 1990. Benthic macroalgal competition: complications and consequences. *Journal of Phycology* 26, 12-17.
- Peckol, P.; M. Harlin and P. Krumscheid, 1988. Physiological and population ecology of intertidal and subtidal *Ascophyllum nodosum* (Phaeophyta). *Journal of Phycology* 24, 192-198.
- Perez-Cirera, J. 1982. Cistocarpos en el tetrasporofito de *Polysiphonia macrocarpa* (Rhodomelaceae, Rhodophyta). *Collectanea Botanica* 13, 887-891.
- Pringle, J. and R. Semple, 1980. The benthic algal biomass, commercial harvesting and *Chondrus* growth and colonization off southwestern Nova Scotia, 144-169. In: *Proceedings of the workshop on the relationship between sea urchin grazing and commercial plant/animal*

- harvesting. Pringle, J.; G. Sharp and J. Caddy, (Eds.). Canadian Technical Report of Fisheries and Aquatic Sciences 954.
- Printz, H. 1956. Recuperation and recolonization in *Ascophyllum*. Second International Seaweed Symposium, 194-199. Pergamon Press. London.
- Reed, D. and M. Foster, 1984. The effect of canopy shading on algal recruitment and growth in a giant kelp forest. *Ecology* 65, 937-948.
- Reed, D.; M. Neushul and A. Ebeling, 1991. Role of settlement density on gametophyte growth and reproduction in the kelps *Pterygophora californica* and *Macrocystis pyrifera* (Phaeophyceae). *Journal of Phycology* 27, 361-366.
- Rice, E.L. and A.R.O. Chapman, 1982. Net productivity of two cohorts of *Chordaria flagelliformis* (Phaeophyta) in Nova Scotia, Canada. *Marine Biology* 71, 107-111.
- Robertson, B. 1987. Reproductive ecology and canopy structure of *Fucus spiralis* L. *Botanica Marina* 30, 475-482.
- Sackville-Hamilton, N.; B. Schmid and J. Harper, 1987. Life-history concepts and the population biology of clonal organisms. *Proceedings of the Royal Society of London B* 232, 35-57.
- Santelices, B.; P. Camus and A. Hoffman, 1989. Ecological studies for harvesting and culturing *Gymnogongrus furcellatus* (Rhodophyta, Gigartinales) in Central Chile. *Journal of Applied Phycology* 1, 171-181.
- Schiel, D. 1985a. Growth, survival and reproduction of two species of marine algae at different densities in natural stands. *Journal of Ecology* 73, 199-217.
- Schiel, D. 1985b. A short-term demographic study of *Cystoceira osmundacea* (Fucales: Cystoseiraceae) in Central California. *Journal of Phycology* 21, 99-106.
- Schiel, D. and J. Choat, 1980. Effects of density on monospecific stands of marine algae. *Nature* 285, 324-326.
- Schiel, D. and M. Foster, 1986. The structure of subtidal algal stands in temperate waters. *Oceanography and Marine Biology Annual Review* 24, 265-307.
- Schiel, D. and W. Nelson, 1990. The harvesting of macroalgae in New Zealand. *Hydrobiologia* 204/205: 25-33. Thirteen International Seaweed Symposium. S. Lindstrom and P. Gabrielson (Eds.). Kluwer Academic Publishers. Belgium.

- Schmid, B. 1990. Some ecological and evolutionary consequences of modular organization and clonal growth in plants. *Evolutionary Trends in Plants* 4, 25-34.
- Schmid, B. and J. Harper, 1985. Clonal growth in grassland perennials. I. Density and pattern-dependent competition between plants with different growth forms. *Journal of Ecology* 73, 793-808.
- Seip, K. 1980. A computational model for growth and harvesting of the marine alga *Ascophyllum nodosum*. *Ecological Modelling* 8, 189-199.
- Sharp, G. 1981. An assessment of *Ascophyllum nodosum* harvesting methods in Southwestern Nova Scotia. Canadian Technical Report of Fisheries and Aquatic Sciences. No. 1012, 28 pp.
- Sharp, G. 1987a. *Ascophyllum nodosum* and its harvesting in Eastern Canada, 4-48. In: *Case Studies of Seven Commercial Seaweed Resources*. FAO Fisheries Technical Paper 281. Rome.
- Sharp, G. 1987b. Growth and production in wild and cultured stocks of *Chondrus crispus*. *Hydrobiologia* 151/152, 349-354. Twelfth International Seaweed Symposium. M. Ragan and C. Bird (Eds.). Dr. W. Junk publishers. Netherlands.
- Sharp, G. 1991. An assessment of *Ascophyllum nodosum* resources in Scotia/Fundy 1990. CAFSAC Research Document 91/52, 30 pp.
- Sharp, G. and D.M. Tremblay, 1985. A tagging technique for small macrophytes. *Botanica Marina* 28, 549-551.
- Sharp, G. and J. Pringle, 1990. Ecological impact of marine plant harvesting in the Northwest Atlantic: A review. *Hydrobiologia* 204/205: 17-24. Thirteen International Seaweed Symposium. S. Lindstrom and P. Gabrielson (Eds.). Kluwer Academic Publishers. Belgium.
- Sideman, E. and A. Mathieson, 1983. The growth, reproductive phenology, and longevity of non-tide-pool *Fucus distichus* (L.) Powell in New England. *Journal of Experimental Marine Biology and Ecology* 68, 111-127.
- Smith, B. 1986. Implications of population dynamics and interspecific competition for harvest management of the seaweed *Laminaria*. *Marine Ecology Progress Series* 33, 7-18.
- Sokal, R. and F. Rohlf, 1981. *Biometry*. Second Edition. Ed. Freeman and Co. New York, 859 pp.

- Solbrig, O. 1980. Demography and Natural Selection, 1-20 pp. In: Demography and Evolution in Plant Populations. O. Solbrig (Ed.). Blackwell Scientific Publications, Oxford.
- Solbrig, O.; R. Sarandon and W. Bossert, 1988. A density-dependent growth model of a perennial herb, *Viola fimbriatula*. *The American Naturalist* 131, 385-400.
- Sousa, W.; S. Schroeter and S. Gaines, 1981. Latitudinal variation in intertidal algal community structure: the influence of grazing and vegetative propagation. *Oecologia* 48, 297-307.
- Southwood, T. 1966. *Ecological Methods*. Chapman and Hall. London, 391 pp.
- Strömngren, T. 1981. Individual variation in apical growth rate in *Ascophyllum nodosum* (L.) Le Jolis. *Aquatic Botany* 10, 377-382.
- Strömngren, T. 1983. Temperature-length growth strategies in the littoral alga *Ascophyllum nodosum* (L.) *Limnology Oceanography* 28, 516-521.
- SPSS: X, 1983. *User's Guide*. 2nd Edition. McGraw-Hill Book Co. SPSS Inc. New York, 988 pp.
- Taylor, A.; L. Cren, B. Smith and L. Staples, 1981. *Chondrus* holdfasts in natural populations and in culture, 140-145. In: *Proceedings of the 8th International Seaweed Symposium*. G. Fogg & W. Jones (Eds.). Wales.
- Thompson, J.; A. Gray and T. McNeilly, 1990. The effects of density on the population dynamics of *Spartina anglica*. *Acta Oecologica* 11, 669-682.
- Underwood, A. 1981. Techniques of analysis of variance in experimental marine biology and ecology. *Oceanography and Marine Biology Annual Review* 19, 513-605.
- Urbanska, K.M. 1990. Biology of asexually reproducing plants. *Biological Approaches and Evolutionary Trends in Plants*. S. Kawano (Ed.). Academic Press. London, 417 pp.
- Vadas, R.; W. Wright and S. Miller, 1990. Recruitment of *Ascophyllum nodosum*: wave action as a source of mortality. *Marine Ecology Progress Series* 61, 263-272.
- Van der Meer, J. 1981. Genetics of *Gracilaria tikvahiae* (Rhodophyceae). VII. Further observations on mitotic recombination and the construction of polyploids. *Canadian Journal of Botany* 59, 787-792.
- Vasquez, J. and B. Santelices, 1990. Ecological effects of harvesting *Lessonia* (Laminariales, Phaeophyta) in Central Chile.

- Hydrobiologia 204/205: 41-47. Thirteen International Seaweed Symposium. S. Lindstrom and P. Gabrielson (Eds.). Kluwer Academic Publishers. Belgium.
- Watkinson, A. 1986. Plant population dynamics, 137-184. In: Plant Ecology. Ed. M. May. Blackwell Scientific Publications, Oxford.
- Watson, D. and T. Norton, 1985. Dietary preferences of the common periwinkle, *Littorina littorea* (L.). Journal of Experimental Marine Biology and Ecology 88 193-211.
- Watson, D. and T. Norton, 1987. The habitat and feeding preferences of *Littorina obtusata* (L.) and *L. mariae* Sacchi et Rastelli. Journal of Experimental Marine Biology and Ecology 112, 61-72.
- Weiner, J. 1984. Size hierarchies in experimental populations of annual plants. Ecology 66, 743-752.
- Welden, C.W. and S.P. Hubbell, 1992. Tropical sapling survival, growth and recruitment in response to canopy gaps and soil moisture. Bulletin of the Ecological Society of America 73, 383.
- Weiner, J. 1988. The influence of competition on plant reproduction, 228-245. In: Plant Reproductive Ecology: Patterns and Strategies. J. Lovett Doust & L. Lovett Doust (Eds.). Oxford University Press, New York.
- Werner, P. 1975. Prediction of fate from rosette size in teasel (*Dipsacus fullonum* L.). Oecologia (Berl.) 20, 197-201.
- Werner, P. and H. Caswell, 1977. Population growth rates and age versus stage stage-distribution models for teasel (*Dipsacus sylvestris* Huds.). Ecology 58, 1103-1111.
- Westermeier, R. and P. Moller, 1990. Population dynamics of *Macrocystis pyrifera* (L.) C. Agardh in the rocky intertidal of Southern Chile. Botanica Marina 33, 363-367.
- Westoby, M. 1984. The self-thinning rule. Advances in Ecological Research 14, 167-225.
- Westoby, M. and J. Howell, 1986. Influence of population structure on self-thinning of plant populations. Journal of Ecology 74, 343-359.
- White, J. 1979. The plant as a metapopulation. Annual Review of Ecology and Systematic 10, 109-145.
- White, J. and J. Harper, 1970. Correlated changes in plant size and number in plant populations. Journal of Ecology 58, 467-485.

- winer, B. 1971. *Statistical Principles in Experimental Design*. Second edition. McGraw-Hill Book Co. New York, 905 pp.
- Zar, J. 1984. *Biostatistical Analysis*. Second Edition. Prentice-Hall, Inc. New York, 718 pp.

Appendix

Report on Damage to the Experiments

An unplanned harvest in my study site took place in November 1989 damaging my experimental plots (in Chapter 2). The area of intertidal harvested extended approximately from the middle of the plots (sometimes higher) and seaward. Some plots were more or less damaged. The effect was direct as well as indirect. The direct effect was when the harvest cut the tagged modules. The indirect effect was when the plants around the transects were cut but the tagged modules were not. The reharvest affected directly and indirectly 10 out of 21 plots. In May 1990 a second unauthorized harvest took place. This damaged the remaining plots. Due to this, I ended the study on harvesting effects three months earlier than planned. Table A shows the treatments, plots and transects affected by the first reharvest. The total number of replications/treatment that were damaged is given in Table B.

Experimental harvesting

Table A. Harvesting treatments, plots (or replications) and transects affected by the November reharvest.

treatment	plot number	transects damaged
winter low	3	medium to low
	13	top to low
	14	
winter medium	6	medium to low
	16	
	20	
winter high	4	medium to low
	10	
	18	
summer low	1	medium to low
	7	medium to low
	9	medium to low

summer medium	12	
	17	
	19	
summer high	2	medium to low
	8	indirectly, near
		low
	21	
control	5	low
	11	
	15	

Table B. The number of replications damaged per treatment.

treatment	number of transects
winter low	2
winter medium	1
winter high	1
summer low	3
summer medium	0
summer high	2
control	1

Modules that were cut or where the adjacent area had been cut were left out. The total number of tagged modules lost to the reharvest (cut) was 133, i.e., 12% of the sample. This estimation was done subtracting the number of modules in April 1990 from that in August 1989 for the damaged plots only. That is 12% of the modules that survived until August 1989 in the above plots. The actual damage, however, may be greater than this. This study has shown that harvesting enhances growth especially in the small size classes (Chapter 2). It is reasonable then, to think that, although modules damaged directly or indirectly were not included in the analyses, the reharvest enhanced the growth of the tagged modules remaining in or near the cut patches.

Also, in this study I found that reproductive state and growth are correlated, reproductive modules growing more than vegetative modules. In enhancing growth then the reharvest may have increased even more these natural differences. Another consequence of the reharvest is a possible bias in the survivorship curves. Even though I excluded all modules damaged, a drop in survivorship at the time of the reharvest can be seen (Fig. 9, Chapter 2). This suggests that the reharvest caused that drop.

Figure 1 suggests that some of the variability in growth may be due to the reharvest. The standard deviations in the plots cut in the summer increased 100% from August to November 1989, when the cut took place. In the plots cut in winter and in control plots high changes in standard deviations occurred at other times, however. The contrast between the variability in summer plots and the other 2 treatments may be partly due to the fact that more plots were damaged (and perhaps more intensely too) in the summer plots than in the others.

The lack of significance of the treatment effects (Chapter 1) may have been due to the reharvest. Since growth is slow, it is possible that treatment effects would have been noticeable 2 years after the harvest. The reharvest, however, lowered the chances of detecting these effects because it reduced the sample size which may have reduced the power of the tests. Another problem is that the effect of the reharvest is confounded with treatment effects. Since, nevertheless, natural variability is high, I collected the available data from the damaged plots hoping that the reharvest would not exert a significant influence on the effect of the treatments.

Experiment: Grazing on zygotes. Fourteen zygote traps and controls, out of 45, were in the damaged plots. The effect of the cut may be 2-fold. It may have altered the density of grazers and resulted in greater light availability thus enhancing zygote growth. This may have influenced survivorship. For instance, the mean

number of zygotes in the exclusion boxes at the end of the study was higher (4,200/tile) in control plots than in harvested stands (3,100/tile). If the reharvest enhanced growth, the low density of zygotes/tile in these may have resulted from density-dependent mortality. Nevertheless, the time interval for this to occur was short and took place in part during the fall and winter when there is no growth and grazing activity was likely low. Thus, data from the affected traps was included in Chapter 4.

Experiment: grazing on adults. This experiment was affected by the second reharvest (May 1990). The damage was indirect. I terminated this experiment in July of the same year. Because growth is slow and variability high, it is unlikely that the reharvest biased the data collected for this study.

Experiment: control for tags. The first reharvest cut through and around the transects of this experiment (Chapter 2). A total of 8 (18%) plants out of 45 were damaged. Thus, 96 modules out of 540 were removed. Due to growth is slow the effect of the reharvest on this experiment was considered non-significant.

Figure Legend

Figure 1. Mean growth over 3-month time intervals between 1988 and 1990 in plots harvested in summer and winter and in control plots. Harvesting intensity treatments and size classes are pooled. Bars are 1 standard deviations.

