PREPARATION OF THIS DOCUMENT

The parallel progress made in recent years both in our understanding of seaweeds, and in the growth of the seaweed industry, were addressed by Dr. J. MacLachlan, then Chairman of the International Seaweed Association, in his opening address to the Eleventh International Seaweed Symposium held in Qingdao, People's Republic of China, June 19-25, 1983. At this same symposium, discussions between FAO, the Academia Sinica and the International Seaweed Association, focussed on the requirement for training in applied seaweed activities. The need for a handbook or guide to practical phycology was also taken into account for the management both of wild seaweed resources and seaweed cultivation by man. From these discussions, it became clear that it is premature to look for such a handbook in the near future, given that although great strides have been made in understanding the biology and natural chemistry of seaweeds, relatively little has been written of global relevance on practical aspects of harvest and cultivation. The present set of case studies, by providing a detailed description of a range of such industries, aims at providing some of the basic elements from which such a broader and more relevant summary can be drawn. At the same time, these studies themselves can be of direct value to those working in the present seaweed industries.

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ABSTRACTS

Seven case studies are presented on commercial seaweed resources; five on wild crops, respectively Ascophyllum nodosum, Chondrus crispus, Gelidium, Laminaria longicruris and Macrocystis, are provided along with case studies of the farmed crops of Eucheuma and Laminaria japonica. Individually the cases range from descriptions of the wild crops and their management to the managed production of farmed crops including, in several examples, some information on economics and/or processing. These initial seven cases range from those emphaizing but one species from but one part of one country, to studies of a genus as it occurs commercially throughout the world.

Foreword

Seaweeds are of direct importance to man as a dietary supplement/food additive/source of industrial feedstock and as a base for synthesis of a wide range of chemical products. They are of indirectly importance as contributors to natural food chains and habitats supporting commercially important marine fish and shellfish. Except for a few areas of the world however; such as in the Asian region/their potential for contributing to coastal economies of developing countries has been largely unrealized to date and there is a general lack of information on how this resource may be used productively. As noted recently by Caddy and Fischer (1984): "Seaweeds pose the same questions to the resource manager with respect to national harvesting strategy as do commercially important marine animals on the one hand, and the optimal management of forest and pasture stands in the terrestrial context, on the other. The same important questions should be asked in relation to harvesting strategy, namely:

"(1) Where are the resources, of what kind, and how much? What are the possible alternative uses and markets for these kinds of resources?

> "(2) What is the rate and time of harvesting needed in order to maintain a sustainable optimal harvest of the wild resources?
>
> "(3) What are the appropriate levels of investment in manpower and equipment needed to achieve the above optimal harvesting rate in both wild and cultivated systems without wasting scarce economic resources?
>
> "(4) What, if any, are the indirect impacts of harvesting wild crops or farming on other resources in the ecosystem?"

Although an attempt at addressing the first of these considerations was made by Michanek (1975), and the second by Naylor (1976) and McHugh & Lanier (1983), we are clearly still at an early stage in beginning to realize the economic potential of this important grouping of organisms. The large scale culture of unicellular algae, and the culture and wild harvest of seaweeds or macrophytes are potentially an important addition to those other major spheres of human activity, namely agriculture, forestry and fisheries, which now provide most of our naturally renewable organic materials.

The utilization of marine algae is still in its infancy, and despite numerous articles scattered through the scientific literature there are few general accounts that provide the manager of coastal seaweed resources with practical information. There is a general lack of guidance on the management of wild seaweed resources; some of which are unexploited, some overexploited. Many are of ecological importance to fisheries and several form the basis for the rapidly growing field of seaweed farming.

Paradoxically, in comparison with mariculture of marine fish and shellfish, the technical problems of growing marine algae commercially are relatively simple, and are fairly well understood, as can be seen by the case studies included here. In contrast, the problems of market development for algal seaweed are generally more difficult than for the animal seafoods. This is because more sophisticated treatments are required for using the algae either directly as food, or extracting them to make a wide range of valuable chemicals available.

The chemical applications of seaweeds in particular support sophisticated, capital-intensive industries in developed countries as extraction and purification of a wide variety of products is now undertaken. Here, economic constraints both with respect to capital, equipment and labour intensive cultivation methods, and generally low unit prices paid for the product, are the main constraints, but are only touched on briefly here. A companion volume to the present series of case studies is now being planned, which will deal in more detail with special topics relevant to seaweed harvest and culture, such as approaches to management and assessment of seaweed resources, processing, legal aspects and economics.

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Introduction

This report applies the case study approach to seven of the more important and diverse world seaweed resources, to bring out some of the main factors affecting their rational production. Less emphasis is placed here on the ultimate uses of seaweeds, which range from their utilization in human food and animal foodstuffs, to their roles as food additives, in water purification systems, pharmaceuticals and as a source of biomass for power production among many other uses.

The editors are conscious of the fact that the seven case studies made available to us within the constraints of the present co-operative study do not cover all of the main types of seaweed resources of importance to man: for example, the production of seaweeds for direct human consumption especially in Japan and China is best represented here by the study on the Chinese Laminaria industry, but some of the economically most important resources are destined for other uses than directly as food. The problems faced on the production side are broadly similar in most cases however, and are likely to be addressed with some modification in one or other of the seven studies presented here.

As human populations increase and strive for better things in life, markets are created for more and more food and the luxury accoutrements of modern society. Among them are many products that require such hydrocolloidal materials as seaweeds produce. These materials are largely suspensoids which tend to keep finely divided particles or droplets separated and in suspension in liquids as in foods that are prepared by suspension in milk or water. As gels they may do the opposite; i.e., keep water suspended in solids, as in the preparation of ice-cream where the result is microcrystals in place of the sandy mouth feel of some ice-creams lacking them. They prevent the scorched taste characteristic of older forms of condensed or evaporated milk. They make many confections, foods and other modern substances possible such as cake icings that don't melt or become sticky at ambient temperatures.

The release of medicines by pills that burst only at the appropriate place as they pass through the intestinal tract are often the result of appropriate coatings of algal materials. Of algal origin are some of the world's most effective antihelminthics. Algal hydrocolloids provide the substratum for many horticultural abd biotechnological procedures such as coating seeds with pesticides and fertilizers and such as used in tissue culture, cytoplast fusion and other genetic mechanics. They produce substances that seem to be effective against some of today's most aggravating viral infections and much more.

Traditionally the seaweed of commerce has been produced from harvesting wild crops. As demands for seaweed have grown, their production by farming has proven attractive for its reliability in respect to quality and volume as well as lower costs. Thus we see the wild crops of Chondrus crispus and Laminaria longicruris, which have contributed so much to the history of seaweed use in the Western Hemisphere, being replaced by the farmed crops from other species in the Orient and Old World Tropics and by other wild crop species from the lower labour cost areas of the Southern Hemisphere. In the case of Eucheuma. shifting from wild cropping to farming has largely involved the same people in the same geographic areas and economic levels; so the change has been welcomed.

The reader will note that there is a wide range of sophistication in respect to the production of the different genera. Gelidium (and most all other agar sources but Gracilaria) is strictly still from wild crops with recognition of clear chemical differences in the agar from the different species involved, though there is little published knowledge of these differences. Our understanding and management of Ascophyllum and, even more so, Macrocystis. wild crops almost approach farming but without great concern in the literature for quality or yield of the hydrocollooid product. Yet the quality of the alginate from different genera and seasons is of primary concern to manufacturers.

Each of the seven seaweed chapters began with the same outline, but as the nature of the production of each is so very different, each chapter has come to have some unique features. However, the basic approach has been to provide the reader with the classical knowledge from science first, then the more experimentally developed specifics leading to crop management and, finally, utilization. The sequence is roughly that of the following ten numbered sections:

1 - Identity of the crop
2 - Distribution, ecology and metabolism
3 - Life history
4 - Population structure and mortality
5 - Productivity of the resource
6 - Method of harvesting and harvesting cycle
7 - Equipment used for harvesting of the resource
8 - Protection and management of the resource
9 - Utilization, processing and economics
10 - References

We hope that the provision of the available information in the above outline will tend to illuminate the gaps in the present information while providing that publicly available for these seven seaweeds. Thus the purposes include encouraging readers to fill the obvious gaps in the technology, to undertake research toward improving present practices and to write new case studies for others of the 25-odd seaweeds of importance in world commerce today.

Ascophyllum nodosum and its harvesting in Eastern Canada

1. IDENTITY
2. DISTRIBUTION
3. POPULATION STRUCTURE
4. GROWTH
5. HARVESTING, BIOMASS RECOVERY AND ECONOMICS
6. AQUACULTURE
7. PROTECTION AND MANAGEMENT OF THE RESOURCE
8. UTILIZATION
9. REFERENCES
APPENDIX I EXCERPTS FROM: MARINE PLANTS/ATLANTIC FISHERY REGULATIONS

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ABSTRACT

Ascophyllum nodosum, a major North Atlantic seaweed resource, is distributed widely from the Arctic Circle to 40 degrees North Latitude. In eastern Canada 45,000 T of wet Ascophyllum are considered harvestable. The present annual harvest ranges is 5/000 to 9,000 wet tons. Hand harvesting has been largely replaced by mechanical harvesting in the last 15 years. Recovery of biomass following harvest is dependent on site productivity/distribution of standing crop, and degree of harvest. After mechanical harvesting residual biomass ranges from 80 percent to 40 percent of pre-harvest standing crop. The economics of harvesting methods were compared, and cost per harvested ton ranged from Canadian dollars 10.65 to Canadian dollars 38.71 per wet ton. Ascophyllum from eastern Canada has been used for a range of agricultural, industrial, and human food products. However, alginate accounts for 95% of the end product.

1. IDENTITY

1.1 Nomenclature
1.2 Taxonomy
1.3 Morphology, anatomy & reproductive structures
1.4 Life cycle and sex composition

1.1 Nomenclature

Ascophyllum nodosum was originally placed in the genus Fucus as Fucus nodosus L. It has numerous synonyms and has been treated various genera as follow:

Ascophylla laevigata Stackh
Ozothallia nodosa Decaisne and Thuret
Physocaulon nodosum Kutz
Halidrys nodosa Lyngb
Fucodium nodosum J. Ag.
Helicoccus nodosus Aresch.

The present accepted name was proposed by Le Jolis in 1863.

1.2 Taxonomy

Ascophyllum nodosum is a member of the order Fucales. These are defined as growing from an apical cell group. Superficial conceptables carry the sporangia where gametes are released and combine outside of the plant. The family Fucaceae have dichotomous or pinnate branches, in some cases with numerous marginal slits or pits (cryptostomata Taylor, 1957). The genus Ascophyllum is distinguished from Fucus by branches un-differentiated into a midrib and a blade. Ascophyllum nodosum has a linear cartilaginous thallus with dichotomous primary branching and pinnate lateral or secondary branching **(Fig. 1).** Single vesicles expand the thallus at varying intervals. Receptacles are oval and yellow when mature.

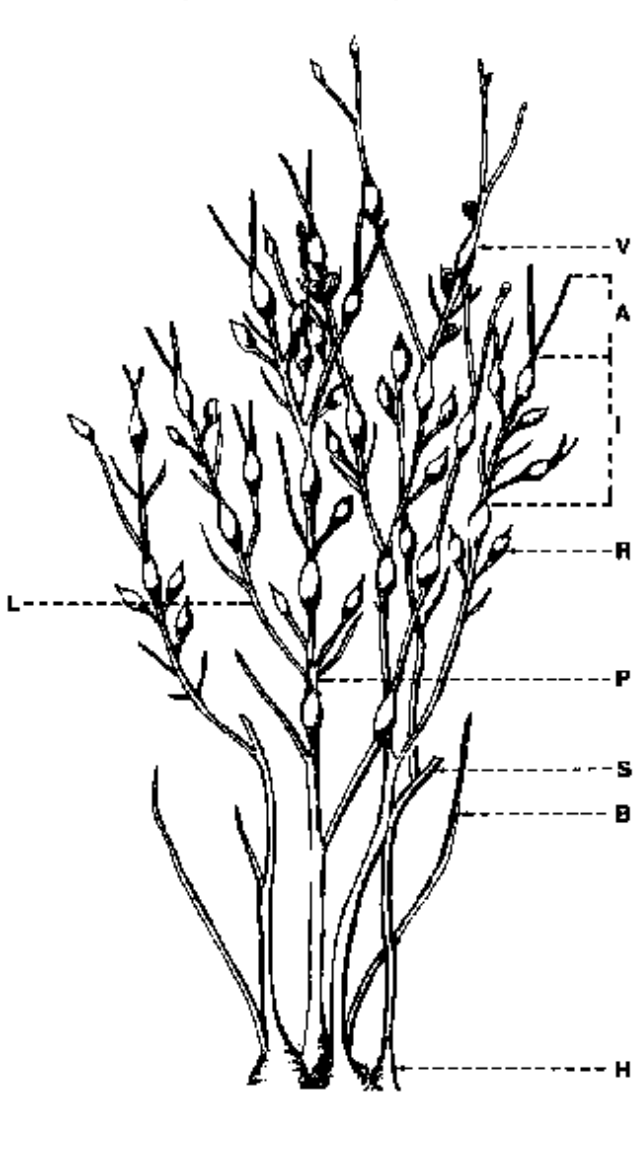
1.3 Morphology, anatomy & reproductive structures

Ascophyllum is an intertidal algae conspicuous due to its ability to float with the changing water surface. Vesicles (air bladders) support the thallus allowing the growing apices to be exposed maximumally to light energy **(Fig. 1).**

The plants are held to the substratum by discoid holdfasts which in dense populations frequently coalesce. The morphological terminology used to describe Ascophyllum has varied with authors. Cousens, (1981a) re-examined these terms and his definitions are adopted for this report as follows with additions to account for harvest related morphology **(Fig. 1).**

Shoot - the axis which results from growth of an apical meristem.
Primary shoot - originating from the holdfast (includes basal shoot of Baardseth).
Lateral shoot - arising from a lateral pit on another shoot. cryptostomata of Taylor/1957).

Figure 1. Ascophyllum nodosum fronds and associated terminology: A, apical tip; B, basal shoot; H, holdfast; I, internode; L/lateral shoot; P, primary shoot; *R,* receptacle; S, stump; V, vesicle.



Stump - a shoot lacking a apical meristem.
Intact shoot - a shoot with at least one apical meristem.
Internode - the portion of a shoot between two adjacent vesicles.
Apical tip - the portion of a shoot distal to the last vesicle. Frond - the system of shoots derived from a single meristematic protrusion of the holdfast.
Plant - an assemblage of fronds arising from a common holdfast.
Stand - a group of plants within a defined area.
Vesicles - dilations of the shoot produced at intervals related to rate of annual shoot elongation.
Receptacles - fertile lateral shoots first appearing April -June maturing in one year and being shed April to June.

Shoot morphology varies greatly between sites and some of this variation can be attributed to environmental gradients. Vesicles are enlarged at sites exposed to wide variations in salinity.

Receptacles can vary in shape and size in the same locality (Baardseth/1970). Receptacles at the most extreme wave exposures were more spherical and had slender long stalks. The most apical internode of unbroken primary shoots reach maximum length at sites of intermediate exposure (Cousens, 1982). Overall length of shoots in relation to water movement increases with velocity up to 1 m/sec but declines thereafter (Mathieson et al 1977). Pigment concentrations increase with wave exposure changing from yellow in sheltered areas to green on the open sea coast (Cousens 1982). A fuller discussion of plant size is contained in Section 3.

1.4 Life cycle and sex composition

Ascophyllum reproduces sexually through the union of eggs and sperms produced in the conceptacular cavities of ripe receptacles. The ratio of male to female plants was reported in early literature as approximating 50/50 (Baarsdeth/1970). Printz, (1956), determined shoot sex by coloration of receptacles; male yellow, female/greenish yellow and described female conceptacles as having larger openings (ostioles) than males. Although there were numerous investigations of reproductive periodicity/no further work has been reported on geographical or vertical distribution of male and female shoots.

Receptacles are initiated in April to June grow and mature for gamete release (also) in April to June. In Maine peak reproduction was April and March of successive years/however/the level of reproduction increased 3-fold in the second year (Mathieson et al. 1976). Mature receptacles were noted in monthly collections from the Bay of Fundy in March and April (Edelstein et al. 1970).

Receptacle initiation is stimulated by photoperiods of 8:16 to 12:12, longer periods of darkness inhibit initiation (Terry and Moss, 1980). The proportion of stand biomass comprised of receptacles ranges from 12.4 to 35.7% in a gradient from wave exposed to wave sheltered (Cousens, 1981a). Maximum dry weight per receptacle is at intermediate wave exposures (Cousens, 1982). However, reproductive effort is greatest at exposed sites, 61.2-60.8% (Cousens, 1981a).

The biomass of the receptacles is equivalent to that of the vegetative tissues during peak reproduction (Josselyn and Mathieson, 1978). The decomposition of the A. nodosum receptacles is rapid; 50% of their original ash free weight being lost within 50 days. Thus the release of A. nodosum receptacle tissue during the spring reproductive period makes a significant contribution to the estuarine detrital pools.

2. DISTRIBUTION

2.1 Geographical

2.1 Geographical

a) Eastern Canada

Until 1933 records of Ascophyllum nodosum in Eastern Canada were limited to individual widely dispersed single collections in localized areas. Collections from a series of 93 sites scattered over the Bay of Fundy, Atlantic and Gulf shores of Nova Scotia, and the coast of Prince Edward Island listed Ascophyllum as abundant in the Bay of Fundy and Atlantic shores and occasionally around Prince Edward Island **(Fig. 2)** (Bell and MacFarlane 1933). Although there have been more recent collections from the Atlantic and Fundy coasts of Canada, (Edelstein and McLachlan, 1966; Neish, 1971) no new extensions of the species range have been reported.

De la Pylaie visited Newfoundland, St. Pierre et Miquelon in 1816 and 1819 and recorded the species of Fucales **(Fig. 3).** Until 1970 records from this area were very limited (Hariot, 1889), (Wilce, 1959) (Lee, 1968). An intensive distributional study of Ascophyllum nodosum and its ecads found the attached form at 50 sites representing all coasts of Newfoundland (South and Hill, 1970).

In the Gulf of St. Lawrence, Bay de Chaleur and Gaspe, Ascophyllum nodosum was common in collections from 46 stations (Cardinal, 1967). Ascophyllum nodosum was reported from 28 of 48 stations along the north and south shores of the St. Lawrence estuary to within 20 km of Quebec City (Cardinal and Villalard, 1971) **(Fig. 3).**

b) World distribution

Ascophyllum is widely distributed in the North Atlantic from Northern Norway and the White Sea to Portugal in the Eastern Atlantic. The arctic circle in the Western Atlantic marks the northern limits and the 40° N latitude the southern edge of Ascophyllum nodosum's range **(Fig 3).** Although more northern exploration has occurred since the description of range by Baardseth (1970) no new northern extension was reported (Lee, 1980).

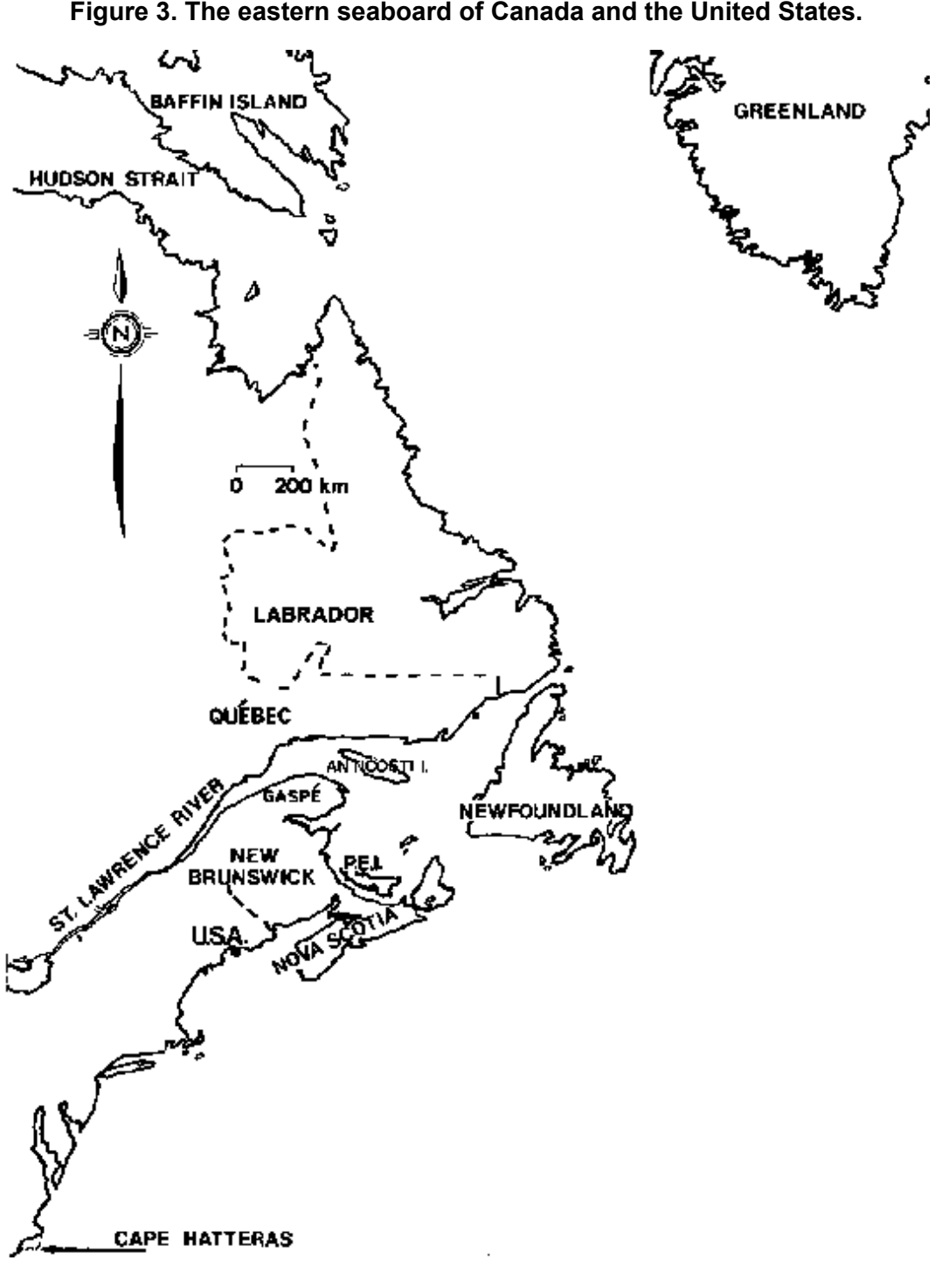
Figure 2. The Maritime provinces of Canada including the Marine Plant Districts as designated by the Atlantic Coast Marine Plant Regulations and area of active Ascophyllum harvest.

c) Vertical distribution

Ascophyllum nodosum is primarily a mid to low intertidal species. Free living ecads can be found in the upper intertidal and attached non floating forms occur in the subtidal (South and Hooper, 1980). In southwestern Nova Scotia A. nodosum occurs from the mean highwater spring tide line +3.5 m to -6 m (**Fig. 4)** (Pringle and Semple, 1980). Within estuaries the vertical distribution of attached A. nodosum is restricted to the mid to lower intertidal. (Chock and Mathieson, 1983). The distribution of biomass is examined in Section 4.3.

The upper limits of Ascophyllum nodosum distribution are controlled by its ability to resist desiccation and high temperatures (Schonbeck and Norton 1978). Ascophyllum nodosum dominates the mid intertidal on shores where it is present. Removal of A. nodosum temporarily allows other fucoids to become established for one or two years. (Hawkins and Hartnoll, 1985: Keser et al, 1981). Ice scour in the St. Lawrence river estuary controls the mix or dominance of A. nodosum and Fucus vesiculosus (Archami-bault and Bourget 1983). In areas of frequent ice scour F. vesiculosus dominates and A. nodosum is dominant in areas without or infrequent ice scour. Juvenile Ascophyllum plants are able to persist under canopies in the field. Once established the shoots are long lived, 5-15 years exceeding the life span of competitive fucoids. Ascophyllum is less susceptible to grazing than are other macrophytes. This is due to the low level of preference of Littorinids for Ascophyllum relative to other fucoids (Menge, 1975).

Figure 3. The eastern seaboard of Canada and the United States.



The factors controlling the lower limits of Ascophyllum in Atlantic Canada have been attributed to grazing pressure in sheltered environments. In exposed locations grazers are less abundant and lower limits are marked by 90% cover of Chondrus crispus. Chondrus survives under the A. nodosum canopy but will bleach if exposed to full light. If C. crispus is removed including the holdfast in its area of dominance, Fucus will colonize the bare surface (Lubchenco; 1980). However/if only Chondrus fronds are removed Ascophyllum re-establishes dominance within two years.

Figure 4. The vertical distribution of Ascophyllum in a semisheltered site southwestern Nova Scotia in relation to chart datum (Pringle and Semple 1980).

3. POPULATION STRUCTURE

3.1 Thallus age, length, biomass
3.2 Mortality

3.1 Thallus age, length, biomass

The minimum age of Ascophyllum nodosum shoots has been determined by the number of vesicles on the longest unbroken shoot; assuming one vesicle is formed annually. The time for the formation of the first vesicle is indeterminate and the length of the first internode varies greatly within a site (Cousens, 1981a). Maximum ages beyond the first vesicle are reported as 16 years in Maine and 12 years in Wales (Keser et al. 1981; David, 1943). In southwestern Nova Scotia maximum age beyond the first vesicle was 15 years (Sharp, unpublished data). Repeated breakage of primary or lateral shoots precludes a meaningful description of age structure. Instead we must examine length weight distributions of these populations. The mean length of primary shoots ranged from 18.6 + 19.9 cm to 11.9 + 14 cm at 5 sheltered to semi-sheltered sites in southwestern Nova Scotia (Sharp, 1981).

The length frequency of primary shoots is extremely skewed to the 0-10 cm class, **(Fig. 5).** The weight of unbroken primary shoots is a power function of shoot length **(Fig. 6).** Shoots above 30 cm in length contribute the majority, of stand biomass. Wave exposure affects the level of biomass within a stand. At exposed sites biomass is concentrated in shoots below 50 cm in length (Cousens 1981a) **(Fig. 7)** compared to sheltered sites where the majority of biomass is above 50 cm from the holdfast **(Fig. 7).** The proportion of shoot density contributing to 50% of the biomass at sheltered sites is 2.5% versus 10.5% in exposed sites (opp. cit).

Figure 5. The distribution of lengths for intact primary (normal) shoots from a wave sheltered site in southwestern Nova Scotia.

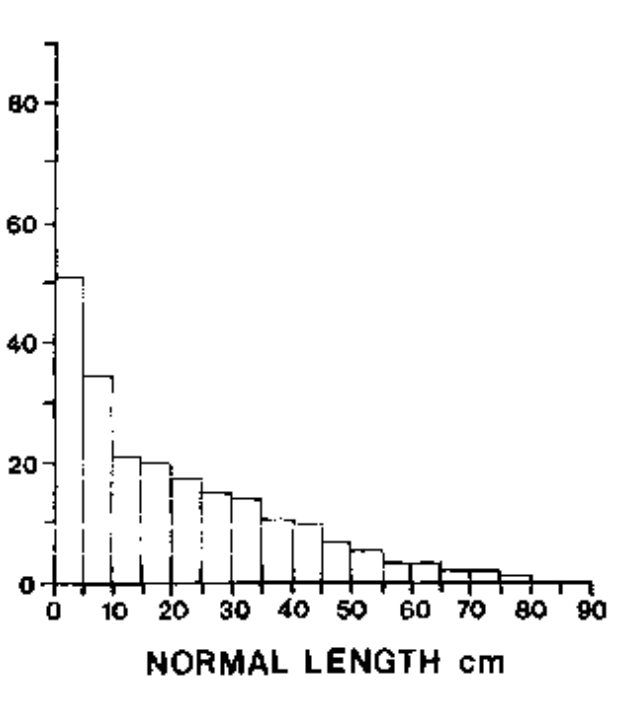


Figure 6. The length to wet weight relationship of intact primary shoots from a sheltered site in southwestern Nova Scotia.

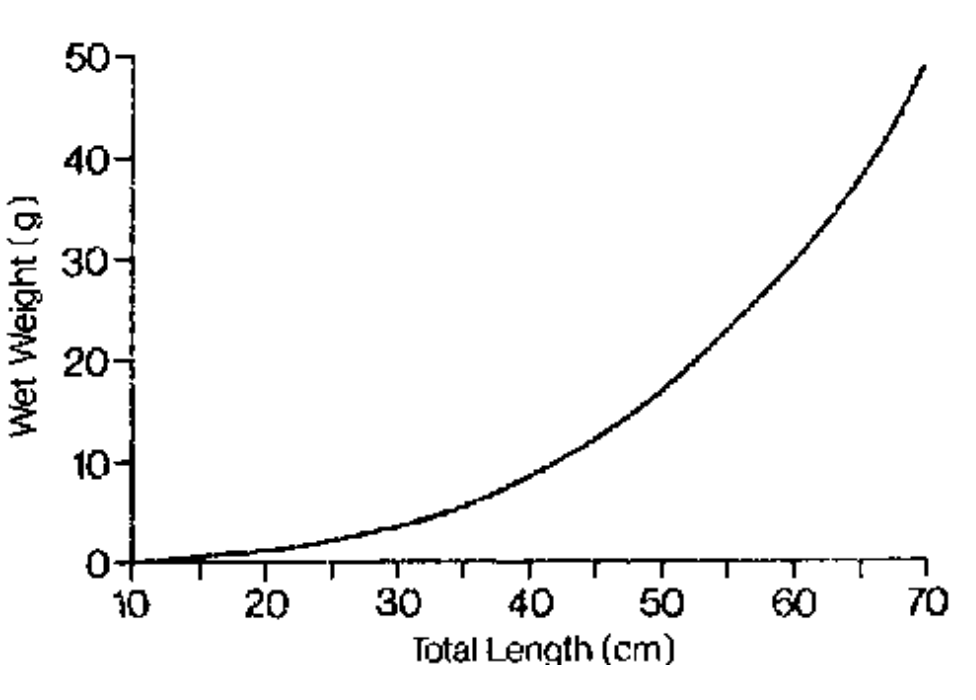
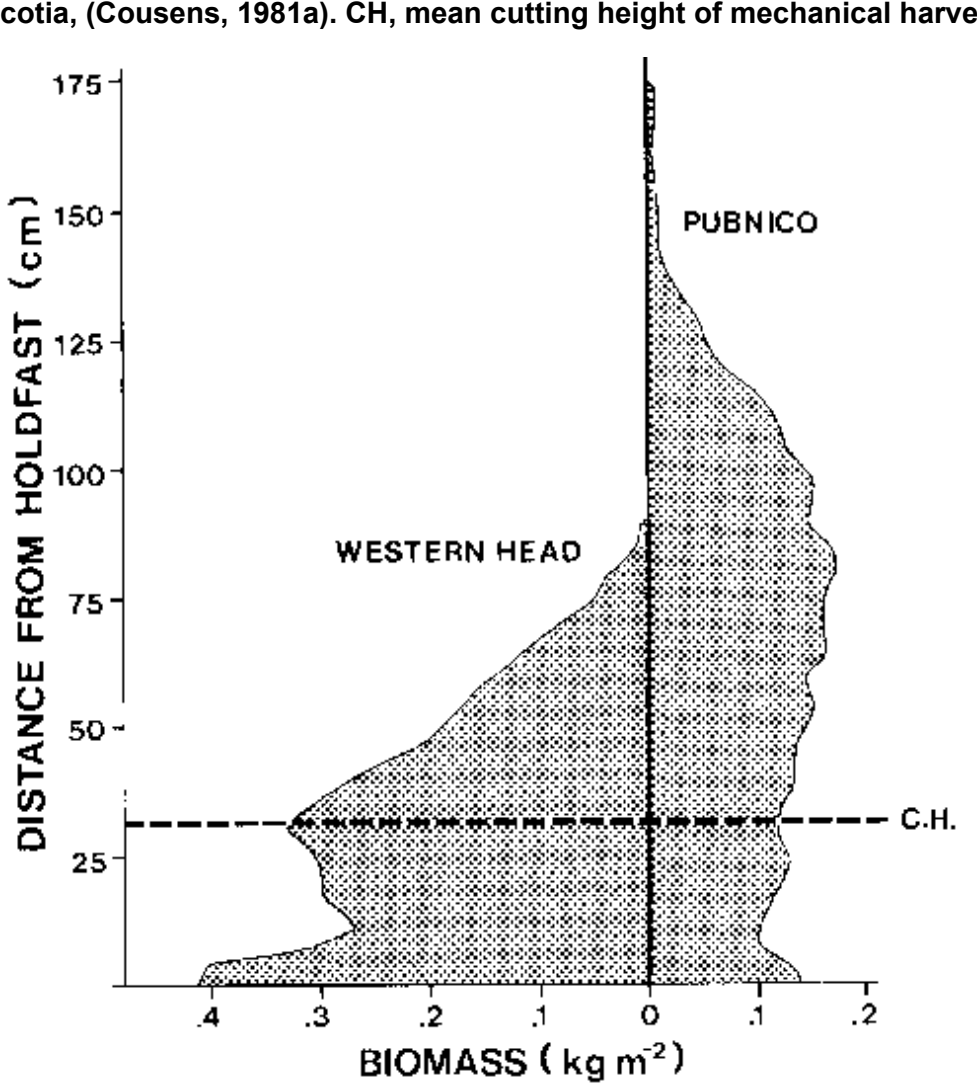


Figure 7. The distribution of Ascophyllum biomass within stand canopies at a wave exposed site (Western Head) and a sheltered site (Pubnico) southwestern Nova Scotia, (Cousens, 1981a). CH, mean cutting height of mechanical harvesters.



3.2 Mortality

The magnitude of natural mortality for Ascophyllum varies annually as significantly as between physical factors of tidal level and wave exposure (Breton Provencher, 1976). Mortality of tagged shoots over the summer was 9% and 16% in successive years in the St. Lawrence River estuary (opp. cit.). Survivorship of shoots (shoot type not identified) in a Maine estuarine site was 75% after one year (Vadas et al. 1976).

If survivorship of each shoot type is examined separately patterns related to environmental gradients are apparent. Survivorship of primary shoots to when an additional vesicle was present increased with increasing wave shelter (Cousens, 1981a). At exposed sites maximum survival was 5 years beyond the first vesicle for primary shoots; in wave sheltered areas the maximum survival was 11 years (opp. cit.). The position of the lateral shoot on a primary relative to the holdfast affects survivorship. Independent of age class laterals in the 0-30 cm (basal) portion of a shoot, had a survivorship of 90% after one year. Mortality of laterals decreased with distance from the holdfast/although mortality increased with age of lateral. The loss of laterals was primarily due to loss of the primary shoot rather than individual lateral shoot loss (opp. cit).

The germling is the most vulnerable stage in Ascophyllum's life. The initial settlement of germlings in an area denuded of Ascophyllum in Maine was 50/000 shoots m^{-2}. Fifty percent mortality occurred within one year of settlement. Shoot densities reached a minimum >8/000 m^{-2} in 2 years covering 60% of the substratum (Keser and Larson, 1984).

Sheltered sites in the North Atlantic are frequently ice covered. Movement and abrasion of ice can be a significant cause of mortality. In the Great Bay Estuary of New Hampshire ice effects removed 1.04 kg m^{-2} dry weight of Ascophyllum fragments per year (Mathieson et al. 1982). In sheltered areas the Ascophyllum zone is a habitat for Littorina species, all potential grazers. However, microscopic A. nodosum was low in the food preference rank in a two way choice presentation of 39 red green and brown algae (Lubchenco/1978). If no other foods were available Ascophyllum was consumed.

Elevated water temperatures caused either by natural or man made phenomena can affect growth or survival of Ascophyllum nodosum . Periodic bursts of high (>20°C) temperature water have inhibited growth for 1.5 years in Maine. In other areas growth was initiated earlier than normal in the growing season (Vadas et al. 1976). Electrical impedence measurements of A. nodosum tissues, an indication of ion movement in extracellular channels, show cell death occurs at -20°C and/or 70% water loss (MacDonald et al. 1974). A. nodosum loses 70% of its fresh weight excluding vesicles after 7.5 hours at 22°C and relative humidity of 40-45% (Dorgelo, 1976). This rate was slower than adjacent Fucus vesiculosus. However, in general, the rate of water loss did not correspond to the tidal level of individual species (opp. cit.).

The upper limits of A. nodosum distribution on the shore were shown in field experiments to be its physiological limits resulting from desiccation factors at these levels (Schonbeck and Norton, 1978). Exposure to long periods of drying resulted in visible tissue damage of A. nodosum after 21 to 28 days (opp. cit.). Winter conditions and rainfall were not critical factors. Transplants of A. nodosum above the normal upper levels of distribution suffered mortalities (opp. cit.).

Ascophyllum nodosum occurs in estuarine locations which are frequently urbanized and industrialized. In approaches to pollution problems, A. nodosum has been utilized in two ways. The ecological approach was to assess the effects of effluents on the distribution, productivity, and reproduction of A. nodosum. The use of A. nodosum as a bioindicator for specific water-soluble pollutants has resulted from its bio-accumulation abilities and perennial nature.

A series of ecological base line studies is available for Oslofjord, Norway, over the period of increasing (1943 to present times) urban and industrial influences on water quality in this fjord. Over this period of increasing pollution, particularly sewage, Ascophyllum nodosum became less common in the inner fjord and at present it does not exist there (Rueness, 1973). Transplantation of mature A. nodosum plants from the outer fjord to the inner polluted area found no significant differences in vegetative or reproductive growth. It was assumed the germlings of A. nodosum could not compete with the Enteromorpha carpet present in the polluted areas of the inner basin (Rue ness opp. cit.). Similar ecological studies were conducted in Iceland (Gunnarsson and Porrison, 1976). Ascophyllum nodosum was among the higher diversity of species which occurred solely away from the sewage outfall.

A decrease in macro-algal species occurred towards a source of pulpmill wastes in the Iddefjord, Norway (Lein et al. 1974). Transplantation of Ascophyllum nodosum and F. vesiculosus to the inner fjord adversely affected their growth and development. Sedimentation and toxicity resulting from this pollution controlled inner boundaries of species rather than salinity in the fjord. Comparisons of Ascophyllum tissues from polluted and unpolluted estuarine areas found lower dry matter, mannitol, and higher phosphate and protein contents in polluted than in unpolluted ones (Munda, 1967).

4. GROWTH

4.1 Thallus length and weight
4.2 Productivity
4.3 Biomass

4.1 Thallus length and weight

Monitoring tagged plants, periods of maximum growth in length of 3.6 to 3.4 cm month^{1} were reported for April and July 1973, respectively in the Great Bay Estuary System of New Hampshire-Maine (Mathieson et al. 1976). Distinct yearly variations were found both in time of/maximal growth and rate of growth. Maximum growth rates were 2.3 and 2.2 cm month-1 in May and October respectively of the second measurement year (opp. cit.). An average of 0.8 cm month-1 was recorded for a Maine population by Vadas & Keser (1972). Three successive years of growth (elongation) measurements of Ascophyllum nodosum in the upper Ascophyllum zone at a site in Maine were 17.4+4.7, 11.5+5.5 and 12.2+5.5 cm (Keser and Larsen, 1984). Breton Provencher (1976) observing A. nodosum elongation in the St. Lawrence river estuary reported 26.4 cm and 24.8 cm in successive years. Nor-mandeau Assoc. Inc. (1977) found spring maximum growth rates of 2.2 cm month^{-1} and winter minimums of 1.2 cm month^{-1} in Maine. MacFarlane (1932) measured inter-vesicle length of Nova Scotian populations and calculated growth rates of 0.33 to 1.2 cm/month.

Maximum rates of shoot elongation were recorded in the central part of the Ascophyllum zone but differences between zones did not exceed annual variation (Keser and Larsen, 1984). The length of the most distal internode (growth in year from formation of last vesicle) on unbroken primary shoots reaches a maximum at sites of intermediate wave exposure (Cousens, 1982). Growth rate increases with the length of intact primary shoots up to 15 cm at more exposed sites and 70 cm at more sheltered sites (Cousens, 1981a). The extremes of exposure were suggested to be suboptimal for growth due to conditions of desiccation/water turnover, and light (opp. cit.).

A relative growth rate comparison was made between Ascophyllum nodosum and Fucus vesiculosus over seven-day periods at depths of 0 to 4 m. Growth in length and fresh weight decreased with depth except except for an increase near compensation depth (Ramus et al. 1977). Ascophyllum nodosum and F. vesiculosus grew in the same pattern but A. nodosum grew at a higher rate (opp. cit.). Maximum photosynthetic activity occurs in tissues of 2-3 years old in shoots with an average age of five to nine years (Khailov, 1976a). This peak of photosynthetic activity was correlated to the maximum dry weight for the 2-3 year age class of tissues (opp. cit.).

A series of unique growth studies was conducted using short term measurements of apical growth in Ascophyllum nodosum with laser diffraction. Irradiance and temperature were correlated with hourly measurements of the growing tip to 1 mm. At artificial light of 12.5 Wm^{-2} and below, plants showed a direct relationship between growth and irradiance (Stromgren, 1977). Irradiance of 35 to 40 Wm^{-2} resulted in a reduced growth rate after 21 day periods. The fucoid species compensation point of 3 Wm^{-2} is only reached in the most extreme low light conditions during winter overcast days under a canopy (Schonbeck and Norton 1980). The saturation point 30-50 Wm^{-2} is not reached at the surface under similar conditions (opp. cit.). Response of apices to temperature was rapid between 2.5 to 30°C for the first few hours, however, experiments of two to three weeks duration showed the optimal temperature or growth was below 17°C (Stromgren, 1976). These laboratory studies correspond to field observations of maximum growth rates in moderate (6-10°C) temperatures and light 150-250 1y d^{-1} (Mathieson et al. 1976). Elongation of Ascophyllum apices is linearly correlated with rapid air temperature increases to 35°C over 1 to 4 hours (Stromgren, 1983). The duration of exposure at low tide and ambient air temperature can account for a large portion of shoot elongation and annual variability in growth.

Growth continues during low nutrient conditions because of direct use of nitrogen from seawater during low ambient nitrogen levels and optimal light (Asare and Harlin, 1983). Tank cultured Ascophyllum nodosum growth is in agreement with previous lab and field observations reaching a maximum of 2.5% d^{-1} (length) at 15°C. Growth was a linear function of light up to 20-30 yEm^{-2} 5^{-1} (Fortes and Luning, 1980).

Growth of zygotes settled on stone and brick substrata and transferred to the sea after ten days was found to be only 1 to 0.2 cm after one year and 0.5 to 1.5 cm after the second year (Sundene; 1973). Maximum growth rates for young Ascophyllum nodosum (10-80 mm) were 7 mm, 5 mm and 10 mm for the periods Sept.- Nov., Nov.-Feb. and Feb.-May in Scotland (Schonbeck and Norton, 1980). Studies of thallus growth immediately after germination in culture showed an increase with light intensity to 10,000 lux with temperature to 20°C (Sheader and Moss, 1975). After 30 days, the thallus was 0.27 mm, corresponding to a growth of 0.32 cm year^{-1} similar to the in-situ values of Sundene, 1973.

4.2 Productivity

In a gradient of wave exposure, annual production (measured by standing crop differences) increases with wave shelter (Cousens, 1981b), **Table 1.** However the maximum production per unit biomass occurred on semi-exposed locations corresponding with an increase of reproductive effort. The turnover time for vegetative biomass ranged from 2.9 years at semi-exposed sites to 10.98 years at extreme wave exposed sites. Annual production varied by a factor of 2 within a 10 km section of coast line (opp. cit.).

Table 1. Standing crop and production (kg dry wt m^{-2} at sites of different exposures to wave action. Sites 1-6 Polly Cove, Site 7 Dover Soi. P/B was calculated from the Modified Baardseth production estimates. (Cousens 1981b).

Site	1	2	3	4	5	6	7
April Standing	0.67	1.50	1.39	2.04	3.25	3.95	3.52
Crop (+2 s.e.)	+0.34	+0.07	+0.09	+0.13	+0.25	+0.97	+0.61
Modified Baardseth method	0.15	0.35	1.10	1.25	1.37	1.66	1.72
Standing Crop	0.05	0.26	0.95	0.94	0.84	1.07	1.05
Difference Method P/B	0.22	0.71	0.79	0.61	0.42	0.42	0.49

Differences between the annual maximum and minimum standing crops obtained in seasonal surveys of Ascophyllum nodosum biomass were used to calculate annual production for a number of widely separated sites (Cousens 1984, **Table 2).** The maximum value of annual production was found in southwestern Nova Scotia equivalent to 1,015 g c m^{-2} (Cousens, 1981a).

Table 2. Annual production and production to biomass ratios for Ascophyllum nodosum populations (Cousens 1964).

Location	t dry wt ha-1	P/B
New England	15	.86
White Sea	13	.65
Spain	23	.64
Nova Scotia (pre-harvest)	20-26	.33-.25
Nova Scotia	6.1-28.2*	.22-.79

*Corrected for growth loss prior to sampling Cousens 1964.

4.3 Biomass

Biomass density in southwestern Nova Scotia is among the highest in the world **(Table 3).** Maine and southwestern Nova Scotia values are similar but Norwegian biomass density is closer to the levels in the St. Lawrence Estuary **(Table 3).** Survey methodology varies greatly between studies from selected samples in the Ascophyllum zone (McFarlane, 1952; Topinka et al. 1981) to a volume "eyeball" estimate (Pielou, 1981).

Table 3. Biomass density of Ascophyllum nodosum populations in the North Atlantic.

Source		Location	Tonnes/Hectare wet weight
McFarlane	1952	Southwestern Nova Scotia	198[a]
Sharp	1981	Southwestern Nova Scotia	120 ± 110[b]
Cousens	1981a	St. Margarets Bay Nova Scotia	96 ± 45[a]
Breton- Provencher	1976	St. Lawrence Estuary Quebec	20 ± 5[a]
Topinka et al	1981	Lincoln County Maine	80[ac]
Chock & Mathieson	1976	Great Bay Estuary New Hampshire	72[a]
Keser et al	1981	Average of six sites Boothbay, Maine	84 ± 60[a]
Baardseth	1970	South Norway	6.9 ± 1.3
		Central Norway	24.1 ± 4.0
		North Norway	14.4 ± 1.7
Munda	1978	Iceland	69

[a] unharvested stock
[b] harvested stocks
[c] includes all Fucoids

Surveys and spot biomass values on the Atlantic coast of Nova Scotia and New Brunswick were combined with existing air photo analysis to estimate standing crops for Ascophyllum nodosum (Smith and Loucks, 1980). Some areas, e.g. the Nova Scotia Eastern Shore, have no ground truthing and other areas had poor quality air photos due to high tides. Taking a conservative estimate from the range of probable values the Atlantic and Fundy coasts of Canada support 442,000 t of A. nodosum wet weight **(Table 4).** A standing crop of 180,000 tons for southwestern Nova Scotia was estimated prior to harvesting and was based on selective sampling methods (McFarlane, 1952).

Mean fucoid biomass per meter of a shoreline in Maine was 352.17 kg m-1 versus 540.0 kg m-1 in southwestern Nova Scotia (Topinka et al., 1981). The primary difference between these areas was a bed width of 45 m in Nova Scotia versus 22 m in Maine.

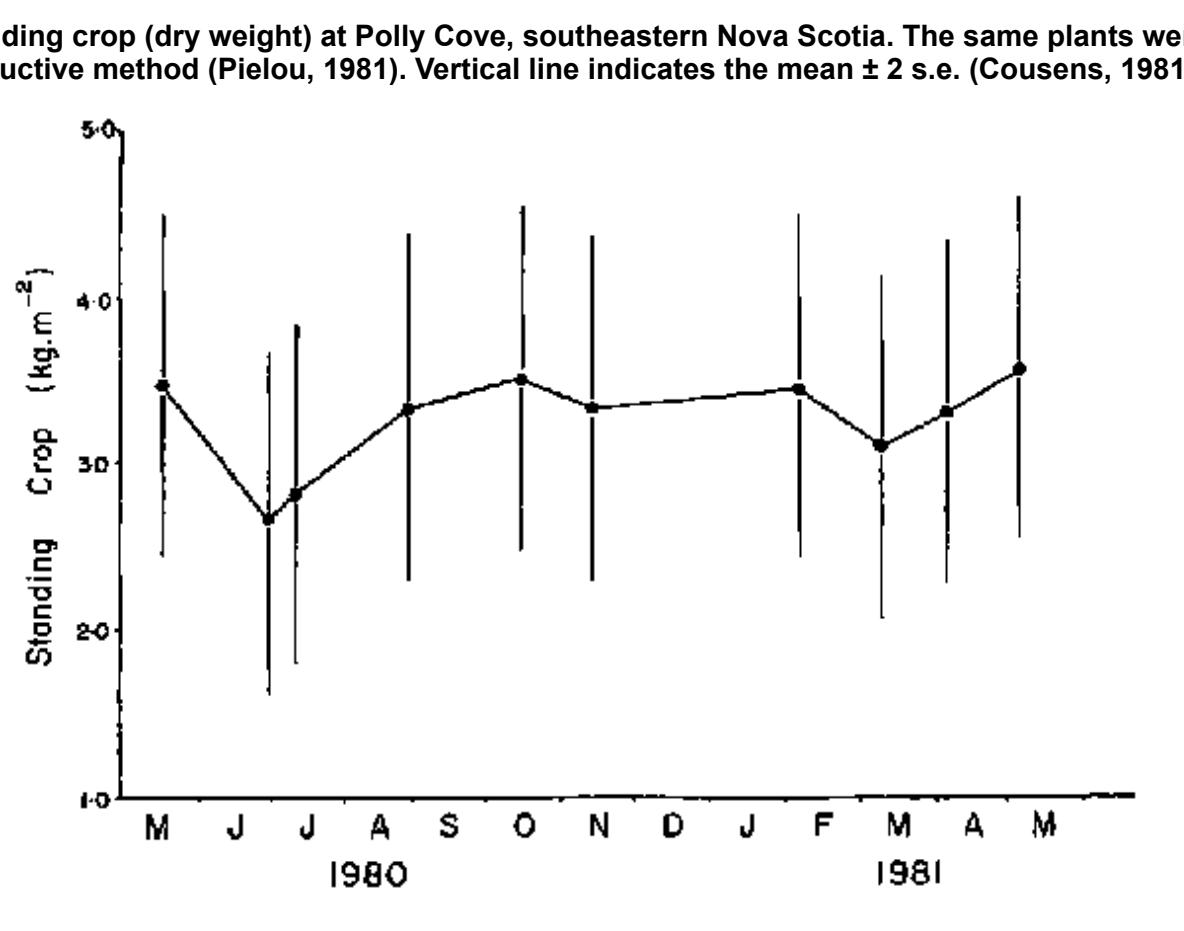
Seasonal variation in Ascophyllum biomass was significant at a New Hampshire site (Chock and Mathieson, 1983). Peak biomass occurred in August 105-135 g· $0.1m^{-2}$ and declined to 25-42 g· $0.1m^{-2}$ in September. However, at a southern Nova Scotian site the only significant change in standing crop occurred **(Fig. 8)** in June-July after the loss of receptacles (Cousens, 1981a).

Table 4. Total standing crop of A. nodosum from the Atlantic and Bay of Fundy shores of Nova Scotia and New Brunswick (Smith and Loucks 1980).

Marine Plant District Area	Standing crop wet t	Fucoids estimated harvestable annual yield wet t
14, Southern New Brunswick	51,000	3,800
12, Minas Basin to Chebogue	42.000+	4,200
12, Chebogue to Cape Sable Island	125.000+	15,000
12, Cape Sable	100.000+	10,000
11, Medway to Chedabucto Bay	154,000	11,500
Total Atlantic & Fundy Coasts of Mainland Nova Scotia & New Brunswick	472,000	44,500
From Smith & Loch 1980		

+ - Discounted by the author due to sampling methodology and assumptions of estimate.

Figure 8. Seasonal variation in standing crop (dry weight) at Polly Cove, southeastern Nova Scotia. The same plants were measured each time by a non-destructive method (Pielou, 1981). Vertical line indicates the mean ± 2 s.e. (Cousens, 1981a).



Biomass density decreases at both extremes of its vertical distribution on the shore (Chock and Mathieson, 1983; Cousens 1981a; Pringle and Semple, 1980) **(Fig. 4).** The spatial distribution of biomass is related to substratal types. In an area of mixed rock and gravel, patches of Ascophyllum averaged 1.5 to 2 m in maximum dimension. Rock and cobble substrata supported larger 2.0-2.5 m patches of A. nodosum (Black[1], unpublished data). Biomass density increases with greater quantities of stable substrata **(Fig. 9)** (Topinka, 1980).

[1] R.Black. Univ. Western Australia, Perth, Australia.

5. HARVESTING, BIOMASS RECOVERY AND ECONOMICS

5.1 Harvesting
5.2 Regrowth
5.3 Economics of harvesting techniques

5.1 Harvesting

a) methods

Commercial harvesting of Ascophyllum nodosum in southwestern Nova Scotia has been active for 20 years by Scotia Marine Products Limited, Lower Woods Harbour **(Fig. 2).** Harvesting methodology made a transition from hand to mechanical methods in the early 1970's (McArthur, 1971). Maximum annual tonnage was 7,000 wet weight averaging between 5,000 and 6,000 t over a 8-9 month operating period. For the first 15 years of operations cutting was managed in a series of 2.2 km by 2.6 km grids, time and tonnage of yields were logged for each grid **(Table 5).**

Figure 9- Standing crop of Ascophyllum on gradients of wave exposure and proportion of stable substrate in Maine (Topinka, 1980).

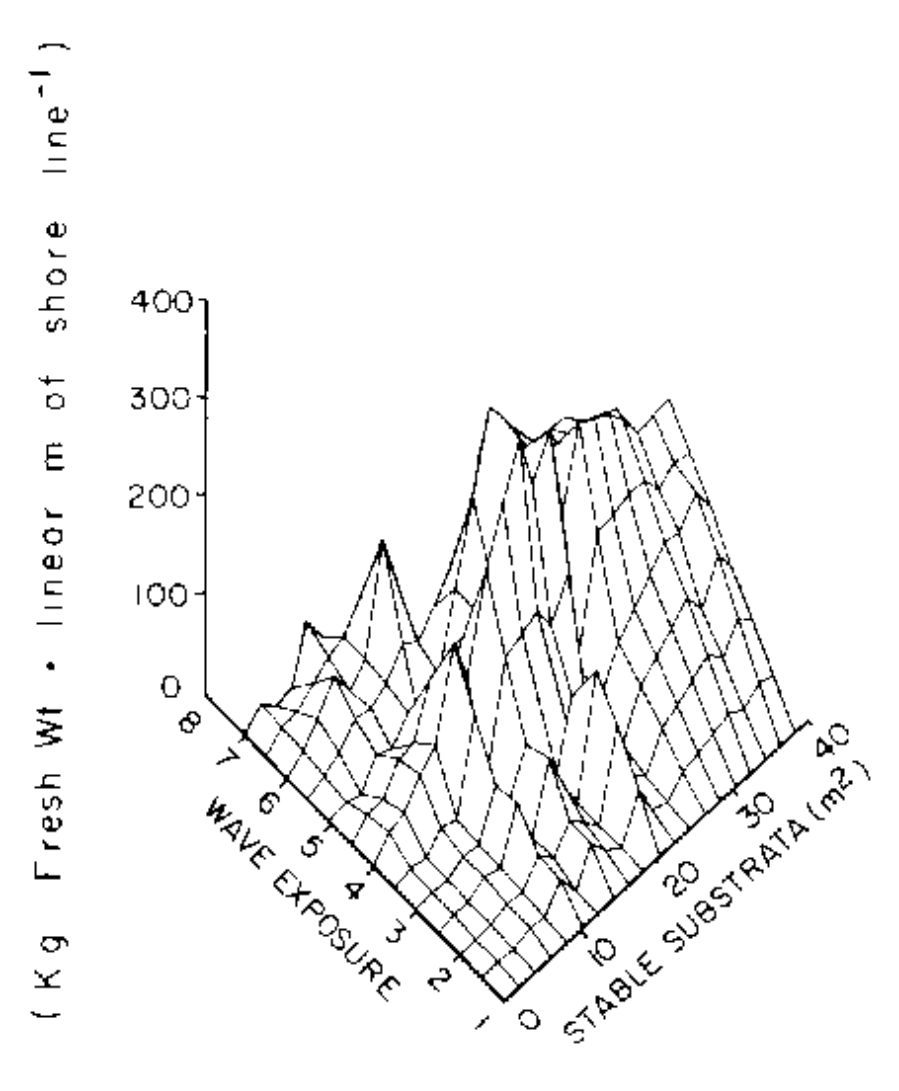


Table 5. Annual harvests from selected 2.2 kg by 2.6 km grid areas by southwestern Nova Scotia. Grid areas were not always completely harvested within one year.

Location	Harvest history by year () = tonnage					
Northwest Roberts Is.	1972[a]	1974[b]	(745)	1975[c]	(747)	1978[c] (818)
Raspberry Is. Woods Harbour		1974[c]		1977[c]		1978[c]
Eastern Wilson Is.	1972[a]	1974[a&c]	(307)	1976[c]	(814)	1977[a]
Tuna Wharf Wedgeport		1974[a&c]	(224)	1976[c]	(414.8)	1977[a]
South Mikes Island		1974[c]		1976[c]	(94)	

[a] Possible hand harvest
[b] Partial harvest
[c] Mechanical harvest

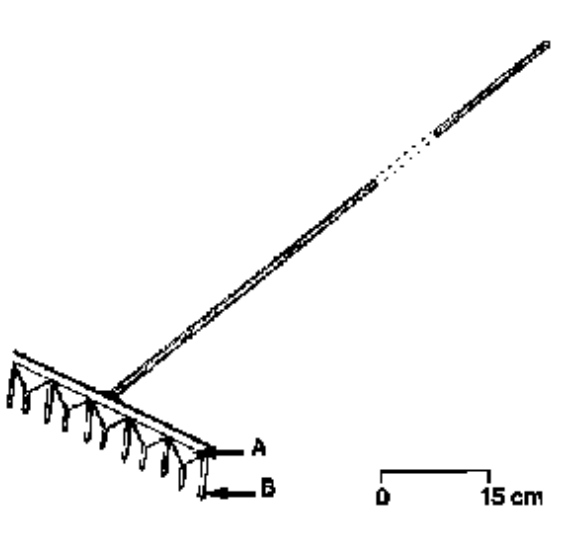
The reharvest interval was 3 years except in areas where hand harvesting was used to reach portions of the resource inaccessible to mechanical harvesting. In the last 5 years the area has been divided in two and reharvested every 2 years. Certain areas exhibiting exceptional growth near the processing plant were harvested annually. (Reharvest intervals are discussed relative to harvester efficiency, Section 5.2).

The existence of only one processor/buyer in southwestern Nova Scotia restricts harvesting to the operational period of the plant. Mechanical harvesters operate 7-9 months of the year dependent upon winter weather conditions. High winds (>30 km h-1) and freezing spray prevent winter operation of harvesters. Hand harvesters use the summer months only since their product must be sun dried to allow its storage for use when mechanical harvesters are unable to operate.

The peak standing crop of Ascophyllum nodosum occurs in the late spring (Section 4.3) corresponding to the maximum size of reproductive structures. Harvesting and processing economics prevent any change in harvesting strategy relative to reproductive periodicity or standing crop.

Hand harvesting of Ascophyllum for commercial use is accomplished with cutting implements sickles and knives. The floating material is encircled by a seine net and loaded by hand or conveyor belt on a vessel (MacArthur, 1971). Later a cutter rake was used consisting of a rake **(Fig. 10)** with widely spaced tines and triangular cutting edges between the tines (Sharp, 1981). These rakes permitted harvesting and loading in one operation.

Figure 10. An Ascophyllum cutter rake as used in southwestern Nova Scotia. A, cutter tooth from a hay mower; B, rake tine constructed from a boat nail.



In Canada hand harvesting techniques account for less than 20% of the annual landings since the introduction of the Aqua Marine[2] H650 harvester to harvest Ascophyllum in 1971. These are a modified aquatic weed harvester 10.5 m long by 4.9 m wide and 2.9 m high driven by paddle wheels through hydraulic motors powered by a diesel engine **(Fig. 11).** A reciprocating cutter blade cuts a 2.4 m swath; shoots are picked up by a conveyor belt and moved into a 1.4 t capacity storage bay. The operator controls cutting height by raising the forward conveyor belt. Once the holding capacity is reached the vessel moves to a barge and off-loads.

[2] Aqua Marine Corp., Wakuseka, Wisconsin.

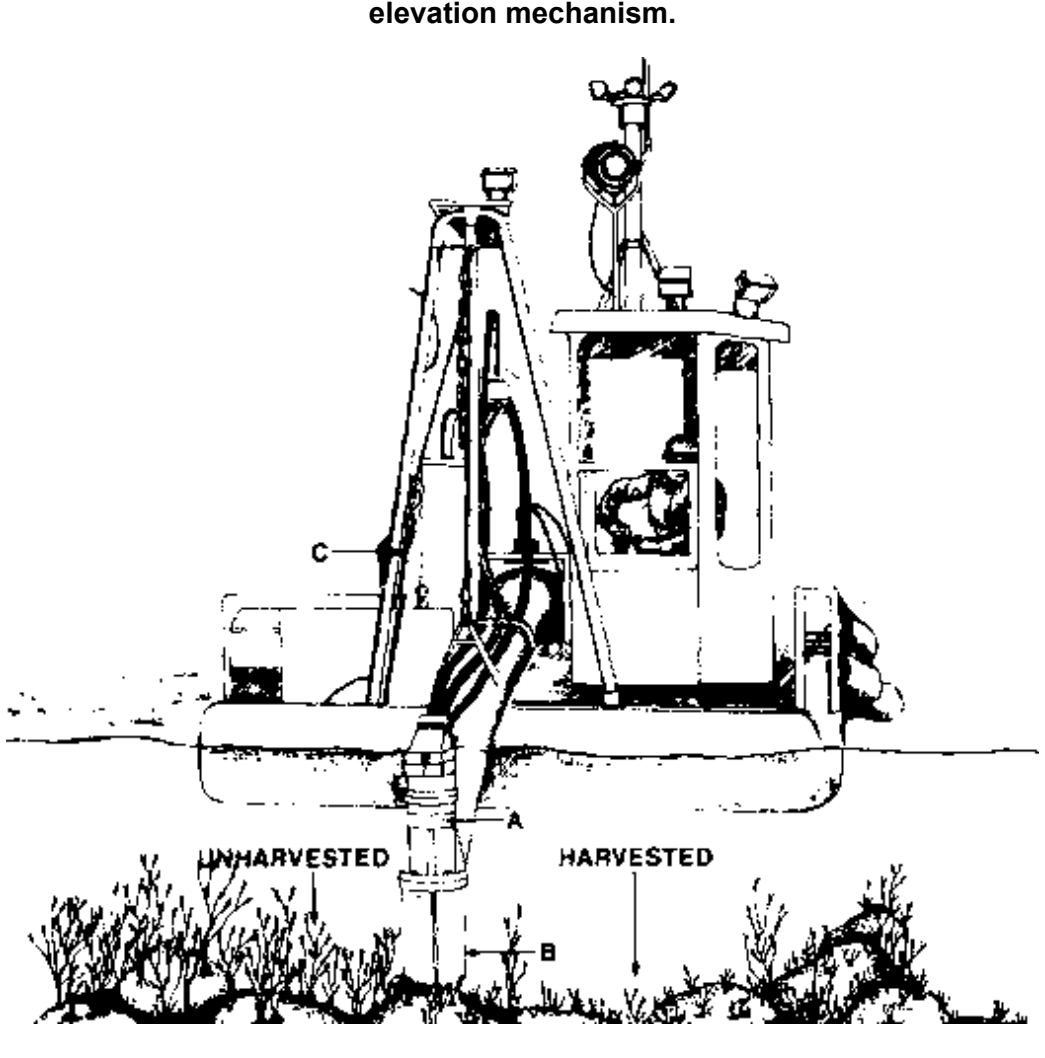
Figure 11. The Aquamarine aquatic weed harvester as modified for Ascophyllum harvest in southwestern Nova Scotia. A, stainless steel mesh conveyor belt for unloading; B, reciprocating cutter blade; C, paddlewheel; D, unloading conveyor; E, air cooled diesel engines.

In 1985 a Norwegian suction/cutter harvester was introduced to southwestern Nova Scotia. This harvester is approximately 5 m long by 2.2 m wide and 2.3 m high. The vessel is propelled by water jets near the stern which point sideways, rearward and forward **(Fig. 12).** A bladed impeller at the end of 25 cm diameter steel suction pipe simultaneously draws up and cuts shoots **(Fig. 13).** The operator hydraulically controls lifting and lowering of the suction head. Water and cut shoots are discharged into a net bag of approximately 1 t capacity **(Fig. 11).** The full bag is ejected and towed behind the vessel or moored together awaiting a collecting vessel.

Figure 12. Rear view of a Norwegian suction cutter Ascophyllum harvester. A, propulsion jet; B, collection bag; C, released bag.

There are few restrictions on the operational area for hand harvesting techniques. Any area reachable by a 5 m boat can be harvested by hand. The intensity of harvesting is largely dependent upon the acceptable level of catch per unit effort. Areas previously cut by mechanical cutters have provided sufficient yield to allow hand harvesting. The mean cutting height of the cutter rake is 23.8+12.9 cm, residual biomass ranges from 10 to 20% of the original values (Sharp, 1981).

Figure 13. Forward view of a Norwegian suction cutter Ascophyllum harvester. A, hydraulic motor drive for impeller; B, cutter/suction head; C, intake pipe and elevation mechanism.



Mechanical harvesters have physical limitations which define the accessibility of a resource. Vessel draft/operational depth of cutter and the seaworthiness of the vessel are the major variables. The ability to operate in wave exposed environments or under high winds is limited due to the danger of cutter impact with rocks. Propulsion systems must be powerful and efficient to overcome wind loads. The Aquamarine harvester has large wind exposed surfaces (15 m²) and an inefficient propulsion system which prevents operations in winds above 30 km h^{-1}. The Norwegian harvester is capable of operating in higher wind velocities due to lower exposed surface (8 m²) but is limited by wave action (>.7 m) (M. Gilje pers. comm[3]).

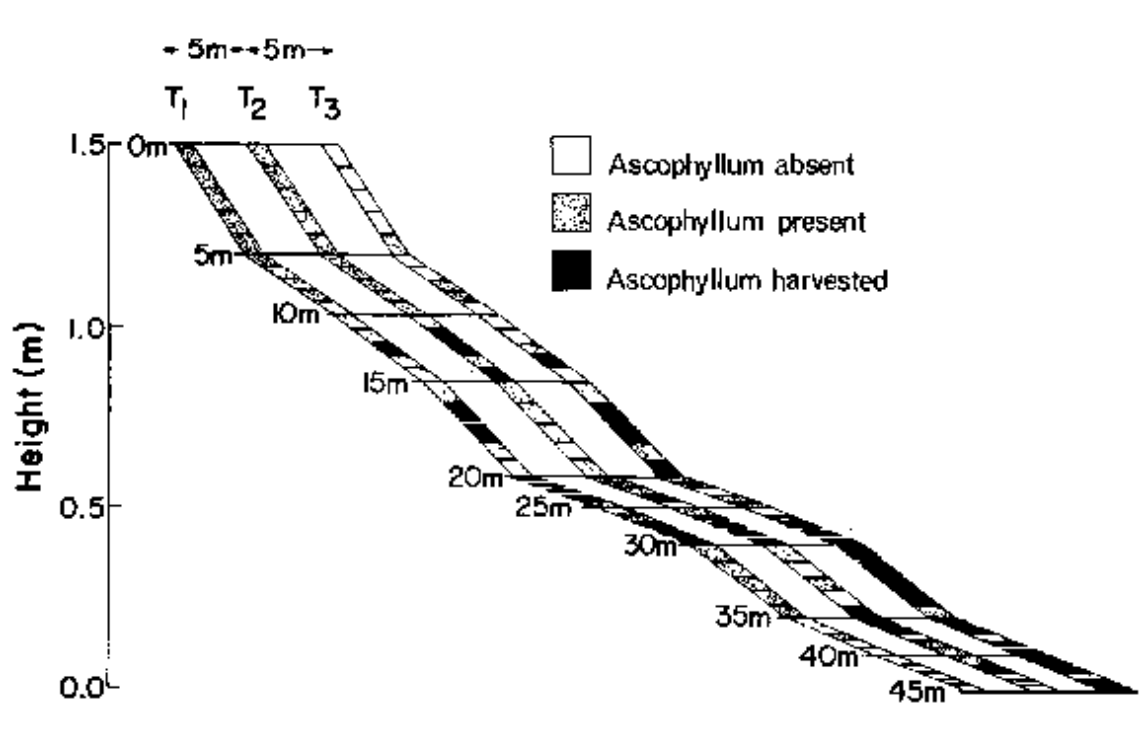
[3] M. Gilje Harvest Manager PROTAN A/S Haugesund, Norway.

The harvesting area of southwestern Nova Scotia has a wide range of wave exposures. In some areas wave exposed shores are close to wave sheltered shores allowing the area of operations to be changed with weather conditions. However extreme wave exposed shores are rarely harvested. (R. Nickerson pers. comm.[4]).

[4] R. Nickerson, Harvest supervisor, Scotia Marine Products Limited.

The draft of the vessel determines the maximum height accessible on the shore and the duration of daily harvesting. The upper and lower most portions of the Ascophyllum zone are vulnerable to harvesting for 2 hours of a six hour operational period on a 0.3 m low tide. Frequently the upper portions of the zone are unharvested **(Fig. 14).** Due to the higher percentage of Fucus in the upper part of the Fucoid zone in southwestern Nova Scotia it is avoided by harvesters (R. Nickerson/pers. comm.).

Figure 14. The harvesting pattern and intensity of the Aquamarine harvester in a trial at a sheltered site, southwestern Nova Scotia. Incidence of harvest in.25 m by 1 in plots in 3 continuous transects from the upper to lower limits of Ascophyllum distribution. Height is relative to chart datum.



The incidence of harvest (proportion of sampled areas 0.25 m² which show evidence of harvest) ranged from 0.27 to 0.61 of areas with Ascophyllum present for the Aquamarine harvester **(Fig. 14).** The Norwegian harvester left evidence of harvest in 0.16 to 0.29 of the areas with Ascophyllum in them **(Fig. 15).** Both types of mechanical harvester leave an uneven or patchy distribution.

An area test harvested by the Norwegian harvester had a preharvest biomass (including the upper inaccessible area) of 15.8+11.6 kg m^{-2} and a post harvest biomass of 11.0+9.6 kg m^{-2}. Excluding the inaccessible zone and areas without biomass, the preharvest biomass was 14.7 kg m^{-2} compared to an 8.7 kg m^{-2} post harvest. In a similar test area the Aquamarine harvester did not significantly change the standing crop as assessed in a strip transect method (Sharp, 1981). In the Norwegian harvester test area, 30.0 t wet weight was removed; it was estimated the Aqua- marine harvester would yield 6 t in this area (R. Nickerson, pers. comm.). The mean cutting height of the Aquamarine harvester was 35.2+.6 cm above the holdfast **(Fig. 16a).** The Norwegian harvester cuts at 29.4+14.9 cm above the holdfast **(Fig. 16b).** Stump length is normally distributed around the mean value in each case.

Figure 15. The harvesting pattern and intensity of the Norwegian suction cutter Ascophyllum harvester in a sheltered southwestern Nova Scotia site. Incidence of harvest in .5 m by .5 m plots on three continuous transects extending from the mean highwater mark on a tidal shoal to ± m above chart datum.

Figure 16a. The distribution of stump lengths following the harvest of a sheltered site by an Aquamarine harvester.

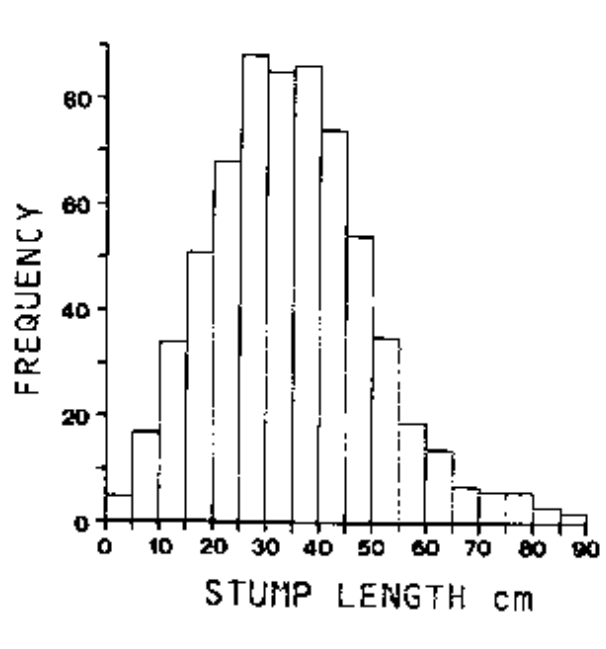
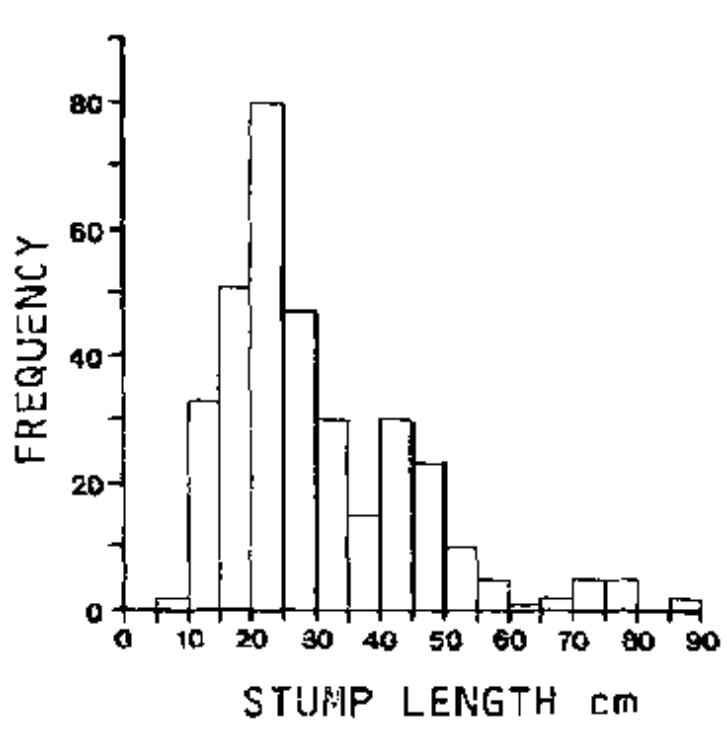


Figure 16b. The distribution of stump lengths following the harvest of a sheltered Ascophyllum bed by a Norwegian suction cutter harvester.



The Norwegian harvester removes more biomass from an area though the incidence of harvest is less overall than the Aquamarine harvester because of the cutting head and its manipulation. The Aquamarine harvester propels itself forward thru the bed while the operator moves the cutter head up or down in its 2.4 m swath **(Fig. 11).** The forward movement of the harvester pushes plants down and away from the cutter thus only a small percentage of shoots is cut in one pass. The machine must make repeated passes over the same area to complete the harvest.

The Norwegian harvester operator lowers the cutter head into a patch of Ascophyllum cutting all shoots within the diameter of the suction pipe **(Fig. 13).** The Norwegian harvester is very maneuverable allowing targeting of the cutter head on specific patches. In Pubnico, N.S., 50% of the biomass is 65-70 cm above the bottom (Cousens, 1981a,b). If an entire area was harvested at the 30 cm level, 73% of the biomass would be removed **(Fig. 7).** The Norwegian harvester removed a maximum of 60% of available biomass in such a test area. Shoots are rarely erect in the harvesters path due to the wide range of tide levels. This prevents consistent cropping.

5.2 Regrowth

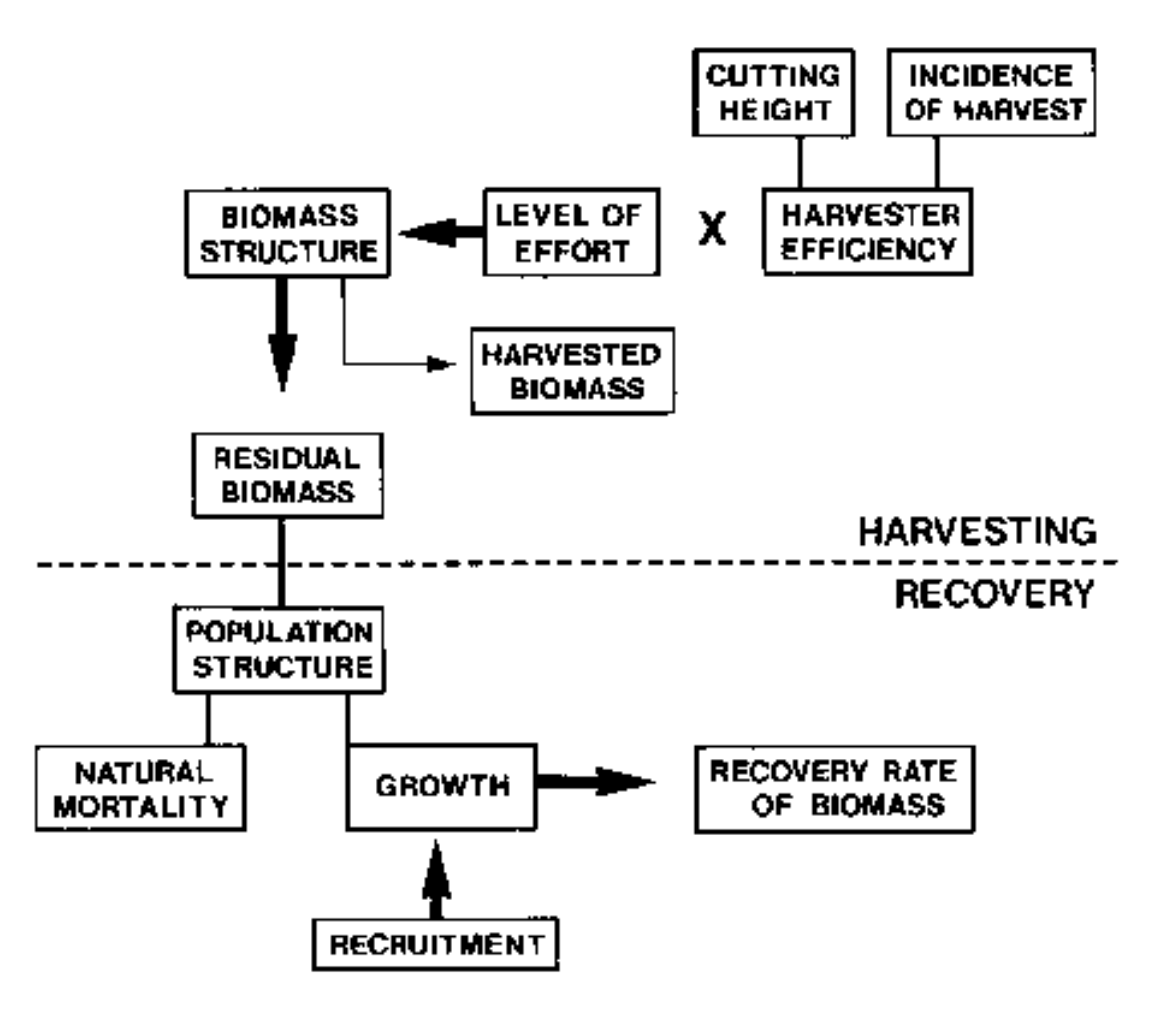
As described in Section 5.1 the harvesting of A. nodosum does not leave the entire population cropped at an even height. Mechanical harvesters leave a remnant biomass of 40%. This remnant biomass consists of stands unreachable by the harvester; shoots uncropped within the path and cutting height of the harvester, shoots below the harvester cutting height, and shoots truncated by the harvester (stumps) **(Fig. 17).** Recovery depends largely on elongation of basal shoots and renewed lateral branching on stumps. In sheltered areas a lower proportion of shoots would be truncated for the equivalent yield at exposed sites **(Fig. 7).** Intermediate wave exposure results in maximum productivity and shortest biomass recovery times **(Table 1).** A recovery of harvestable biomass after one year has been observed at some sites in southwestern Nova Scotia over the 20 years of harvesting. The large amount of residual biomass (40%) is markedly different from the 2% (carrying capacity) biomass remaining in Norway after hand harvest (Seip, 1980). Harvesting models based upon lower degrees of harvesting intensity projected an increase of yield by 40% to 70% on a 2 year reharvest with larger amounts of residual biomass (opp. cit.).

Homogeneous cutting of Ascophyllum at 15-25 cm in 2 of 8 sheltered sites of Maine recovered biomass within one year (Keser et al. 1981). Within sixteen months, following complete denudation of a portion of the Ascophyllum zone and subsequent incursion of Fucus spp., Ascophyllum shoots in the 3-4 cm size class covered 52% of the area (Keser and Larson, 1984). Although in commercial harvesting complete denudation does not occur, over-harvesting using hand cutting methods did occur in a few sites in southwestern Nova Scotia in the early years of the industry (McArthur, pers. comm.[5]). Normally harvested Ascophyllum populations have a large capacity for biomass recovery. Frond densities average 529 m^{-2} in Maine and 957-5655 m^{-2} on Nova Scotian sites (Keser et al. 1981; Cousens, 1981a; Sharp, unpublished). At exposed and sheltered locations on the Atlantic coast of Nova Scotia 10.47% and 2.48% respectively of these shoots carry 50% of the biomass (Cousens, 1981a). Therefore, at cutting heights above 25 cm the shoot density will be relatively unaffected. Prior to harvest primary apices and lateral apices are 60 times shoot density (Keser et al. 1981). Primary growing points will not be reduced in proportion to shoot truncation since the majority of primary shoots are below 15 cm **(Fig. 5).** Lateral apices are more significantly affected because few laterals are below 15 cm, (Cousens, 1981a). Cutting may provide growth stimulation enhancing biomass recovery. Removal of the Ascophyllum canopy above 15 cm at a semi-sheltered Atlantic site increased primary shoot linear growth by 75% and lateral density per centimeter of shoot by 200% (Cousens 1981a). This effect was attributed to greater light intensity rather than removal of apical dominance (opp. cit.).

shoot by 300% (Cousens 1981a). This effect was attributed to greater light intensity rather than removal of apical dominance (opp. cit.).

[5] A. McArthur, former Manager, Scotia Marine Products Ltd., Woods Harbour, Nova Scotia.

Figure 17. The major factors affecting recovery of Ascophyllum biomass.



5.3 Economics of harvesting techniques

Harvesting Ascophyllum with sickles or cutter rakes yields 2-3 wet tons per individual per tide (4-6 hours). Capital investment is dependent on the size and type of vessel used for harvest and transport. A 3-5 m outboard powered boat costs were Canadian \$18.50 d^{-1} in 1975 dollars. Most operations require a larger boat or barge for several harvesters and such may cost Canadian \$32.50 d^{-1} if amortized over 10 years (Sharp and Neish, 1976). To complete drying of the raw material a transport vehicle and a drying field are added to the costs **(Table 6).** The return to the harvester was assumed to be Canadian \$4.00 hr however, due to inflation and competition for labor, present day costs would be at least doubled. One wet ton required 2.3 hours of labor costs in travel/harvest and unloading **(Table 7).** Exclusive of drying operations; labor and capital costs were Canadian \$10.65 respectively per wet ton; drying added Canadian \$4.78 labor and Canadian \$0.47 capital.

Mechanical harvesting increases the productivity per individual but greatly increases capital costs. The Aquamarine harvester harvests 2 to 3 t h^{-1} but costs Canadian \$70/000 per unit. An average yield of 12.5 wet ton per day and 120 operational days per year was used to calculate operational costs **(Table 8 and 9).** If fresh materials are utilized directly, costs are reduced by Canadian \$7.32 per wet ton **(Table 9).** Operations in southwestern Nova Scotia requiring a tow vessel and 120 t capacity barge require Canadian \$250,000 capital costs, amortizable over 15 years with daily operational costs of Canadian \$240 resulted in a total daily cost of Canadian \$370. If daily production is a multiple of harvesting units (x12-18 t d^{-1}) total costs are Canadian \$38.71 per ton. The Norwegian harvester capital cost is approximately Canadian \$138,000 but daily production is 50 t per unit. The harvesting operation does not require a barge or large tow vessel assuming the harvest boat can tow bags directly to the plant. Under these circumstances capital and operating costs per ton are 9.78 per ton. Transport overland would involve a 25 t capacity truck and crane at a cost similar to the tow vessel and barge combination.

Persons hand harvesting Ascophyllum use this activity as a 5% to 20% supplement to their annual income. Alternative income sources during the summer months are ground fish, fishing or processing, herring fishing by seine or gillnet and Chondrus crispus (Irish moss) harvesting (Sharp and Roddick 1982).Some individuals combine Ascophyllum and Chondrus crispus, harvesting them on either alternating tides or using the low tide period for Chondrus and rising or falling tides for Ascophyllum . The remainder of the year fishermen either captain or deckhand on a lobster fishing vessel (Sharp and Roddick 1982). Individuals employed directly by the processing company to operate Aquamarine machines are active from March-April to November-December depending on weather conditions in the early fall and spring. Alternate employment is lobster fishing or utilization of the Canadian Unemployment benefit program. Harvesting income comprises 60 to 100% of employment income for these individuals. Family income in southwestern Nova Scotia averages Canadian \$20,000 to \$22,000; the male contributes 55 to 65% of this income (Raymond 1985). Primary industry, including fishing and marine plant harvesting employs 26 to 34% of the labor force (opp. cit.).

Table 6. Capital and operating costs associated with hand harvesting of rockweed in Year 1, assuming that all equipment except holding nets and the collecting seine are shared with other fisheries and that these nets would be used for at least 50 days per year (or would have proportionately extended amortization rates if used less). A mean daily harvest of 8.4 net metric tons per day was assumed for a three-man harvest crew. (Sharp and Neish 1975).

		Gross	Amort. Rate	Deprec. Cost	Hourly Op. Cost	Maint. Cost as % of	Maint. cost	Days of use in all	Daily cost for Rockweed
a)	Harvesting boat and barge	20,000	10	2,000	5.00	10	2,000	200	32.50
b)	Winch, mast and boom	4,000	10	400	-	10	400	100	8.00
c)	Dory or skiff	1,000	10	100	-	10	100	100	2.00
d)	25-HP motor	1,400	5	280	2.00	10	140	100	6.20
e)	Large holding nets (20)	1,000	2	500	-	20	200	50	14.00
f)	Collecting seine(100 x 2m)	600	5	120	-	20	120	50	4.80
g)	Truck (3 ton)	14,000	5	2,800	6.00	10	1,400	200	24.00
h)	Drying field(0.2 ha)	1,250	20	63	-	10	125	100	1.88
	Daily Cost								93.38
	Cost/wet metric ton								11.12
	Cost exclusive of drying								10.65

Table 7. Labour costs associated with hand harvesting of rockweed assuming a desired return to the fisherman of \$4.00 per hour and a daily harvest rate of 8.4 wet metric tons per day (Sharp and Neish 1976).

Activity (See Figure 1)		Crew size	Man-Hours Day-1	Labour Cost at-\$4.00 Hr-1	Labour Cost per wet metric ton (\$)
Travel	(1)	3	0.75	3.00	.35
Harvest	(2)	3	15.00	60.00	7.14
Return to port	(3)	3	0.75	3.00	.35
Unload Harvest	(4)	3	3.00	12.00	1.43
Ship	(6)	3	1.50	6.00	.71
Unload Truck	(9)	4	1.50	6.00	.71
Spread Crop	(10)	4	4.00	16.00	1.90
Attend Crop	(11)	-	-	-	-
Collect and pack *	(12)	4	6.00	24.00	2.85
Hill and pack	(13)				
Totals			32.50	130.00	15.47
exclusive of drying					10.69

*Costs associated with drying.

Table 8. Labour costs associated with mechanical harvesting assuming a desired return to the fishermen of \$4.00 per hour and a daily harvest of 12.5 metric tons. All figures are estimates based on experience with other crops (Sharp and Neish 1976).

Activity (See Figure 1)	Crew size	Man-Hours Day-1	Labour Cost at \$4.00 Hr-1	Labour Cost per wet metric ton (\$)
Travel	2	2.00	8.00	0.64
Harvest	2	12.00	48.00	3.84
Return to port	2	2.00	8.00	0.64
Unload boat	4	8.00	32.00	2.56
Ship	2	1.00	4.00	0.32
Unload Truck	4	8.00	32.00	2.56
Spread Crop*	4	12.00	48.00	3.84
Attend Crop*	-	-	-	-
Collect and pack*	4	12.00	48.00	3.84
Mill and pack*				
Totals		57.00	228.00	18.24
Total exclusive of drying and packing				10.56

*Costs associated with drying operations

Table 9. Capital and operating costs associated with mechanical rockweed harvesting in Year 1 using the Aquamarine HN462 harvester. A harvest rate of 12.5 wet metric tons per day and sharing of boat and truck costs with other fisheries are assumed. Harvest rate is based on estimated rates achieved by Scotia Marine in Nova Scotia (Sharp and Neish 1975).

		Gross	Amort. Rate	Deprec. Cost	Hourly Op. Cost	Maint.Cost as% of	Maint. cost	Days of use in all	Daily cost (\$) at 12.5m.t./day
a)	Harvest boat & skiff	20,000	10	2,000	5.00	10	2,000	200	32.50
b)	Winch, mast, boom	4,000	10	400	-	10	400	200	4.00
c)	HN462 Harvester	70,000	7	10,000	5.00	10	7,000	-	182.00
*d)	Holding nets (50)	2,500	2	1,250	-	20	500	-	14.58
*d)	Tractor	8,500	10	850	5.00	10	850	-	54.00
*f)	Spreader	3,500	10	350	-	10	350	-	5.83
g)	Baler and handling gear	10,000	10	1,000	-	10	1,000	-	16.67
h)	3-Ton Truck	14,000	5	2,800	6.00	10	1,400	200	24.00
*i)	Drying ground(1 ha.)	6,000	20	1,200	-	10	600	-	15.00
	Daily Cost								348.58
	Cost/wet metric ton								27.89
	Exclusive of drying								20.57

*Costs of drying

6. AQUACULTURE

Until recently the aquaculture of macrophytes, such as Ascophyllum , which dominate the intertidal algal biomass of many North Atlantic shores was not considered economically viable. The desire to control composition of phycolloid end products has justified applied research on culture techniques.

A spray technique first developed by L. Hanic University of Prince Edward Island for grow out of macrophytes has been further developed to grow Ascophyllum on draining surfaces (Rheault and Ryther, 1983). Spraying with unenriched seawater and pulse feeding of nutrients obtained 14.3 g m^{-2} d^{-1} Similar experiments with a multiple tier growing system and continuous addition of nutrients produced 40 g m^{-2} d^{-1} of dry matter (Moeller et al. 1984). Excluding land and inoculum costs this system produced one ton of Ascophyllum at a cost of U.S. \$1620 per dry ton (opp. cit.). Present costs of harvesting and delivering the factory naturally grown Ascophyllum is approximately US \$140 per dry ton (See Section 5.3).

7. PROTECTION AND MANAGEMENT OF THE RESOURCE

7.1 Regulations
7.2 Management

7.1 Regulations

Local phycologists recognized the problems of over harvesting Ascophyllum resources, as observed in Europe/were possible in the Maritime Province (C. MacFarlane, pers. comm.). Provincial governments enacted Sea Plants Harvesting Acts in response to the advice of seaweed experts. These regulations included harvesting gear restrictions requiring the use of cutting implements only to prevent holdfast loss by regulating cutting height at 12.7 cm above the substrate to allow regrowth.

The Sea Plants Act of Nova Scotia made provision for exclusive licenses for designated portions of the shoreline for up to 15 years. Licenses were granted to companies providing a monopoly for raw material from that area. It was the responsibility of the licensee to respect the regulations within his region. A company could then have numerous harvesters as contractors in this license. In 1975 the responsibility for management of marine plant resources were transferred to the Federal government of Canada. The Sea Plants Harvesting Act was incorporated under the Atlantic Coast Marine Plants Regulations within the Fisheries Act. In 1985 the Atlantic Coast Marine Plant Regulations were incorporated in the Atlantic Fishery Regulations Part I (Appendix I). The regulations were not altered but provision was made for alteration of the harvesting season and setting of quotas, Part I **(Appendix I).**

There were two major changes in regulations from the Provincial Act. Marine Plant Harvesting districts No.'s 1-14 were established **(Fig. 1)** and licenses were personal and annually renewed. No exclusive privileges to the resource were provided and a fisherman's boat registration and general fisherman's license were required. Enforcement of regulations is the responsibility of the Department of Fisheries and Oceans, Operations Branch regional fisheries officers. All purchases of marine plants must be recorded on individual purchase slips for statistical reporting. Due to the large number of small (<1 t) transactions purchasing companies are permitted to report total monthly landings by port to the Statistical Branch of Fisheries and Oceans Canada. In areas where less than 2 companies are active landings are not made public.

As marine plants form a part of the fish habitat Section 31 of the Fisheries Acts of 1977 provides protection against disruption of the habitat. "No person shall carry on any work or undertaking that results in the harmful alteration/description or destruction of fish habitat".

7.2 Management

There are no additional restrictions/quota/season or area of operations which require annual assessment of standing crop. The Research Branch of the Federal department of Fisheries has the mandate to obtain that biological information relevant to resource management.

Biologists are provided with species and regional responsibilities within the branch. Information relevant to management advice must pass thru a peer review process known as the Canadian Atlantic Fisheries Scientific Advisory Committee (CAFSAC) and thence as advice to upper level fisheries managers.

To communicate information to the industry/regional Marine Plant Advisory Committees were established including representatives of government, processors/buyers and harvesters. The biologist can present his advice to these committees and the committees can provide recommendations directly to the Minister of Fisheries via an area manager.

8. UTILIZATION

8.1 Chemical and nutritional content
8.2 Human food
8.3 Animal fodder
8.4 Fertilizer
8.5 Industrial products and processes

8.1 Chemical and nutritional content

The early industrial utilization of Ascophyllum nodosum required for practical purposes an analysis of its constituents. Baardseth (1970) recorded studies of a wide range of organic and inorganic substances in A. nodosum. Seasonal/geographical, and inter-thallus variations of water content, trace elements, alginates, and pigments were among the topics reviewed **(Table 10).** Since 1970, more detailed data on some of these constituents were recorded and additional substances identified.

Pharmacological research continues to find potential in seaweeds. Fucoidan, as prepared from Ascophyllum nodosum, shows excellent metal binding abilities and binds lead most efficiently of the divalent metal cations (Paskins-Hurlburt et al. 1976). In vivo experiments a 75% reduction in lead absorbed by rats from their gastrointestinal system was observed.

The antihypercholesterol activity of sterols in algae has led to studies of their content in Ascophyllum nodosum (Knights, 1970; Safe et al. 1974). Fucosterol comprises over 95% of the sterol content of A. nodosum. The presence of other sterols was considered the result of oxidation (Knights, 1970). A more detailed study of sterol content found 0.10% sterols of dry weight, of which fucosterol was 90% with positive identification of five other sterols of which saringosterol was 6% (Safe et al. 1974). Hemagglutinic activity was found with solutions of powdered A. nodosum tested on human blood groups. No differences were found in hemagglutinic activity between thallus regions (Blunden et al. 1975).

Table 10. Average composition of Norwegian seaweed meal (Baardseth, 1970 from Jensen Nebb and Saester 1966).

Component	Content		Component	Content	
Moisture	12-15	%	Crude fibre	8	%
Ash	17-20	%	Crude protein	5-10	%
Alginic acid	20-26	%	Ether extract	2- 4	%
Mannitol	5- 8	%	Fucoidan	10	%
Laminaran	2- 5	%	N-free extractives	45-60	%
S	2.5-3.5	%	Caloric value	0.56	SPU/kg*)
K	2- 3	%	Ascorbic acid	500-2000	mg/kg
Cl	3.1-4.4	%	Carotene	30-60	mg/kg
Na	3- 4		Biotin	0.1-0.4	mg/kg
Mg	0.5-0.9	%	Folic acid	0.1-0.5	mg/kg
Ca	1- 3	%	Folinic acid	0.1-0.5	mg/kg
P	0.1-0.15	%	Niacin	10-30	mg/kg
B	40-100	mg/kg	Riboflavin	5-10	mg/kg
CO	1-10	mg/kg	Tocopherols	150-300	mg/kg
Fe	150-1000	mg/kg	Vit.B_{12}	0.004	mg/kg
Mn	10-50	mg/kg	Vit.K	10	mg/kg
I	700-1200	mg/kg	V	1.5- 3	mg/kg
Zn	50-200	mg/kg	Ni	2- 5	mg/kg
Mo	0.3- 1	mg/kg	Ba	15-50	mg/kg

*) SFU = Scandinavian feed units
Alginic acid 150-1000 mg/kg N-free extractives 500-2000 mg/kg

Vitamin content of Ascophyllum nodosum was extensively catalogued by Baardseth (1970). However, several concurrent papers were not included in the synopsis. Tocopherol (Vitamin E) content and its variation with individual diurnal, and seasonal changes/was investigated after a rapid and accurate analytical technique was developed (Jensen, 1969a). Total tocopherol was maximal in September and February at 500 mg/kg dry matter (Jensen/1969b). Proportions of tocopherols varied with immersion and emersion periods. Optimally growing plant sections contained less total tocopherol than older portions of the plant (Jensen opp. cit.). Choline is one of the B complex vitamins which is included in commercial feeds. The choline content of A. nodosum was 0.9 to 3.2 mg/g dry weight over one year. Highest choline content occurred in winter and spring, dropping in June, July, and August (DaSilva and Jensen, 1973).

Anti-microbial compounds were detected in Ascophyllum nodosum as early as 1954 (Vacca and Walsh/1954). Recent studies have found summer antimicrobial activity but none in spring or winter (Horsney and Hide 1976). This points out the further need for year round sampling in any study of chemical constituents.

Several recent studies of Ascophyllum nodosum chemical composition relate directly to an overall metabolic strategy within its geographical and zonal ranges. Amino acid composition was found to change with decreasing salinity (Munda, 1977). Nitrogen content increased with lower salinities. This change was attributed directly to the increasing presence of glutamic acid which is a key amino acid in the synthesis of other amino acids (opp. cit.).

Exposure and season were found to have the greatest correlation with caloric value of Ascophyllum nodosum tissues (Breton-Provencher/1976). Maximal calorific values occur in July in the period of maximum growth. The highest overall calorific values corresponded to locations where A. nodosum was dominant over other Fucoids.

Growth hormones were extensively investigated in higher plants and have only recently been examined in detail for algae. G.L.C. analysis of water soluble components from Ascophyllum nodosum found compounds similar to abscisic acid. These compounds were found to inhibit growth of lettuce hypocotyl (Hussain and Boney, 1973). Auxin-like/gibberellin-like, and cytokinin-like substances were found in A. nodosum extracts using a bio-assay system (Kingman and Senn, 1977). A seasonal survey of gibberellin activity in three fucoids showed a maximum activity of extracts occurred in October for A. nodosum and a minimum of gibberellin activity in January (Wildgoose et al. 1978).

Descriptions of alginate structure and its composition in a variety of algal species has been ongoing since 1970. The sequences of uronic acid, building blocks of alginate, were described for Ascophyllum nodosum (Smidsrod & Glover 1973). Although earlier studies have described wide difference between the relative amounts of the various uronic acid groups, recent work indicates all young tissue is rich in manuronic blocks (Haug et al. 1974). Therefore, any differences in composition of alginates occurs in older portions of the plants (opp. cit.). Other polysaccharides were isolated from A. nodosum and their structure examined. Fucoidan was isolated and described as a sulphated glucuronoxylogucan, existing as a building block of the complex macromolecule (Larsen et al 1970).

Concern for the effects of hydrocarbon spills in our coastal environment lead to an assessment of natural hydrocarbon background levels in various benthic algae (Youngblood et al. 1971). N-pentadecane predominates in Ascophyllum nodosum and other tested brown algae. Polyunsaturated hydrocarbons occur only in the reproductive tissues of A. nodosum.

8.2 Human food

Ascophyllum nodosum is not normally used directly as a foodstuff but may appear as a constituent of health food tablets. The polysaccharide algin extracted from Ascophyllum as alginic acid is used in the form of salts as a viscosity control gelating and emulsifying agent. Alginic acid is composed of polymannu-ronic acid segments, polyguluronic acid segments and alternating segments of these acids. Ascophyllum nodosum alginic acid is composed of 65% mannuronic acid, 35% guluronic acid the ratio of these components can range between 1.40 and 1.95 (Cottrell and Kovacs, 1980). Common food uses for alginates include prepared pie fillings, instant mixes and sauces.

8.3 Animal fodder

Ascophyllum nodosum is used as a stock feed additive. It may make up to 5% of the diet for poultry, sheep, cattle, pigs and horses. The trace element and vitamin components of Ascophyllum meal are the active ingredients for growth of cattle, milk production, color in eggs and improving wool color in sheep (Neeb and Jensen 1965). Canada has imported seaweed meal for use as a fodder supplement. Agricultural committees near the sea have allowed farm animals access to storm tossed seaweed.

8.4 Fertilizer

The use of fresh Ascophyllum as a soil conditioner, source of trace elements and general growth stimulant began in the earliest settlements of Maritime Canada. European settlers brought this custom from centuries of use in Europe. Liquid seaweed extracts developed since 1950 and wetable powders are used as in foliar sprays. Extracts have proven chelating properties that improve the utilization of minerals (Lynn 1972). Application of extracts to seeds increases germination and early growth (Britton and Nayes, 1964). Auxin and gibberellin like activities are reported for seaweed extracts but the results are conflicting. Soluble powders as foliar sprays increased protein content of soybeans, soluble solids in tomatoes and yield of Southern pea (Annon, 1978).

A liquid extract of Nova Scotian Ascophyllum nodosum was produced in Yarmouth by Argosy Seaweeds Ltd., but commercial production did not follow.

8.5 Industrial products and processes

Sodium alginate is used as a part of a sizing solution for liner-board. Alginate enhances penetration of adhesives, acts as a dye carrier in fire reactive dyes. Its gelling properties are used in air fresheners and explosives. As an emulsifier it is used in polishes. The stabilizing properties of alginates make them useful in ceramics, welding rods and cleaners. The industrial processing of Ascophyllum nodosum includes a fixative step in addition to those shown in **(Fig. 18)** to prevent coloration of the final product.

Figure 18. Flow chart describing major steps in the manufacture of alginic acid (Cottrell and Kovacs, 1980).

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APPENDIX I EXCERPTS FROM: MARINE PLANTS/ATLANTIC FISHERY REGULATIONS

PART I GENERAL

Variation of Close Times and Quotas

4. A Regional Director-General may, by order, vary any close time or fishing quota fixed by these Regulations.

5. Where, pursuant to Section 4, a Regional Director-General varies a close time or a fishing quota, he shall, by one or more of the following methods, give notice of the variation to the persons affected or likely to be affected by the variation:

SCHEDULE XXVI
(s. 94 and 96)

MARINE PLANT HARVESTING DISTRICTS AND CLOSE TIMES+

Item	Column I: Harvesting Districts	Column II: Period
1.	District 1. Waters adjacent to the west shore of Prince Edward Island between West Point, Prince County, and North Point, Prince County.	November 1 to June 10
2.	District 2. Waters adjacent to the north shore of Prince Edward Island between North Point, Prince County, and the Prince, Queens Counties boundary.	November 1 to July 30
3.	District 3. Waters adjacent to the north shore of Queens County, Prince Edward Island.	November 1 to June 30
4.	District 4. Waters adjacent to Kings county, Prince Edward Island.	November 1 to June 30
5.	District 5. Waters adjacent to the south shore of Queens County, Prince Edward Island.	November 1 to June 6
6.	District 6. Waters adjacent to the south shore of Prince County, Prince Edward Island, between the Prince, Queens Counties boundary and West Point.	November 1 to June 6
7.	District 7. Waters adjacent to the north and northeast shores of New Brunswick between the Quebec and Nova Scotia borders.	November 1 to June 6
8.	District 8. Waters adjacent to the north shores of Cumberland, Colchester, and Pictou Counties, Nova Scotia.	November 1 to June 30
9.	District 9. Waters adjacent to the shores of Antigonish and Inverness Counties, Nova Scotia.	November 1 to June 30
10.	District 10. Waters adjacent to the shores of Victoria, Cape Breton, and Richmond Counties, Nova Scotia.	November 1 to July 15
11.	District 11. Waters adjacent to the shores of Guysborough, Halifax, and Lunenburg Counties, Nova Scotia.	November 1 to June 30
12.	District 12. Waters adjacent to the shores of Queens, Shelburne, Yarmouth, Digby, Annapolis, and Kings Counties, Nova Scotia.	November 1 to June 6
13.	District 13. Waters adjacent to the shores of Kings County and the south shores of Colchester and Cumberland Counties, Nova Scotia.	November 1 to June 6
14.	District 14. Waters adjacent to the south shore of Westmoreland County and the shores of Albert, Saint John, and Charlotte Counties, New Brunswick.	November 1 to June 30

+Close times apply to Irish moss (Chondrus crispus) and Gigartina stellata) only.

PART IX
MARINE PLANTS

94. In this part,

"District" means a harvesting district described in Schedule XXVI; (arrondissement)
"rockweed" means a brown marine plant of the species Ascophyllum nodosum; (Ascophyllum n nodosum) "holdfast," in relation to a marine plant, means that portion of the marine plant by which it is attached to the ocean floor, (pied)

Harvesting Methods and Gear

95. (1) Subject to the conditions of a licence, no person shall harvest rockweed unless he

(a) uses an instrument that severs with a cutting action; and
(b) leaves a length of at least 127 mm above the holdfast.

(2) No person shall have in his possession any rockweed plant to which the holdfast is attached.

Chondros crispus Stackhouse[1]

1. IDENTITY
2. DISTRIBUTION, ECOLOGY AND METABOLISM
3. LIFE HISTORY
4. POPULATION STRUCTURE AND MORTALITY
5. PRODUCTIVITY OF THE RESOURCE
6. METHOD OF HARVESTING AND HARVESTING CYCLE
7. EQUIPMENT USED FOR HARVESTING AND CULTURE OF SEAWEED RESOURCES
8. PROTECTION AND MANAGEMENT OF THE RESOURCE
9. UTILIZATION
ACKNOWLEDGMENTS
10. REFERENCES
APPENDIX I: Terms of reference for the southwestern Nova Scotia Marine Plants Advisory Committee Committee

[1] Also a Scientific Contribution from the New Hampshire Agricultural Experiment Station and Jackson Estuarine Laboratory Contribution Number 197.

by
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ABSTRACT

The Northwest Atlantic Chondrus fishery is the basis of a phycocolloid industry. Harvesting is centered in the Gulfs of Maine and St. Lawrence where the species is an ecological dominant. The extensive ecological-physiological data base is reviewed as is the biosystematics. Annual catch peaked in 1974 (approx. 50,000 t) and troughed in 1983 (approx. 18,000 t). Catch decline was due/in part, to a decrease in crop demand caused by international marketplace competition from other carra-geenophytes. Harvesting and handling techniques are described. Resource management structure is outlined, as are stock assessment and assessment science programs. The international aspect of resource utilization is discussed.

1. IDENTITY

1.1 The crop
1.2 Taxonomy
1.3 Nomenclature
1.4 Morphology and anatomy

1.1 The crop

The north Atlantic red alga Chondrus crispus Stackhouse **(Fig. 1)**, which is referred to as Chondrus, Irish moss, or "moss" in this text, is the basis of a western world multimillion dollar phycocolloid industry (Levring et al., 1969; MacFarlane, 1956; Michanek, 1983). However, its share of this industry has declined from ³ 75% before 1975 to £ 20% at present, primarily due to the successful farming of Eucheuma spp. in the Philippines (Parker, 1976).

The steady increase in carrageenan demand in the 1960's led to a concern about future sources of raw material. The Canadian federal government, through the National Research Council's Atlantic Regional Laboratory (=NRC), began, in the late 1960's, to develop aquaculture techniques for Chondrus. The program was turned over to Marine Colloids Canada Ltd. in 1972 and to Genu Canada Ltd. (subsidiary of Copenhagen Pectin) a little later. NRC funded these ventures through various granting schemes (see Anderson et al. 1977). Genu stated in 1981 (Norve[1], personal comm. to J. Pringle) that it would likely not be cost effective in the near future, and dissolved their aquaculture program. Acadian Seaplants purchased Marine Colloids Canada Ltd. in ~ 1980 **(Table 1)** and continued their aquaculture development program, recently their facility was expanded, but they are not yet independent of government support (R. Foxall, personal comm. to J. Pringle)[2]. In the present account, the descriptions of productivity and harvesting will concentrate on the wild harvest and in particular the Irish moss fishery of eastern Canada, as 95% of the crop comes from this fishery.

[1] Mr. H. Norve, former manager of Genu Canada Ltd., Halifax, N.S.
[2] Dr. R. Foxall, Director, Atlantic Regional Laboratory, Oxford Street, Halifax, N.S.

1.2 Taxonomy

Chondrus crispus Stackhouse belongs to the division Rhodo-phyta, class Florideophyceae, order Gigartinales and family Gigartinaceae (Dixon and Irvine, 1977). Stackhouse (1797) established the generic name and C. crispus has become its type. As outlined by Taylor and Chen (1973), Chondrus is separated from other genera in the Gigartinaceae (i.e. Besa, Gigartina, Iridaea and Rhodoglossum, sensu Kylin, 1956) by having gonimoblasts diffusely extended among medullary filaments in the distal portions of female fronds, by producing totally immersed carpo-sporangia with no clear separation of vegetative tissues, by lacking any special external cystocarp opening, and by having bundles of cruciately divided tetrasporangia produced from branches of medullary filaments in the upper parts of the fronds.

Figure 1. Morphological variation of Chondrus crispus populations at an estuarine (Dover Point) and two open coastal sites (Rye Ledge and Jaffrey Point), in New Hampshire, U.S.A. (from Mathieson and Burns, 1975)

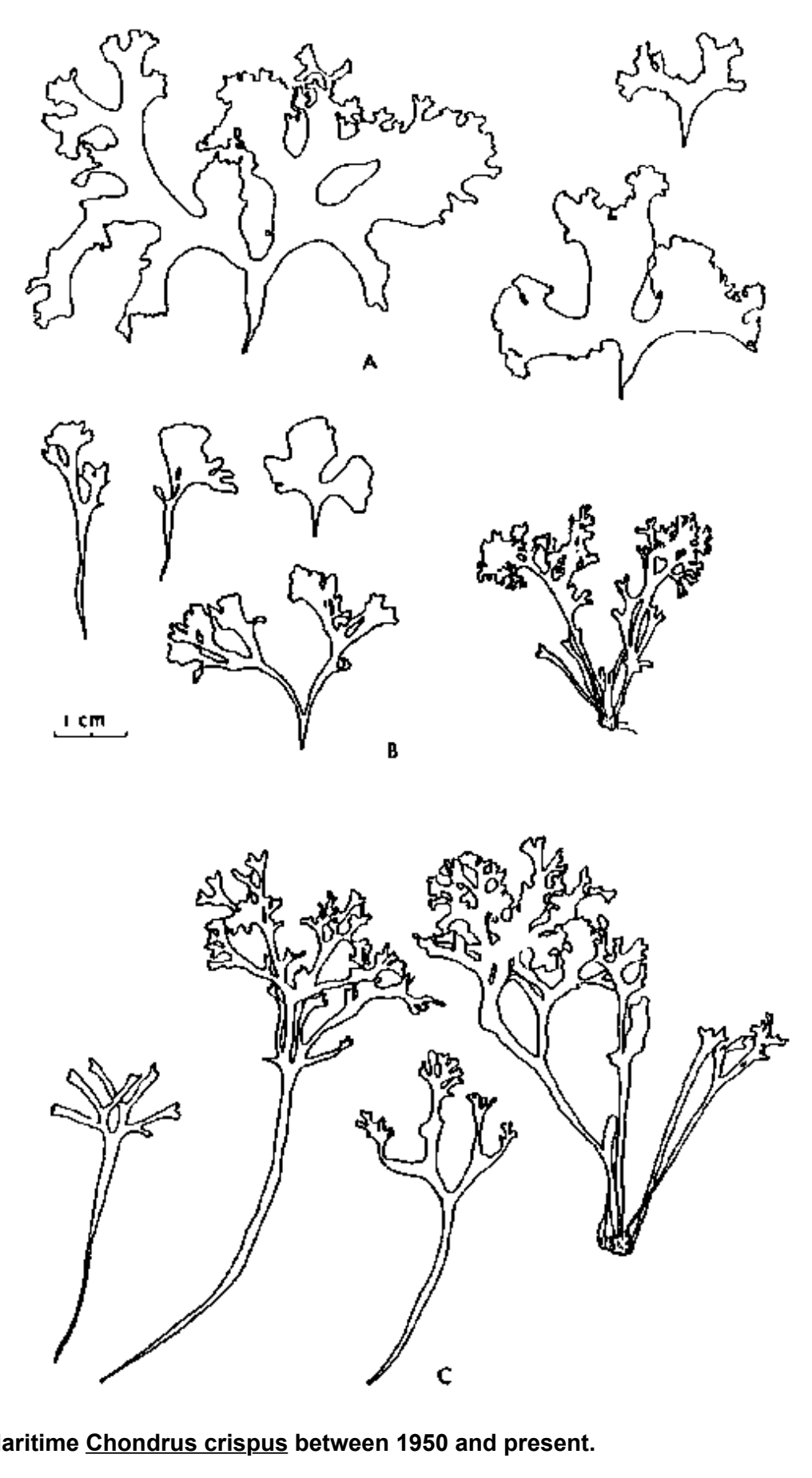


Table 1. Major companies directly buying Maritime Chondrus crispus between 1950 and present.

Companies	1950 1965	66	67	68	69	70	71	72	73	74	75	76	77	78	79	80	81	82	83	84	85
Marine Colloids	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X					
Cunningham & Sons	X	X	X	X	X	X	X	X	X	X	X	X	X*								
Litex - P.E.I.Seaweeds Ltd.		X*	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X**		
Genu Canada Ltd.		X*	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
P.E.I. Marine																					
Plants Cooperative									*X	X	X	X	X	X	X	X					
Stauffer Chemicals														*X	X**						
Litex - N.S. Seaweeds Limited																X	X	X			
Acadian Seaplants																	X	X	X	X	X
Wendell Stewart[1]																*X	X	X	X	X	X

*Approximate date of first direct buying activity.
**Aproximate termination data of buying activity.
[1] Was a buyer for many years for commercial companies.

Additional species of Chondrus have been described from the Pacific Ocean (e.g. Chihara, 1970; Mikami, 1965) although their delimitation is uncertain (Guiry and Masuda, 1984; Taylor and Chen, loc. cit.).

1.3 Nomenclature

Taylor and Chen (1973) state that the earliest binomial applied to Chondrus was Fucus filiformis Hudson (1762), but this was never taken up and Okamura and Segawa (in Segawa, 1935) applied the combination Chondrus filiformis to a Pacific species. Fucus crispus Linnaeus (1767) is believed to refer to Irish moss, but it is a later homonym of Fucus crispus Hudson (loc. cit.), the first legitimate combination describing the plant currently known as Phyllophora crispus (Hudson) Dixon (1964). Stackhouse (1797) separated certain taxa from the wide-embracing genus Fucus L. and proposed Chondrus and included C. crispus as his first species among six. Thus, the name for Irish moss is continued as Chondrus crispus Stackhouse. See Taylor and Chen (loc. cit.) for a detailed listing of the synonyms.

MacFarlane (1968) and Madlener (1977) list common names for Chondrus crispus as Irish moss, others, such as carrageenan, carrageenan moss, jelly moss, sea moss, etc. Carrageenan refers to Carragheen, a town in Ireland where the plant is believed to have been first utilized (Vadas and Ring, 1969).

1.4 Morphology and anatomy

Dixon and Irvine (1977) give a detailed account of the plant's morphology and anatomy, which consists of a perennial discoid holdfast and erect fronds in tufts **(Fig. 1).** The upright fronds consist of compressed unbranched stipes, expanding gradually into fan-like blades, up to 220 mm long. The fronds are undulate in younger parts, membranous to cartilaginous, repeatedly (to 5 times) dichotomous, with rounded axils, 2-15 mm broad between dichotomies, occasionally proliferous from the margins, usually expanding but occasionally tapering towards rounded apices; dark reddish or purplish brown, bleaching to a greenish yellow, frequently iridescent at the tips. The multi-axial thallus consists of medullary filaments that are thick-walled, 7-16 m m in diameter to 80 m m in length; cortical cells are arranged radially, 4-8 x 3-4 m m. The species is dioecious. Spermatangia are colorless, produced in white or pink superficial sori on terminal portions of young branches. They are liberated through distinct pores in the thickened cuticle, 7.5-10 x 4-5 m m. Cystocarps protruding strongly, usually as concavo-convex swellings about 2 mm in diameter, with a pore; carposporangia 20-30 x 14-25 m m. Tetrasporangial sori only slightly protruding, oval to linear, 1-5 x 0.5-1.0 mm, numerous, particularly in the younger regions and often confluent. Tetrasporangia terminal or intercalary, immersed in the medulla, 17-40 x 11-30 m m, cruciately divided.

2. DISTRIBUTION, ECOLOGY AND METABOLISM

2.1 Geographical extent
2.2 Local vertical and horizontal distribution
2.3 Effects of ecological determinants
2.4 Seasonality of growth
2.5 Nutrition and growth

2.1 Geographical extent

Chondrus crispus extends from Labrador to New Jersey, northern Russia to southern Spain and possibly Morocco and Cape Verde Isles, as well as in the western Baltic and Iceland (Dixon and Irvine, 1977).

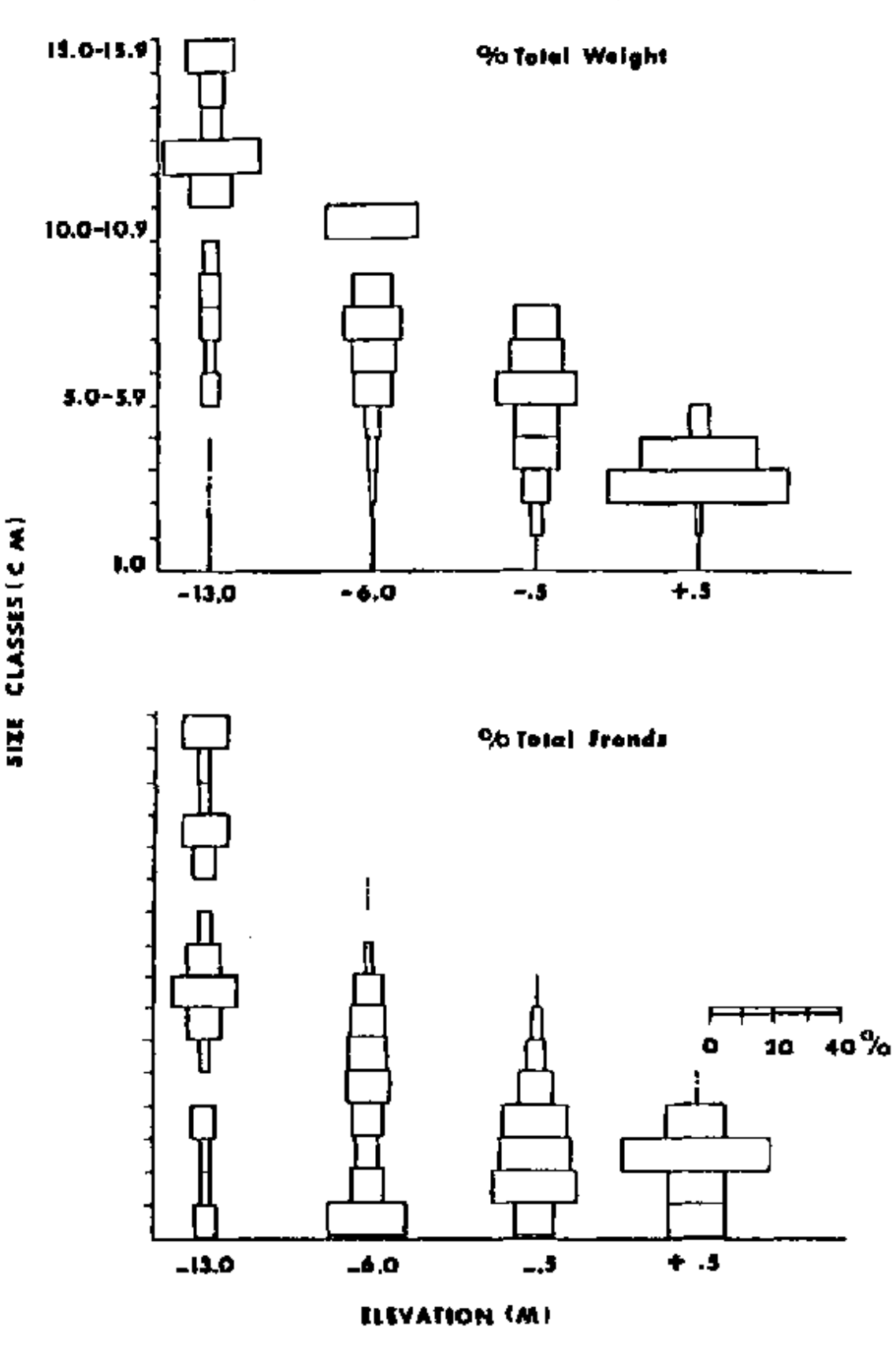
2.2 Local vertical and horizontal distribution

Irish moss extends from the littoral fringe (sensu Lewis, 1964) to -20m below mean low water, depending upon wave action, transparency and other local topographic conditions (cf. Bird et *al.,* 1983; Femino and Mathieson, 1980; Mathieson and Prince, 1973; Prince and Kingsbury, 1973b). Even so, it is usually most abundant near M.L.W. to the mid subtidal zone (Mathieson and Prince, loc. cit.), with varying densities and morphologies occurring throughout this gradient **(Fig. 2-4).**

2.3 Effects of ecological determinants

Chondrus crispus grows most abundantly on massive and stable outcrops (ledges) and boulders, with substantially reduced populations on smaller rocks and sand/or sediment-covered rocks (cf. Daly and Mathieson, 1977; Pringle and Semple, 1984). Occasionally, it will occur as detached populations (cf. Norton and Mathieson, 1983). Chondrus usually grows on shelving and horizontal surfaces, while adjacent vertical surfaces that are impacted by strong wave action, desiccation and freezing (Green, 1983; Lewis, 1964) are often dominated by Gigartina stellata (cf. Burns and Mathieson, 1972; Green, loc. cit.; Mathieson and Burns, 1975). Chondrus grows most abundantly on semi-exposed, open coastal sites; in addition, it is common in estuarine habitats, being particularly abundant where strong tidal currents occur (Conover, 1968; Kent and Buggeln, 1972; Mathieson and Hehre, 1986, Mathieson et al., 1983). The plant's extensive distribution in estuarine habitats (cf. Doty and Newhouse, 1954; MacFarlane, 1966; Munda, 1977, 1978) suggests a broad tolerance to temperature' salinity and light (cf. Mathieson and Burns, 1971; Mathieson and Prince, 1973). Even so, polluted harbor water and oil contamination can be harmful (cf. Boney, 1965; Grenanger, 1957; Marshall et al., 1949), while ice erosion in "northern" areas can be damaging, reducing the plant's reproductive potential and restricting it to crevices (cf. Bird et al., 1983; Hooper et al., 1980; Lilly, 1968). See Sections 4.3 and 4.4 concerning a variety of animals, bacteria, fungi and other plants that can adversely affect the survival and growth of Irish moss.

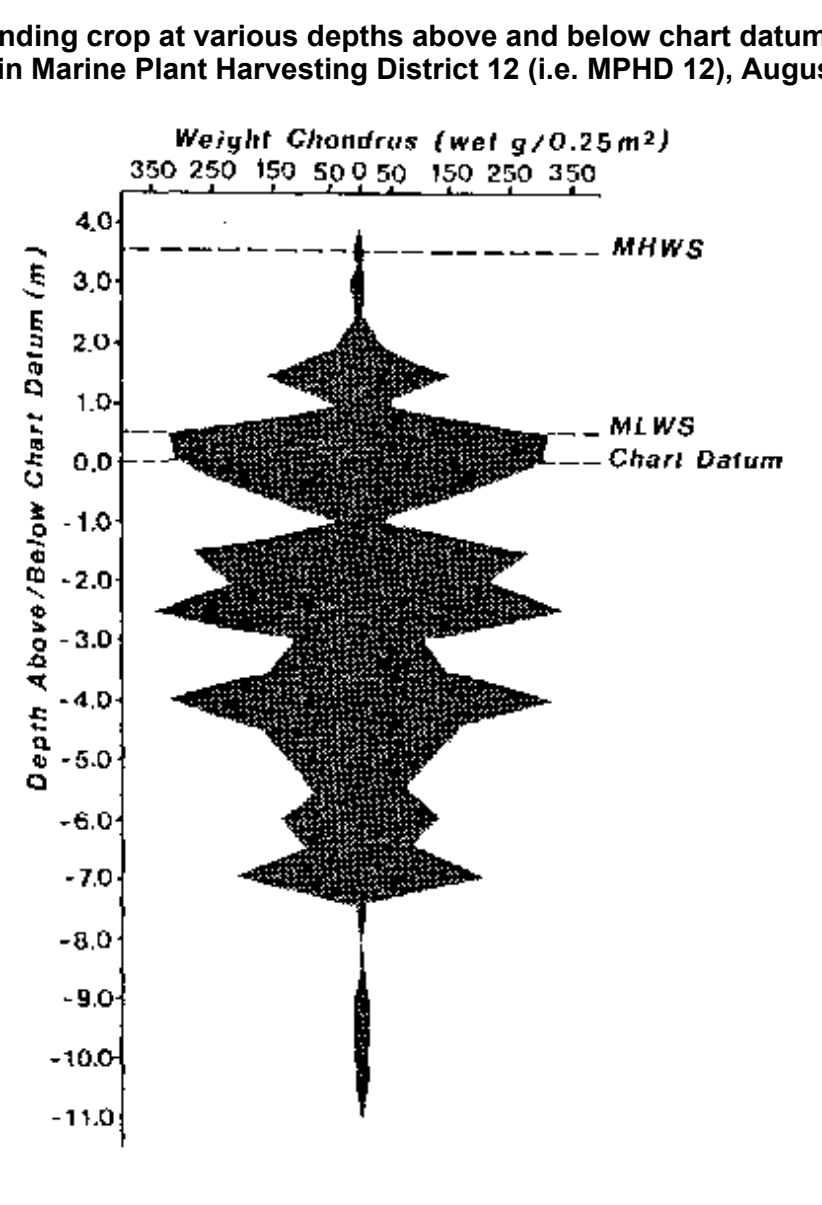
Figure 2. Size and weight distributions of Chondrus crispus fronds in the intertidal and subtidal zones at Jaffrey Point, Newcastle, New Hampshire, U.S.A. (from Mathieson and Burns, 1975).



2.4 Seasonality of growth

The seasonal growth of Chondrus crispus is maximal during late spring or summer and minimal during the winter (cf. Koop and Perez, 1979: Mathieson and Prince, 1973; Mathieson and Burns, 1975; Prince and Kingsbury, 1973a,b; Pybus, 1977). For example, Prince and Kingsbury (loc. cit.) found that growth was minimal during November-February; thereafter, it increased nearly linearly, reaching a maximum of approximately 0.37 mm/day in September or October. See Kanwisher (1966) and Taylor (1954, 1970) for further information on growth rates. Prince and Kingsbury (loc. cit.) suggest that the plant's growth patterns are coincident with temperature variations. However, Neish and Fox (1971) state that decreasing autumn growth rates are primarily due to declining solar radiation. Mathieson and Burns (1975) note that maximum nutrient levels (i.e. nitrate-N, nitrite-N and ortho-phosphate-P) are evident in early spring when growth is initiated, while lower levels occur during the summer and fall when maximum growth occurs. Hanic and Pringle (1978), Pringle (1979) and Taylor et al. (1975, 1981) emphasize that the holdfasts of Irish moss grow slowly. For example, Hanic and Pringle (loc. cit.) found that it took two years to produce a holdfast of 4-mm^2.

Figure 3. The distribution of Chondrus crispus standing crop at various depths above and below chart datum along the West Pubnico Peninsula, Nova Scotia, Canada, in Marine Plant Harvesting District 12 (i.e. MPHD 12), August, 1975.



2.5 Nutrition and growth

Recent aquaculture experiments with Irish moss have shown that adequate carbon is essential for normal growth and that photosynthetic uptake is proportional to HCO_3^- concentrations up to 2 m (Bidwell and McLachlan, 1985). The same authors found optimal growth with ammonium nitrate or ammonium phosphate, and that the addition of macronutrients other than N and P was not critical. Chondrus seems to grow equally well on NO^{-3} or NH^{+4}; in addition/it grows better on inorganic nitrogen than on urea (cf. Laycock et al., 1981; Neish and Fox, 1971; Neish and Shacklock, 1971; Prince, 1974). The dipeptide L-citrullinyl-L-argine accumulates to high concentrations when Chondrus is supplied with nitrate or ammonium at low temperatures; much of this reserve is readily mobilized for growth during periods of higher temperatures, increased irradiance and reduced nutrients (cf. Laycock and Craigie, 1977; Laycock, et al., 1981).

Figure 4. The vertical distribution of macrophyte taxa (in relation to chart datum) a single transect off the West Pubnico Peninsula, Nova Scotia, (MPHD 12), August, 1975.

3. LIFE HISTORY

3.1 Life cycle and reproduction

3.1 Life cycle and reproduction

Chondrus crispus has been shown to have a triphasic isomorphic life history in culture consisting of separate male and female gametophytes, carposporophytes parasitic on the female gametophyte and free-living tetrasporophytes (cf. Chen and McLachlan, 1972; Guiry, 1979). A cytological alternation of generations involving haploid gametophytic, diploid carposporophytic and diploid tetrasporophytic phases has also been documented (Hanic, 1973; Magne, 1964). Released carpospores and tetraspores develop identically in culture (e.g. Chen and McLachlan/loc. cit.; Prince and Kingsbury, 1973a; Ring, 1970; Taylor and Chen, 1973). Initially; they swell and then undergo a series of anticlinal and periclinal divisions, which result in a hemispherical cushion (i.e. holdfast initial) that initially produces a cylindrical frond primordia and ultimately a flattened dichotomous frond.

Reproductively mature fronds have been observed in culture after the growth of carpospores from 91 days-21 months and tetraspores from 114 days-21 months (cf. Chen and McLachlan, loc. cit.; Guiry, loc.cit.; Prince, 1971). Procarp-bearing plants produce carpospores only when male plants are in the same culture - e.g. Guiry (loc. cit.) records carpospore production 45 days after being mixed. If the density of spores is high or if inadequate spore contact occurs, an initial rhizoidal sequence may occur, which ultimately leads to formation of the holdfast initial. Juvenile gametophytic and sporophytic plants can also exhibit a high frequency of sporeling (i.e. holdfast) coalescence (Tveter and Mathieson, 1976; Tveter-Gallagher and Mathieson, 1980), which is associated with an accelerated production of frond primordia **(Fig. 5 and 6)** and an obvious ecological advantage (cf. Jones, 1956). See Section 4.1 regarding patterns of in situ longevity and reproductive maturity.

Field studies have documented different life history patterns (e.g. Craigie and Pringle, 1978; Mathieson, 1982; Mathieson and Prince, 1973; Section 4.2). **Figures 7 and 8** summarize the in situ life history patterns of Chondrus crispus populations in New England, employing a variety of procedures as suggested by Prince and Kingsbury (1973a) - i.e. seasonal spore discharge rates, percent viability of spores, the number of sori/frond segment and diverse habitat sampling. These studies and those of Taylor et al. (1975, 1981) demonstrate a reproductive strategy involving prolonged sporic as well as broad-scale vegetative reproduction (cf. Section 4.5), with the former consisting of unimodal carpo-sporic and bimodal tetrasporic maxima and the latter of extensive holdfast regeneration. The duration and phenology of sporic and sexual reproduction varies spatially (Mathieson, 1982; Tveter-Gallagher et al., 1980, **Fig. 7 and 8).** Tetrasporic plants have maximum discharge rates in May - June (36-48 x 10^3 spores/sorus) and a smaller maximum in December-January (29-31 x 10^3 spores/sorus). Tetraspore viability was lowest during February -April (68-74%); thereafter, it ranged from 82-92% **(Fig. 8).** Cystocarpic plants showed maximum discharge rates during summer (48 x 10^3 spores/sorus), a clinal decrease during fall-winter, and lowest discharge rates and number of reproductive sori during April (20 x 10^3 spores/sorus). Overall, cystocarpic plants exhibited their highest sustained viability (85-92%) during summer. In demographic studies of intertidal populations in the Canadian Maritime Provinces, Bhattacharya (1985) found that the carpospore and tetraspore discharge rates never fell below 106 spores/m^2/month, while they were maximal during September (i.e. 8.7 x 10^9 carpospores and 10.4 x 10^9 tetraspores/m^2/month). Overall, the annual release rates of carpospores was 4.7 times greater than that of tetraspores. In contrast to Bhattacharya, Mathieson (1982) employed subtidal plants and emphasized individual frond discharge rates; thus, the two studies are not directly comparable.

Figure 5. The relationship between sporeling area and the stature of upright fronds with Chondrus crispus; the plants were collected from the upper subtidal zone at Jaffrey Point, Newcastle, New Hampshire, U.S.A. (from Tveter and Mathieson, 1976 and Mathieson, 1982).

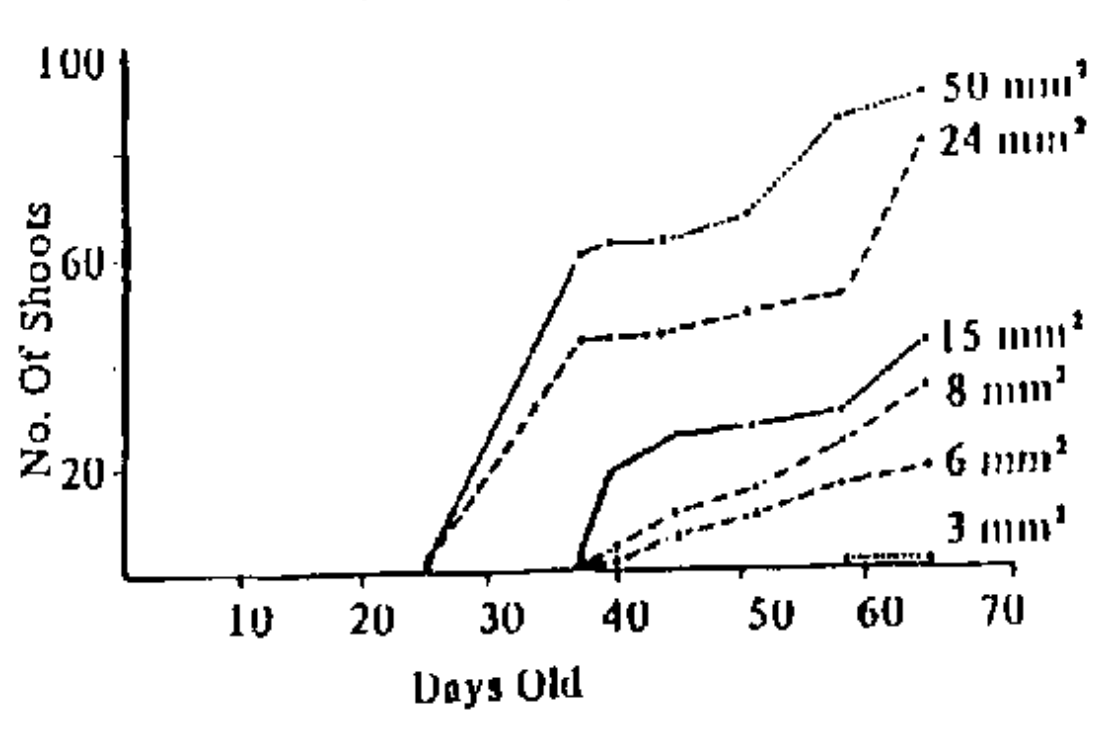


Figure 6. The relationship between sporeling area and number of upright fronds with Chondrus crispus; the plants were collected from the upper subtidal zone at Jaffrey Point, New Hampshire, U.S.A. (from Tveter and Mathieson, 1976 and Mathieson, 1982).

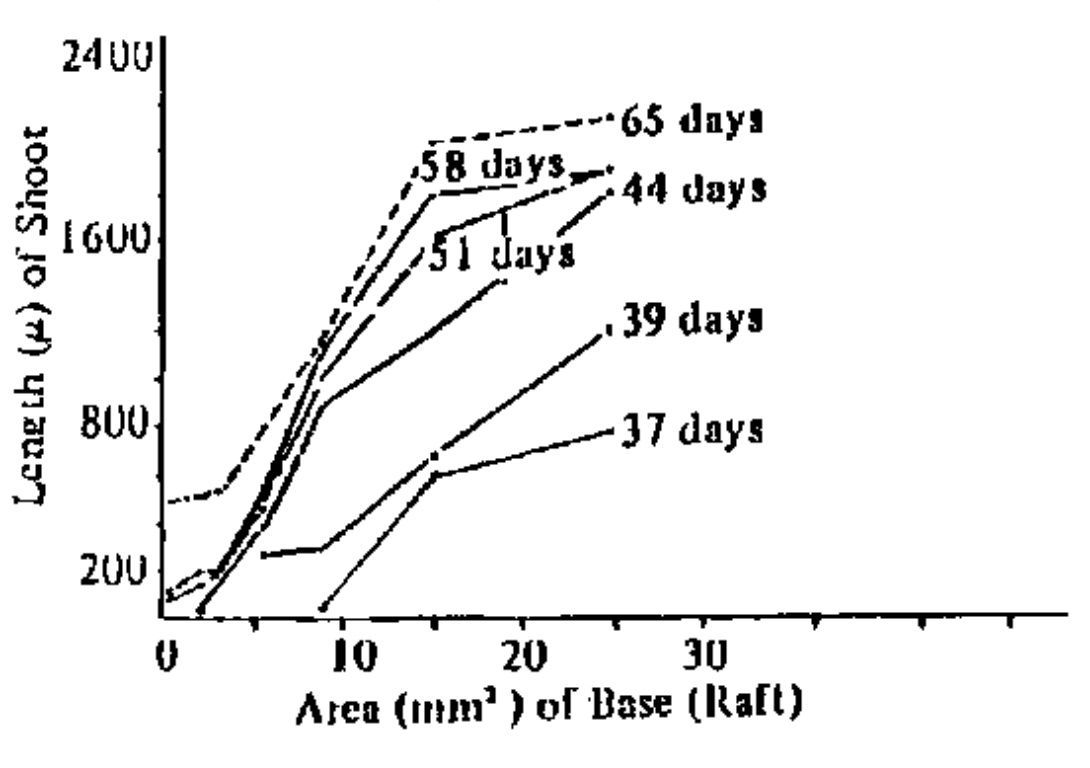


Figure 7. The reproductive phenologies of spermatangial, cystocarpic and tetrasporic plants of Chondrus crispus within the upper subtidal zone (-3m) at an open coastal site at Jaffrey Point, New Hampshire; as well as within the mid (+1.0m) and lower-intertidal zones at an estuarine site at Adams Point, New Hampshire; expressed as number (%) of each reproductive phase/sample (from Tveter-Gallagher, et al.; 1980).

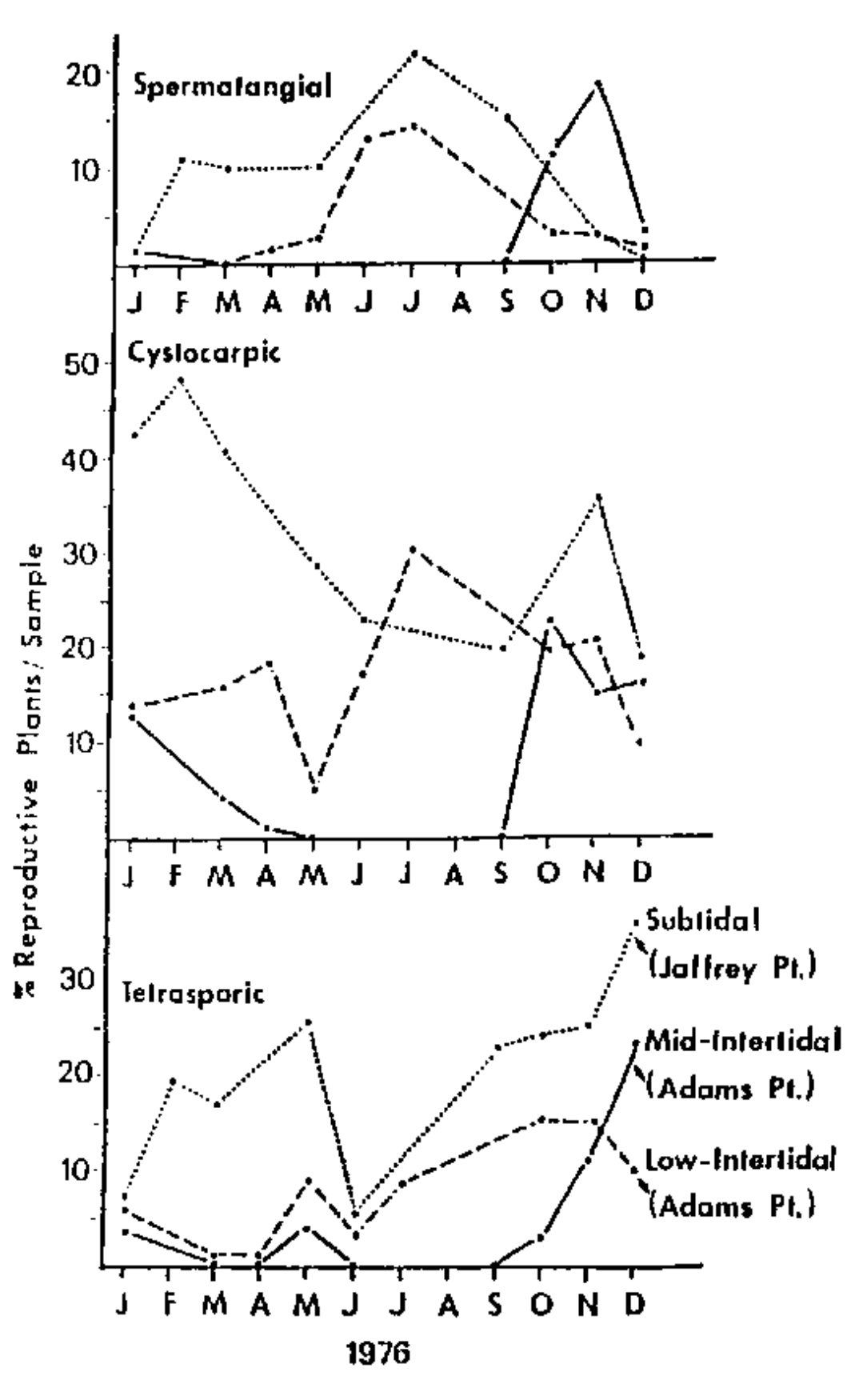
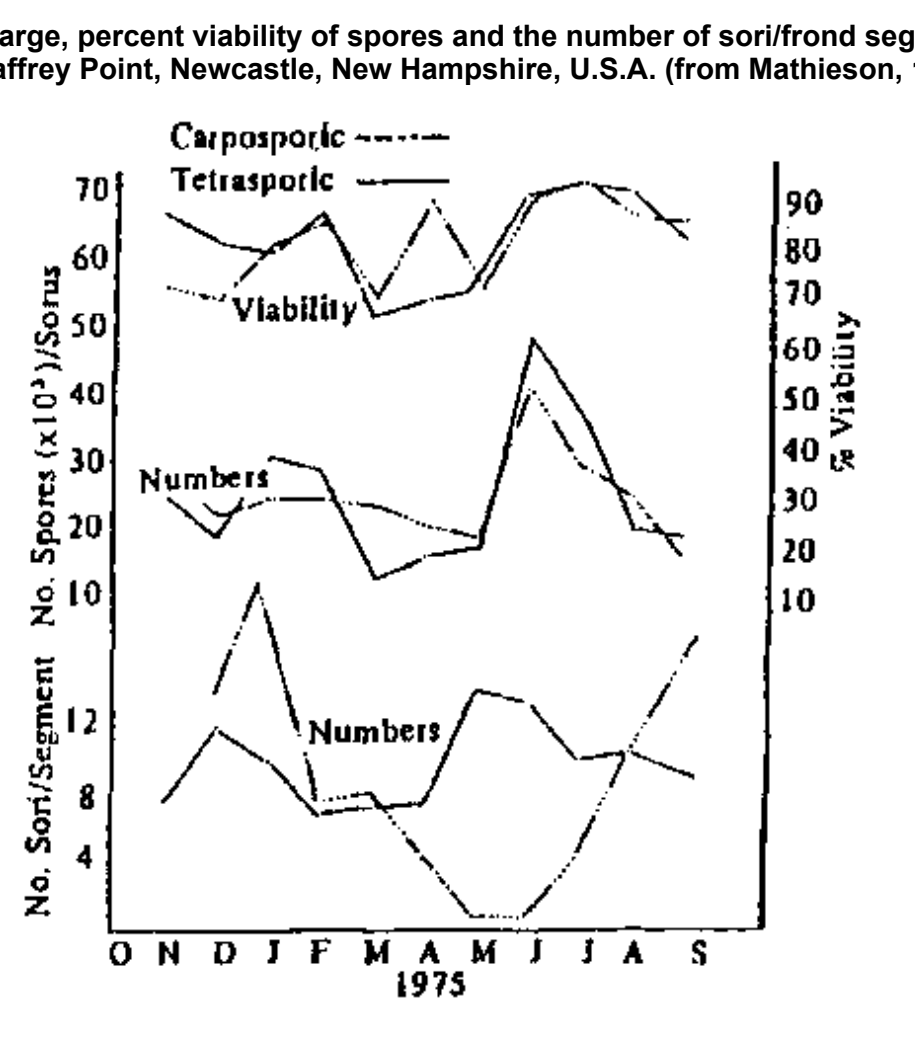


Figure 8. A summary of seasonal spore discharge, percent viability of spores and the number of sori/frond segment in Chondrus crispus; the plants were collected from the low intertidal zone at Jaffrey Point, Newcastle, New Hampshire, U.S.A. (from Mathieson, 1982b and Mathieson and Tveter, 1977).



4. POPULATION STRUCTURE AND MORTALITY

4.1 Age, weight or size composition
4.2 Sporophyte-gametophyte and sex composition
4.3 Mortality, morbidity
4.4 Grazing
4.5 Regeneration

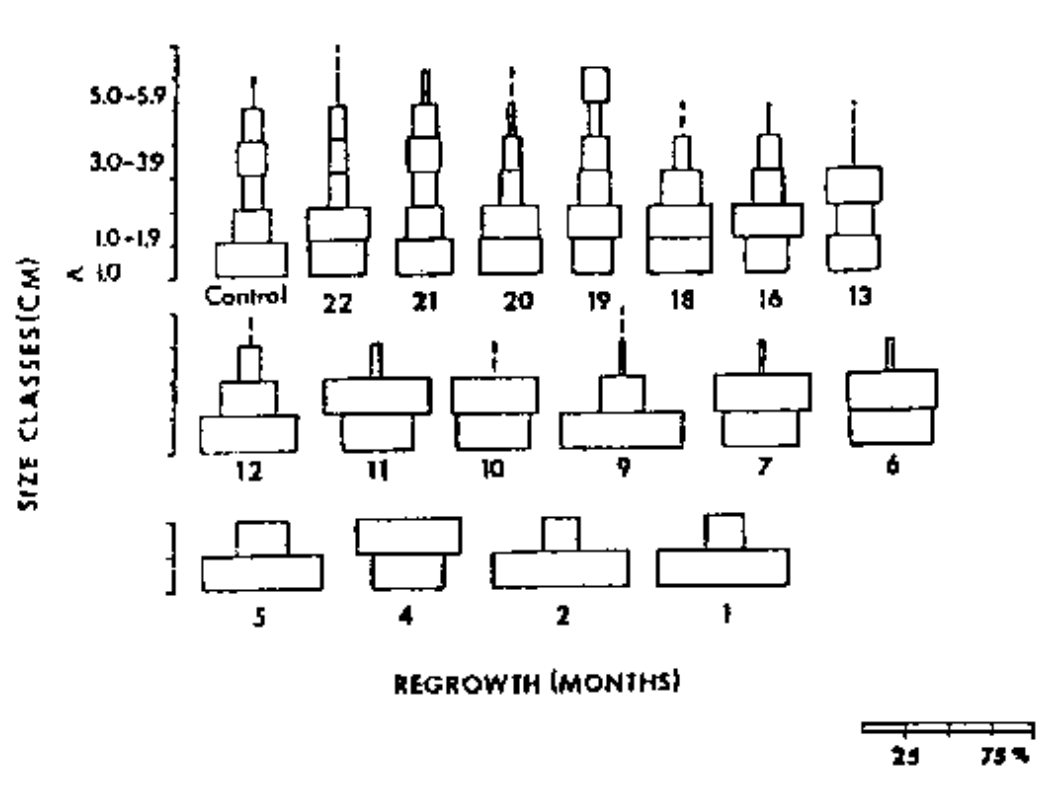
4.1 Age, weight or size composition

Fronds of Chondrus crispus can potentially grow 2-6 years while holdfasts have an even greater longevity (cf. Taylor and Chen, 1973; Taylor et al., 1975, 1981). Estimates of reproductive maturity for in situ plants range from 20 months to 5 years (MacFarlane, 1968; Mathieson and Burns, 1975; Rosenvinge, 1931). Shorter periods (13 months) have been recorded after regrowth from residual holdfasts (Mathieson and Burns, loc. cit.).

Taylor (1956, 1958/59, 1959, 1970, 1971, 1972, 1973) examined the composition and morphology (i.e., size and degree of branching) of fronds from Canadian locations ranging from the southern Gulf of St. Lawrence, to the Bay of Fundy, New Brunswick and Fife, Scotland. He divided fronds from these populations into arbitrary size-development classes (see Fig. 9), originally seven classes (Taylor, 1956), but later four (Taylor, 1959, 1970, 1971). As young fronds are formed throughout each growing season and older ones continuously lost, a large percentage (20-40%) occurs in Classes I-III, and a small percentage (3-10%) in Class IV (cf. Prince and Kingsbury, 1973b as well). Taylor and Chen (1973) noted a consistent percentage distribution pattern during different years and at various locations. The largest plants in Class III and those in Class IV were most vulnerable to storm removal. Mathieson and Burns (1975) observed the same patterns, particularly for low intertidal and shallow subtidal populations **(Fig. 2).** The size frequency distribution patterns also vary substantially depending upon the severity and time since harvesting **(Fig. 10).** After 16-18 months of regrowth on sequentially denuded quadrats, the size frequency distribution of various frond populations was basically at control levels, similar to those described by Taylor (1959, 1970, 1971).

Figure 9. Four arbitrary size development classes of Chondrus crispus fronds as outlined by Taylor (1959, 1970, 1971) - Taylor and Chen (1973).

Figure 10. Size frequency distribution of Chondrus crispus fronds on sequentially denuded quadrats at Rye Ledge, New Hampshire (from Mathieson and Burns, 1975).



Several investigators have described the density and/or standing crops of Chondrus crispus and/or Gigartina stellata (cf. Boney, 1965). Marshall et al. (1949) found that G. stellata made up 50-90% of the standing crop at several sites in England, Scotland and Wales. The standing crops of harvestable Gigartina, and smaller amounts of Chondrus, on Scottish shores varied from 1.4-146 tons and 0.5-60lbs./linear yard. Approximately 460 Chondrus fronds greater than 2.5 cm were found per m^2. Pybus (1977) found frond densities (as $\log_{10}(n+1)/dm^2$) for C. crispus and G. stellata in Galway Bay, Ireland, of 0.3-1.9 and 0.3-1.7, respectively. Monthly estimates of standing crop for Irish moss at three sites varied from 1.3-79.2 g dry weight/m^2, with the mean annual values for the three sites being approximately 14.6, 18.0 and 40.0g dry weight/m^2.

MacFarlane (1952) states that the average standing stock of Chondrus crispus in southwestern Nova Scotia varies from 1-2.5 lbs/ft^2 (i.e. 0.453-1.132 kg). In one 30 mile stretch of coastline in the same area, the average standing stock was approximately 1,361,000 kg/mile^2 (MacFarlane, 1968). In a study off Prince Edward Island, Taylor (1970, 1972) found approximately 11,000 fronds/m^2 for about 1000m in a shoreward direction. The mean dry weight of Irish moss on this same transect was 426 g/m^2, With a conversion factor of approximately five (Stoloff, 1949), this would correspond to a wet weight of 2.13 kg/m^2, On another of Taylor's transects off Prince Edward Island, he found approximately half this density. Pringle (1979) states that the mean standing crop off southwestern Nova Scotia is approximately 436 g dry weight/m^2, In reviewing the standing stocks of Chondrus in southwestern Nova Scotia and approaches to the Bay of Fundy/Michanek (1971, 1975) records wet weights of 5-12 kg/m^2, Gigartina stellata replaces C crispus within the Fundy area and its standing stock (i.e. wet weight) is approximately 5-15 kg/m^2.

Foster (1953, 1954, 1955b, 1956) records 0.6-7.5 kg wet weight/m^2 of Irish moss in Maine, with the most productive areas of Washington County (i.e. northern Maine) having 6.0-7.5 kg/m^2, In New Hampshire, Burns and Mathieson (1972) found 7-8 kg wet weight/m^2 of Gigartina stellata under ideal conditions of elevation and wave action. Similar studies of Chondrus crispus showed approximately 11-13 kg wet weight/m^2 (Mathieson and Burns, 1975) although both of these values were extremely variable depending upon elevation and local habitat characteristics. Prince and Kingsbury (1973b) state that the seasonal biomass of Irish moss at Plymouth, Massachusetts, varied from 5,035-12,768 fronds/m^2 (x = 7,409) and 739-1517 g dry weight/m^2 (x = 1084) at -3.0m versus 2,466-8,266 fronds/m^2 (x = 5,783) and 677-1,182 g dry weight/m^2 (x = 911) at -6.1m.

4.2 Sporophyte-gametophyte and sex composition

Although the life history of Chondrus crispus is triphasic in culture (see Section 3.1), several investigators have reported spatial differences in haploid and diploid dominance (Bhattacharya, 1985; Craigie and Pringle, 1978; Mathieson and Burns, 1975). While working in three subtidal sites in Prince Edward Island and one in Nova Scotia, Craigie and Pringle (loc. cit.) found that the number of tetrasporic plants varied from 22.2-31.2% at the former to 51.4% at the latter. In contrast, Bhattacharya (loc. cit.) found 6-10% of the intertidal populations at another Nova Scotian site to be tetrasporic. Mathieson and Burns (loc. cit.) found a greater number of tetrasporic than carposporic plants within the subtidal zone in New England **(Fig. 11);** pronounced spatial differences were noticed in the intertidal composition of tetrasporic plants depending upon the degree of exposure to water motion **(Fig. 12).**

4.3 Mortality, morbidity

Although Chondrus crispus is a perennial taxon, its fronds may be ephemeral or annual (cf. Hooper et al., 1980; Lilly, 1968; MacFarlane, 1968; Marshall et al., 1949) in fluctuating habitats. Shoots of different ages are present on a single discoid holdfast, and if left undamaged, it continues to produce shoot primordia for a number of years (MacFarlane, loc. cit.). Holdfasts damaged by storms, harvests, grazing, etc., may regenerate and give rise to new shoots (cf. Chen and McLachlan, 1972).

Ice scouring can result in ephemeral or annual frond populations, reduced plant stature and limited reproduction (cf. Section 2.3). Mathieson and Burns (1975) emphasize that winter storms cause pronounced fluctuations in the weight and size of Chondrus populations, particularly in exposed open coastal areas. Demographic studies by Bhattacharya (1985) on intertidal Irish moss demonstrated a strong relationship between size (maturation) and survivorship after storms.

Figure 11. Changes in reproductive capacity of Chondrus crispus with vertical position on the shore at Jaffrey Point, Newcastle; New Hampshire; U.S.A. (from Mathieson and Burns; 1975).

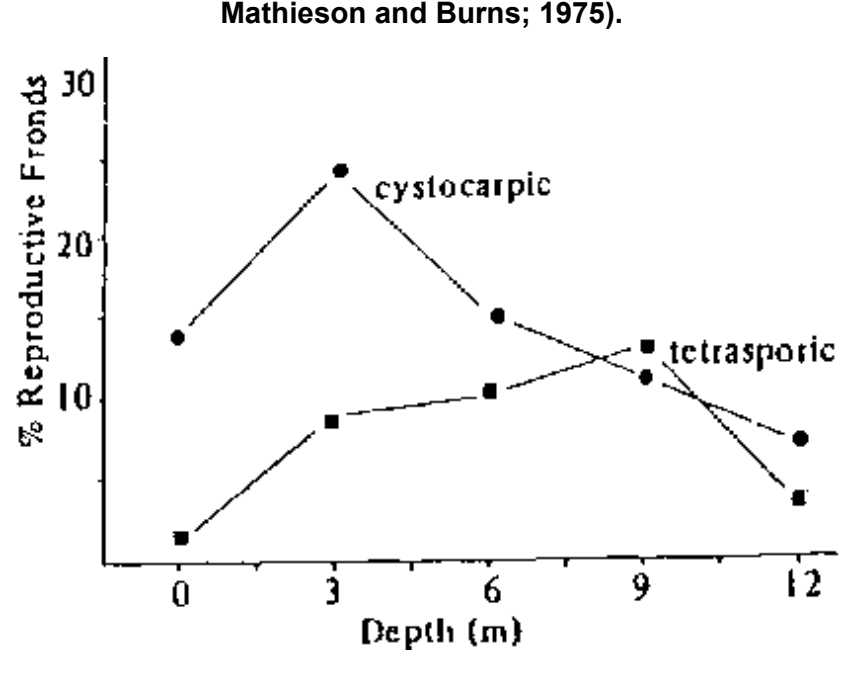
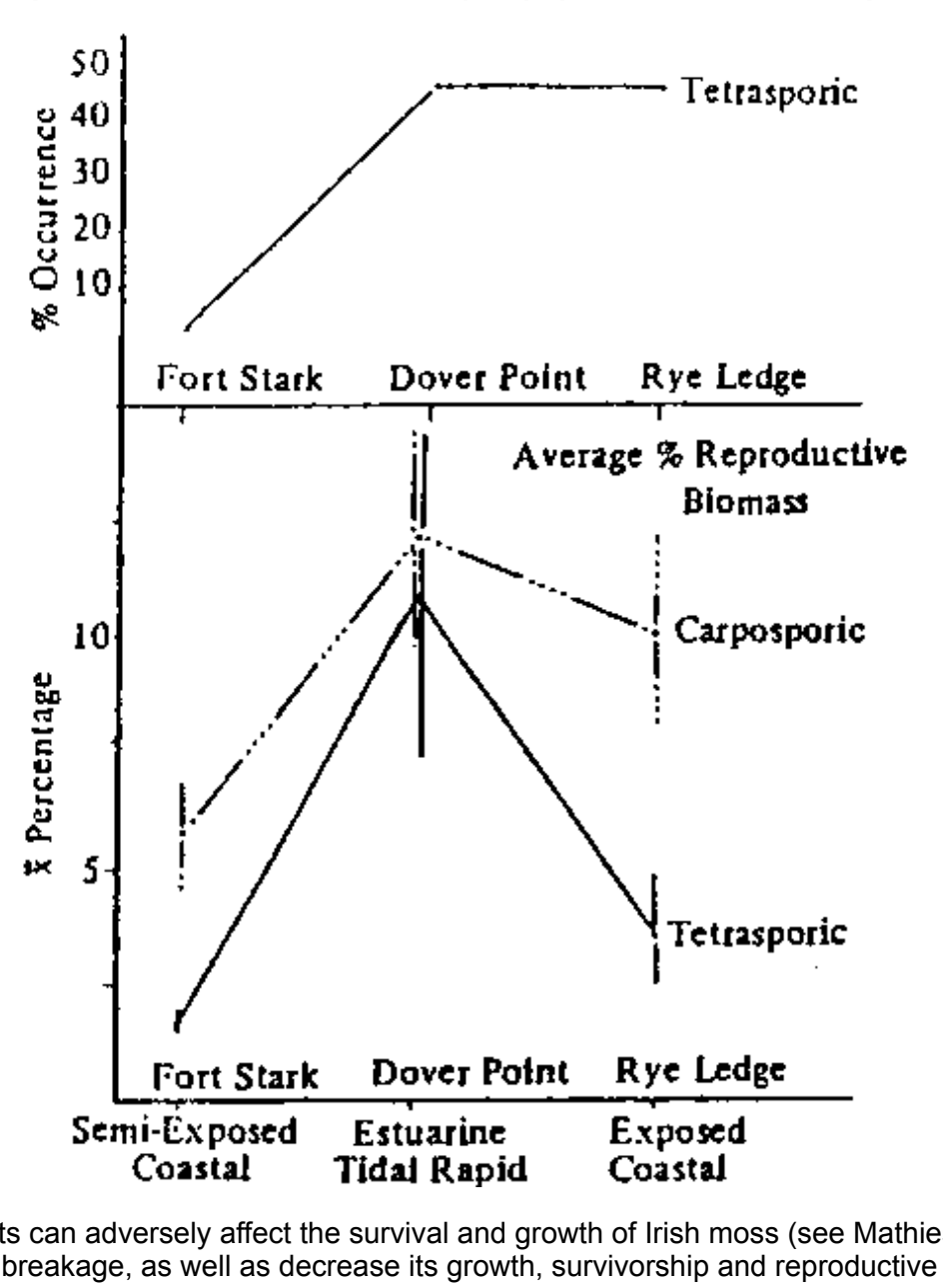


Figure 12. Horizontal variations of reproduction with Chondrus crispus populations in New Hampshire; U.S.A. (from Mathieson; 1982).



A variety of animals, bacteria, fungi and other plants can adversely affect the survival and growth of Irish moss (see Mathieson and Prince, 1973, for a synopsis). Thus, epiphytic algae can increase the potential of frond breakage, as well as decrease its growth, survivorship and reproductive output (D'Antonio, 1985; Prince, 1971; Pybus, 1977), while several fungi and bacteria can parasitize and badly infect the plant (e.g. Andrews, 1976; Cantacuzene, 1930; Chemin, 1927, 1931; Ring, 1970; Prince 1971).

4.4 Grazing

Most animals found on or amongst Chondrus crispus are small forms (e.g. amphipods, bryozoans, crustaceans gastropods, nematodes, etc.) or juvenile stages of larger organisms like urchins, mussels, crabs and sea stars (Lilly, 1968). Recent population explosions of the green urchin Strongylocentrotus droebachiensis have caused extensive damage, perhaps as a result of overfishing of one or more predators or pollution (Mann, 1977; Pringle et al., 1983; Sivertsen and Bjorge, 1980; Wharton and Mann, 1981). Similarly, Mytilus edulis can cause the plant's demise **(Fig. 13)** via altered sediment deposition patterns, reductions of light and while intense grazing by Littorina littorea of epiphytic species on Irish moss may cause similar effects (Lubchenco, 1978; Lubchenco and Menge, 1978; Menge, 1975). Haliotus and Acmea testudinalis browse on a variety of seaweeds, including Chondrus (MacFarlane, 1968).

Figure 13. Changes in biomass of Chondrus crispus and Mytilus edulis on a pier piling at an estuarine tidal rapid site at Dover Point, New Hampshire, U.S.A. (from Mathieson et al., 1983; Reynolds, 1971). space, etc. (Lilly, loc. cit.; MacFarlane, 1956, 1968; Reynolds, 1971),

4.5 Regeneration

Several workers (Foster, 1955a; MacFarlane, 1952; Marshall, et al., 1949; Mathieson and Burns, 1975; Taylor, 1959/60) have evaluated the regrowth of Chondrus after harvesting. Mathieson and Burns (loc. cit.), working in New Hampshire, found that carefully and moderately harvested plots (i.e. 1/3 and 2/3 of longest fronds removed) established during the summer (July) allowed regrowth to control levels of biomass after 5-6 months, while comparable winter plots took a year or more to reach control levels **(Fig. 14 and 15).** Totally harvested plots of summer took approximately one year for regrowth to control levels, while comparable winter plots took two years. Winter harvests had a drastic and long-range effect on regrowth. Foster (loc. cit.) evaluated regrowth of Chondrus in Maine after raking at monthly intervals (June-September, 1955). Regrowth was greatest in June and decreased in succeeding months. Marshall et al. (loc. cit.) found that harvesting in Great Britain during September had little or no effect on yields during the subsequent summer. Plots scraped totally in August began to colonize by January, and more than 460 plants exceeding 2.5 cm in length were counted in a metre square. They suggest that Chondrus is a more rapid colonizer than Gigartina stellata, even though the former is more sensitive to harvesting than the latter. The same authors showed that regeneration of harvested populations occurs from holdfasts, as well as from the surface and margin of cut or broken fronds.

Figure 14. Changes in biomass of Chondrus crispus within the low intertidal zone at Rye Ledge, New Hampshire, U.S.A., following harvesting in July, 1969 (from Mathieson and Burns, 1975).

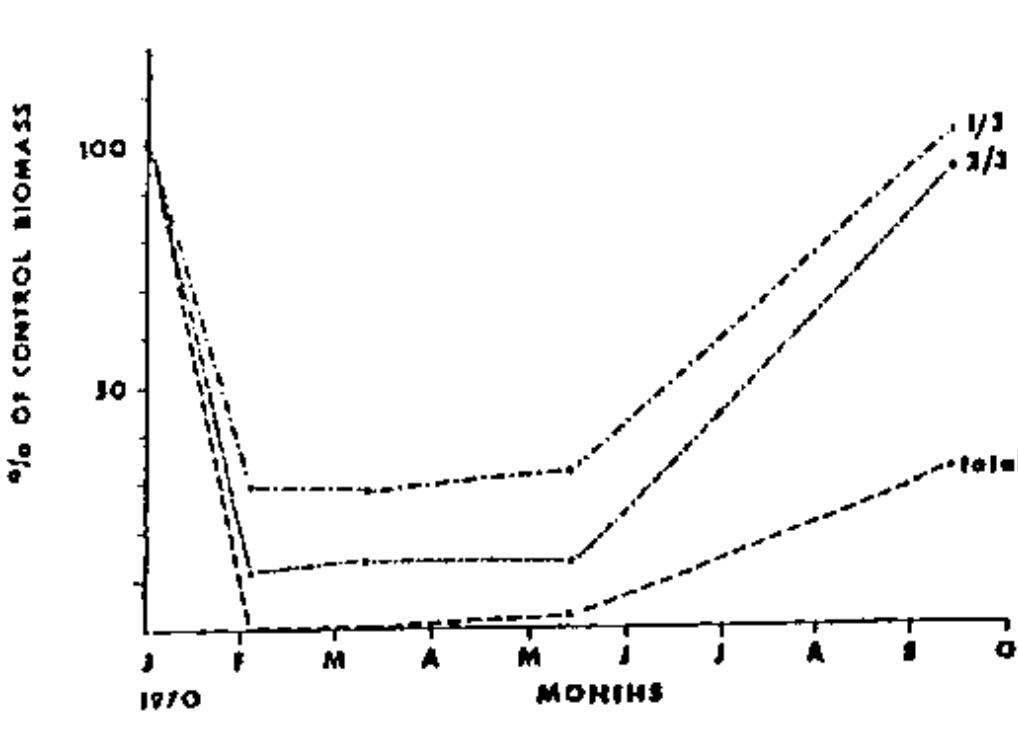
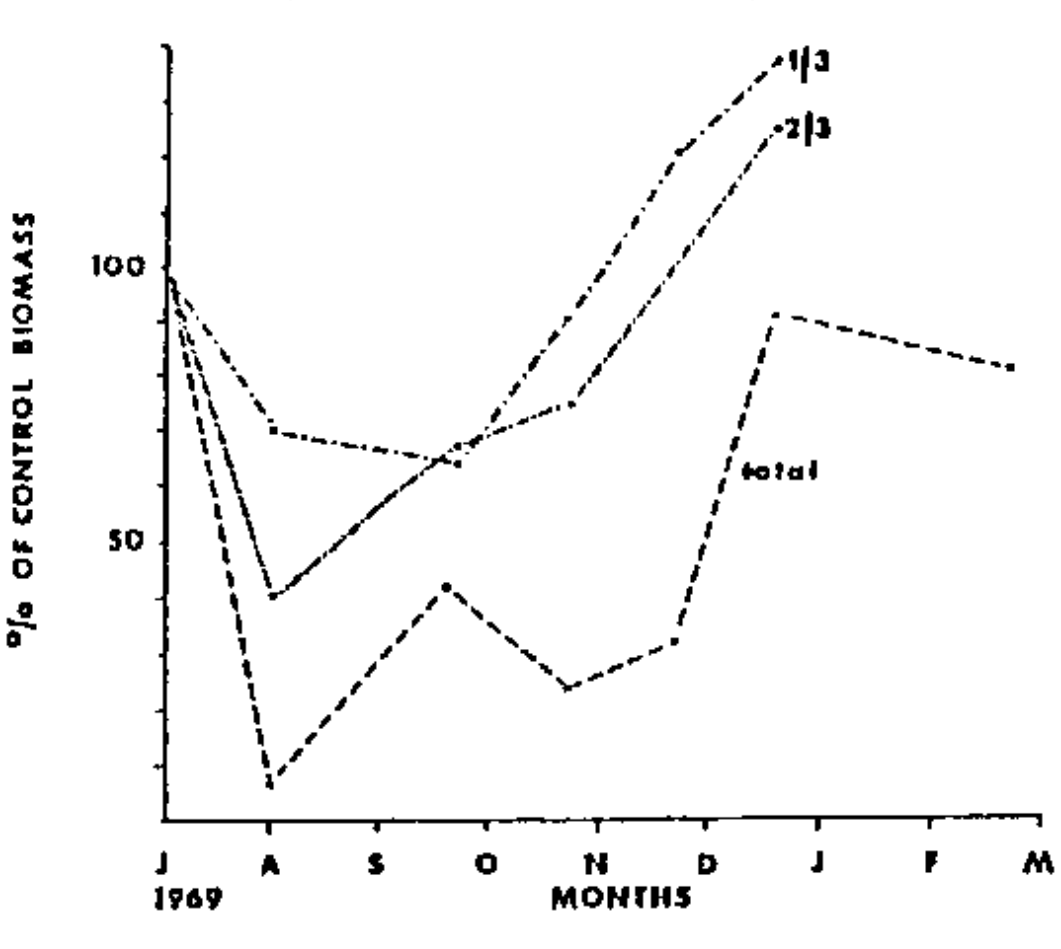


Figure 15. Changes in biomass of Chondrus crispus within the low intertidal zone at Rye Ledge, New Hampshire, U.S.A., following harvesting in January, 1970 (from Mathieson and Burns, 1975).



MacFarlane (1952) and Taylor (1959/60) recorded the effects of differential levels of harvesting on intertidal Chondrus in the Canadian Maritime provinces. MacFarlane (loc. cit.) found that plants cut with sheep shears, as closely as possible, returned to control levels after 18 months. In agreement with Mathieson and Burns (1975), she found that careful raking allowed control levels after six months. Taylor (loc. cit.) found that plucking the crop, in order to simulate intensive raking, reduced the harvestable population after 12 months to 24.5% of the previous year. Clipping the tops of fronds reduced the population after 12 months to 29% of the previous year. MacFarlane (1956) emphasized that severe holdfast injury can ruin a bed for several years. If raking is done properly, only the largest fronds will be removed leaving the short shoots for subsequent regrowth.

Mathieson and Burns (1975) summarized the effects of total harvesting (i.e. only residual holdfasts left) of intertidal quadrats for 20 consecutive months -i.e. starting in February, 1969, and ending in August, 1970 **(Fig. 16).** Plants were allowed to regrow until September, 1970, when the quadrats were simultaneously reharvested. Control levels of biomass and population structure (i.e. size distribution of fronds) were evident after 12-13 months of regrowth **(Fig. 10 and 16).** Younger plots showed differential levels of productivity and/or size.

Figure 16. Regrowth of sequentially denuded quadrats of Chondrus crispus within the low intertidal zone at Rye Ledge, New Hampshire/U.S.A. expressed as g fresh weight/cm^2 (dry weight = 10% of fresh) (from Mathieson and Burns 1975).

Mathieson and Burns (1975) evaluated the effects of differential levels (careful, moderate and total) and times of harvesting on the reproduction of Chondrus **(Fig. 17).** Carefully and moderately harvested plots of July were at or near control levels (80%) of reproduction after nine months of regrowth; similar December harvests were at 20% and 10%, respectively, of control levels after four months (April) and near control levels after a year. Totally harvested quadrats (both July and December) took over three years to reach control levels. Mathieson and Burns (loc. cit.) summarized the reproductive capacity of Chondrus on totally harvested quadrats established for 20 consecutive months (see previous description). Reproductive structures were found after 13 or more months. In addition, no intact frond less than 2 cm was reproductive. See Boney (1965) regarding further details on the effects of harvesting, including the percentage of holdfasts and juvenile fronds collected by various harvesting gear.

Figure 17. Seasonal changes in reproductive activity in Chondrus crispus populations within the low inter-tidal zone at Rye Ledge, New Hampshire, U.S.A., following harvesting at various levels (1/3, 2/3 and with residual holdfast) in July and January, 1970 (from Mathieson and Burns, 1975).

5. PRODUCTIVITY OF THE RESOURCE

5.1 Standing stock and yield
5.2 Physical and biological factors affecting yield
5.3 Genetic improvement of wild stocks
5.4 Contributions of sexual and vegetative reproduct ion and regeneration
5.5 Enhancement of wild stock environments

The annual landings of Irish moss within the Canadian Maritime Provinces, including a "mixture" of Furcellaria lumbricalis Lamouroux from Prince Edward Island (P.E.I.) since 1966 are summarized in Table 2. The latter material from P.E.I. in Marine Plant Harvesting District #4 (i.e. MPHD 4, cf. Fig. 19) consists of 50 percent "moss" and 50 percent Furcellaria harvested as "storm toss". It has been purchased by Prince Edward Island Seaweeds Co. Ltd., a subsidiary of the Danish Company Litex. since 1974 Furcellaria has constituted 13.0% of the P.E.I. harvest. Between 1948 and 1961 annual landings were similar for both Nova Scotia and P.E.I. Landings from Nova Scotia increased by 39% in 1962 and remained at these levels until 1979. Since 1981, landings have dropped to 1953-54 levels. Sharp and Roddick (1982) analyzed the 1978 to 1980 MPHD 12 fishery, which accounted for 75%-95% of the Nova Scotian annual harvest. The landings decreased 48% in this period due to the following reasons: bio-mass was down 25%; there were 28% fewer daylight low tides; weather conditions were poor; and Irish moss returns/kg were not competitive with other fisheries.

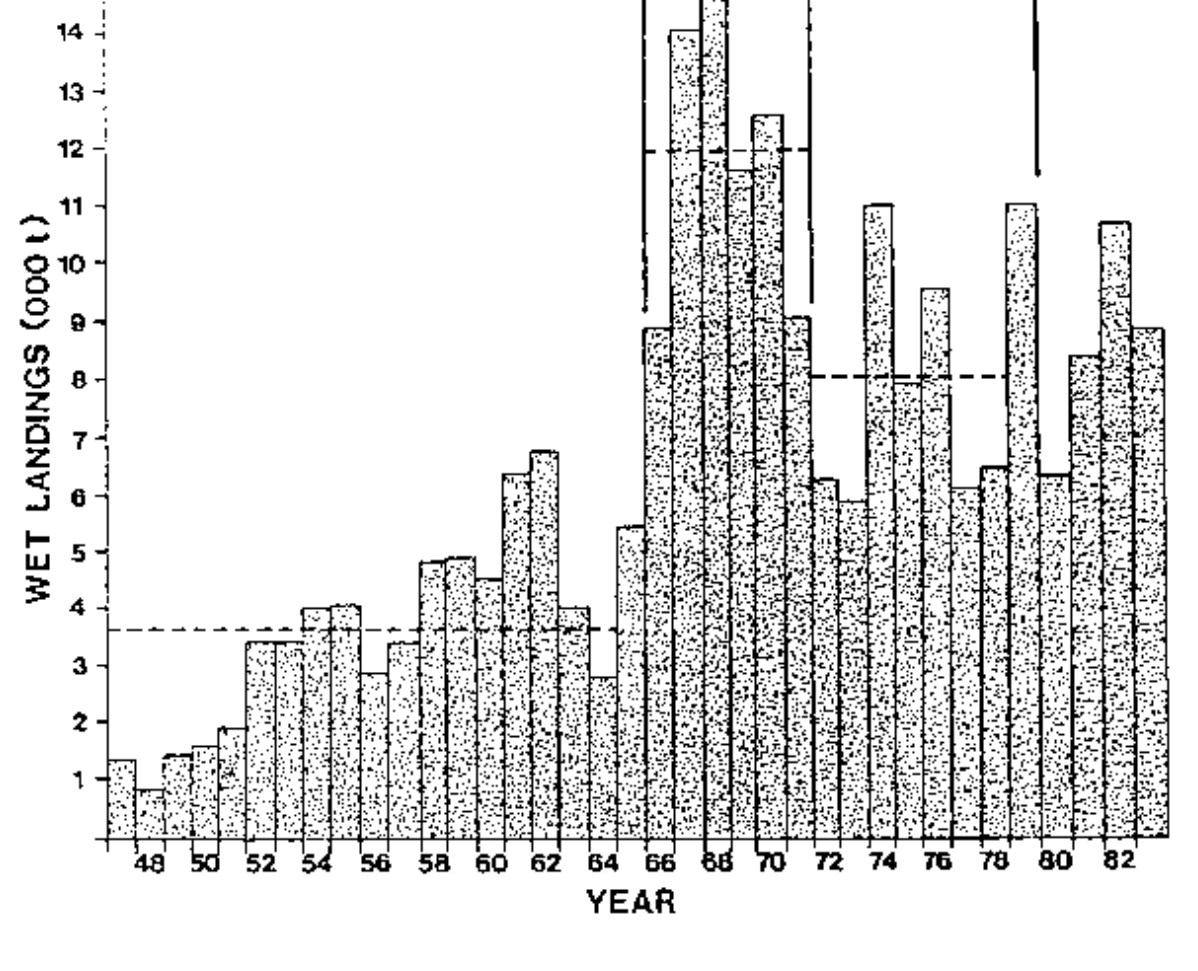
Landings from P.E.I. increased markedly in 1966, and nearly doubled again in 1967. Subsequently, they peaked in 1970 and 1974 (30/000 t) and then dropped to 15/000 t by 1982. The causes of the latter decrease were twofold. First, after 1974, demand decreased, coincident with the success of the Philippine Eucheuma spp. harvest (Parker, 1976). The direct result was a reduction in, or a closure of, buying efforts in marginally productive districts (e.g. MPHDs 5, 6, 7, and 9). Secondly, biomass in MPHD 1 appeared low. Pringle (1981) showed that the wild oscillations in landings **(Fig. 18)** were due to standing crop fluctuations and not effort and price/kg fluctuations. Biomass in 1978 on the Cape Gage bed was the lowest measured in the previous 11 years **(Fig. 20).**

Table 2. The landings of Irish moss (includes Furcellaria sp. in P.E.I. from 1966) per Canadian Maritimes province between 1948 and 1982.

Year	Nova Scotia (MT)	New Brunswick (MT)	Prince Edward Is. (MT)	Total Maritimes (MT)	Percentage of total harvest from MPHD 1 and 12
1948	1,255.0	-	1,327.7	2,582.7	
1949	2,784.1	-	2.220.4	5,004.5	
1950	3,030.4	-	2,126.4	5,156.8	
1951	3,891.8	-	2,538.2	6,430.0	
1952	4,511.8	-	4,000.4	8,512.2	
1953	5,396.4	33.2	4,813.2	10,242.8	
1954	6,583.2	-	5,240.0	11,823.2	
1955	7,834.5	-	5,174.1	13,008.6	
1956	6,841.8	-	4,204.1	11,045.9	
1957	6,942.7	-	4,845.0	11,787.7	
1958	8,015.4	-	6,795.9	14,811.3	
1959	6,660.9	4.0	5,373.6	12,038.5	
1960	7,259.0	4.0	5,678.6	12,941.6	
1961	7,014.5	139.5	0,430.0	15,584.0	
1962	11,491.3	397.2	7,882.2	19,770.7	
1963	11,903.2	49.5	4,779.5	16,732.2	
1964	9,386.8	196.4	3,238.1	12,821.3	
1965	10,069.1	-	7,790.4	17,859.5	
1966	11,634.5	431.4	111,120.0	23,185.9	
1967	13,755.4	519.0	[1]21,784.5	36,058.9	
1968	14,613.2	565.4	[1]24,389.1	39,567.7	
1969	18,568.6	1,707.3	123,540.4	43,816.3	
1970	14,224.1	3,547.3	[1]30,237.2	48,008.6	
1971	12,017.7	1,496.8	[1]23,074.1	36,588.6	
1972	9,676.4	1,085.9	113,853.2	24,615.5	
1973	10,673.2	1,034.5	[1]22,328.6	34,036.3	
1974	15,378.2	4,696.4	[1]30,326.2	50,400.8	[2]56.8
1975	14,158.5	3,271.9	[1]18,958.3	36,388.7	[2]63.9
1976	10,653.5	565.5	[1]16,293.3	27,512.3	[2]83.1
1977	12,199,5	1,010.1	[1]12,000.1	25,209.7	[2]76.0
1978	13,155,5	985.6	[1]15,356.5	29,497.6	[2]68.9
1979	9,463,8	687.5	[1]17,840.1	27,991.4	[2]77.3
1980	7,036,3	1,091.1	[1]15,929.5	26,050.6	[2]62.8
1981	6,598,6	763.9	[1]14,707.3	22,069.8	[2]64.4
1982	5,207,5	661.7	[1]14,519.3	20,388.5	[2]65.9
1983	5,622,0	73.0	12,736.0	18,431.0	
1984	4,459,0	-	15,751.0	20,210.0	
1985	5,426,0	-	17,419.0	22,845.0	

[1] Includes "mixture" which constituted 13% of the harvest.
[2] The percentage of the total annual landings harvested in MPHD 1 and 12.

Figure 18. Annual Irish moss landings in MPHD 1 (Prince Edward Island, Canada) between 1947 and 1982. The broken horizontal lines represent the mean annual landing for each of three periods.



5.1 Standing stock and yield

Thirteen commercially important Irish moss beds have been identified in MPHD 1. Based on distribution of commercial effort (Pringle and Semple, 1984) seven of these beds **(Fig. 21)** yielded the bulk of the crop. In 1979 these seven beds were surveyed for their type of substratum, area, percent cover of Chondrus and other species (Pringle and Semple, 1983). The seven beds ranged in size from 16.3 ha (at Horses Head) to 104.4 ha (at Pleasant View), with their total area being 512 ha. The area of the remaining six beds would not exceed 100 ha; consequently, the total productive area in MPHD 1 is about 600 ha.

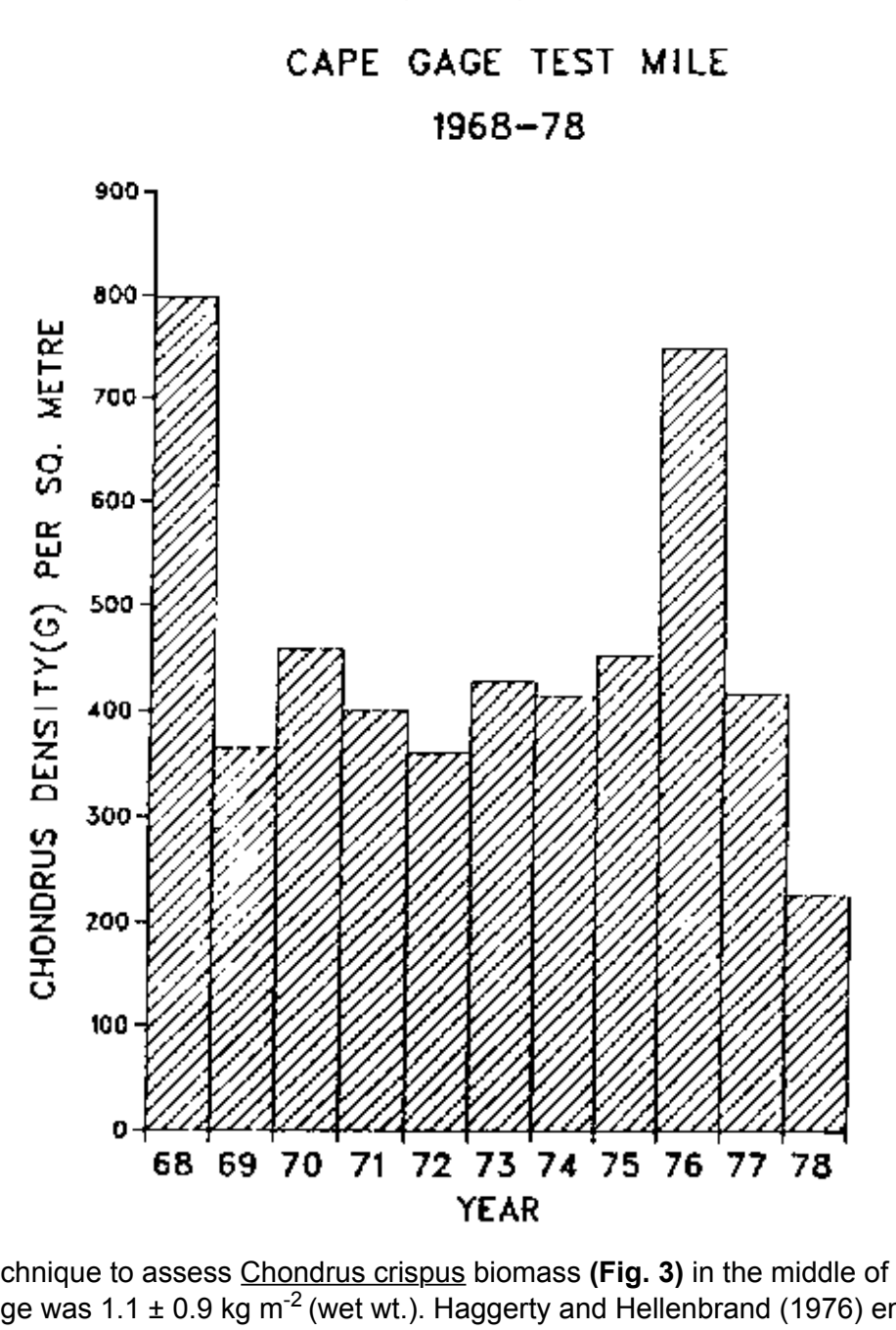
Figure 19. The designations of MPHDs 1-14 as per the Atlantic coast marine plant harvesting regulations. "Oceanic" Nova Scotia extends from the southeastern portion of MPHD 12 to the eastern portion of MPHD 10.

Annual landings for MPHD 1 are available from 1947 to the present **(Fig. 18).** The mean annual landing (wet wt.) between 1966 and 1971 was 12,000 t (Pringle, 1981); this value declined to 8,029 t between 1974 and 1982. The respective yields for the former and latter periods were 20 and 13.4 t/ha or 2.0 and 1.3 kg/m² respectively.

Preseason standing crop was measured on the Cape Gage Irish moss bed (cf. Pringle and Semple, 1983 for location) between 1968 and 1978, using a point transect technique (Johnstone and Herring, 1968). The mean annual standing crop fluctuated markedly through this period **(Fig. 20),** ranging from 0.23 kg/m² (1978) to 0.80 kg/m² (1968). The estimated standing crop for this 92 ha bed was 211.6 t in 1978 and 736 t in 1968.

A modified, random stratified, sampling technique (Pringle and Semple, unpublished) was employed in 1980 to assess preseason standing crop in MPHDs 1, 2, 6, 7, and 9 **(Fig. 19; Table 3).** The total macrophyte standing crop/m² (dry wt.) ranged between 24.5 g(MPHD 7) and 251.6 g (MPHD 9). Irish moss standing crop (dry wt.) ranged between 12.8 g/m² (MPHD 6 - by catch was 81.6%) and 199.5 g m^{-2} (MPHD 9). As summarized in **Table 3,** the catch per unit effort (i.e. CPUE) values for the dragrake "winchers" (cf. Section 7.0) employed in each district ranged from 141 to 470 kg/h (dry weight) in MPHD's 6 and 2, respectively.

Figure 20. The mean standing crop/m² of Chondrus crispus (i.e. all that could be removed by SCUBA divers) on the Cape Gage (Prince Edward Island) commercial Irish moss bed (MPHD 1) between 1968 and 1978.



Pringle and Semple (1980) used a point transect technique to assess Chondrus crispus biomass **(Fig. 3)** in the middle of MPHD 12. At the end of the harvest season in August, the mean standing crop throughout the range was 1.1 ± 0.9 kg m^{-2} (wet wt.). Haggerty and Hellenbrand (1976) employed a qualitative assessment technique. That is, a sled with a SCUBA diver was towed along the transects, while the percent cover was estimated and converted to biomass using fresh weight harvested from selected quadrats. An estimated 1,600 ha of commercial beds occurred in this area between the eulittoral and -4m. Chondrus wet weight/m² from 0 to -1.8 m, -1.8 m to -3.6 m and >-3.6 m was 1.5, 0.64 and 0.46 kg, respectively; a crude estimate of standing crop would be 13,920 t (i.e. 1,600 ha x 0.87 kg/m²). The mean annual handrake (see Section 7.0) landing for 1975/1976 was 12,405 t. Sharp and Roddick (unpublished data) demonstrated that the prime harvest area accessible to handrakes was above -1 m below chart datum. Thus, they concluded that only 800 ha is accessible to handrake harvesters in MPHD 12.

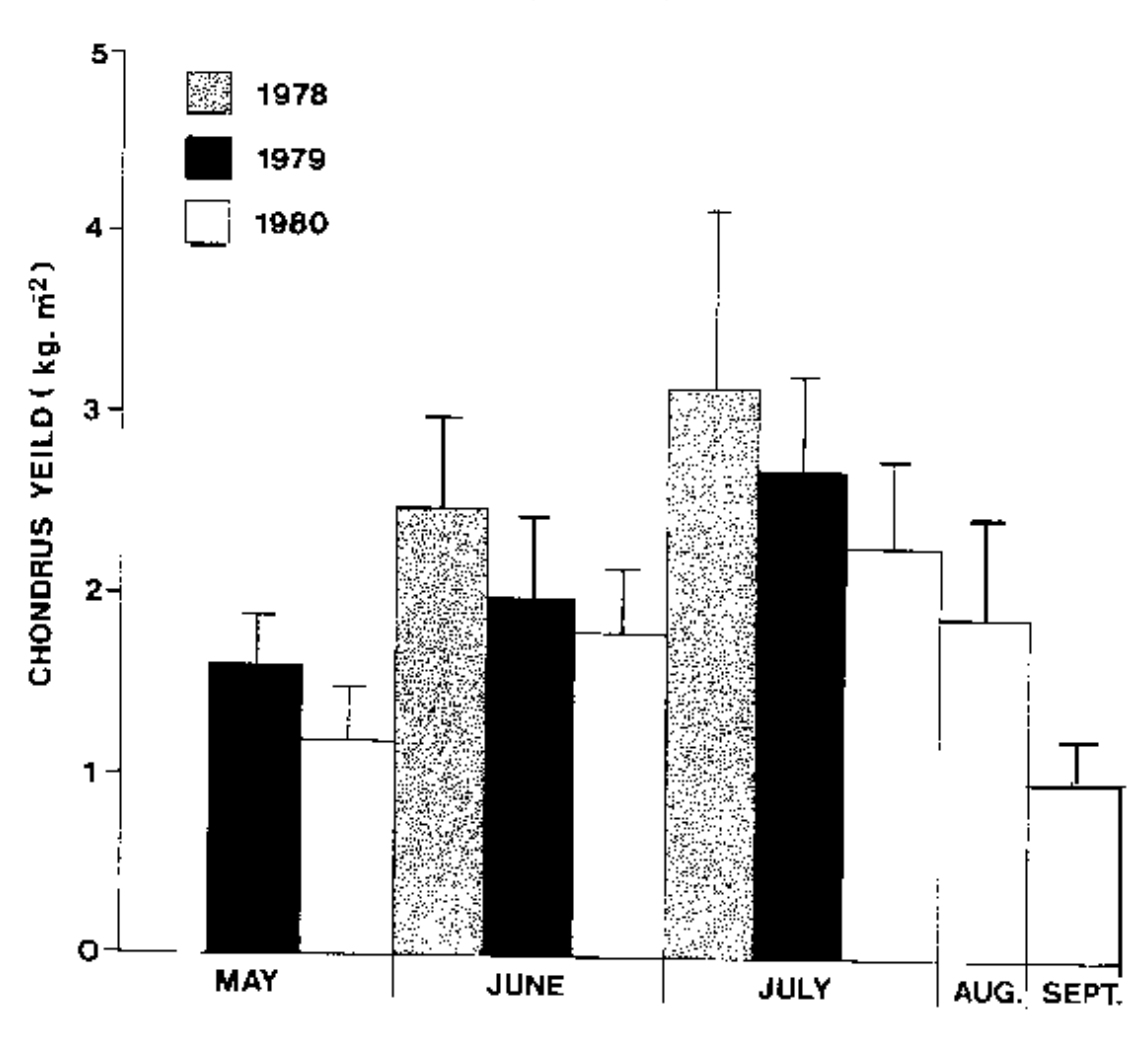
Figure 21. The location of the seven major commercial Irish moss beds in MPHD 1 (Prince Edward Island) between 1975 and 1981.

Table 3. Preseason CPUE and biomass of Chondrus and other taxa in commercial Irish moss beds in Marine Plant Harvesting Districts 1, 6 and 7

		Biomass (g-1m² = dry wt.)					
District	Bed	CPUE (kg h^{-1})	Chondrus	Other Species	Total Total	% Chondrus	% Other Species
6	Chelton Beach	141.9	35.4	7.8	43.2	81.9	18.1
	Redhead	249.7	12.8	56.7	69.5	18.4	81.6
7	Spruce Point North & south	213.8	24.3	0.2	24.5	99.2	0.8
1	Roseville South(Sullivan's)	280.4	-	-	-	-	-
	Pleasant View	306.5	38.4	3.0	41.4	92.8	7.2
2	Coop Dryer (Anglo)	470.7	101.2	7.2	109.6	92.3	7.7
	Sea Cow Pond North	454.0	96.1	4.6	100.7	95.4	4.1
9	Cape Jack	230.0	199.5	49.7	249.2	80.1	19.9
	Blue Rock	296.7	165.2	86.3	251.6	65.7	34.3

To assess annual yield/m² and to explain the above discrepancy/Sharp and Roddick (unpublished data) employed an experimental Irish moss bed (i.e. Lears Island that was closed to hand-raking after the 1977 season). Six successive biweekly harvests were made with a handrake having 5 mm tine spacings. Peak harvestable standing crop between May and September (1978-1980) occurred during early July **(Fig. 22).** The mean yield per harvest was 0.75 kg/m² or 4.5 kg/m² over the three month period. The mean yield per crop was 0.95 kg/m² when harvested monthly for four successive months (total yield was 3.8 kg/m²). There was a complete recovery of biomass with bi-monthly inclusive harvests between June and September.

Figure 22. Harvestable Chondrus crispus biomass/month between 1978 and 1980 on the "closed-to-raking" Lears Island/Nova Scotia, commercial Irish moss bed (MPHD 12).



The Whitehead Island commercial Chondrus bed above -1 m² consists of 12/078 m². Its May biomass was 2.6 ± 1.6 kg/m². The cumulative yield from the harvestable zone of this bed on four test harvests was 2.8 kg/m² or 33,818 kg. However, this estimate did not include the crop removed by commercial harvesters which was estimated at 3.0 kg/m² (wet wt.).

5.2 Physical and biological factors affecting yield

Chondrus crispus, although ubiquitous through eastern Canada (Ffrench, 1971), is commercially harvested in only a few areas with >60% of the annual harvest coming from MPHDs 1 and 12 **(Fig. 19)**. Extensive sea urchin (Strongylocentrotus droebachiensis) grazing in southern and southeastern New foundland (Himmelman, 1980; Hooper, 1980) restricts Chondrus to the eulittoral. Small, sublittoral beds occur in isolated areas of western Newfoundland (Lilly, 1968). They were infrequently harvested in the early to mid 1970s. Standing crop, however, appeared insufficient to sustain a commercial buying/drying operation (Norve, personal comm. to J. Pringle).

Bell and MacFarlane (1933) divided the Nova Scotia biogeo-graphic province (see Watling, 1979) into the following districts based upon the distribution of benthic algal taxa: (1) coastal Bay of Fundy including the western portion of MPHD 12; (2) Nova Scotia's oceanic coast (MPHD 11 and the eastern portion of MPHD 12); and (3) coastal Gulf of St. Lawrence (MPHD 1-9). The flora within each region is uniform with respect to dominant forms and growth characteristics.

The oceanic climate varies between these three regions. For example, MPHD 12 occurs shoreward of an upwelling area (Garrett and Louck, 1976); hence, nutrients for kelp growth are not limiting throughout the year (Gagne et al., 1982), while light may be. Annual summer water temperatures peak at 12°C. By contrast, nutrients are limiting for 8 months of the year along oceanic Nova Scotia (Gagne et al., loc. cit.). Here, late summer surface water temperatures peak at 16°C. In the southern Gulf of St. Lawrence, waters are even warmer, averaging 17°C in summer with 23°C peak surface temperatures. Nutrient levels are ~ 3 times higher than those on the Scotian Shelf (Bugden et al., 1982).

The optimal light requirements for Chondrus crispus are lower than for many intertidal algae (Luning, 1981). Kanwisher (1966) noted a compensation point of only 25 ft. candles (6.3 m e/cm²/sec.) or less than 1% of full sunshine. The plant's low compensation point is no doubt an important factor accounting for the high productivity of Chondrus in both the fog bound coast of MPHD 12 and the turbid waters of MPHD 1.

High production values are only important in establishing a low valued macrophyte (Chondrus equals $0.14/kg wet) as a commercially important species if biomass is large, and the physical environment, including weather, permits efficient harvesting. The tidal range in MPHD 12 is very large; in this district C. crispus has the widest vertical distribution, and it is the second most abundant macrophyte **(Fig. 4).** The rugged granitic substratum also provides a large surface area **(Fig. 23).** The tidal range in the southern Gulf of St. Lawrence is low, but the sandstone, nearshore ocean bottom slopes gently seaward. Consequently/although the center of a commercial bed can be 1 km from shore in MPHD 1, the mean depth of the beds is only 3.0 m below chart datum (Pringle and Semple, 1983). The prominent substratum in these beds is sandstone ledge (x 31%). Four other types of substratum were identified based upon their size (fines, cobble, rock, and boulders). A positive correlation was recorded between percentage of ledge and Irish moss cover in each bed (Pringle and Semple, 1983). The deposition of fines over a ledge or the movement of boulders and rock by water and ice reduces the standing crop.

Figure 23. A typical Irish moss handraker and hand powered (oars) boat from MPHD 12. Note the rugged granitic, glacial till of Lobster Bay, Nova Scotia (1976).

The maximum frond size varies significantly (P £ 0.05) between Gulf districts (Pringle and Semple, unpublished data, in **Table** 4). Harvesting pressure and local environmental conditions may cause this variability with the mean frond dry wt. being much greater in MPHD 9 than in MPHD 1/6/and 7. Harvesting pressure is extremely high in District 1 (Pringle and Semple, 1984) and much lower in Districts 7 and 9. The beds are deeper in MPHD 9, which may be the cause of the larger fronds.

The single most important cause of frond and holdfast mortality in commercially important cropped beds is raking. Pringle (1979) showed that 5% and ~ 30% of the fronds in the harvests from MPHDs 12 and 1/respectively/were attached to holdfasts.

Table 4. Catch characteristics of preseason harvesting trials in districts 1, 2, 6, 7 and 9

Location	Mean Frond No./Sample Unit	Frond Mean Dry Wt. (9)	Percentage Chondrus	Percentage By Catch	% (by weight) of each Morphological Class in the Harvest					
					I	II	III	IV	V	VI
District 1 (Sullivan's)	1638.8±314.1	0.17	85.0	15.0	0.5	1.9	2.3	31.1	53.7	10.5
District 1 (Pleasant View)	1850.5± 87.9	0.19	79.2	20.8	0.5	1.8	2.4	17.8	68.9	8.6
District 2 (Anglo)	1259.7± 138.4	0.23	79.0	21.0	0.2	2.5	0.8	37.3	49.7	9.4
District 2 (Sea Cow Pond)	1333.3± 326.6	0.20	86.2	13.8	0.4	2.0	0.8	33.4	56.1	7.3
District 6 (Egmont Bay)	504.8± 150.9	0.15	15.0	85.0	2.2	3.4	1.5	1.6	79.8	11.5
District 6 (Chelton Beach)	3485.8± 611.9	0.08	61.1	38.9	1.3	7.3	9.8	18.3	54.5	8.8
District 7 (Pt. Sapin)	1556.3± 309.1	0.18	97.3	2.7	0.4	3.6	6.7	43.8	37.4	13.2
District 9 (Blue Rocks)	950.2± 59.0	0.35	93.5	6.5	0.1	0.2	0.1	0.5	92.3	6.8
District 9 (Caps Jack)	977.6± 86.5	0.29	86.3	13.7	0.1	0.3	0.2	1.3	90.1	8.1

Although dragrakes tend to select mature fronds, 35.8% in the harvest vs. 12.2% in the beds **(Tables 5 and 6),** immature fronds occur in the harvests (63.9% vs. 87.8% in the bed). Handrakes from MPHD 12, on the other hand, have 73.5% mature fronds in their crop (Pringle and Semple, 1978).

Table 5. The percentage of mature and immature Chondrus plants in both the commercial beds off Caps Cage, Prince Edward Island, and in commercial harvests from the same area during 1976.

Source or samples	Immature plants (I and II) (%)	Mature plants (III and IV) (X)
Scraped from the benthos	87.8	12.2
From the harvesters	63.9	35.8

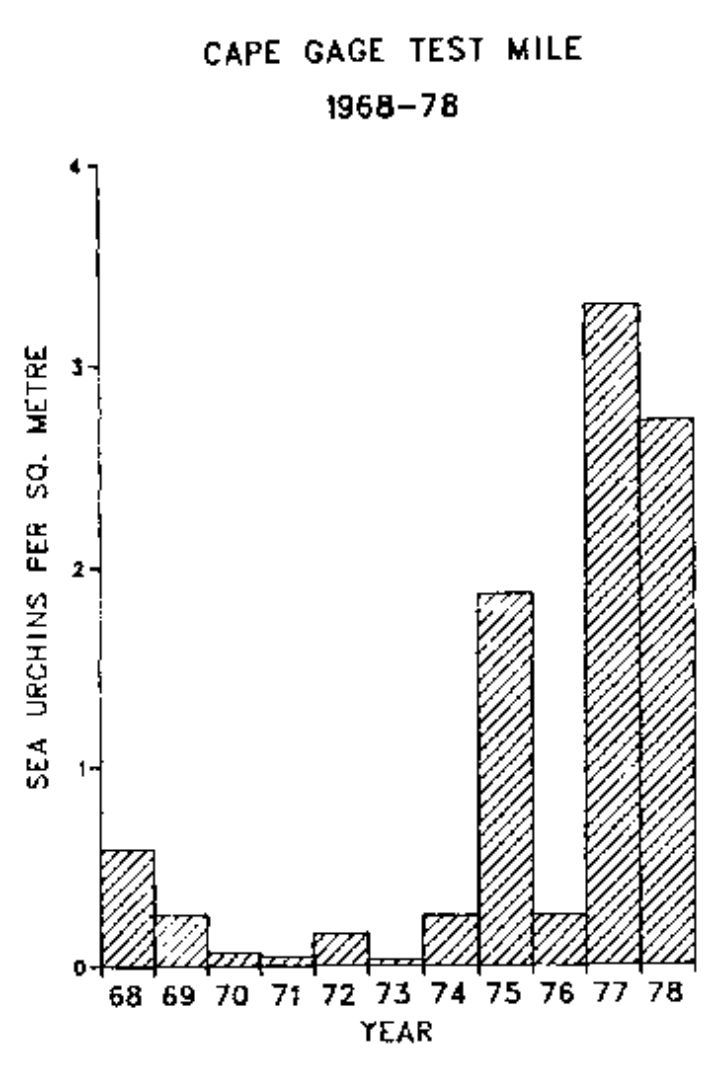
Table 6. The number and percentage of the commercial harvest that was mature, or immature, from the Miminegash, Prince Edward Island, area during June, July, and August, 1976.

Date of Harvest	Immature Chondrus		Mature Chondrus	
	Number of Plants	Percent of Harvest	Number of Plants	Percent of Harvest
June 7-9	728.3	68.0	342.7	32.0
June 14-17	469.4	61.4	294.5	38.6
July 16-21	784.3	67.6	376.5	32.4
August 18-19	594.2	57.7	435.5	42.3

The major herbivore in northwest Atlantic waters is the green sea urchin, Strongylocentrotus drobachiensis (cf. Pringle et al., 1980). It limits the abundance of sublittoral macrophytes throughout the Bay of Fundy and southern and eastern Newfoundland. Episodic overgrazing may occur along oceanic Nova Scotia (e.g. MPHD 11, see Miller, 198; Miller and Colodey, 1983). Urchins are rare in the commercially important beds of MPHD 12, but they are locally abundant in the southern Gulf of St. Lawrence. Sea urchins in the Cape Gaqe bed (MPHD 1) ranged in density from <0.10/m² (1973) to 3.0/m² during 1977 and 1978 **(Fig. 24).** Sea urchins tend to graze unattached macrophytes (Mattison et al., 1977) unless starved, which may explain their frequent aggregation along the borders of dragraked beds (e.g. MPHD 1 and 2) where many unattached fronds occur. Evidence of extensive overgrazing has not been observed.

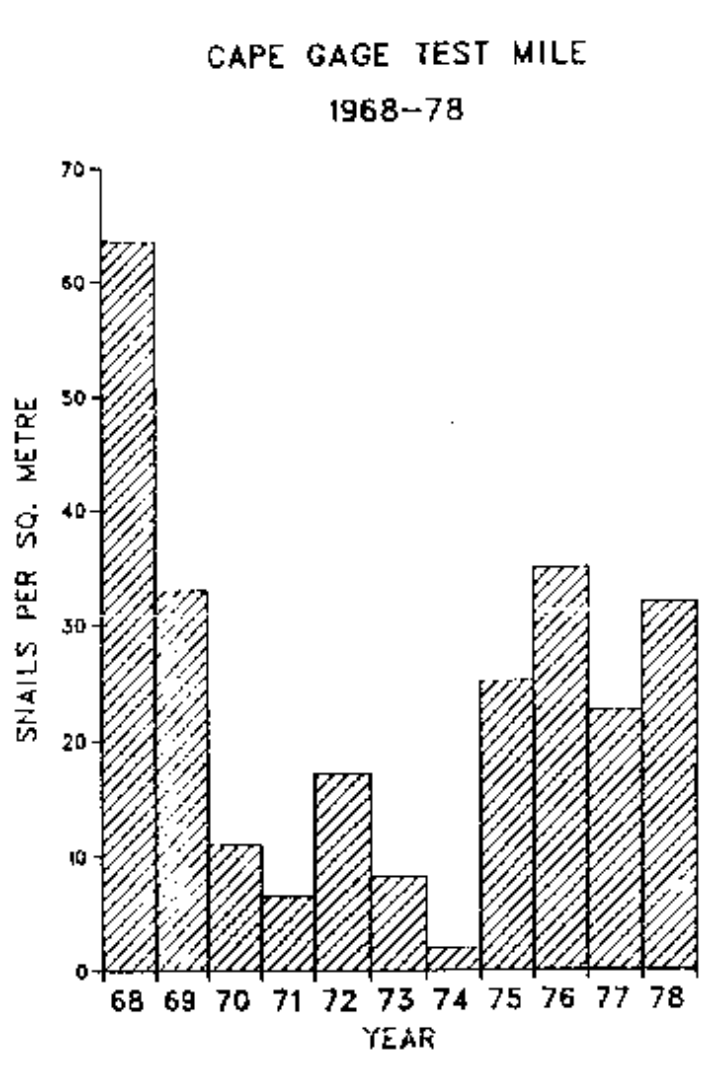
Littorina spp. may also occur abundantly in MPHDs 1 and 12, but extensive grazing has not been noted. The mean densities of snails in the former district can range from 3 to >60/m² **(Fig. 25).**

Figure 24. The mean sea urchin (Strongylocentrotus droebachiensis) density/m² on the Cape Gage, Prince Edward Island, commercial Irish moss bed (MPHD 1) between 1968 and 1978.



The holdfast of Irish moss adheres well to the substrata, increases in diameter annually (Taylor et al., 1981) and may bear up to 100 fronds of varying size classes (Pringle, unpub. data). With optimal harvesting (MacFarlane, 1968), larger fronds are selectively removed over immature fronds, and the plant's holdfast is left intact for vegetative regrowth. None of the other northwest Atlantic macrophytes occurring in the same zone has such an extensive vegetative recruitment system, and this may explain the competitive dominance of Chondrus crispus **(Table 3 and Fig. 4)** in commercially raked beds (Pringle, unpublished data). For example, many fishermen in various districts have observed that the size of beds increases following a few years of dragraking. That is, competitors are selectively removed from the margins, allowing C. crispus to dominate. Hanic and Pringle (1978) in a series of outplanting studies noted that Irish moss was the competitive dominant over Fucus spp. and Laminaria spp. on cement blocks placed at +5 cm. in MPHD 12 (also cf. Pringle and Semple, 1980).

Figure 25. The mean snail (Littorina spp.) density/m² on the Cape Gage, Prince Edward Island, commercial Irish moss bed (MPHD 1) between 1968 and 1978).



Grazer control in commercially important Irish moss beds has not been attempted. Prior to the massive declines of sea urchins due to disease (Miller and Colodey, 1983), quickliming was successfully attempted in localized habitats (Bernstein and Welsford, 1982). Large scale disease of locally occurring/wild Irish moss has not been recorded.

5.3 Genetic improvement of wild stocks

The potential exists for genetic manipulation within wild Irish moss stocks. The value of the resource, however, precludes this happening in the near future. Previous genetic studies carried out on economic seaweeds, with the exception of the Chinese breeding experiments with Laminaria japonica, have tended to be in concert with aquaculture ventures. Simple strain selection studies with Chondrus crispus have improved its growth rates, carrageenan concentrations, susceptibility to epiphytes, etc. (Chen et al., 1982; Chen and Taylor, 1980; Cheney and Mathieson, 1977, 1978, and 1979; Cheney et al., 1981). Wild stocks of Chondrus were assayed for genetic differences using starch gel electrophoresis (Cheney and Mathieson 1977). Differences were noted. As well, Cheney et al. (1981) showed that biomass productivity differed amongst strains grown under identical conditions. However, they warned growth differentials might be environmentally specific. Cheney (1984) has gone on, with some success, to explore macrophyte genetic engineering using protoplast fusion-somatic hydridization techniques.

5.4 Contributions of sexual and vegetative reproduct ion and regeneration

Plants of Chondrus crispus following 49 years of handraking in MPHD 12 still maintain a dense carpet **(Fig. 4),** whereas in MPHD 1 between 1.2-21.1% of the prime substrata (sandstone ledge) is devoid of plants (Pringle and Semple, 1984). They hypothesized that the major source of recruits in MPHD 1 was via vegetative growth of upright shoots from existing holdfasts. Spores repopulate barren areas (Bhatacharya, 1985; Pringle and Semple, 1980) caused by ice scouring, handrake holdfast removal, dragrake boulder rotation (Sharp and Roddick, 1980), grazing etc. but these barrens are a small portion of the bed.

The adherence of Chondrus crispus holdfasts to sandstone in the southern Gulf of St. Lawrence (i.e. MPHD 1) is more susceptible to interference (Pringle, 1979; Taylor et al., 1981) than that on the granite substratum of MPHD 12. The heavy harvesting intensity (Pringle and Semple, 1984) in MPHD 1 plus ice scouring, annually creates barrens, which can only be successfully recolonized by *C.* crispus sporelings. Pringle and Semple (unpublished data) and Hanic (unpublished data[3]) have shown that Chondrus recolonization by spores will occur on chisel-cleared, sandstone surfaces. However, recolonization of cement outplant blocks(Hanic and Pringle, 1978) was considerably slower in M'PHD 1 than in MPHD 12. Colonization of blocks occurred swiftly in MPHD 1 when there was an overhang of reproductively mature fronds (Pringle, unpublished data), while, elsewhere, C. crispus spore-lings were sparse. Similarly, clay pottery, control outplant units (Hanic and Pringle, 1978) were rarely colonized by in situ produced spores.

[3] Dr. L. Hanic, Professor of Biology, University of P.E.I., Charlottetown, P.E.I.

5.5 Enhancement of wild stock environments

Few investigations have attempted the enhancement of wild Chondrus crispus production. Marshall et al. (1949) conducted weeding experiments on the British coast, but their techniques were not cost effective, although physically possible. Hand-raking at sheltered sites within MPHD 12 removed the "green thread weed" Chaetomorpha spp. from C. crispus, but again it was not cost effective(MacFarlane, 1968). MacFarlane (1952 and 1958) also found that raking reduced encrusting polyzoans on C. crispus.

Pringle (unpublished data) designed trial techniques to "reseed" barren areas in MPHD 1. To date, these techniques have not been employed.

6. METHOD OF HARVESTING AND HARVESTING CYCLE

6.1 Annual cycle of operations
6.2 Manpower productivity
6.3 Alternate employment

6.1 Annual cycle of operations

Individual inshore fishermen in eastern Canada tend to prosecute a number of fisheries. Of these, lobstering is usually the most important (Pringle et al., 1983). Thus, if and where possible, the auxiliary fisheries seasons are dictated by the seasonal occurrence of the lobster fishery which varies markedly between different Lobster Fishing Districts. For example, in MPHDs 1 and 2, the lobster fishing seasons are August 10 - October 10 and May 1 - June 30, respectively, while the corresponding opening dates for Irish moss harvesting are June 10 and July 1. The lobster fishing' season closes May 15 in MPHD 12, and the Irish moss season opens June 1. As a result of this schedule, bona fide fishermen begin mossing prior to the influx of students into the fishery in late June (Sharp and Roddick, 1982). Several other factors may influence the Irish moss harvesting seasons, including annual cycles of weather, tides, frond growth and reproduction, carrageenan concentration and epiphyte abundance (cf. MacFarlane, 1968).

Irish moss is harvested from small boats in MPHD 12 (see Section 7.0) 2 h on either side of low tide. The extreme tide range and fine summer weather permit this successful harvesting technique (40 years - Sharp and Roddick, 1982). In attempting to explain the marked (48%) decline in annual landings between 1978 and 1980, they note that the latter year's season had 28% fewer extreme low tides during daylight than the former year (cf. Sharp et al., In Press).

Frond growth rates increase in late spring, prior to season opening, in both MPHD 1 (Pringle, unpub. data) and 12 (Sharp and Pringle, unpub. data), but maximum growth does not occur until late summer/early fall - i.e. long after the harvestable biomass has been removed. Where exploitation rates are high, as in MPHD 1 (Pringle and Semple, 1984), this may have resulted in overharvesting (Pringle, unpub. data).

A study of the reproductive phenology of Chondrus crispus in MPHD 1 is currently underway. Initial data available from an experimental harvesting study **(Table 7)** shows that the percentage of carposporangium- and tetrasporangium-bearing fronds peaks in May and June, respectively, i.e., just prior to or during the start of the annual harvest. Nevertheless, decreased spore production may be the cause of persistent barrens within MPHD 1 (Pringle and Semple, 1984). Reproductive activity peaks in the Gulf of Maine during late fall/early winter following the harvest (cf. **Fig. 7 and 8**). Although this is a concern, it is presently felt that spore recruitment plays only a minor role in this area as compared to vegetative recruitment.

Table 7. Percentage carposporangial and tetrasporangial bearing fronds in the crop of experimental Irish moss dragraking in MPHD I (Prince Edward Island) in 1977 (n = 224.003).

	Percent reproductive fronds	
Month	Carposporangial bearing	Tetrasporangial bearing
May	6.9	6.1
June	5.3	8.4
July	2.9	4.4
August	2.3	3.4

Within the southern Gulf of St. Lawrence (i.e. MPHD 1 and 2) the inshore fishing grounds are ice-bound from early December to about mid April. High winds in early spring and late fall blow across the exposed grounds. This tends to shorten the fishing seasons further. Another problem is partially silted harbors, which make entrance during storms dangerous. Prior to 1977 (regulation promulgation), the Irish moss season was initiated by harvesters usually in late April to early May. The season opening has since been moved back to June 11 and July 1 in MPHDs 1 and 2 respectively (Pringle, 1985), due to concerns regarding both recruitment and growth overharvesting.

A study of seasonal spore production in an experimental dragraking area (MPHD 1) is only now underway. A preliminary evaluation of the data for 1977 **(Table 7)** demonstrated the highest frequency of tetrasporangium-bearing fronds in June, while the percentage of fronds bearing carposporangia was maximal in May. If these data hold up, then there is a chance of recruitment overharvesting, particularly in MPHD 1. The holdfasts are attached to sandstone in this district. Thus, up to 30% of the harvested fronds are attached to holdfasts as opposed to <5% of the harvested fronds in MPHD 12 (Pringle, 1979). See Section 7.0 for further information regarding harvesting techniques, etc. Holdfast removal by dragrakes (particularly basket dragrakes, cf. Pringle et al., 1979), along with the coincidental occurrence of spore production and commercial harvesting may, in part, be responsible for the large percentage (14.5%) of barren substrata within MPHD 1's commercial beds. That is, 9.3% of the prime ledge substrata are barren within these beds (Pringle and Semple, 1983).

6.2 Manpower productivity

See Section 7.0.

6.3 Alternate employment

To attain a Canadian commercial fishing license for most fisheries one must be full-time or have ³ 60% of his/her total annual income derived from the fishing industry. The above described license procedure is in effect for the dragrake fishery in the southern Gulf of St. Lawrence (MPHDs 1, 2, 6-9). Individuals gathering "storm toss" in MPHDs 3-5 require no license (cf. Section 7.0); those desirous of handraking need not be "full-time" fishermen. Other sources of income (many are students in MPHD 12) for "storm toss" harvesters are from farms, as farm laborers; fishermen, school teachers, etc., and governmental (welfare) assistance.

7. EQUIPMENT USED FOR HARVESTING AND CULTURE OF SEAWEED RESOURCES

7.1 For wild resources

7.1 For wild resources

Irish moss is either harvested by gathering unattached fronds or by cropping attached fronds with a drag- or hand-rake. The major, commercially important beds in the southern Gulf of St. Lawrence are located in MPHDs 1-4 **(Fig. 19),** along the western, northwestern and northeastern shores of P.E.I. The average daily wind speed for P.E.I. is high. Wave surge is frequently sufficient particularly in the spring and fall, to crop the larger fronds (Classes IV and V, see Prince 1971). The latter fronds are tossed (hence the term "storm tossed") along the shore in windrows **(Fig. 26).** Beginning as early as 1927 in St. George Bay, Nova Scotia or MPHD 9 **(Fig. 19),** harvesters gathered this crop (MacFarlane, 1968; Pringle, 1976).

Figure 26. "Storm toss" harvesters forking windrowed Irish moss into trucks along MPHD 1 (Prince Edward Island). Note horse and rider gathering unattached Irish moss with a horse scoop (1976).

The Gulf of St. Lawrence is ice bound from late December to mid April. Often ice will be driven onshore by winds where it gathers in piles up to 5 m thick. During ice breakup/these piles may be wind driven seaward, shoreward and/or laterally several times. Bottom ice scouring removes attached Irish moss crops (termed "spring moss") which may then be wind driven onshore. Harvesters are constantly checking the shore for "storm toss". Where the beach is accessible, searching is carried out on or in bicycles, horses, cars, trucks, tractors, etc. **(Fig. 27).** Elsewhere, the shore is surveyed from cliff tops.

Harvesters may enter the water wearing waterproof; chest length boots **(Fig. 28)** to gather the unattached "moss" concentrated in the surf; they will either pull a scoop with runners or dip the "moss" with a hand net **(Fig. 29).** Horses are also used to gather the unattached moss **(Fig. 30);** they are rigged with a "horse scoop" **(Pig. 26 and 27),** and the harvester either rides the horse into the water **(Fig. 26)** or sends the horse into the surf, guiding it from shore via long reins **(Fig. 30).**

The crop from this operation and the windrowed "storm toss" is forked into horse or tractor drawn wagons **(Fig. 29)** or truck beds **(Fig. 26).** It is then transported to a suitable location such as the harvester's yard or the border of an adjacent road **(Fig. 31 and 32)** for drying and the cleaning/removal of non-commercially acceptable material. The crop is then transported to a buying station.

Figure 27. "Storm toss" harvesters in MPHD 1 (Prince Edward Island) preparing to load horse scooped Irish moss into waiting vehicles (1976).

The land abutting the shores of the southern Gulf of St. Lawrence is frequently excellent farm land. The productive waters support a wide variety of fisheries with lobster as the mainstay of the inshore fishermen. The demand for Irish moss during World War II and the resultant economic value encouraged the gathering of "storm toss". Farmers with wagons, horses and tractors had an advantage over the fishermen in securing this moss. The fishermen in the late 1940s (A. Wedge, personal commun. to J. Pringle[4]) took the advantage from the farmers by going to sea and handraking from their fishing boats. The drag-rake in present use **(Fig. 33)** evolved from the handrake (Pringle et al., 1981). The dragrake weighs 25 kg, is 1 m wide and 0.9 m long; the 42 teeth, 12.5 mm x 12.5 mm x 20.0 cm, each spaced 6.5 mm apart, are secured to the bottom of a steel bar.

[4] Wedge, fisherman, Miminegash, Prince Co., P.E.I.

Dragrake boats are rigged for Irish moss harvesting in one of two ways, with the size of the vessel generally dictating the method **(Fig. 34).** Harvesters with smaller boats (7-10 m) use the "hauler" technique **(Fig. 35)** where up to 6 dragrakes are secured independently to the bulwark by rope (2.5 cm x 20 m). The boat is run in a circular direction when cropping. The dragrakes are returned to the boat via the lobster trap hauler **(Fig. 33)** which is a steel cone-shaped cap driven in a circular motion via the power takeoff of the vessel's engine. The skipper assists in the rake recovery operation.

Figure 28. "Storm toss" harvester equipped with rubber chest waders and modified "horse scoop" in MPHD 1 (Prince Edward Island). Harvester wades through the surf dragging scoop (1975).

"Winchers", vessels up to 14 m x 4.0 m are rigged with a centrally located iron spar (3.6 m x 10 cm); a pair of iron booms (5 cm x 8 m), secured at 45° angles to the deck amid ship **(Figs. 34 and 36)** and a pair of winches (12.5 cm diameter drum) forward of the boom base. Cable (9 mm x 60 m), attached to each drum, is strung through pulleys (10 cm in dia.) and attached to an iron tow bar.

Dragrakes are hooked in triplicate to the tow bar, but they are not attached laterally to each other. A set of dragrakes is used for both the starboard and port sides of the boat.

Figure 29. "Storm toss" harvesters gathering Irish moss from MPHD 1 (Prince Edward Island) waters with dip nets and loading it into a tractor drawn wagon just out of the picture (1975).

Figure 30. Horse and scoop entering surf to gather unattached Irish moss form MPHD 1 (Prince Edward Island) waters. Note long reins used by shore based harvester (1978).

Figure 31. "Storm toss" crop (Irish moss) drying along clay road verge in MPHD 1 (Prince Edward Island) Harvester is turning the crop with a lawn rake to permit faster drying (1979).

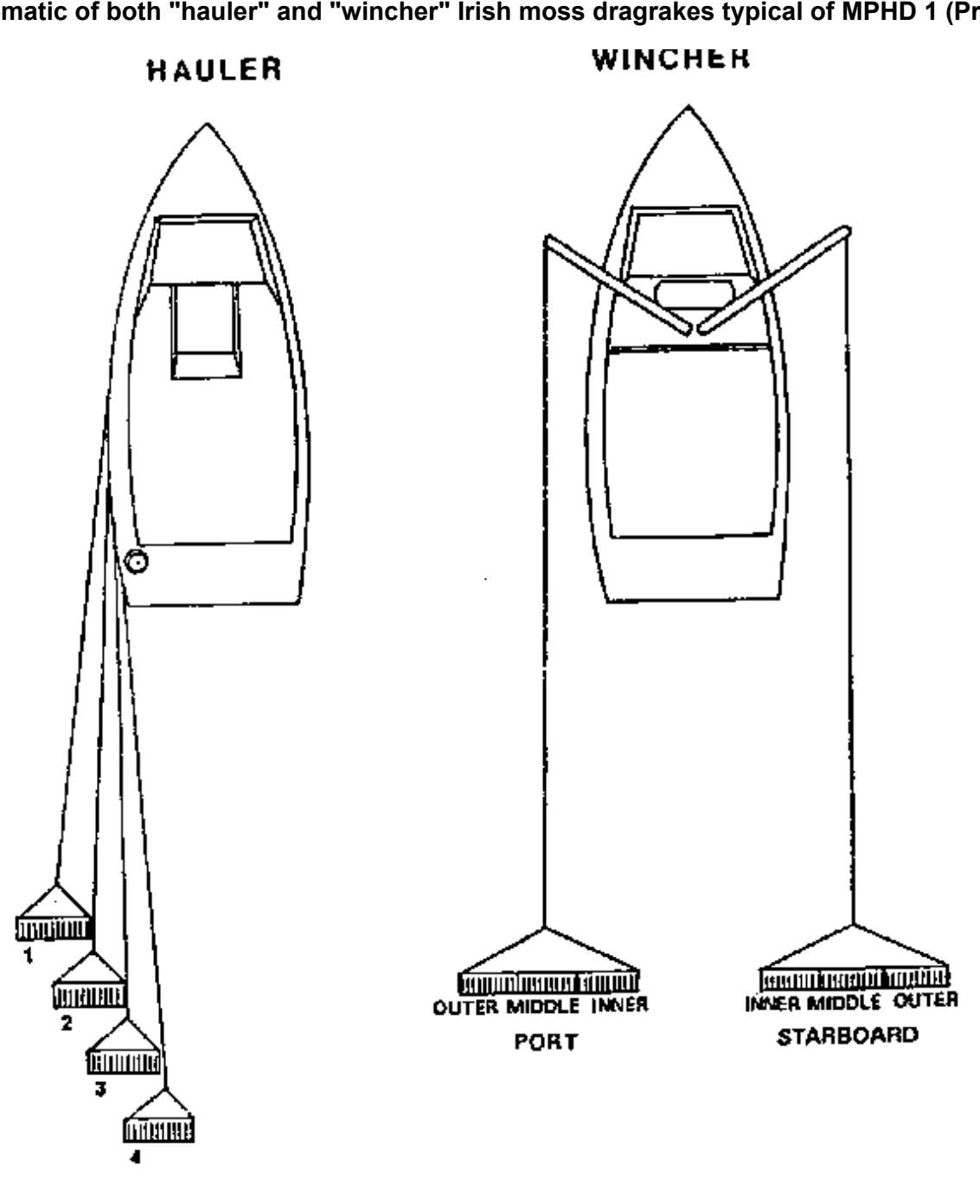
Figure 32. Children and mother "cleaning" (removing large, non-Irish moss, matter) "storm toss" harvest while it sundries in MPHD 1 (Prince Edward Island) during 1975.

Figure 33. "Hauler" boat captain (at lobster trap hauler) winding dragrake rope around lobster trap hauler (powered by a power-takeoff from boat engine) while the deckhand cleans a single dragrake (1975).

The boat, while harvesting, moves continuously on a straight course; the skipper runs the winches and the boat. While one set of dragrakes is cropping, the deckhand removes the harvest from the opposite rakes **(Fig. 37).** The crop is loosened from the tines with a couple of blows to the dragrake by an iron bar **(Fig. 38).**

Prior to the introduction of the Atlantic Coast Maine Plant Harvesting Regulations (cf. Pringle, 1976, for details), harvesting was often begun in April following ice breakup. Present regulations dictate a closed season from 11 October to 10 June in MPHD 1 and from 11 October to 30 June in MPHD 2. The number of haulers and winches operating in MPHD 1 and 2 in 1975 and 1976 is given in **Table 8.** The July increase in harvesters is due to the season opening in MPHD *2,* while the August decrease is due to diminished crops and the opening of the lobster fishing season.

Figure 34. Aerial schematic of both "hauler" and "wincher" Irish moss dragrakes typical of MPHD 1 (Prince Edward Island).



The daily mean number of harvesting hours per day for both haulers and winchers for each of the prime harvesting months of 1975 and 1976 is given in **Table 9.** The mean number of potential harvest days for June, July, and August during 1975-1982 was 13.4, 20.5, and 20.*3,* respectively. The mean length of time for each tow during 1975 and 1976 is given in **Table 10;** the two year (1975 and 1976) mean for harvester production for both haulers and winchers was 147.2 and 209.5 kg/h, respectively **(Table 11).** The mean area harvested by winchers and haulers was 7.2 and 6.2 ha/d, respectively (Pringle and Semple, 1984). Haulers and winchers cropped on average 1.1 and 1.72 metric tons/day respectively in 1975/1976 **(Table 11).** Mean annual production per harvester day (2 man-days per boat-day) in 1975/1976 for haulers and winchers was 0.55 and 0.86 t, respectively **(Table 12).**

Figure 35. A "hauler" (the steel booms for the winching technique are rigged as well as this boat was under charter for experimental raking studies) towing seven independently rigged dragrakes in the Pleasant View bed in MPHD 1 (Prince Edward Island) during 1977.

Figure 36. A typical "wincher" dragraking off MPHD 1 (Prince Edward Island). Note the midship attachment of the two steel booms. The winches are operated within the cabin by the skipper. Two cable blocks are visible at the distal end of each boom. The deckhand is resting on the Irish moss crop (1980).

Figure 37. Deckhand on a "wincher" cleaning crop from the port dragrake tines while the starboard dragrakes are cropping Irish moss. Three dragrakes are hooked in triplicate on both port and starboard (1975).

Figure 38. A "wincher" deckhand beating the dragrakes with a steel bar to loosen the tightly bound Irish moss harvest from the tines. Note the single chain bridle linking all three dragrakes to a single towbar. The equipment over the stern is the banned (1977) "basket dragrakes" and a hay fork for moving the crop within, and from the boat (1975).

Table 8. The number of both haulers and winchers observed harvesting the Irish moss beds in MPHD 1 and 2 (Prince Edward Island) in 1975 and 1976

Year	June	July	August
1975	119.8	211.2	63.0
1974	125.3	154.0	39.3

Accurate measures of the harvesting efficiency of dragrakes have not been made. Subjective estimates by SCUBA divers were 10-15% removal of harvestably mature fronds. Probably another 5% is removed but not tine bound; the latter probably forms a portion of the free-floating crop once gathered by basket dragrakes (Pringle et al., 1979 and **Fig. 38).** The free-floating crop is now either swept seaward by currents and lost to the annual yield or swept shoreward by waves and harvested as "storm toss".

About 75% of the Irish moss boats are multipurpose, inshore fishery vessels used in the lobster, herring and groundfish fisheries. Such multipurpose boats tend to be larger and better equipped electronically than those only employed for "mossing". Consequently, the range of boat costs is substantial, varying from about $5,000-25,000 (Canadian). Low interest government loans and grants were available in the past to construct inshore fishing vessels, but this program is no longer available. Boat and gear insurance is offered by the Department of Fisheries and Oceans, but frequently the fishermen fail to purchase it. Harvesters having worked 10 full weeks in areas where the unemployment is ³ 20% are able to collect unemployment insurance for 40 weeks. Through the 1970s, dragrake gear including winches and dragrakes were available from the buying companies, but this subsidization is no longer available. Dragrakes cost about $60.00 apiece (Canadian) and last about one season. The approximate annual (1985) cost estimates **(Table 13)** for gasoline, engine oil, boat paint, and miscellaneous items necessary to run an Irish moss "wincher" in MPHD 1 was $6,610 (Canadian). This does not include annual amortization of boat construction.

Irish moss harvesting in MPHD 12 **(Fig. 19)** is an important supplementary income for bona fide inshore fishermen, area non-fishermen, and area students. Harvesting technology has not developed beyond the use of the original handrake (MacParlane, 1966; Pringle, 1979) from "moss boats" **(Fig. 39).** These crafts are 4-5 m in length. They are generally powered by outboard motors **(Fig. 40),** but some are rowed as well **(Fig. 23).**

Table 9. Mean daily number of hours harvesting for Irish moss harvesters (haulers and winchers) In MPHD 1 (Prince Edward Island) in 1975 and 1976.

	Daily Mean Number of Harvesting Hours								
	1975				1976				
	June	July	August	Season Mean	June	July	August	Season Mean	Two year Mean
Haulers	6.9	6.4	7.4	6.9	9.1		7.9	8.5	7.5
Winchers	8.0	5.2	9.6	8.1	10.3	7.9	-	9.1	8.2
Mean	7.5	5.8	8.5	7.3	9.7	7.9	7.9	8.8	7.9

Table 10. Mean length of tow (minutes) for Irish moss harvesters in MPHD 7 (New Brunawick) during 1975 and 1976. Harvesters employed both basket-dragrakee and dragrakes.

Mean length of tow (min)								
Basket-dragrakes					Dragrakes			
	June	July	August	Seasonal Mean	June	July	August	Seasonal Mean
1975	9.9	8.9	11.3	10.0	2.7	2.8	-	2.8
1976	6.2	8.6	-	7.4	2.0	4.4	-	3.2
Two year mean	8.1	8.8	11.3	8.7	2.4	3.6	-	3.0

Table 11. Mean seasonal hourly production of Irish moss harvesters (haulers and winchers) in MPHD 1 (Prince Edward Island) in 1975 and 1976.

	Production h^{-1} of harvest (kg)								
	June	July	August	Season mean	June	July	August	Season mean	Two year mean
Haulers	258.3	159.2	82.2	166.6	125.5	-	110.9	118.2	147.2
Winchers	215.3	126.6	173.9	171.9	398.7	133.2	-	265.9	209.5
	236.8	142.9	128.1	169.3	262.1	133.2	110.9	192. 1	169.0

Table 12. Harvester production for both haulers and winchers in MPHD 1.

1	2	3	4	5	6	7
Harvesting method	Mean daily area harvested (ha da^{-1})	Mean harvesting day (h da^{-1})	Mean hourly production (kg h^{-1})	Mean area (ha) harvested h^{-1}	Mean daily boat prod. (t da^{-1})	Prod. per harvester day (t)
Hauler	[1]6.2	[1]7.5	[2]147.2	[3]0.82	[4]1.1	[5]0.55
Wincher	[1]7.2	[1]8.2	[2]209.5	[3]0.88	[4]1.72	[5]0.86

[1] From Pringle and Semple (1984)
[2] From Table 11
[3] Column 2/Column 3
[4] Column 3 x Column 4
[5] Column 6 x 0.5

Table 13. The approximate annual coat of items required to run an Irish moss "wincher" in MPHD 1 (Prince Edward Island) In 1985 ("hauler" costs Mould be slightly less).

Description or Item	Individual cost ($Cdn)	Number yr^{-1}	Total cost ($Cdn)
Dragrakes	60.0	8	480.00
Dragrake teeth	0.15	600	90.00
Cable blocks	50.00	8	400.00
Cable	2.00 m^{-1}	300 m	600.00
Gasoline or	50.00 da^{-1}	60 da	3,000.00
Diesel	30.00 da^{-1}	60 da	(1,800.00)
Engine Oil	1.50 da^{-1}	60 da	90.00
Boat upkeep (paint, etc.)			*1,000.00
Miscellaneous			60.00
Boat hauling		60 da	*50.00
Food (2 harvesters)	14.00 da^{-1}		840.00
Total			**6,610.00

*These costs are amortized over 3 fisheries for winchers.
**Calculated for gasoline.

Figure 39. A schematic sketch of a MPHD 12 (Nova Scotia) handraker cropping attached Irish moss fronds. The plants always cover the substratum much more thickly than shown here (sketch by G. Jeffrey).

Figure 40. A typical outboard motor powered Irish moss boat in MPHD 12 (Nova Scotia) during 1976.

The granitic substratum off southwestern Nova Scotia is glacial till, hence, the bottom is rugged **(Fig. 23).** There are 61 distinct commercial Irish moss beds between Cape Sable Island, Shelburne Co., and Pinkney's Point, Yarmouth Co., (Pringle and Semple, 1980). Commercial beds occur between +1 and -5m (chart datum). Due to a 5m mean tidal amplitude, handraking is restricted to 2 h on either side of low tide.

The harvester places "mossoil" (fish oil) on the water, creating a slick that reduces wave chop and improves visibility. The rake has a 6 m wooden handle; head dimensions are listed in **Table** 14. The harvester wears both rubber boots and pants when standing in the aft cropping the moss with a raking, then pulling motion **(Figures 23 and 40).** The rake is cleaned in the boat and then returned immediately to the water. The moss is generally sold wet at dockside, although, as with dragrakers in the Gulf of St. Lawrence, a few sell "sundried moss".

With the introduction of outboard motors, about 10% of the harvest (Sharp and Roddick, 1980) is cropped with dragrakes **(Fig. 41).** Thus, both the depth and the harvesting hours have been extended (i.e. not restricted to low tides). However, the rugged bottom restricts the use of this technique.

The total cost of boat and motor are $2,000 (Canadian); they last about six years. Handrakes cost approximately $50 (Canadian); the head and handle are replaced two and three times/season, respectively. Unemployment insurance is available to these harvesters as well.

Figure 41. A typical dragrake towed behind outboard motor powered Irish moss boats (cf. Figure 40) in MPHD 12 in Nova Scotia (a = tines; b = runner and c = tow bar).

Table 14. Handrake dimensions in MPHD 12 (Nova Scotia) during the 1975 harvesting season.

Rake dimensions									
Area studied	Number measured	Head length (cm)		Tine width (mm)		Tine spacing (mm)		Tine length (cm)	
		Range	Mean	Range	Mean	Range	Mean	Range	Mean
Westport	66	22.9-44.4	36.3±4.1	3.18-6.36	4.45±1.06	3.18-12.70	6.80±2.9	6.2-12.5	9.8±1.9
Pubnico	114	22.2-45.7	33.8±4.3	3.18-7.70	4.80±0.36	3.18-12.70	6.28±2.2	6.2-16.3	10.8±1.5
Cape Sable	26	30.5-33.1	33.3±2.5	4.76		3.18-4.76	3.18-4.76	8.6-12.5	10.3±1.3

8. PROTECTION AND MANAGEMENT OF THE RESOURCE

8.1 Management of seaweed resources

8.1 Management of seaweed resources

The British North American Act of 1867 ceded all Canadian, renewable marine resources from, and including, the intertidal zone and below, to the federal government. The resource is considered common property, belonging to the Canadian public; resource leases are not permitted. Harvesters are given the right to harvest on behalf of the Canadian people, but the resource does not belong to them. To prevent a "tragedy of the commons" (sensu Hardin, 1968) the resource is managed; all aspects from resource development through assessment science to resource allocation being under one government agency (see Pringle, 1986), Fisheries Management of the Department of Fisheries and Oceans (DFO). The Minister of Fisheries (elected representative) is the resource manager, but certain responsibilities are relegated to the Directors General (DG) of each of the seven fisheries regions.

The two most important commercial marine plant regions are the Gulf (Gulf of St. Lawrence) and Scotia-Fundy area **(Fig. 18).** Resources are managed via the techno-centric model of Larkin (1977) where harvest rates by species, area, season, gear type, etc., are controlled by the State. The DG receives input from biologists (Fisheries Research Branch), economists (Economics Branch) and industry via a marine plant advisory committee (see **Appendix I** for committee mandates). Members of this committee consist of elected representatives of the harvesters, buyers/processors, provincial government personnel, a DFO biologist, an economist and regulation enforcement personnel. Biological advice is presented to the committee and the DG, only after it has been vetted by the Canadian Atlantic Fisheries Scientific Advisory Committee (CAFSAC), which is made up of Atlantic Canadian DFO fisheries scientists. Generally, resource management plans are modified annually in large part by this advisory committee.

Canadian fisheries (marine plants are "fish" under the Canadian Fisheries Act) are managed under the concept of optimum sustained yield (OSY). Regulations (see Pringle, 1976, for the Canadian Atlantic Coast Marine Plant Regulations) are enforced by fisheries officers and judicial courts. Marine plants specifically are managed by controlling both the annual number of harvesting days (seasons) and effort within marine plant harvesting districts **(Fig. 19).** Harvesting gear type is also controlled based on impact to the target species (Pringle, 1979; Sharp and Roddick, 1980) and other commercially important species in the community (Scarratt, 1972; Pringle and Jones, 1980; Pringle and Sharp, 1980).

Due to fears of both overharvesting in MPHD 1 and 2 **(Fig. 19),** a freeze was placed on the issuance of new licenses in 1978. To reduce the adverse impact of dragraking, the most deleterious implement, the basket dragrake **(Fig. 38)** was banned in 1977 (Pringle, 1985; Pringle et al., 1979). Further, dragraking **(Fig. 36)** which was thought to be deleterious to the commercially important alga Furcellaria (Scarrat, 1972), was prohibited in MPHD 4 until its impact could be assessed. A minimum handrake tine spacing of 7.0 mm was introduced in MPHD 12 in 1979 based on a study by Pringle and Semple (1978). There is evidence from this district that annual yield would be enhanced by varying each season's opening date in order to better correspond with seasonal growth (Sharp and Roddick, 1982) and tide regime (Sharp, unpublished data). Regional DGs have only recently attained the ability to vary seasonal opening dates on short notice; this harvesting strategy will now be permitted.

9. UTILIZATION

9.1 Chemical and nutritional content
9.2 Human foods
9.3 Animal fodder
9.4 Manure
9.5 Industrial products and processes

9.1 Chemical and nutritional content

Much of the ash in Chondrus crispus (i.e. 17.6 - 21.8%) is represented by the calcium salt of a non-dialyzable sulfate, which is linked to the colloidal polysaccharide, carrageenan (Buggeln and Craigie, 1973). Even so, a wide variety of other minor ash constituents are also evident (e.g. calcium, sodium cobalt, etc.). The plant's major carbohydrates are carrageenan, cellulose and mannitol, with the former being the most important economically (cf. section 9.5). Upon extraction in boiling water, Irish moss is found to be composed of 70 - 79% by weight gelatinous carrageenan substance, plus 15% minerals and 7% proteins (Chapman, 1970). Carrageenan is a hydrophilic, sulfated polyanionic phycocolloid that is a structural component of the cell walls; it is composed of two polymers, D-galactose and 3,6 anhydro-galactose (Anderson and Rees, 1966; Patell, 1972). The percent Nitrogen in the plant varies from 1.3 - 4.6%, depending upon the season and site of collection (cf. Buggeln and Craigie, loc. cit.). Young and Smith (1958) record 20 amino acids, some of which (e.g. gigartine) may have a role as N-storage compounds (Laycock and Craigie, 1977; Laycock et al., 1981). Buggeln and Craigie (loc. cit.) also summarize the variety of lipids, sterols, vitamins and pigments. The vitamin and pigment contents within the plant seem fairly typical of other red algae, except for the relatively high riboflavin content (25 m g/g dry weight).

9.2 Human foods

Chondrus crispus is only palatable when cooked; even then, it still contains a high proportion of indigestible carbohydrates (Chapman, 1970). In New England and western Europe, fresh or hydrated Irish moss is boiled, and the gel sweetened and flavored with sugar, salt, vanilla, honey, nutmeg, lemon or orange powder to taste; it is then used as a gelatin dessert called blanchmange or used to make aspic dishes and jellies. Boehmer (1982), Chapman (loc. cit.) and Stephenson (1968) note its usefulness in a variety of other recipes, such as in vegetable stews, in soups, and sauces.

9.3 Animal fodder

Irish moss has at various times been used as a "favorite food" for farm animals; as well as for the curing of "wasting disease" in calves, the reduction of gastric ulcers in guinea pigs, as a dietary supplement for dairy cows and pigs providing beneficial effects on their pregnancies, etc. (Boney, 1965; Stephenson, 1968). Even so, there are some accounts of negative effects of carrageenan extracts on experimental animals, including toxicity and suppression of antibody response in mammals (cf. Bird, 1972; Brewer et al., 1974; Thompson and Home, 1976; Yaphe, 1973).

9.4 Manure

Irish moss has been used by maritime farmers in Europe to create soils where little exists and to enrich soils for increased yields (Boney, 1965; MacFarlane, 1968; Stephenson, 1968). It is either added straight from the beach, partly composted or mixed with various barnyard manures; in contrast to the latter manures, it releases nitrogen and phosporus more slowly, has more trace elements (cf. section 9.1) and growth substances and contains no weed seeds or soil micro-organisms (Scagel, 1961).

9.5 Industrial products and processes

Carrageenan from Irish moss is used extensively in dairy products as a stabilizer, gelling and viscosity control agent. A milk protein-carrageenan interaction is employed in products such as ice cream to stabilize the product and in chocolate milk to provide body and suspend the cocoa. It is also used as a gelling agent in baby, dietetic and instant foods, in bakery and candy products, plus in the cosmetic industry as a stabilizing and thickening agent for creams, lotions, toothpastes, etc.

Michanek (1983) notes that the advantage of carrageenan relative to other emulsifiers and stabilizers in foods is that it is possible to manufacture "tailor-made" products, to control texture, mouth-feel, and stability in gels, liquids, pastes and suspensions. That is, different types of carrageenans (kappa and lambda plus, from other seaweeds, iota) can be mixed and blended for diverse uses.

The commercial Irish moss harvest from the northwest Atlantic and, in particular eastern Canada, is purchased by one of a number of buying companies/extractors **(Table 1)** that have been in the region for a varying number of years. The first commercial export of Irish moss was harvested in George Bay, Nova Scotia, in 1927. It was sun-dried by the harvesters and then shipped by them to France (Pringle, 1976). The first P.E.I. Irish moss was purchased and shipped in 1944. Since then the bulk of the crop has been purchased by Canadian subsidiaries of foreign based extractors such as Marine Colloids of the U.S.A. and Litex and Copenhagen Pectin, both of Denmark.

The harvesters in P.E.I. formed a cooperative in the early 1970s and developed mechanical drying capacity, but, without an extraction facility, they were dependent on the foreign extractors. Their market dried up in the late 1970s (cf. Anderson et al. 1977 for details).

Until 1975 Canada produced up to 75% of the western world's raw material source for carrageenan. Even so, no initiative was taken to build an extraction facility, and government agencies did little to encourage local extraction. The provincial government of P.E.I, sought advice from the American based Arthur D. Little consulting firm (Anon., 1971) regarding the potentials of building an extraction plant; they advised caution as the major extractors dominated the markets. This, despite a lack of, or very little, raw material in the countries of extraction. Since then other countries with little or no raw material such as Spain, Japan and New Zealand have developed carrageenan extraction facilities!

Chile is determined not to make the same mistake. The harvests of carrageenophytes (Iridaea and Gigartina spp.) in this country increased by 53% between 1979 and 1983 (Lopehandia, personal comm. to J. Pringle[5]). The bulk of this crop is exported. Recently, the Chileans took the initiative and constructed a carrageenan extraction facility which should permit a marked increase in the value-added to their carrageenophyte harvest.

[5] Mr. Lopehandia, Biologist, National Fisheries Service, Santiago, Chile

By contrast, the value-added for the Canadian harvest is low. Irish moss when purchased wet, is put through a shaker to rid the crop of sand, stone, etc. It is then dried in an oil-fired drum drier, baled and transported to the foreign-based extraction facilities.

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APPENDIX I: Terms of reference for the southwestern Nova Scotia Marine Plants Advisory Committee Committee

1. Purpose and Objective

The South West Nova Scotia Advisory Committee will serve as a forum for discussion and consultation among those sectors of the industry and provincial governments having an active interest in the fishery and the Federal Department of Fisheries and Oceans. The Committee shall provide advice and recommendations to the Department's Regional Director-General, through the prescribed reporting relationship, on all policies pertaining to conservation, utilization and enhancement of the marine plants resource.

2. Duties and Responsibilities

The Committee will be responsible for reviewing and offering comment, advice or recommendations on the following:

(a) The establishment of policies to enable implementation or better use of management measures, including examination of guidelines relating to such matters as seasons, closed areas, fishing methods and licensing for the local marine plant fishery;

(b) The establishment of regulations to ensure sufficient conservation and best utilization for its harvest, as well as methods to enable adequate enforcement for such regulations; and

(c) Review the necessity for development programs, including examination of environmental, biological, technical and economic considerations

3. Membership

Meeting on behalf of the Regional Director-General, the Department's Area Manager in the Southwestern Nova Scotia area will be the Chairman of that Committee. Representation will be drawn from all sectors dependent upon the marine plank resource. Membership shall normally be limited to a maximum of sixteen. The Committee will draw representation from among the following:

- Commercial fishermen/harvester
- Processors
- Provincial government
- Federal government

4. Technical Expertise

As required, the Committee may draw upon the expertise of the Department's biologists, engineers, economists or other scientific and professional advisors, and may request that these individuals attend meetings for specific purposes.

The production and use of Eucheuma

1. IDENTITY
2. DISTRIBUTION, ECOLOGY AND METABOLISM
3. LIFE HISTORY
4. POPULATION STRUCTURE AND MORTALITY
5. PRODUCTIVITY OF THE RESOURCE
6. METHODS OF HARVESTING AND HARVESTING CYCLE
7. EQUIPMENT USED FOR HARVESTING AND CULTURE OF EUCHEUMA
8. PROTECTION AND MANAGEMENT OF THE RESOURCE
9. UTILIZATION
10. REFERENCES

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ABSTRACT

Three commercial kinds of Eucheuma are being used for their carrageenans. The three kinds, the annual production of each and their specific carrageenans are, respectively: **cottonii,** 30,000 tons producing kappa carrageenan; **spinosum,** over 6,000 tons producing iota carrageenan; and **gelatinae,** about 100 tons producing a mixture of gamma, beta and kappa carrageenans. The principal carrageenan uses are as suspensoids in dairy, luxury human and pet foods and drug products. Over 95% of the annual commercial Eucheuma crop is from farms in the tropical far western Pacific. In addition to foreign exchange earnings for those countries exporting the seaweed and the final use values of its carrageenans, the labor-intensive farming of Eucheuma is of great socio-economic value to the often nearly indigent shore dwelling families who grow it.

1. IDENTITY

1.1 Taxonomy
1.2 Nomenclature and terminology
1.3 Morphology and anatomy

1.1 Taxonomy

Eucheuma production from wild crop sources has dwindled to insignificance, and over 95% of the crop is farmed E. alvarezii Doty (as **cottonii),** E. denticulatum [Burman] Collins & Hervey (as **spinosum)** and E. gelatinae [Esper] J. Agardh (as **gelatinae).** Only the latter is predominantly from wild crops. The others are almost all farmed.

The taxonomy of the Eucheuma section Cottoniformia, which produces the cottonii of commerce, is most difficult due to the wide range of environmentally induced forms. This was not realized until strain selection commenced in the early 1970's (Doty & Alvarez 1975) and one kind, Eucheuma alvarezii var. tambalang Doty, was found to be consistently different physiologically and to have its own gamut of variation in form. It proved to be so much more easily grown that it has completely replaced the other species, such as E. striatum (elkhorn variety), formerly dominating the farming.

Likewise, many of the former wild crop components of commercial lots of Eucheuma were either never farmed (such as E. cottonii), are no longer farmed (e.g., E. striatum), or are not now recognized (e.g., E. spinosum, E. edule, E. muricatum, E. okamurae and E. serra) (Doty & Norris 1985).

Table 1. provides the key characteristics of the three commercial species. They are illustrated in Figures 1, *2,* and 3. Doty & Norris (1985) provide a key to the commercial species and those sometimes seen in wild crop lots of Eucheuma.

Table 1. Distinguishing Characteristics of the Three Kinds of Eucheuma Currently in Commerce. A common and a scientific binomial name are given for each. The presence and nature of special core tissues usually requires microscopic study.

	Morphological attributes		
Common names and the species of Eucheuma	**Branching**	**Axis & habit**	**Carrageenan and sulfate content**
SPINOSUM E. denticulatum (Figure 1)	Whorled or at predictable intervals	Terete, erect w/a rhizoidal core	Iota. 3 0 % sulfate or over
COTTONII E. alvarezii (Figure 2)	Irregular	Terete, erect & w/o rhizoidal core	Kappa. 28% 1 sulfate or less
GELATINAE L. gelatinae (Figure 3)	bi-lateral or dorsi-ventral	Flattened & erect to procumbent w/a rhizoidal core	Gamma, beta & kappa 20% sulfate

Fig. 1. Eucheuma denticulatum branch showing the cylindrical axis with rings of spinous primary initially-determinate branches, some of which have become indeterminate but are yet small.

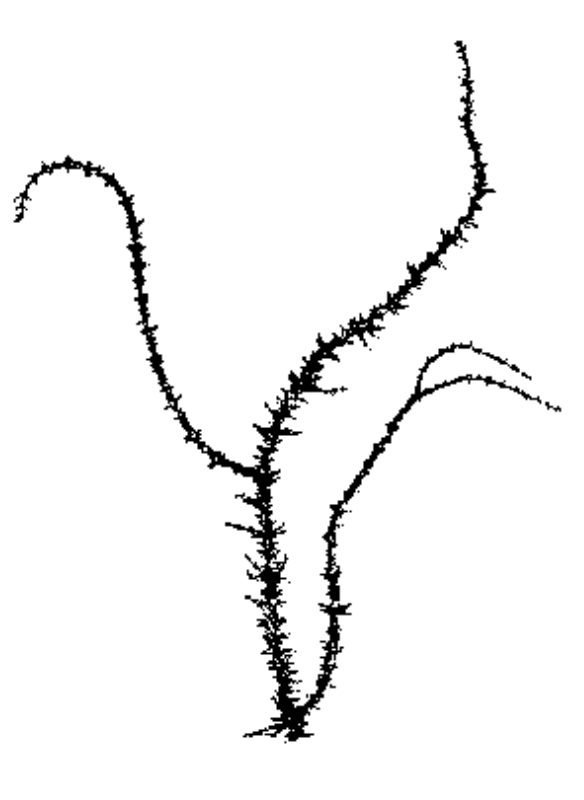


Fig. 2. Eucheuma alvarezii branch showing its cylindrical axis with branches that are commonly enlarged maximally just beyond a basal curvature toward the light.

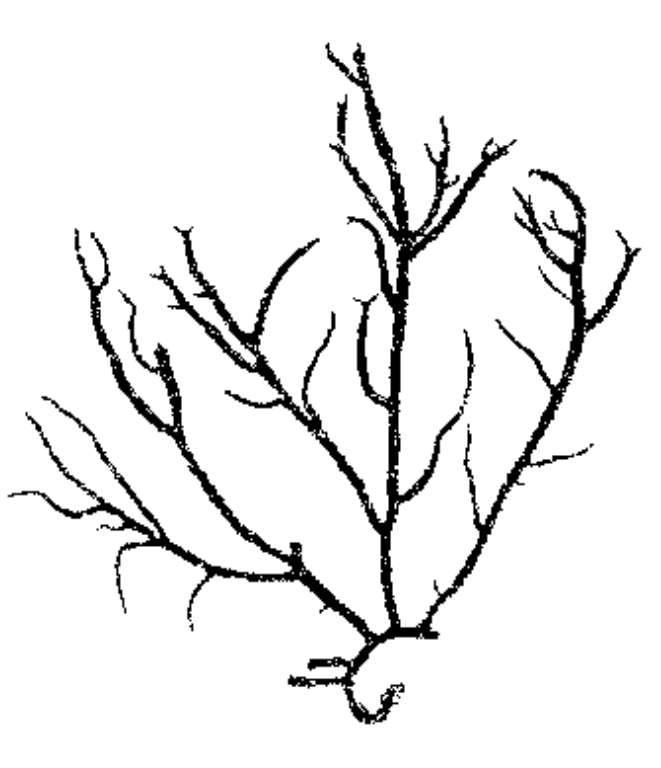
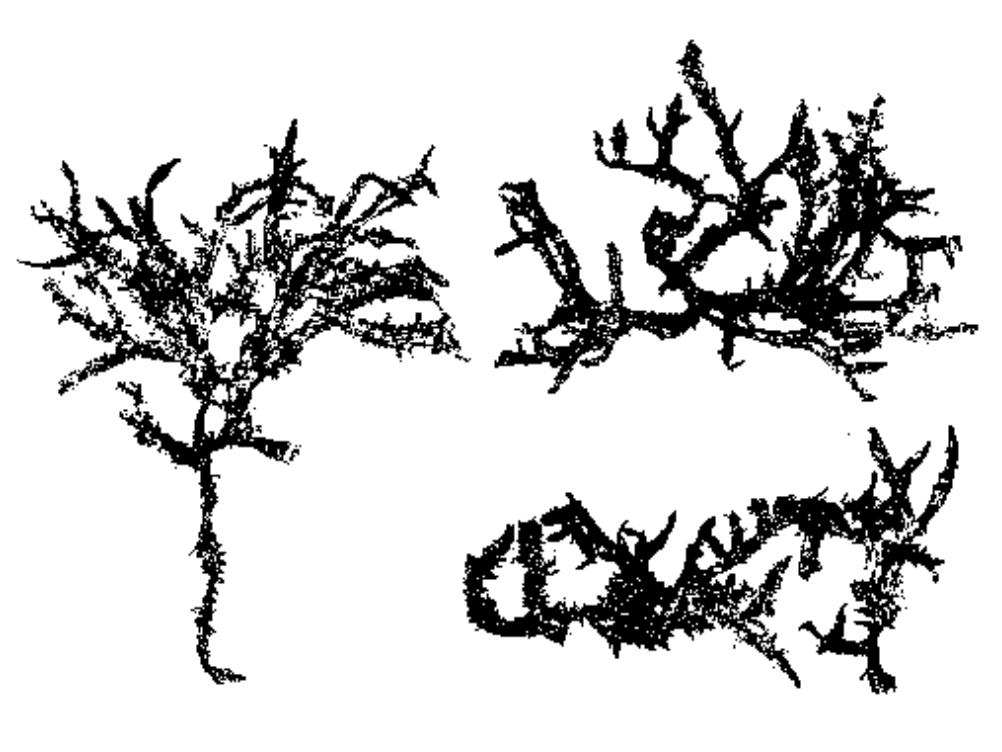


Fig. 3. Eucheuma gelatinae showing the flat branches arising from marginal cylindrical teeth. The scale bars represent 3 centimeters.



1.2 Nomenclature and terminology

The first name applied to a Eucheuma was Fucus denticulatus N. L. Burman in 1768 and the use of this specific epithet is continued today as E. denticulatum (Burman) Collins & Hervey 1917. That Linnaeus (in 1771) sought to substitute Fucus spinosus for Burman's name, which has been used as E. spinosum (L.) J. Agardh, has no standing (Dixon 1962) in view of the priority of Burman's epithet, a priority acknowledged by Linnaeus himself.

Eucheuma was first distinguished as a genus and named by J. Agardh (1847), who included seven species one of which was E. "spinosa" based on Sphaerococcus spinosus C. Agardh, in turn based on earlier species including Fucus spinosus Linnaeus and F. muricatus Gmelin, in turn based (Dixon 1962) on Burman's yet earlier F. denticulatus. The Lectotype is the specimen in the Linnaean Herbarium as #1274-104 and illustrated by Turner (1808) as Figure "a" of his Plate 18.

There is no question as to the nomenclature of this species, Eucheuma alvarezii Doty (1985). The Holotype is in the B.P. Bishop Museum in Honolulu, Hawaii, bearing the author's voucher number 28727.

Among the species originally included in Eucheuma by J. Agardh (1847) was E. gelatinae, the specific epithet for which was first applied by Esper(1797) in the combination Fucus gelatinus. Thus today one uses E. gelatinae (Esper) J. Agardh for this third commercial entity. The Lectotype is Esper's material in the Hamburg (Germany) Herbarium.

1.3 Morphology and anatomy

The thalli of commercial Eucheumata are often up to a kilogram in mass but in one form of cottonii they have been weighed at 56 kilograms alive. Basically it is a multiaxial filamentous red algal genus which becomes strongly pseudoparenchymatous. The nature of their triphasic life history results in their relegation to the family Solieriaceae of the order Gigartinales as these taxa are defined by Kylin (1956) and more recent authors.

The species vary greatly in form as a result of the environments in which they grow. This is particularly true of those in the section of the genus to which the cottonii forms belong. Commercial spinosum and cottonii are composed of cylindrical branches that are rigid. Mature gelatinae branches are apically flat, somewhat flexible, have marginal teeth and arise from a cushion of strongly compressed branches.

Gabrielson (1983) and Gabrielson & Kraft (1984) provide much of the structural detail which Kylin (1956) does not include. None of these authors treats the sections of the genus, Anaxi-ferae, Cottoniformia or Gelatiformia, from which the commercial cottonii and gelatinae crops arise. Weber-van Bosse (1928) and

Doty (1985) provide some of the structural details of the section Cottoniformia but they are still largely undefined anatomically. (See Section 4.5).

2. DISTRIBUTION, ECOLOGY AND METABOLISM

2.1 Geographical distribution
2.2 Local horizontal and vertical distributional determinants
2.3 Effects of non-distributional ecological determinants
2.4 Environment and growth
2.5 Life form versus environment

2.1 Geographical distribution

The two major commercial forms, spinosum and cottonii, are native to the Old World Tropics (Weber-van Bosse 1928; Laite & Ricohermoso 1981) westward to East Africa (Anderson 1953; Mshigeni 1982, 1984). A very small amount of the third, gelati-nae, comes from the Philippines and China (Hainan Island and Taiwan). These three species of the genus are almost entirely restricted to the same brightly lit waters **(Figure 4)** in which coral reefs form. Eucheuma is now being commercially produced in the far western Pacific. Cottonii has been introduced eastward through Micronesia into Kiribati and Tonga to the Society and Hawaiian Islands.

Figure 4. Sea Temperature Habitat for Commercial Eucheuma. Production both north and south of the equator occurs between the paired winter 21.1 and 23.9 C isotherms shown near both 20 deg. N. and S. Latitudes. (Anonymous 1944)

In some seasonally substropical/temperate parts of the Southern and Northern Hemisphere, e.g., in Australia, Florida (U.S.A.), the Gulf of California (Mexico), and southern Japan, a variety of non-commercial species may flourish during the warmer brighter times of the year. The anticipated micro-forms persisting during the off-season are not known (See Section 3).

2.2 Local horizontal and vertical distributional determinants

Tolerance to aerial exposure appears to govern the upward distributional limits of the Eucheuma species, although otherwise, the brighter the light the faster they grow. Possibly the tolerance of spinosum is greater than that of cottonii and gela-tinae is the least tolerant. Since Eucheuma grows almost entirely in open ocean water in areas of high water motion, light and temperature are not significant factors in local distribution. Water motion is most important. In some cases there may be some influence of run-off from land. Spinosum especially appears to be sensitive to water quality.

Both the commercial wild and farmed kinds of Eucheuma are mostly found in water less than a half meter deep at extreme low tide level. The greatest depth recorded is that of Weber-van Bosse (1913), 26 fathoms. For Eucheuma, deep water habitats are of no commercial importance.

2.3 Effects of non-distributional ecological determinants

Tides of greater range allow less working time at a site for either wild crop harvesting or farming than do tides of lower range. Also tides may exert an influence on productivity through light intensity and water motion control. Thus generally commercial production is in areas with low tide ranges.

Pigmentation is characteristically more or less dense at brighter light levels. Thalli may be black in intense light and relatively redder in the shade or in deeper water due to relative abundance of phycoerythrin. Pale yellower thalli are found in some bright light conditions.

Some cottonii forms may become negatively phototropic in intense light, and the spininess of some spinosum forms may be reduced to bilaterality, and the axial segments may then suffer some dorsiventral compression.

Cottonii thalli exposed to air tend to form "heads," or become prostrate and dorsiventrally flattened. Bushy thalli are formed in turbulent water, and trailing cottonii forms are found (Doty 1985) where current dominates. Cottonii may form erect cane-like forms seasonally in pools or deeper water.

At greater depths the species may change in morphology as though etiolated in a phycological sense. See Dawes (1981, Chapter 14) for the basic physiological nature of the responses expected of such a seaweed as Eucheuma as its extremes of vertical distribution are approached.

Cottonii and spinosum are composed of cylindrical branches **(Figures 1 & 2)** which, in cottonii, sometimes reach diameters of over two centimeters. The rigid and bush-like thallus form enhances thinning of the boundary layers wherever they are subjected to water motion. Thus, since materials move into and out of algae such as Eucheuma by diffusion, their growth increases as water motion increases, up to the point where drag or force produces excessive physical damage. Only gelatinae tolerates direct wave action. It is **(Figure 3)** the smallest of the three, and the fronds are apically flat and pliable.

Commercial production is from level sedimentary bottoms that are under water except during the lowest of tides. Level sedimentary bottoms are desirable for they are uniform and easily workable whereas sloping or irregular areas are not. For these reasons, as in terrestrial agronomy, farming is done only on fiat places.

Local horizontal and vertical distribution are correlated with the variations in the above factors. The chemical nature of the substratum is of little importance. The physical nature of the substratum is important as a stable anchorage for wild crop thalli. Its stability correlates with water movement, which, in turn, is essential (See Section 2.5) physiologically. In the Hawaiian experiment (See Section 2.4) water movement was found to be the most important environmental factor (Doty 1979) influencing growth. (See Section 5.2).

2.4 Environment and growth

A few laboratory respirometric studies of Eucheuma have been done, but only some of them related to micro-nutrient water content; e.g. by Dawes et al. (1974a & b), Mathieson et al. (1974) and Glenn & Doty (1981). For the commercial forms of Eucheuma, beyond the results in Section 5.2, there have been no quantitative simultaneous measurments of seaweed growth and environmental quality; thus, to date no statistically valid cause-and-effect relationship has been experimentally demonstrated between, e.g., Eucheuma growth or hydrocolloid quality and any putatively causal micro-nutritional element in the farm environments. Clear water and stable salinities (of 29 to 34‰) are desirable.

Temperature and light are felt to be relatively independent of water motion and its quality. It is not economic for farmers to provide control of these factors directly, so in selecting sites it is essential all be within tolerable limits. Water motion especially is a factor that must be taken into account in selecting sites. It often affects sediment in the water, which, in turn, affects light.

Mineral nutrition is surely important in view of the high mineral content of the species. **Table 2** provides various cation as well as nitrogen and phosphorus, values for the commercial species. They are similar among other Eucheuma species. Unfortunately, the variation in these elements in different commercial lots is not publicly known. Arsenic is below the U.S. Federal Drug Administration limits.

Table 2. Inorganic Cation Plus Phosphorus and Nitrogen Concentrations in Different Eucheuma - related Materials. The cation determinations were made by atomic adsorption methods in replicate. The means shown for K, Na, Ca and Mg are in terms of per cent dry weight; Zn, Cu, Fe and Mn are given *as* parts per million dry weight. Phosphorus and nitrogen are in terms of percent dry weight. The values for Fe were from thalli ground in porcelain.

Cations plus nitrogen and phosphorus									
Source	**K**	**N**	**Na**	**Ca**	**Mg**	**P**	**Zn**	**Cu**	**Fe**	**Hn**
A- **THALLI** rinsed and redried free of surface salt										
Spinosum	11.91	0.46	4.79	0.589	0.758	0.043	13	7.5	66	14
Cottonii	9.33	1.19[a/]	3.97	0.234	0.619	0.030	16.5	2.5	52	4
B- **SALTS** as crystals washed from thallus surfaces										
Cottonii	52.82	---	0.290	0.120	0.027	0.012	1.1	6.5	18	5
Spinosum	36.52	---	10.45	0.240	0.15	nil	18	1.1	24	1.1

[a/] N value was that of a different Sample No. 26551.

In an unpublished study the fixed nitrogen and dissolved phosphorus contents of the water, as well as other factors, were determined weekly as the water passed through about 15 meters of (usually) dense Eucheuma planting. Among the results **(Table 3)** there appeared to be a reduction of 24% of the nitrate/nitrite ion as the water passed through the seaweed and 6% of the phosphate. This provided the material used by Glenn & Doty (1981) and is spoken of below as the 55-week Hawaiian experiment or study. In a different (unpublished) study the average N/P ratio in 9 species of the genus was near 15 though perhaps 12 or 13 was the mode. Thus, in the present case, the N/P ratio in the water of 8.5 may indicate non-detection of ammonium ion uptake due to its being produced (or recycled) by the animal population that had become resident in the planting.

Table 3. The Hawaiian Eucheuma Experimental Habitat. The values are mean microgram atoms per liter from all weekly measurements made over the 55 weeks of a 1976-77 study period.

Sample site	Water motion	Micro-nutrients		
		NH_3-N	NO_3+NO_2-N	PO_4-P
Upstream		1.98	1.44	0.66
Downstream		2.01	1.10	0.62

Fertilizing is not thought to be economically worthwhile though it does provide some increases in productivity.

2.5 Life form versus environment

Water movement of all kinds is of major significance. It affects growth in such ways as change in mass (growth rate), differentiation (form), reproduction and production of the hydro-colloid materials for which Eucheuma is prized. These topics are discussed above and in Section *5.2,* below.

In the commercial Eucheuma species, the relationships of form to environment have not been described adequately, and they are only cursorily mentioned (Doty 1985; Doty & Norris 1985) with respect to their cause and effect relationships. Yet these relationships are important for farm production. For example, in regard to the space occupied and diffusion as a whole, the Eucheuma thallus is analogous in its relationships to the (sea) water in the same way the root system of a terrestrial flowering plant is related to the soil water. Unpublished results indicate that, in a desirable commercial Eucheuma habitat, the water in a one-liter thallus space may be laterally changed over a half million times a day.

3. LIFE HISTORY

The wild crops appear to follow the triphasic Polysiphonia life history scheme common for red algae. A diploid vegetative phase (Phase 1) produces haploid non-motile spores called tetra-spores. The tetraspores produce haploid gametophytes (Phase 2) that in turn produce diploid carposporophytes parasitic in the female thalli. The carposporophytes (Phase 3) release diploid carpospores which initiate the diploid tetrasporic stage again.

The details of the reproduction of Eucheuma from a classical point of view are readily available in Kylin (1956), and considerably updated by Gabrielson (1983) and by Gabrielson & Kraft (1984). Superfically spinosum, cottonii and gelatinae all appear to be triphasic though the strains being farmed may not be.

The contumacy of the species of red algae for the above described triphasic life history is well known to those who have sought it. There is no detailed study of the life history of any member of this genus. Male thalli are as yet unknown for the commercial forms. Santos & Doty (1978) found both cystocarpic and tetrasporic thalli in quantity in only 6 of the 15 species in which they were sought. They did not find them common in the commercial species and found no male thalli. Shallow water, line-farmed Eucheuma (and, incidentally, pond-grown Gracilaria thalli) are almost always sterile. While this may be a blessing to the marine agronomist and farmer in some ways, it hinders utilizing the advantages of sexual reproduction in improving the crop.

Eucheuma alvarezii carpospores produce morula-like tetra-sporophytic embryoes **(Figure 5)** that attach by rhizoids and differentiate an erect pyriform, then cylindrical form as the typical cluster of apical cells develops opposite the substratum. The younger embryos have a thick gel coat and a large number of very fine hairs, each ten or twenty times longer than the diameter of the embryo. Perhaps they may represent the micro-form in which some species of the genus persist in "off" seasons.

Figure 5. Diploid sporeling of Eucheuma alvarezii about fifteen days old. Maximum diameter 150 microns. (Photo 32696.24A)

The Eucheuma farmed crop is produced without regard to the life history phase concerned. Prices paid to the commercial producers is the same for the two macroscopic stages.

4. POPULATION STRUCTURE AND MORTALITY

4.1 Population structure of wild crops
4.2 Population structure of farmed crops
4.3 Morbidity, mortality and health
4.4 Grazing
4.5 Storm and other mechanical damage
4.6 Wound healing, regeneration, and secondary attachment

Eucheuma farm production is by vegetative propagulae grown to harvest size on farms from stocks that appear to live indefinitely. Therefore the conventional phenomena of population structure and mortality have little meaning.

4.1 Population structure of wild crops

Nothing has been published on the population structure of the communities in which Eucheuma appears. Overharvesting appears (Doty, 1973a,b; Doty & Alvarez 1973; Parker 1974) to cause wild crop population declines. Exports from the Philippines climbed in the 1960's to at least 800 tons in 1966 but fell in the late 1960's (Doty 1973a/b) and the early 1970's (Doty 1978) to less than one fourth of that amount. At that time most of the world's supply was coming from the Philippines. Earlier, when the crops were nearly all coming from Indonesia, the wild crop harvesting was not nearly as intense and apparently at most places well below the level of maximum sustained yield. Yet it was observed in two places along the southwest coast of Sulawesi (Indonesia) during this time that such harvests were bringing in spinosum of very small sizes that had been harvested from between finger coral branches as though all possible was being picked.

A nearly ten-fold decrease in wild crop density, seemingly related to over-harvesting, appears to have taken place (Table 3 in Doty 1972) at least at one time in the Sulu Sea area. A great deal of community composition information, including the masses of other seaweeds found in the random ring-toss samples, is available in the same data report and in Kraft (1969), a similar raw data report. There is almost nothing more, either published or in the grey literature on the commercial species comparable to that published on E. isiformis by Dawes et al (1967, 1974a,b) or in the brief study by Kraft (1972) on E. arnoldii and neither of these has data that imply cause-and-effect relationships. Kraft does describe E. arnoldii var. alcyonida as (loosely quoting) being restricted to association with the branched coelenterate corals in silt-free, rapidly moving water near the seaward margins of reefs.

Kraft (1969) provides a wealth of information on the communities in which commercial Eucheuma species occur, based on one or a few observation periods at many Philippine sites over a wide geographic range. Doty (1972) describes repeated observations of the same populations of commercial species relative to the non-Eucheuma seaweeds at some 31 sites just in the Sulu Archipelago. These two appear to be the largest sources of community information on the genus.

4.2 Population structure of farmed crops

Farming quite naturally was developed as a result of over-harvesting and to obtain desirable size, stability and quality of crop. Farming routines soon result in very uniform populations. The very valuable work of Lim et al. (1982) at one site for a good many months is the major source of published information.

No attempt is being made here to describe farm siting, construction and operation beyond what is to be found in other sections of this case study. The early history of the farming (Doty 1973a,b; Doty & Alvarez 1973, 1975, 1981; Parker 1974; Deveau & Castle 1976; Lim & Porse 1981) provides the essential generalities. Each farming area displays characteristics which are to a large extent the result of field expediency.

Farms nowadays consist **(Figure 6)** of parallel rows of stakes bearing nylon monofilament line to which there are tied branches of Eucheuma broken from previous farmed, or from wild crop, thalli. For good growth the habitat is especially important in reference to bottom elevation, water movement, the nearness and nature of the bottom materials and the pests that may be in the area. The successful farms are over sedimentary bottoms with the thalli near or on the bottom and where problems such as those discussed in the following subsections are minimal.

Figure 6. Above: about one tenth of a hectare of cottonii farm at Pohnpei, Federated States of Micronesia. Below: closeup underwater view of a portion of the same farm on which the largest thalli of Eucheuma alvarezii shown are two to three kilograms in weight and over 30 cm tall. From Doty 1986.

4.3 Morbidity, mortality and health

In experiments, individual vegetative thalli of cottonii have lived for 14 months, and one farmed population is known to have thrived by vegetative cuttings for over 10 years. Farmed strains of spinosum and gelatinae have not been as closely observed but they seem to have prospered for years.

Thallus colors and growth rates are often considered indicative of the health of a planting. There is no finished study of the former but it is well known that yellowing indicates a lowering of vitality in the red algae. In Chondrus this is sometimes associated with the production of a higher yield of stronger gel and can be (Neish & Shacklock 1971) artificially induced by holding the live thalli in high light and low mineral nutrient water for a few days before the final harvesting. (See Section 2).

It is practical in test plots to use the coefficient of variation (mean growth rate/standard deviation) as a comparative measure of population health. This value, C, may be high due to genetic variability in the population or due to uneven grazing, responses to environment, different ages of seedstock branches orientations and exposures of the thalli. Values of 0.20 are good, less than 0.10 excellent.

The lack of healthy growth, very low rates of growth and lack of reproductive fertility may be due to environmental imbalances or agronomic practices. It must be recognized that farms are often located where Eucheuma does not occur naturally, and this may not always be just due to a lack of suitable substratum. The major cottonii form, tambalang, may not become fertile on farms, though the typical form is freely fertile in its native habitat. Whether this is due to its genetic constitution or to farm practice is unknown, but juvenile thalli are rarely if ever seen. Juvenile spinosum thalli are often seen on farms.

Other specific poor health situations seen on farms are discussed below. (Gross physical damage is included under Section 4.5).

The most common symptom of malaise, ice-ice, is often spoken of as a disease. Actually it is only a symptom. No microorganism-caused or contagious disease is known (Uyenco et al. 1981). Infections and infestations are known. In itself the word ice-ice is (Doty & Alvarez 1975) a malay treatment of the Middle English word, ice, applied to the white segments that appear between branches usually in the more basal parts of the thalli.

Ice-ice seems to be related most often to intolerable physio-chemical stresses, such as increased ceil permeability following low growth rates or relatively low counter-movement of photosynthate. The onset is a sharply limited greening of a segment which, the next day, is clearly green and in one or very few more days very pale, then white. The segment may remain there for a day or two but soon dissolves away, separating the two adjacent parts of the thallus, which seem to be otherwise unaffected. In this way ice-ice acts as an agent in vegetative reproduction: the ice-ice does not normally spread to the adjacent segments. The two such thalli resulting continue their normal growth though one is unattached. Of course, the one not attached may become lost to the farm.

A second malaise is "pitting," the formation of a cavity penetrating the cortex in one place and expanding in the medullary regions beneath. It can lead to thallus breakage. This phenomenon has been studied by various students and by Dr. Gordon Sill (unpublished personal communication) who carried out Koch's postulates with pure cultures of the bacteria isolated from them. In no case has the pitting been obtained without a mechanical wounding of the cortex. In time the pit surfaces become covered by regenerated cortex and are then the same color and nature as the adjacent natural cortex. At least if small, the pits do not adversely affect the thalli. It does not spread.

A third malaise is "tip darkening," relative to the adjacent segments below the affected branch apices. This may well be due to senescence or cold weather. In time the lower parts of the thallus so affected may lose color and disintegrate; the tips fall to the bottom. Isolated, or after a change in environmental conditions, the tips may resume growth and regenerate new thalli of normal size and appearance.

A fourth malaise is "tip discoloration" relative to the adjacent segments below the affected apices. This is usually a change toward pinkness and eventually the tips soften, discolor further, become white and dissolve away. It is as though respiratory metabolism were affected and usually has been thought to be (unpublished) related to intolerably warm water or aerial exposure

A fifth phenomenon is a slowing of growth, the appearance of epiphytes and usually the onset of pigment loss followed by a general decay through softening of all tissues. Possibly this is most often due to intolerable changes in water motion, salinity or mineral content such as appear at some sites seasonally or randomly. Moving the thalli to higher water-motion areas usually offsets this if done soon enough. It indicates a poor season, place or way of farming.

In some cases, general decay has been seen to result in the death and disappearance of ail but the very oldest basal, often horizontal but unattached, segments. These may remain alive though reduced to an unbranched cylinder. If the environment becomes favorable again such segments may generate a plethora of vigorous shoots and regenerate a new thallus of normal form.

In one case in Sitangkai (Philippines) a great deal of die-off occurred, with the thalli displaying the above general discoloration symptoms. Similar losses have occurred in the Malay-sian part of the Sulu Archipelago. This general die-off phenomenon has been thought due to pools of fresher water forming off the mouths of the large rivers that drain into the sea along the north shore of Borneo (i.e., in the Malaysian State of Sabah) and, breaking away, drift so as to temporarily cover reef-flat farm areas to the east and south. In some dialects of the region this phenomenon is apparently referred to as HAUS, pronounced as is the English word for a residence. (See below under micro-grazers.)

4.4 Grazing

Grazing organizms can be recognized as individual species, with some being categorized as micro- forms and others as macro-forms. Yet, in reality, they form the continuum illustrated through the following two subsections. In different places and different times different ones of them are a problem. Some that may prevent farming in one place will be completely absent in another place.

4.4.1 Micro grazers

Micrograzing occurs when organisms, generally less than 2 cm long, both take up residence on a thallus and consume the thallus materials in some way. It has not been studied in Eucheuma. In the slowing of growth, described above, there have been cases of nematodes attaching in great numbers to the decadent thallus surface. Ordinarily micrograzers are not visible on healthy Eucheuma.

Micrograzing forms could be defined to include certain sizeable echinoderms that are sometimes bad pests in Eucheuma farms. There are two types in this category. The first is a Tripneustes that arrives in planktonic form and settles on the seaweed. As it grows it becomes visible, orange, and up to perhaps 5 or 6 cm in diameter. In serious infections there can be at least one of these sea urchins developing to adulthood in almost each Eucheuma thallus. Their grazing hollows the central area of the thalli affected. As they sever major branches, those branches not tied to a farm line fall from the farm planting **(Figure 6)** and may be lost.

The second type of similarly arriving micrograzer that becomes a macro-organism is exemplified by synaptid holothurians. In Hawaii, as Ophiodesma spectabilis, they arrive as net piankters and become up to 2 cm in diameter and half a meter long. These are first obvious as residents of Eucheuma thalli when they are soft pink objects just above a centimeter in length. They soon grow to be sizeable, adherent but otherwise innocuous, snake-shaped animals that may slip Eucheuma branch tips into their "mouths" where the seaweed disintegrates.

4.4.2 Macro-grazers

These grazing organisms arrive as adults, and they are usually 5 or more centimeters in their major dimension.

The first macrograzer is the common asteroid echinoderm, Protoreaster nodosus, which climbs into Eucheuma thalli when this alga is farmed on microalgal-dominated (as to color) sedimentary bottoms. Once there it everts its stomach over the branches, and the branches die where they are covered. This often causes major branches to separate from the part secured to the farm lines and become lost, as do branches separated by ice-ice. This can be a bad pest, but it appears to be restricted to near or within sea grass, Enhalus acoroides or Thalassia hemprichii, communities. The activities of Protoreaster have been described (Thomassin 1976) in regards its microalgal herbivory.

The heterospinous long-spined "poisonous" sea urchins, usually Echinothrix or Diadema, are notorious pests. They combine the ill effects of the above-mentioned Tripneustes and Protoreaster with the threat of injury to the farmer who may try to remove them. Fortunately their populations are usually downstream (on falling tides) from the best farm areas.

Fishes of different kinds browse on Eucheuma avidly. The rabbit fishes (Siganidae) and puffers (Tetraodontidae as well as Canthigasteridae) are common. The former are by far the most destructive. When about two centimeters long they appear as dark schools by the "millions" (often with the longest days of the year) and mow the diatoms off the edges of such eel grasses as Thalassia. As they grow larger they will turn to any Eucheuma available. The schools are gradually decimated as the individuals lengthen. Medium-sized Siganus species will attack a thallus here and there among the many on a farm and remove the normally reddish to greenish olivaceous brown cortex leaving a still-living white skeleton which, as though displaying a heroic ice-ice symptom, disintegrates in a few days. By the time the schools of thousands are reduced to scores; perhaps 4 to 5 months after their initial appearance as vast numbers of tiny individuals/the siganids nip off the branches beginning at the tips and continue this grazing until some inhibiting diameter is reached...perhaps related to the size of the fishes in the local school. After some months the remaining few rabbit fish are timid and, being fast agile swimmers, are usually seen from above the water surface as swiftly darting shadows. Though by now relatively few, they can still destroy a Eucheuma farm. Human presence and active overfishing may well control them.

The grazing of fishes can reduce dense Eucheuma beds to a few large-diameter segments that persevere as gnarled relics among the bottom debris. Russell (1983) has provided an often perceptive and quantitative study of this and related non-Siganid fish grazing phenomena. He reports the fish eating as much as 20 tons per month of live cottonii from a patch about 3 meters horizontally wide and 500 meters long.

Turtles are the largest of the macrograzers of concern. They pose a special problem for two reasons. First; it is usually the green turtles that are the problem, and they seem to take large bites and crawl over a farm, thus devastating their way through it. Secondly, the farmers pay no attention to the purported endangered species nature of this (or other) species. Human feelings about turtles are very strong in different places in very different ways. In some places the turtles are considered in a class with pork and therefore anything to do with them may be rejected. In some places they are traditional parts of particular celebrations. In yet other places they are avidly sought out and eaten.

4.5 Storm and other mechanical damage

For the most part, mechanical damage comes about as a result of a few discrete causes. Water motion tends to move the thalli about and, especially when they are large, this can cause branches to become abraded or break off entirely and be washed away. Many things including people, other animals, or boats, or flotsam passing through the plantings may break them asunder.

4.6 Wound healing, regeneration, and secondary attachment

Damage, whatever the cause, is soon repaired by production of a new cortical layer covering the wound. Branches may regenerate from this new surface, if brightly lit. Near preexisting meristoderm or axial tissue, one or more cellular lumps may appear on the new cortical layer and differentiate a central tuft of apical cells and, then, a new branch.

Secondary attachments are normally formed when an apical cell tuft is held against a surface. Spinosum has many tips at right angles to the stems on which they are borne and is often seen with apical attachments to a wide range of objects including other Eucheuma thalli. Cottonii tips are mostly directed toward the light, parallel to each other and thus away from surrounding objects; thus its having secondary attachments is not common.

Wound healing from breakage or abrasion, e.g., by being rubbed against a coelenterate coral, is rarely seen to have led to attachment directly. Russell (1983) found that where corals and algae had rubbed together due to water motion, the corals more often grew around the seaweed than visa versa.

As a result of heavy grazing or nearly lethal conditions, large-diameter short segments of Eucheuma thalli may remain alive and fall onto the bottom, where their surfaces regenerate. During a successive favorable growth period these old gnarled segments may produce hosts of new branches quickly. Such regeneration is described by Russell (1983) when there is respite from grazing. (See Section 4.3).

5. PRODUCTIVITY OF THE RESOURCE

5.1 Global tonnage and dollar productivity
5.2 Natural determinants of Eucheuma production
5.3 Genetics and high technology in Eucheuma production
5.4 Relative contributions of sexual and vegetative reproduction
5.5 Anticipated agronomic improvement of Eucheuma production

5.1 Global tonnage and dollar productivity

Productivity data in terms such as world crop, number of families concerned or dollar values are very scarce or nonexistent, and those discussed below are much of what is available. There are even fewer published values for productivity in terms of tons/ha/year for even one site, but **Table 4** provides a few of the earliest.

Table 4. Eucheuma Growth Rates. E. gelatinae plus three other kinds, i.e., spinosum, elkhorn and tambalang, which are believed to be referable to E. denticulatum, E. striatum and E. alvarezii, respectively; with the latter two being cottonii. The many measurements of Lim et al. (1982) and Doty (unpublished) made in the field are not summarized here.

Author	Kind	Percent per day	Tons/ha/year
Tham (1969)	sp.[a/]	1.1 to 4.7	
Doty (1971)	elkhorn	2.64	
Doty (1973a,b)	elkhorn	1.5 to 5.5; x 2.3	36
Parker (1974)	elkhorn	1.5 to 5.5[c/] (x 2.3[d/])	36
		2 to 4	13
Dawes, et al. (1974b)	spinosum	1 to 2[b/]	
Doty & Alvarez (1975)	elkhorn	1.73	42
	tambalang	>5.20	
Glenn & Doty (1981)	(all three)	2.3 to 5.34[b/];	
Lim et al. (1982)		2 to 6[e/]	
Liu & Zuang (1984)	gelatinae	0.41[g/]	
		0.44 to 0.63[g/]	
Doty & Glenn (unpub.[f/])	spinosum	3.51	
	elkhorn	3.51	
	tambalang	5.05	

[a/] Species unknown. The author and Dr. Tham Ah Kow were working cooperatively at the time and only with cottonii.
[b/] Determined from respirometry.
[c/] Range in first week.
[d/] Mean of same thalli the second week.
[e/] Determined simultaneously from weight change.
[f/] Each value was reduced from 55 consecutive weeks' weights.
[g/] Calculated from data provided.

Laite & Ricohermoso (1981) provide the statistics on the early growth of Eucheuma exports leading to the undocumented estimate of 35,000 tons in 1985-86. If 30,000 tons of the 35,000 probably is farmed, then between 1000 and 2000 hectares is probably in Eucheuma farms. Lim & Porse (1981) provide yet other tonnages. These two sources of information concerned the Philippines at a time when perhaps 90 percent of the world's Eucheuma was coming from there. At present (Adnan & Porse In Mss) some few thousands of tons per year come from Indonesia too. Other places produce at best a total of a few hundred tons per year.

Most of the Eucheuma crop goes to the U.S.A., Denmark, France, Australia, Japan and China. These markets are largely for pre-export-treated material and thus their tonnages do not reveal the total crop harvested. Their declared values do not necessarily indicate the dollars returned to either the first seller or the exporter.

The import values of Eucheuma shown in **Table 5** are for the countries importing cottonii predominantly in rough dried form. The discrepancies between general export prices of $350 (cottonii) and $400 (farmed spinosum) to $600 (wild clean spinosum) for those in this table are considered to have been produced largely by the import tonnages being mixtures of kinds and qualities as well as proportions of semi-processed and raw seaweed.

Table 5. Declared Dollar Value of Eucheuma Exported from the Philippines, 1980 and 1984. The terms are metric tons and U.S. dollars per ton. Only countries receiving very predominantly non-modified cottonii in 1980 are included.

Country of destination	1980		1984	
	Tonnage	Value	Tonnage	Value
Argentina	154	357.14	256	437.50[a/]
Denmark	4859	342.25	5408	429.36[a/]
France	2360	296.19	3129	285.39
Spain	1802	330.74	879	470.99[a/]
South Korea	191	314.14	842	451.31[a/]
HongKong	55	363.64	2223	25.1.46
Taiwan	60	333.33	453	238.41

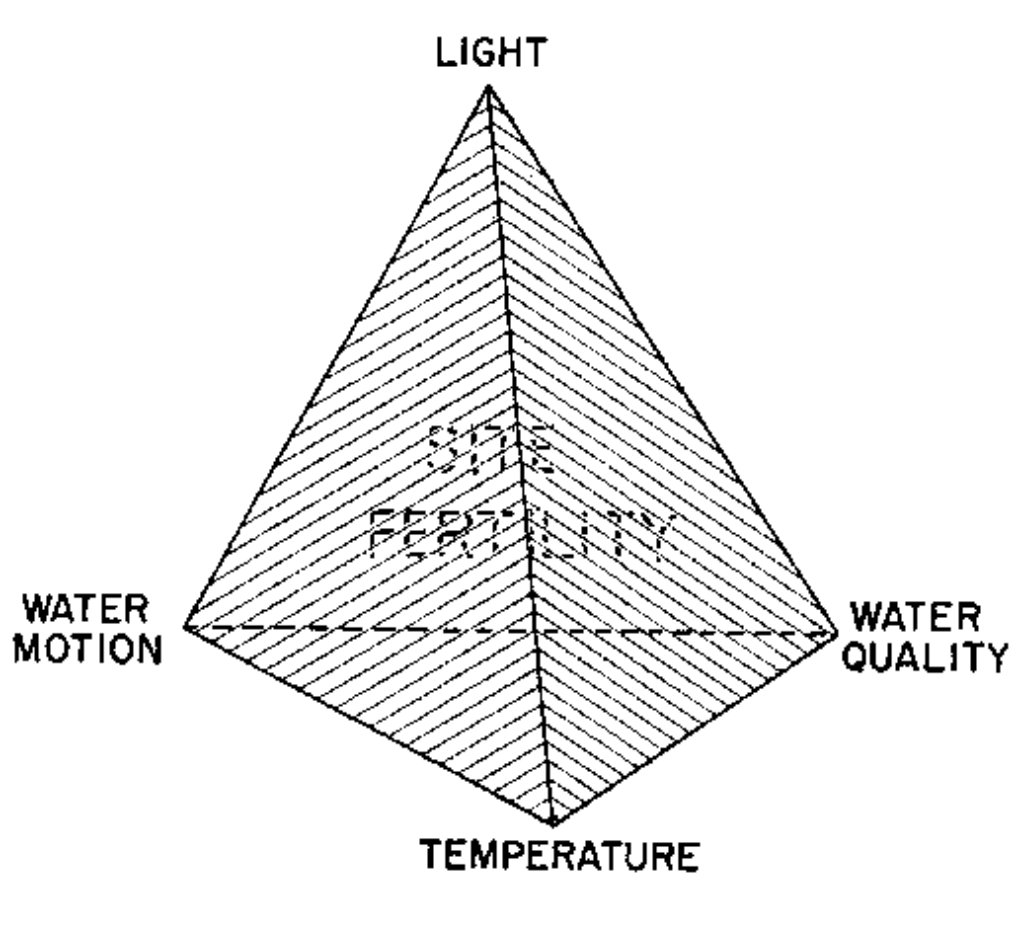
[a/] These high values must be presumed to reflect part of export was AMC or spinosum.

5.2 Natural determinants of Eucheuma production

5.2.1 Physical determinants of productivity

For wild crops the summation of the four complexes of physico-chemical factors (categorized as water motion, light, temperature, and water quality) was initially **(Figure 7** and Doty 1971, 1979) considered to control "site fertility." Later, as farming came to dominate Eucheuma production, farm "productivity" in terms of mass/area/time, became the objective and water motion was recognized (Doty 1982a) as a prime factor in both successful site selection and productivity. Unless farm site selection has provided these four conditions suitably, and favorable tidal and bottom relationships as well, farm productivity is not satisfactory. (The similarly essential biological factors are considered in Section 5.2.3).

Figure 7. An hypothetical compensatorial relationship of site fertility to environment. Each of the four vertices of the tetrahedral figure represents respectively one of the four classes of physical environmental elements. The volume so established by the four plane surfaces of the tetrahedron represents both site fertility and productivity. (From Doty 1982b)



5.2.2 Seasonality and longer term variation in productivity

Field conditions have frustrated attempts to obtain reliable measurements of Eucheuma seasonality, except for the 55-week Hawaiian unpublished study of Doty & Glenn. Seasonal farm production data is undependable because of the lag between the time the seaweed is harvested and the time it reaches a level in the market chain where the quantity can be measured consistently. Added to this, one has no way of correcting the market chain for farmer, consolidator and extractor effort and these elements in themselves, have few seasonal constraints. The Hawaiian study reveals some of the environmental parameters **(Table 3)** within which Eucheuma thrives; it also indicates that spinosum and the two principle strains of cottonii grow **(Table 6)** at different rates and may have different seasonalities. Where these seaweeds are grown commercially nearer the equator, seasonality has appeared to be weaker except in monsoon areas.

Incident sunlight varies with latitude and longitude (List 1966) and varies **(Figure 8)** as much as 20 percent over periods of a few years. Sunlight intensity has a seasonal maximum, and commercial crop productivity seems to vary with it.

Sea temperatures are usually correlated with (but lag behind) sunlight intensity in an annual cycle. The global sea temperature **(Figure 4)** shows the area of the Indo-Pacific where the 23 to 33°C temperature range occurs. Geographically this temperature range indicates the latitudes favorable to Eucheuma commercial production.

Several year variations in water temperature and sea level changes surely influence Eucheuma production. These long-period changes are seemingly related to variations in the Southern Oscillation Index (see Ramage, 1986, for review) and this may in turn be related to such items as the pattern of variation in sunlight **(Figure 8).**

5.2.3 Human and other biological determinants of population density

The most important factors regulating the degree to which the highest economically sustained yields are obtainable are found among the biological factors controlling pests (Section 4.3 and 4.4), genetics (See Section 5.3) and the dedication with which wild and farmed crop agronomic practice are applied.

Table 6. Mean Growth Rates for Cottonii and Spinosum on the Hawaiian 55-week Experiment Plot. Cottonii was represented by "A" Eucheuma alvarezii and "B" by E. striatum with spinosum being represented by "C" E. denticulatum. "UP" and "DN" refer to the place of growth at, respectively, the upstream or downstream edge of the plot and growth is in terms of percent increase in weight per day. Only upstream values are given in the seasonal part of the table.

Season	Growth rates as percent per day		
1976-7	**A**	**B**	**C**
Spring	5.25	3.95	3.51
Summer	6.23	3.33	4.05
Fall	4.41	2.98	3.52
Winter	4.15	3.76	3.35
UP X	5.05	3.51	3.61
DN X	2.07	1.43	2.29

Figure 8. Year to year variations in sunlight. The values are for Honolulu, and the solid horizontal line indicates the mean value (From the 1983-84 Hawaii Natural Energy Institute Report).

5.3 Genetics and high technology in Eucheuma production

Though not done, it would apparently be relatively easy to produce new strains by traditional hybridization. There is no place equipped to do this now. There are two principle barriers to success: one is that the thalli are large and require both a large amount of desirable water and its movement; so in vitro work is limited. The other is the lack of recognizable, genetically-different strains and males in this genus. Eucheuma has not yet proven amenable to gene mechanics or protoplast fusion, and the costs and returns of this may not be favorable from an economic standpoint.

5.4 Relative contributions of sexual and vegetative reproduction

Sexual reproduction has little influence on crop production: all farmed crops are reproduced vegetatively.

Sexual reproduction and rearing crops from spores or very small vegetative propagulae of some kind do not seem practical in view of farm conditions. The size of Eucheuma thalli makes it economic in the Old World Tropics to break off and plant individual large pieces of the thalli, and this has become the routine for starting a farm or individual crop. Thus macro-vegetative reproduction is used. Inducing regeneration (Section 4.6) is not a part of the farming manipulations.

The farming routines advised (e.g., (Doty 1973a,b; Doty & Alvarez 1973), i.e., of harvesting and selling the small thalli after a crop growth period and replanting with vegetative fragments of the largest, would seem to be effective insofar as local genetic variability in the crop is concerned when farming is initiated from wild thalli. After a few crops, further use of this selection procedure produces neglible results insofar as improvement is concerned.

Early in the development of Eucheuma farming, a very significantly better variety was found (E. alvarezii var. tambalang Doty) by a selection program involving over 23 strains and species of wild cottonii. Such improvement has not been obtained in the case of spinosum despite many efforts. The most striking strains are strongly green thalli, principally, but other color and some morphological varieties are seen commonly. None of these appears to be superior from either the farm production or gel extraction points of view.

5.5 Anticipated agronomic improvement of Eucheuma production

All farming involves environmental enhancement; in the case of Eucheuma it is largely provision of substratum. It may be concrete posts (Liu & Zhuang 1984) or nets (Doty 1973a,b, 1979; Doty & Alvarez 1973, 1975; Deveau & Castle 1976; Parker 1974) or more commonly lines nowadays **(Figure 6)** that hold the thalli in place in a desirable environment. It appears to be essential for such an environment to have water movement so strong near the sedimentary bottom that, at peak intensities, the seaweed would be washed away if they were not attached. The lower growth rates reported (e.g., **Table 4)** may be due to the plantings having been off the bottom or in calmer water.

Raking the bottom under the farm lines and fertilizing seem to enhance productivity, but perhaps will not produce economically significant increases in it. There is no shortage of suitable farm area, and the capital cost per hectare is very low; so unless there is a great labor saving, there is not much pressure for higher Eucheuma productivity.

Crop quality, not its productivity, is the greatest agronomic concern. The quality of the Eucheuma produced is affected by the agronomic practices of the farmers. The highest crop yields are produced by frequent harvesting, and this leads to harvesting what may be called immature material. Rational harvesting routines that replant young material and sell the oldest can be instituted; these will yield more carrageenan per ton of seaweed and higher quality-gel. **Table 7** provides examples of value indices for a better standard cottonii and for a low grade cottonii, such as one can expect from poor harvesting practices. This table shows that if a crop indexed at 0.280 is worth $350 dollars per ton, a crop valued at but 119/280ths of that is worth only $145 per ton to the same processor if used for the same period.

Table 7. Linear Factoring as a Method of Evaluating Eucheuma for Extraction. The Value Index resulting is equal to the product of the individual evaluations in the columns to the left. While the individual percent values given may be characteristic they refer to no particular lot or source of the seaweed. The terms used are the Dry to Wet Weight Ratio (=Dry wt.), Clean Anhydrous Carrageenan Yield (=CAV) and Gel Strength (=Gal str.) and are standard terms to which a cost of processing (=Process) factor is added.

Seaweed quality	Dry wt.	CAY	Gel str.	Shipping	Process	Value index
Standard	0.70	0.40	1.00	1.00	1.00	0. 280
Low Grade	0.60	0.30	0.60	1.00	1.10	0. 119

6. METHODS OF HARVESTING AND HARVESTING CYCLE

6.1 General harvesting cycle
6.2 Farm productivity
6.3 Eucheuma farming as an alternative means of employment

6.1 General harvesting cycle

Wild crop production involves repeated periods of harvesting, regrowth and reharvesting with the addition of pre-sale treatment. Farming adds maintenance of the farm structures, planting, replanting and pest control. (See Section 4). Harvesting is breaking off part of each thallus by hand and removing it from the wild crop or farm area.

Immediately after harvesting, the most common treatment is sun drying. For this purpose the seaweed is usually scattered on rock or bamboo surfaces as this obviates sand, soil and trash being added. The more sophisticated drying is on slatted bamboo decks surrounding farm houses erected at the farm sites.

It takes about three days of hot sun to produce commercially dry Eucheuma, during which time the farmer should be alert to protecting his harvest from rain. Rain washes off salt and small organic solubles and causes bleaching. Such losses in weight and color increase the value of the crop, but this is at the farmer's expense, unless the greater effort and loss of weight bring a compensatory higher first sale price. Bone-dry Eucheuma rinsed in sea or fresh water for less than a minute will lose about 16% of its bone-dry weight.

To obtain greater value in the dried Eucheuma, there have been buying stations located among the farms. These consist of platforms surrounding the station's building(s) upon which, after the live crop is purchased, the cleaning and drying of the harvested lots is done uniformly by the consolidator. The buying stations, like the farm buildings, are constructed on posts driven into the reef flat surface so as to endure storm winds and waves. They are, thus, over water but elevated above the highest sea levels.

Initially the buying stations merely dried the seaweed and transported it the relatively long distance (for individual farmers) to the main consolidation areas. Recently there has arisen the commendable practice of purchasing live seaweed at the buying stations with the post-harvest treatment being done by the first purchaser. Under this regime variously sophisticated post-harvest treatments have been introduced at the buying stations.

6.2 Farm productivity

The productivity of a farm depends on the inherent nature of the strain of seaweed and the agronomic practices being used, as well as the environmental conditions. (See Section 5).

Site fertility and the agronomy applied are so variable that there is little consistency in yield from place to place. Furthermore it is almost impossible to obtain such information without living at the farm being studied. Two of the best reports of field observations are Lim et al. (1982) and Adnan & Porse (In Mss) though incomplete in many respects. Yields as high as 74 (spinosum) to 104 (cottonii) dry tons per hectare per year have been verbally reported. However, a usual range **(Table 4)** of 15 to 30 tons per hectare per year is recognized.

Returns to the farmer vary from place to place. Lim & Porse (1981) provide the only published recent first sale values. Outside the Philippines first sale values are believed to range from perhaps 10% to 80% of the export value. Doty (1986) provides a method of relating the farmer's productivity to his cash returns from first sale, assuming 75% of the export price is returned as is common in the Philippines. The grey literature contains more information.

Farm growth rates of Eucheuma **(Table 4)** routinely range from 2 percent per day toward ten percent per day, depending upon strain and environment. Better quality Eucheuma is produced when the growth rates are such that the crop doubles in size in each lunar cycle of 28 days. This is a growth rate equal to 2.51 percent per day. More practically speaking, a growth rate of 3.5 percent per day is thought to offset the generally anticipated negative factors and provide a doubling of the crop and so yield a harvest of one half of it every month. In some places the thalli will double in weight in less than 14 days.

It is obvious that in starting a farm, the farmer should plant the largest thalli feasible. However, the larger the thalli become, the more susceptible they are to physical damage and loss. Thus the size at which harvesting would best take place, the mature size, is different in different places, though the strain and agronomic treatments may otherwise be the same.

The mature size is usually between 512 and 1028 grams. Especially seasonally, the mature size may be **(Figure 6)** much larger. The size of large mature Eucheuma thalli make it practical to handle, tie in place, tend and harvest individuals. The productivity can be calculated from the number of thalli involved, the mature size of the thalli, and time between harvests. Many farms have about 100,000 thalli per hectare.

6.3 Eucheuma farming as an alternative means of employment

A large, successful farm could require several people for its proper operation, and a small farm might be successful even though it does not require all the time of even one person. The farming of Eucheuma is not on an annual cycle; it is rather continuous in the same sense as poultry farming. Eucheuma farming is excellent as an alternative means of employment.

When the farm is small, the artisanal fisherman who has become a Eucheuma farmer can often continue his traditional ways of obtaining a livelihood, and it is often his wife who farms the seaweed. Thus, Eucheuma farming is a ready way of improving family income.

The farms are on reef flats or other horizontal bottoms near extreme low-water level. Since working at high tide is often much more exhausting than working at low tide, seaweed farming tends to become a part-time occupation. Furthermore, since the tides are not governed by calendar or solar time, but vary in lunar month (siderial time) cycles, the formal employment conventional to the developed world is hardly appropriate. It is sometimes difficult for those not working in the sea to cope with this idea, that favorable conditions for work are not in accord with the civil or religious calender days, weeks, weekends, holidays or seasons.

Incentive and free enterprise are major factors in farm productivity. Early experience (Doty 1973a,b) in developing the farming of Eucheuma led to the statement "having the farms small, and owned and operated by the workers who benefit in proportion to their investment of material and effort seems to be the key to successful production of this seaweed." From a different series of experiences, Lim & Porse (1981) have pointed out that Eucheuma from an absent-owner estate-managed farm costs $0.34 per kg to produce. Comparably from a resident-owner farm hiring workers, they found the cost was $0.37 per kilogram, but only $0.20 per kilogram from a family farm where there are no paid employees. Doty & Alvarez (1981) provided the further figures of 2 to 3 kg/man-hour on a non-seasonal family farm and 1 to 2 kg/man hour on an estate farm.

7. EQUIPMENT USED FOR HARVESTING AND CULTURE OF EUCHEUMA

7.1 Wild resource management
7.2 General statements regarding capitalization
7.3 Sources of credit and insurance of the crop

7.1 Wild resource management

Wild crop harvesters normally forage on the reef flats for much of their livelihood and so are already equipped to forage for Eucheuma. This equipage may be as little as just the essential knowledge of what seaweed is to be harvested and where it is found. The first level of sophistication might be a container in which to accumulate the Eucheuma as it is picked. Their locally made family boat is often used. While harvesters usually carry a large knife; this and even hats and shoes are not requisite to wild crop harvesting.

7.2 General statements regarding capitalization

When wild crop harvesters or fishermen shift to farming Eucheuma, they may start with a single piece of monofilament line obtained at no cost and, as they sell their crop, use some of the proceeds to obtain more line. Creating circumstances which allow them to do this is one of the better ways to get this farming undertaken. Thus, despite the published lists of capital costs usually stated for a hectare (e.g./Doty 1973a/b), the costs may increase so gradually from negligible to such as the example tabulated **(Table 8)** as to be no barrier to undertaking farming. Most farms are probably near one tenth of a hectare or far less than a hectare in extent.

Table 8. Estimated Costs for Capital Investment in a Eucheuma Farm. Parameters are one acre of average quality bottom and Eastern Sabah (Malaysia) minimal costs in 1982 Malaysian dollars. 2.47 acres = 1 hectare.

I. Material expenses:				
Item & Description	**Number needed**	**Length needed**	**Weight needed**	**Cost in M$ in 1980**
A. For the farm:				
1) Mangrove posts, 2 inches in diameter by 3' @ M$1.68 each	565	3' or 1 m		942.38
2) Mangrove posts, 12 feet long @ M$0.30 each	4	12' or 3 m		1.20
3) Nylon mono filament line 120 lb test strength (this is not the #120 on most packages)		14,700	5.8 lbs or 2.6 kg	100.00
4) Tie-tie material cut into pieces 10" long (25.4cm) each split into 3 pcs.	4,839	1,344' or 409 m		20.00
B. Seedstock				
1) Seedstock, M$0.20 per kilo, (100g per plant initial, weight) at 1.5'x1.5'	17,689		1,769 kg	354.00
C. Total estimated cost of materials				1418.58
II. Labor expenses:				
A. Mangrove posts				
1) Delivered to site				100.00
2) Total cost of labor (for cutting and sharpening 565 stakes at $0.10 each)				60.00
B. Staking (installation costs)				
1) 565 stakes per acre, 10 minutes to set a stake or ca 100 man-hours per acre = 25 4-hour low tide periods with travel time each day @ M$8.00/such 4-hr day.				
Labor cost				200.00
C. Tying of seedstock				
1) 125 to 240 thalli per hour - 1000 to 1920 thalli per man-day @ 50/man-days per acre @ $10.00/day at dense spacing				
Cost of 5,000 thalli				1,000.00
D. Setting and planting of monofilament lines (4 hours low tide working time per day.)				
1) 32 man-hours per acre to make and install mono-lines and obtain thalli, M$8/day for 8 days.				64.00
2) 16 man-days to set up monolines and plant 4,839 (a minimal number of) thalli on one acre				128.00

E. Estimated total cost of labor w/o supervisory time.	1552.00
III.. Equipment needed	
1 crow bar	18.00
2 heavy knives (e.g. bolo)	12.00
2 stainless steel knives	7.60
4 rattan baskets	28.00
1 plastic container for water	10.00
1 plastic container for gasoline	10.00
Miscellaneous	14.40
Total	100.00
IV. Total estimated cost of materia1s and installation of a one acre monoline Eucheuma farm	3070.00a/

a/In 1985 this was equivalent to about U.S.$1330.

When government or tradition intervenes, rather than cost of materials, etc., a stumbling block to farming from the would-be-farmer's point of view could be obtaining the right to farm.

An investor would find the weakest place in Eucheuma farming to be in the availability of competent personnel for selecting a site, installing a farm and managing it. The cost of such a manager could be equivalent to the local costs for a non-college-graduated school teacher. In addition the investor would have to obtain clearance to use the site and obtain the initial planting material. **Table 8** displays the materials and their costs for one acre farms constructed in easternmost Sabah, Malaysia, for the State Fisheries Department. These Sabah costs are surely more nearly maximal than minimal if for no other reason than that they included **(Table 9)** two surrounding sets of nets and devices to control herbivorous fish (largely Siganus) and Chelonia midas, the green turtle.

The amount of time required is increased by the travel time to and from the farm construction site and by the tides. At the Sabah sites to which Tables 8 & 9 refer the time on the job was about four hours per man day. This would be different elsewhere.

7.3 Sources of credit and insurance of the crop

Essentially there are no sources of credit or insurance for seaweed crops. In practice the most to be had is provided by the strong ties among the pre-sale seaweed producers and credit with the local merchants.

8. PROTECTION AND MANAGEMENT OF THE RESOURCE

8.1 Management of seaweed resources
8.2 Regulation of seaweed

8.1 Management of seaweed resources

As in many such agricultural industries, there are three levels of management concern plus the government. These may be separated conveniently into a) pre-first sale level of wild crop harvesters and farmers; b) post-first sale entrepreneurs and exporters, and c) the ultimate processors. Hollenbeck (1983) and Vellin & Hollenbeck (1982) provide much more.

8.1.1 Commercial relationships

Management of wild crop harvesting has always been largely in local, usually informal or traditional, hands. A typical operation is for a post-first sale entrepreneur to make arrangements to buy Eucheuma from a shoreside village merchant. This merchant is often the de facto local government insofar as the harvesters are concerned. In Indonesia he is (Lee Hollenbeck, personal communication) often the traditionally recognized village leader who gets the artisanal fishermen to collect seaweed, often a given or traditional amount. The village leader accumulates the seaweed and sells or barters it to the entrepreneur or trader, who will probably be but a representative of a traditional exporter. In a money-economy situation the village leader, the trader and the exporter may be considered second level interests. The third level interests, the processors, establish commercial relationships which are often agreements to buy a certain tonnage within certain time/quality limits "free and on board" a ship bound for the port nearest the processor's plant.

Table 9. Fish and Turtle Exclosure Fences and Trap Costs. The list of materials is for a square one acre farm ca 210 feet on a side in an area where the tides may rise as high as two meters. Values are in 1982 Malayaian dollars.

Item & Description	Number needed	Length needed	Weight needed	Amount in M$
A. For fencing:				
1) Mangrove posts	148	12 ft. long & 2 " diam.		44.40
2) Stranded fish net Twine: PE. 380/6 Mesh: 2 1/4" Width: 300 cm Length: 150 ft./roll	3 rolls	880.6 ft.		750.00
3) Border-line for stranded fish net, 150 lb test.			2 kilos	24.00
4) Wire for securing fish net to posts, 16 inches long	444 pcs.	592 ft.		20.00
5) For turtle net, 2.5 x 5 meters in standard net units	60 pcs.	946 ft. or 288.5m.	5 kilos	228.00
6) Mangrove posts for turtle net fencing	60 pcs.	12 ft. by 2" in diam.		20.00
7) Wire for securing turtle nets to posts, wire pieces 16" long.	174 pcs.	232 ft.		8.00
B. Two fish traps:				
1) Mangrove stakes, 3 meters long by 2 1/2 " in diam.	8 pcs.	10 ft.		2.40
2) Mangrove stakes, 2.5 meters by 2 1/2" in diam.	8 pcs.	9 ft.		2.40
3) Many rove stakes, 1 meter by 2 1/2" in diam.	8 pcs.	4 ft.		1.20
4) Stranded fish net; Twine: PE. 380/6 Mesh: 1 1/4" Depth: 300 cm		32 ft.		7.00
C. Total fencing & trap material costs				1,107.40a/

a/In 1985 this was **equivalent** to **about** U.S.$480.

8.1.2 Government roles

Two governmental groups are often the official bodies of concern: economic development authorities and the fisheries departments (often) of the agriculture department. They usually arise after-the-fact due to their lack of entrepreneurial and phycological capability as well as incentive, the need to heed the wishes of the politico/economic interests and their traditional fin/shellfish concerns.

The private sector has been the initiator (Doty 1973b; Adnan & Porse In Mss) and has been initially in control of the first two levels in almost all successful production areas: e.g., to the extent that there is production in Indonesia, Philippines, Taiwan and Tanzania. In Indonesia the Agency for the Assessment and Application of Technology and in Kiribati and Malaysia the fisheries departments have been very positively active in seeking to establish farming.

In the Philippines the national fisheries department research section played an unusually successful role by coordinating and contributing its facilities to the expatriate academic and processing interests of industry at the initial development level of both the wild crop harvesting and later the R & D leading to pre-eminence of the Philippines in both cottonii and spinosum farming.

There are no effective formal mechanisms for consultation between the levels of concern in the Eucheuma industry.

There are essentially no regulations effectively governing the harvesting/culture of Eucheuma. What arrangements exist for leasing or private ownership of nearshore or intertidal areas for this purpose have been ineffective or have been applied at the initiative of local fisheries officers and the private sector by what might be called field expediency. In southernmost Philippines, village councils have shouldered the responsibility for individual farmer concessions under the umbrella protection of master concessions from the government obtained by the processors. In some other places government participation in efforts to "facilitate" farmer leasing have been as much a barrier to success as an aid.

The concession plans in Indonesia and Malaysia; at least, were established so as to leave passageways for local boat traffic. On reef flats there is no conflict with fisheries useage or with ocean navigation. The farms result in enhanced fish crops, and fish traps and Eucheuma farms do not compete for the same space.

8.2 Regulation of seaweed

To date no specific legislation is known that affects Eucheuma farming. In Hawaii it has been effectively prevented in the past by the classification of all sub-tidal land as conservation, a designation that prevents its economic development. This situation in Hawaii is changing favorably through new legislation. In the Philippines legislative and executive bodies have considered legislation and various regulations, but these have not been effected. Regulations have been instituted to obtain advantages for individuals, but they are ineffective and largely ignored. Notably in one African country a monopoly has resulted in no development of farming and apparently no increase in export during the past 20 years. In two other countries government has entrusted development to innocent hands that despite goodwill have been unable to move to the economic export level. In some others nothing has happened. Only in those countries where there was no contrary legislation and the ultimate processing companies from abroad have sent in expatriate management has introduction led to farming and regular export.

9. UTILIZATION

9.1 Chemical and nutritional content
9.2 Human food
9.4 Animal Fodder
9.5 Manure
9.6 Industrial products and processes

9.1 Chemical and nutritional content

Industry's only concern for Eucheuma is its carrageenans. Carrageenan is a cell wall component which represents 40 to 75 percent of the seaweed's salt-free dry weight. In addition to carrageenan the cell walls of a Eucheuma contain a small amount of cellulose and minor amounts of other unspecified materials.

Eucheuma reaches the ultimate consumer as whole or particulated, dried material in one of several forms. Commonly the carrageenan may be extracted carrageenan (with or without chemical modification) or in the non-extracted modified form.

Basically carrageenans are d-galactopyranoses alternately paired by alpha 1-3 and beta 1-4 linkages. Their molecular weights may be as high as 400,000. They are typically sulfated though sulfate is lacking (Greer & Yaphe 1984) in beta carrageenan. Seven types are recognized and referred to by the greek letters, beta, gamma, kappa, lambda, iota, mu and nu. Infra-red absorption peaks are present for total sulfate and, respectively, that at any of the 2, 4 or 6 positions. In addition, the different carrageenans are distinguished by their solubilities in water at different temperatures (Greer & Yaphe 1984) and reactions to different salt solutions as well as the physico-chemical properties of their gels. At present there is considerable question as to their structure, e.g., whether they are purely one or another of the seven types listed above or whether there are blocks of one type in combination with blocks of other types. Relatively low sulfate content and 3-6 anhydro linkages are found to be related to high gel strengths. Milk reactivity and gel strength may be related to potassium and sulfate, respectively, at the 4-carbon positions. Various other radicals may be attached especially at 6-carbon positions.

The nutritional value of Eucheuma and its contained carrageenan are unknown. Its effect on humans is believed to be nil and, in foods containing it, the carrageenans are minor components by weight, though often indispensable for contributing a specific quality to the product.

9.2 Human food

Culinarily speaking, Eucheuma, the fresh or non-dried seaweed itself, adds delightful variety, novelty, and bulk to peoples' diets in various countries where it grows, e.g., as a fresh salad component or as pickles.

The extracted carrageenans provide stabilization and quality to the products in which they are combined. Today, many instant foods that come in powdered form for mixing with cold milk to make them comestible owe their speed and permanence of suspension to the carrageenan modification they contain. A desirable mouth feel is sometimes obtained by adding a carrageenan. Some major toothpastes contain it for its way of holding water in the product and, thus, extending shelf life. The successful suspension of chocolate in milk is perhaps best done with carrageenan. Most if not all evaporated milk nowadays contains carrageenan as the component that makes possible its pleasant flavor and thick, creamy quality.

Aside from "extracted carrageenan", there is the alkali-treated Eucheuma (sometimes spoken of as AMF or AMC, i.e., alkali modified flour or alkali modified carrageenan or semi-processed carrageenan). Making alkali-treated Eucheuma seems to consume most of the cottonii Eucheuma produced, for it is far less expensive than extracted carrageenan. It can usually substitute for extracted carrageenan where a little cloudiness from the small percentage of cellulose present does not interfere.

Both the alkali-modified Eucheuma products and the extracted carrageenans must compete with other hydrocolloids on the basis of amount required to do the job and cost per pound. An outstanding exception is their special effect in some milk products wherein carrageenan is often essential or nearly so. Carrageenans form synergistically desirable substances with other hydrocolloids and are chemically modifiable in many ways, giving them a wide variety of useful special qualities. Guiseley et al. (1980), Whistler & BeMiller (1973) and Glicksman (1969, 1982) provide four of the most useful treatises on applications of the different carrageenans and their modifications.

9.4 Animal Fodder

The carrageenans and Eucheuma are not normally used in animal fodder. However, the largest volume of alkali-treated Eucheuma is in pet foods where it is used as a powdered, granulated or hydrated gel component in the various formulations.

9.5 Manure

Eucheuma has essentially no use as a manure. Though its addition as an organic component in conditioning sandy soils is in some cases attractive, the cost is high. Some effort has been put forth to obtain use of the filter aid waste from the carrageenan extraction plants as a soil conditioner. Such waste filter aid is the major nonsoluble product from Eucheuma processing

9.6 Industrial products and processes

The carrageenans extracted from Eucheuma are modified by proprietary methods and even the relatively simple alkali-treatment process is hardly publicized. The assayed plant yields of extracted carrageenan may vary (Adnan & Porse In Mss) from 23 to 36 percent. A simple diagrammatic flow sheet is provided **(Figure 9)** though it is hardly applicable to any one actual alkali-modification plant.

The carrageenan extraction process itself is well known to be a hot water, high pH, process. The principal costs are in heat and separating the carrageenan from the extraction water. Three approaches are in use for water removal after centrifugation, filtering and sometimes vacuum removal of some water: a) spray drying on steam-heated drums as in the making of powdered milk; b) cold-water extraction of the seaweed (when Chondrus is the source) such that the lambda carrageenan is separated from the kappa, with the kappa being extracted and precipitated separately later; and c) precipitation with alcohol. Each process has its merits, and some large companies use more than one method to obtain different qualities in their final products. Moss & Doty (In Press) provide a flow sheet **(Figure 10)** for the latter plant type.

Aside from the raw seaweed material, the principal costs of carrageenan (Moss & Doty, In Press) are in inventory, warehousing, water, power, alcohol recovery (only in alcohol precipitation plants), filter aid (diatomite or expanded mica as a rule) and chemicals (largely calcium and potassium hydroxides).

Figure 9. The alkali-treatment process for cottonii. Depending upon end product specifications, live or dried cottonii with or without preliminary treatment is often treated first in a hot alkali solution containing about 8.5 percent potassium hydroxide and then rinsed in successive tanks of water. The seaweed may be handled in baskets by an overhead traveling crane. Following a final draining, the treated material may be dried whole, or chopped and dried. The lower part of the figure shows a succession of processing steps that may follow depending on control laboratory analysis and desired nature of the final product

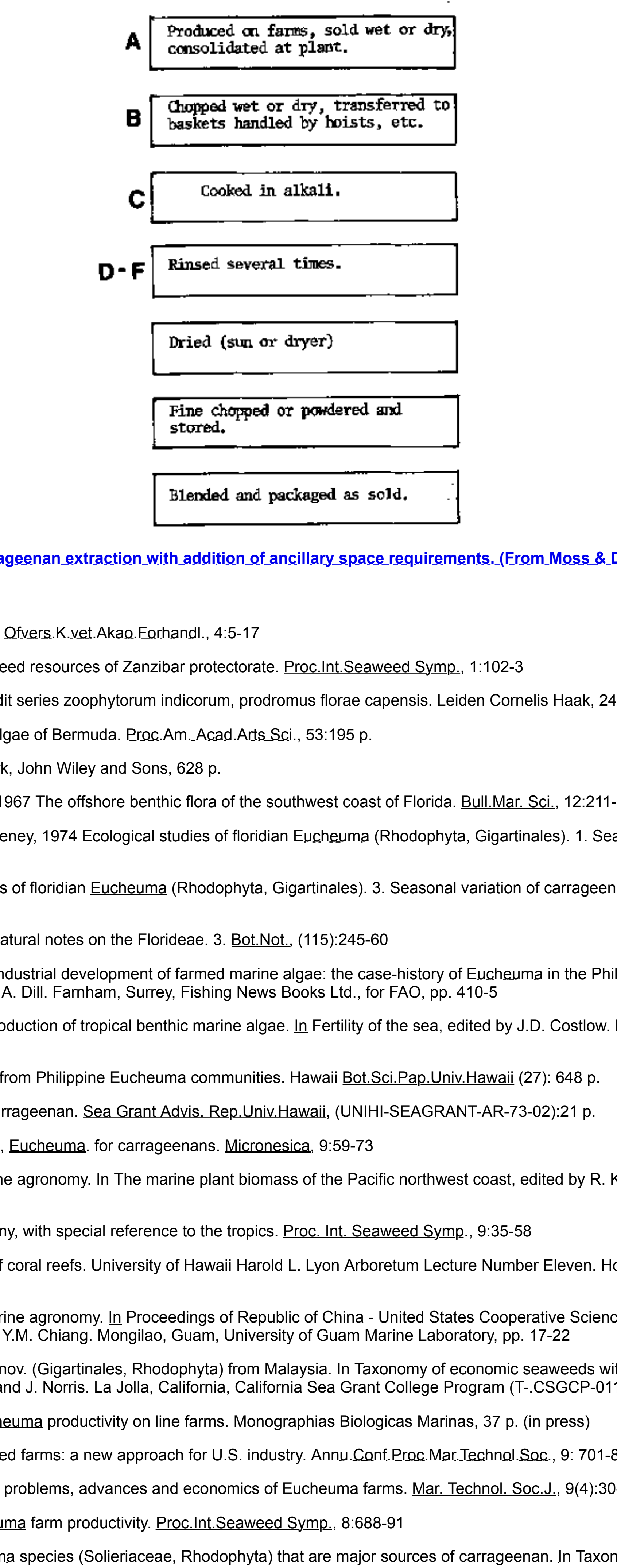

A
B
C
D
E
F
A Produced on farms, sold wet or dry; consolidated at plant.
B Chopped wet or dry, transferred to baskets handled by hoists, etc.
C Cooked in alkali.
D-F Rinsed several times.
Dried (sun or dryer)
Fine chopped or powdered and stored.
Blended and packaged as sold.

Figure 10. The alcohol process for carrageenan extraction with addition of ancillary space requirements. (From Moss & Doty In Press.)

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The wild harvest and culture of the economically important species of Gelidium in Chile

- 1. IDENTITY
- 2. DISTRIBUTION, ECOLOGY AND METABOLISM
- 3. LIFE HISTORY
- 4. POPULATION STRUCTURE AND MORTALITY
- 5. PRODUCTIVITY OF THE RESOURCE
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ABSTRACT

Gelidium chilense, G. lingulatum and G. rex are economically important in Chile. Gelidium lingulatum extends from central to southern Chile (33 to 41 S) while the two other species extend from central Chile to central Peru (35 to 14 S). All three species occur in low intertidal belts along the more wave exposed rocky coasts. Light intensity, temperature, water movement and interspecific interference have been proven to be ecologically important in regulating distribution and production. Daily growth rates of 2.5 to 4 percent have been reported. The Chilean wild crops (100 - 150 tons per year) are a minor part of the world crop of Gelidium-Pterocladia (15,000 to 19,000 tons per year). Gelidium rex has grown 2.5 to 3 percent per day in experimental field cultivation. Gelidium chilense is able to grow under free floating conditions. All three are gathered by hand picking as a part-time activity.

1. IDENTITY

- 1.1 Nomenclature
- 1.2 Taxonomy
- 1.3 Morphology and anatomy

1.1 Nomenclature

1.1.1 Valid scientific name

In Chile, three species of Gelidium are economically important, Gelidium chilense (Montagne) Santelices et Montalva, G. lingulatum Kutzing and G. rex Santelices et Abbott.

1.1.2 Nomenclatural synonyms

The basionym of Gelidium chilense is Acropeltis chilensis Montagne (1837, p. 355). Previous to clarification this common species of Gelidium in Central Chile (Santelices and Montalva, 1983; Santelices and Abbott, 1985) passed under the name of G. filicinum Bory (Montalva and Santelices, 1981; Santelices, Oliger & Montalva 1981).

Gelidium lingulatum was originally conceived by J. Agardh, who gave it the manuscript name Suhria lingulata. Yet, it was first described by Kutzing (1868, p. 27, fig. 65). J. Agardh published further descriptions in 1872 and 1876. The species was found in Chile by Montagne (1852, p. 330) but misidentified as G. filicinum Bory, an opinion also held by Navas (1966). Skottsberg (1923, p. 5) and Levring (1960, p. 34) have confused Chilean materials of G. lingulatum with G. crispum Howe.

The recently described Gelidium rex Santelices and Abbott (1985, p. 33) had been referred to previously as G. spinolosum Kutzing prox. (Oliger and Santelices, 1981; Montalva and Santelices, 1981; Santelices, Oliger & Montalva 1981).

1.1.3 Vernacular name

In Chile fishermen refer to the various species of Gelidium under the common name of "chasca".

1.2 Taxonomy

1.2.1 Affinities

1.2.1.1 Suprageneric

The genus Gelidium belongs to the family Gelidiaceae, which also includes eight other genera. The family Gelidiaceae has been considered a member both of the order Gelidiales and of the Nemalionales (=Nemaliales). The classification of the family depends upon acceptance of the Gelidiales as a distinct order, a taxonomic status which has been under dispute over the last twenty years (Dixon, 1961; Papenfuss, 1966; Pueschel and Cole, 1982).

1.2.1.2 Generic

The genus Gelidium was established by Lamouroux (1813) with the European species Gelidium corneum (Hudson) Lamouroux as the Type. The following is a diagnosis of the genus.

The thallus is cartilagineus, sometimes crispate, 2 to 40 cm tall, composed of one or several erect terete or compressed axes. Axes distichously, plumosely or irregularly branched, red to deep purple although in some species deep green, blackish or caeru-lean. Erect axes arise from cylindrical or compressed, branched or unbranched creeping axes with numerous short haptera extending as individual axes or forming massive disc-like holdfasts. Plants sometimes occurring in mats of algal turf with extensive basal parts or in rather discrete clumps. The erect fronds can be cylindrical at the base, subcylindrical above and frequently compressed at their apical ends. Margins of the axes can be entire or subentire. Often they are subentire in the basal third, irregularly sinuous-dentate or erase dentate above and variously branched along the edges of the upper half of the erect axes. Cortex with several rows of pigmented cells, generally smaller towards the outside, mostly 2-15 m m diam., generally irregularly arranged in surface view. Medullary cells in cross section generally rounded, up to 30 m m diam., colorless, compact or loosely appressed, with or without evident starch granules. Rhizoidal filaments thick-walled, up to 5 m m diam., in medullary and/or cortical tissues, varying in number and position within species. Tetrasporangia in sori occupying the entire or the somewhat expanded or broadly rounded tips of lateral branches or main axes. Fertile branches simple or pinnately compound, somewhat twisted and densely congested. Often with sterile margins. Tetrasporangia cruciately divided, up to 35 m m and generally arranged without order in the sori. Spermatangial sori sometimes apparent as relatively unpigmented areas on apices of branchlets, usually conspicuous by presence of a sterile darker margin. Carpogonial filaments unicellular, fusing with adjacent cells after fertilization. Mature cystocarp protruding equally on both surfaces of the branch, usually with one or, more rarely, several openings on each surface of the frond. Occasionally two cysto-carpic cavities coalesce laterally, forming compound cystocarps up to 1 mm long.

It should be noticed that cystocarpic structure is the only presently accepted morphological difference distinguishing Gelidium from the closely related genus Pterocladia. However, due to the common scarcity of sexual thalli this character is of limited application for routine taxonomic purposes. Other morphological characters have been suggested as segregation characters (Okamura, 1934; Akatsuka, 1981; Stewart, 1976), including hyphal distribution, shape of medullary and cortical cells and degree of basal incurvation of branches and branchlets but they have not recieved general recognition (see Santelices, 1974 for a review).

1.2.1.3 Specific

The Type specimen of Gelidium chilense was collected at Coquimbo, central Chile (30°S), and is now deposited in the Montagne Herbarium, Museum National d'Histoire Naturelle, Paris (Santelices and Montalva, 1983). The Lectotype of Gelidium lingulatum Kutzing is a plant labelled 'Herbarium Kutzing No. 46' deposited at the Rijksherbarium, Leiden. Previously; the specimen No. 33241 in Herb. Agardh, University of Lund, identified by J. Agardh had been chosen as lectotype by Levring (1960). Both plants probably came from the same place in southern Chile in the proximity of Valdivia (Santelices and Montalva, 1983).

The holotype of Gelidium rex Santelices et Abbott bears the Herbarium No. 102652 and is deposited in the Museo Nacional de Historia Natural in Santiago, Chile. Isotypes have been deposited in the Herbarium of the Sala de Sistematica, Pontificia Universidad Catolica de Chile (SS UC), the Algal Collection of the U.S. National Herbarium/Smithsonian Institution, Washington, D.C. (U.S.A.), and the Herbarium of the B.P. Bishop Museum, Honolulu, Hawaii (U.S.A.). All plants were collected from their normal low intertidal to high subtidal habitats, among holdfasts of Lessonia nigrescens Bory, at Pelancura (ca 5 Km north of San Antonio Port) Santiago Province, Chile, on a wave-exposed rocky platform (Santelices and Abbott, 1985).

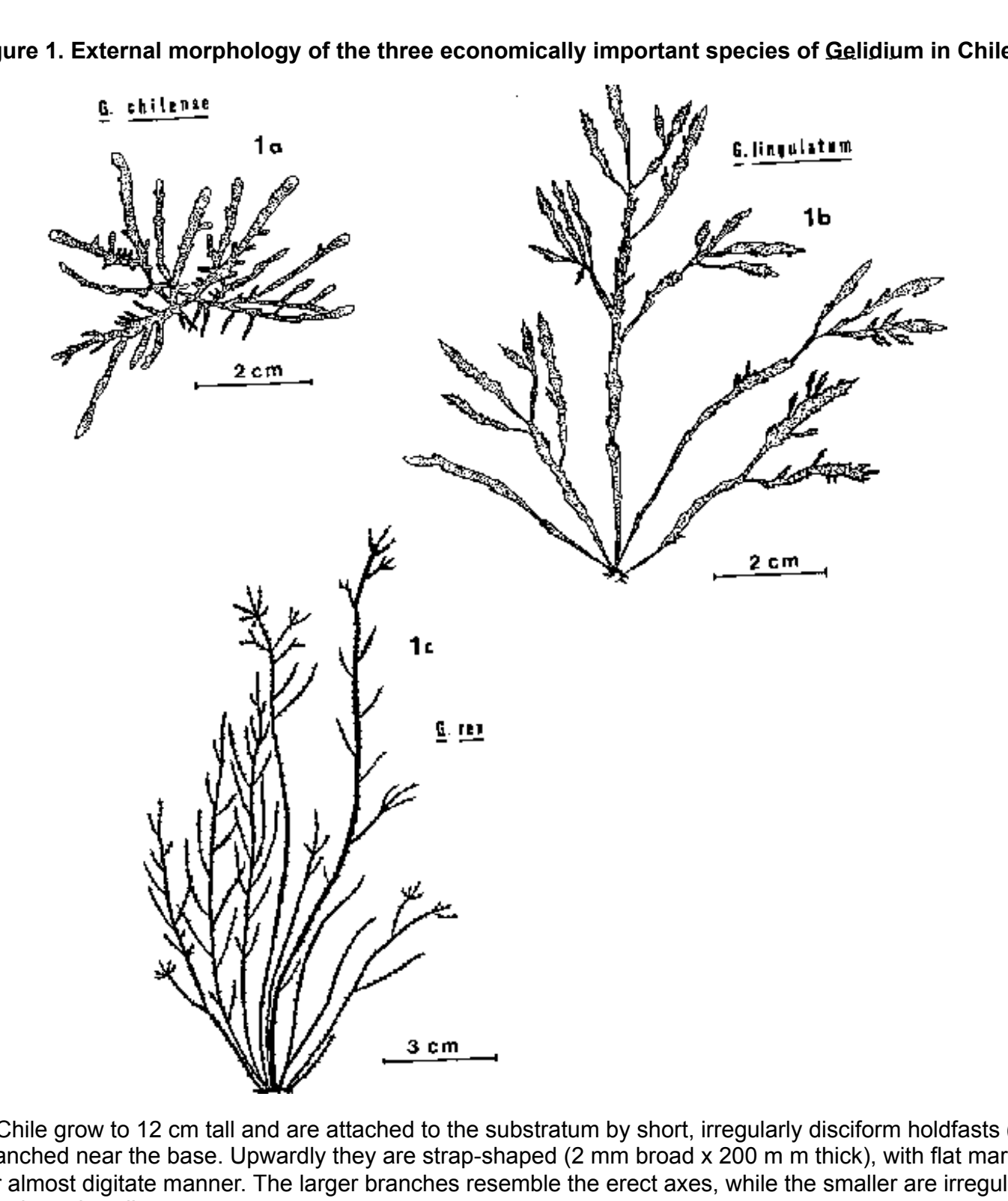
1.3 Morphology and anatomy

The plants of Gelidium chilense are composed **(Fig. 1a)** of several erect, flat axes similar to a sword blade but with rounded and somewhat widened apices. Attachment is by a cylindrical creeping axis with stolons at irregular intervals. Branches can be found along most of the axis, although they are scarce in the basal third. Branching can be of up to three orders. First-order branches are similar to the main axis, frequently disposed in an irregular manner and generally producing second-order or terminal, ovate-lanceolate branchlets. Often first order branches end in a truncate (grazed) apex whence a group of ovate-lanceolate or heart like branchlets originate.

A transection of the frond **(Fig. 2a)** shows a cortex of 2-3 layers of globose-ovoid pigmented cells with their diameters less towards the medulla. The medulla is composed of colorless cells of up to 20m m diameter. Rhizoidal filaments are extremely abundant in inner cortex and outer parts of the medulla, decreasing in density towards the inner medulla.

Tetrasporangia are produced in short, heart-like, rounded or irregularly shaped proliferations, commonly with toothed or dentate margins or on rounded and somewhat expanded apices of main axes (Pig. 3a). They are globose-ovoid, 10-30 m m diam. and 20-50 m m long, cruciately divided. Cystocarps are borne on small, rounded branchlets with dentate margins **(Fig. 4a).** They are ovoid in surface view, up to 600 m m thick and 800 m m long, with two locules, each with one or two ostioles opening on each surface of the frond.

Figure 1. External morphology of the three economically important species of Gelidium in Chile.



The plants of Gelidium lingulatum in Chile grow to 12 cm tall and are attached to the substratum by short, irregularly disciform holdfasts **(Fig. 1b).** The erect axes are cylindrical and simple or sparingly branched near the base. Upwardly they are strap-shaped (2 mm broad x 200 m m thick), with flat marginal branches in the upper parts disposed in an irregularly alternate or almost digitate manner. The larger branches resemble the erect axes, while the smaller are irregularly shaped. The margins of main axes and primary branches often have branch rudiments.

Figure 2. Transections of fronds of Gelidium chilense, G. lingulatum and G. rex.

A transection through the flat, erect axis shows (Fig. 2b) a cortex with three to four layers of rounded, pigmented cells of 5-15 m m diam., inwardly increasing in size and decreasing in pigmentation. Rhizoidal filaments are not very abundant and are scattered in the inner cortex and medulla.

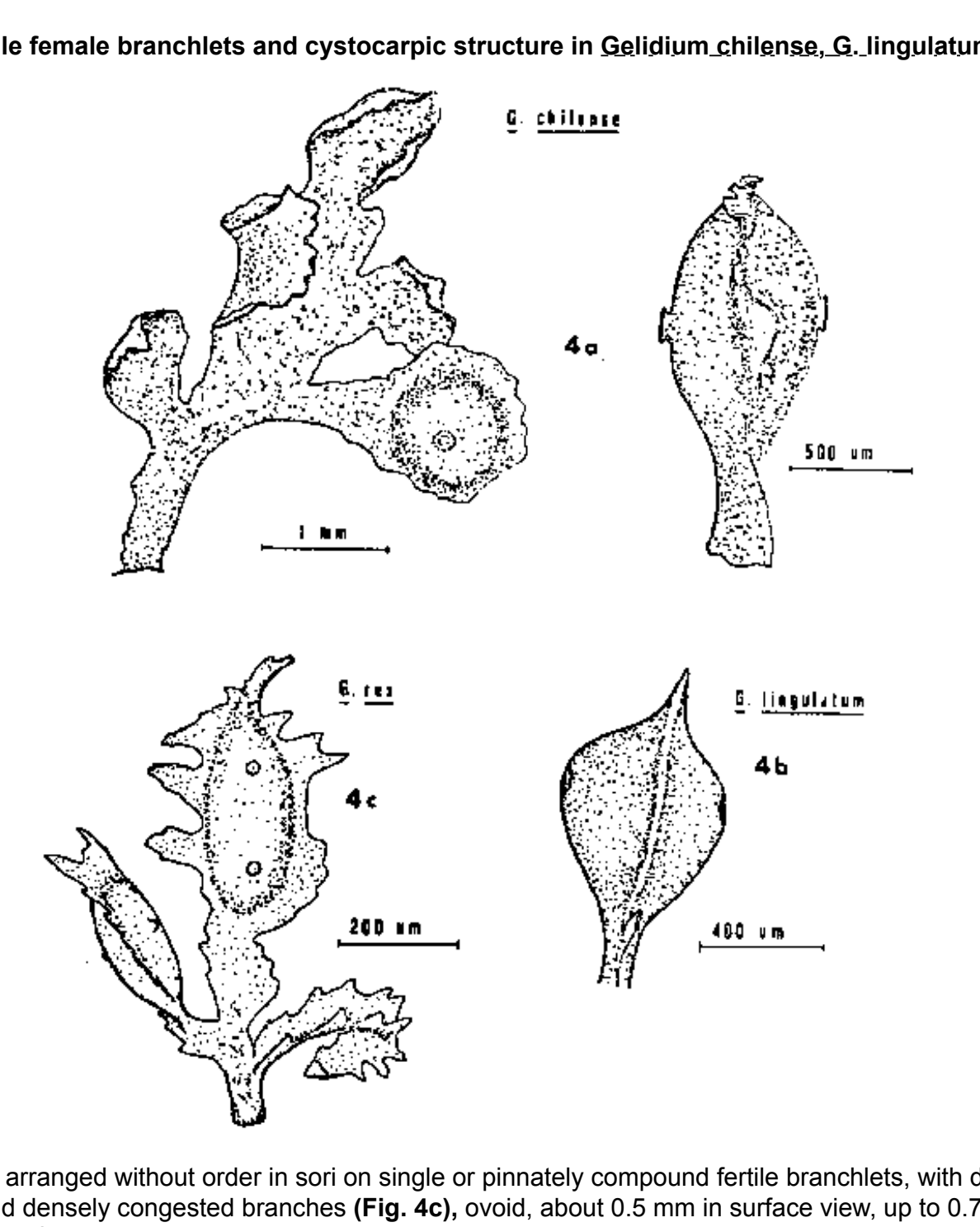
Tetrasporangia and cystocarps occur in pinnately or subpin-nately arranged proliferations **(Figs. 3b and 4b)** that are irregularly compound, commonly crisped or contorted and with serrate margins. Tetrasporangia are ovoid, cruciately divided, 16-25 m m diam. and 19-38 m m long. Cystocarps are elongate, up to 800 m m thick and 1 mm long, with an ostiole on each side of the frond.

The thallus of Gelidium rex is rigid, crispate and cartilaginous, up to 30 cm tall, consisting of one to several erect axes devoid of branches in the basal half and irregularly branched in the apical portion of the thallus **(Fig. 1c).** Erect axes arising from cylindrical creeping axes that have downward projecting numerous short haptera that form massive discoid holdfasts. Erect axes cylindrical at the base, flattened above and slightly compressed at the apical end; to 2 mm wide, 0.8 mm thick at the cylindrical base. Margins of axes and branches conspicuously dentate, particularly in upper portions. Branches in young specimens and in sterile adult plants scarce, generally of one order, disposed alternately along the axis and externally similar to the erect axes. Fertile thalli abundantly branched in their upper third and consisting of axes of elongated, bladelike branches with margins conspicuously dentate. Fertile branchlets lobate, or pinnately compound.

Figure 3. Tetrasporangial branchlets (sporophylls) of the three economically important species of Chilean Gelidium.

Cortex of erect axes **(Fig. 2c)** of 4-6 pigmented cell layers, the most external cortical layer conspicuous, of cuboidal cells with rounded corners, to 12 m m high by 8 m m diam.; inner cortical cells increase slightly in size inwardly, surrounded by numerous, colorless, rhizoidal filaments. Medullary cells rounded and ovoid in transection, to 30 m m diam., with extremely thick cell walls; rhizoidal filaments scarce in inner medulla.

Figure 4. Fertile female branchlets and cystocarpic structure in Gelidium chilense, G. lingulatum and G. rex.



Tetrasporangia cruciate, 20-40 m m diam., arranged without order in sori on single or pinnately compound fertile branchlets, with dentate margins **(Fig. 3c).** Cystocarps on pinnately compound, somewhat twisted and densely congested branches **(Fig. 4c),** ovoid, about 0.5 mm in surface view, up to 0.7 mm thick, with one or, more rarely, several openings on both surfaces of the frond.

It should be noted that all three species and especially G. chilense and G. lingulatum have several morphological variants which appear under different environmental conditions.

2. DISTRIBUTION, ECOLOGY AND METABOLISM

- 2.1 Geographic extent
- 2.2 Local vertical and horizontal distribution
- 2.3 Effects of ecological determinants
- 2.4 Nutrition and growth

2.1 Geographic extent

Gelidium chilense and G. rex have an approximately similar geographic distribution. Gelidium chilense extends from 14°S in central Peru to approximately 35°S in central Chile. Likewise, G. rex has been found from southern Peru (ca 16°S) to southern (40°S) Chile (Santelices and Montalva, 1983; Santelices and Abbott, 1985).

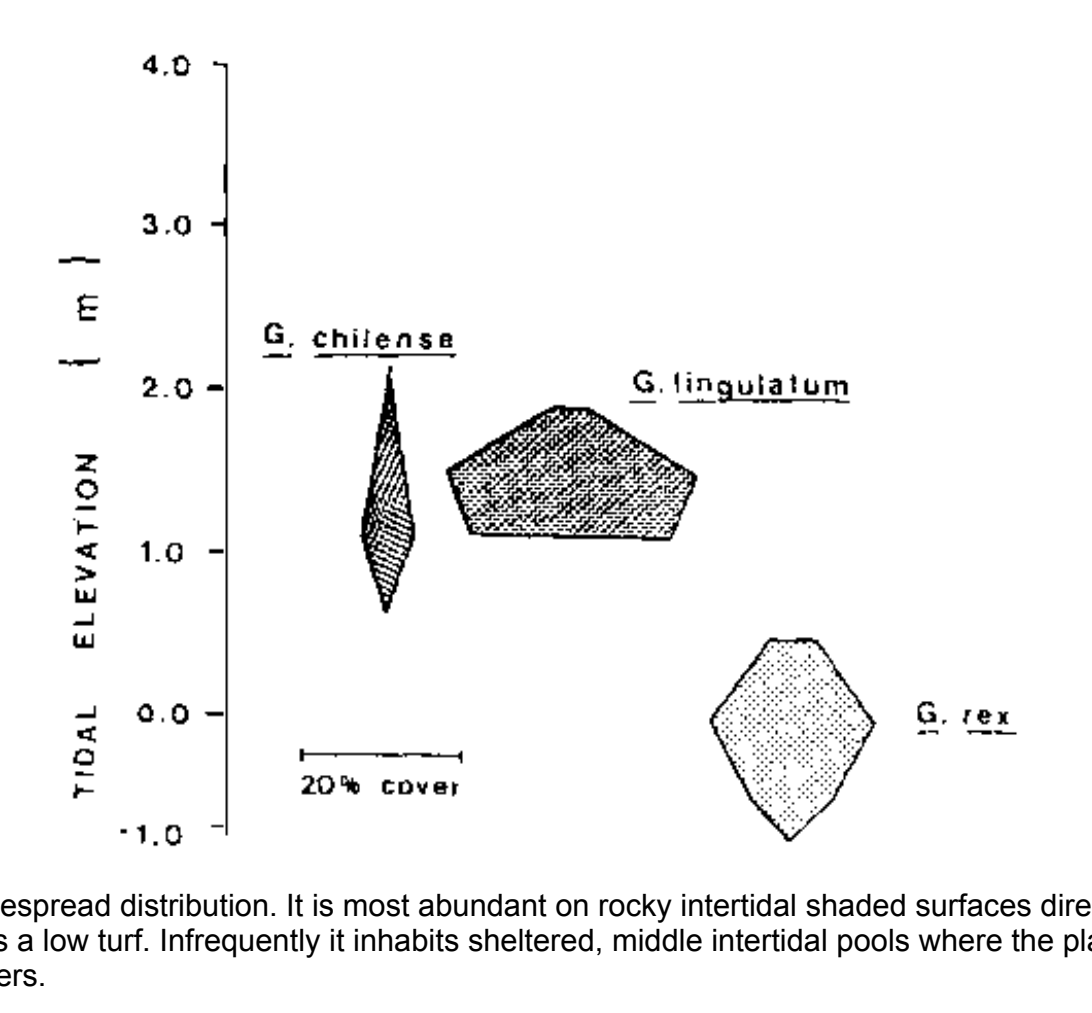
Gelidium lingulatum has been repeatedly collected from Valparaiso, in Central Chile (ca 33°S) to Puerto Montt (41°S). Levring (1960) also reported the species from the Strait of Magellan (53°S) but the species has not been found there again.

2.2 Local vertical and horizontal distribution

All three species of Gelidium occur as belts around the lower limits of the spring tides on rocky bottoms in exposed and semi-exposed habitats.

In the rocky intertidal of central Chile, Gelidium chilense and Gelidium lingulatum occur **(Fig. 5)** at the same tidal elevations with no evidence of zonation or other type of spatial segregation between them although G. chilense extends slightly higher and lower than G. lingulatum. Gelidium rex occurs in low intertidal to high subtidal clumps of plants, sometimes forming a belt, and is frequently under the shade of the kelp Lessonia nigrescens (Oliger and Santelices, 1981; Montalva and Santelices, 1981).

Figure 5. Vertical distribution of Gelidium chilense, G. lingulatum and G. rex in wave exposed, rocky habitats of Central Chile.



Gelidium chilense is the species with most widespread distribution. It is most abundant on rocky intertidal shaded surfaces directly exposed to strong waves. Yet, the species also occurs on boulders where it forms a low turf. Infrequently it inhabits sheltered, middle intertidal pools where the plants have elongated, almost cylindrical creeping axes which are pinnately branched to three orders.

Gelidium lingulatum also is abundant on rocky intertidal surfaces exposed to strong waves. However, the species is most abundant and reaches larger sizes in middle intertidal pools with frequent water exchange. When growing on barnacles and mussels on wave exposed, vertical walls, G. lingulatum is rather rigid, sparingly and often irregularly branched below, irregularly 1-2 pinnately branched above.

Gelidium rex has the least widespread ecological distribution. It occurs only on shallow subtidal shaded rocky surfaces exposed to very strong waves and high water exchange rates.

2.3 Effects of ecological determinants

Available data (see Santelices, 1974 and 1978 for reviews) point to general patterns of ecological responses for the species of Gelidium. They occur on rocky substrata, often on top of coralline crusts, normally associated with high levels of water movement, extending up to 1.5 m of intertidal elevation and down to 25 m deep. Their standing crop is maximal in shaded habitats and during summer. In Temperate latitudes seasonal growth is correlated with temperatures while in Tropical waters growth is correlated best with light intensity and water movement. Laboratory studies have confirmed these as low light saturation species. Growth can be increased by temperature increments up to 25°C or by long photoperiods combined with low light intensities. Increments in water movement or nutrient enrichments (especially nitrogen and phosphorus) can reverse to some extent the bleaching effects of high light and high temperatures. Grazing and interspecific interference often seem to affect field productivity but few quantitative data exist on this matter.

The few ecological studies performed with the three Chilean species of Gelidium (Oliger and Santelices, 1981) have shown that they have temperature tolerance ranges from 10 to 25°C. Growth does not occur above and below these limits (Oliger and Santelices, 1981). Growth rates are maximum at 20°C for Gelidium chilense and at 15°C for G. ligulatum and G. rex **(Fig. 6).**

Figure 6. Effects of temperature, light intensity and photoperiod on the growth of Gelidium chilense, G. lingulatum and G. rex.

The combined effects of light intensity and photoperiod affect in various ways the above three species **(Fig. 6).** The lower intertidal Gelidium rex is the species with the least tolerance to extended photoperiods under the higher experimental quantum dose used in these studies (120 m Em^{-2}S-1). Growth under photoregimes of 16 h of daily light is achieved only when the quantum dose is reduced to 45 m Em^{-2}S^{-1}. By contrast, the middle intertidal species G. lingulatum and G. chilense will maintain their optimal growth rates under conditions of higher quantum dosage and long days (16 hours of daily light). None of the three species could survive in continuous light as, in all experiments, the thalli normally bleached under long day regimes of 24 hours of light.

Physiological ecological responses of sporelings to different temperature-light regimes are somewhat different from the responses shown by adult thalli (Correa et al., 1985). Both, in Gelidium chilense and G. lingulatum the sporelings are light-saturated at 50 m Em^{-2}S^{-1}. In the case of G. chilense maximum growth of the sporelings requires a shorter photoperiod (12 h) than the mature thalli. These findings are consistent with predictions indicating that mature plants should have greater light requirements than those of sporeling stages because of their increased proportions of non-photosynthetic internal tissues.

Field studies with Gelidium chilense and G. lingulatum in the rocky intertidal habitats of Central Chile have stressed the importance of interspecific interactions in the distribution of these species (Santelices, Montalva & Oliger 1981). As previously indicated, in these habitats both species of Gelidium occur at the same tidal levels with no evidence of zonation or other type of spatial segregation between them. Both are perennial (Montalva and Santelices, 1981). Gelidium lingulatum is maximally abundant in summer; the peak being correlated with temperature and photoperiod. The stocks of G. chilense, by contrast, scarcely vary seasonally. Temporal standing stock changes in this species, however, were significantly negatively correlated with the stocks of G. lingulatum. The negative correlation occurred at each of the three intertidal levels studied and the significance increased from the higher to the lower levels. Since in both species there was a direct correlation between total standing stock and tetrasporangial standing stock, the interspecific interaction affected their reproductive potentials (Montalva and Santelices, 1981).

Gelidium chilense also can interact with Lessonia nigrescens at low intertidal levels and the outcome of the interaction is heavily depending on season. Gelidium chilense is fertile all year round whereas the sporophyte of L. nigrescens is fertile only during late winter. If the kelp is removed during late fall or early winter, G. chilense temporarily extends into the low intertidal levels previously occupied by L. nigrescens. Yet, the newly settled juveniles of the kelp start appearing by the end of winter and are able to overgrow, shade and cover the thalli of G. chilense with their massive holdfasts (Santelices and Ojeda, 1984; Ojeda and Santelices, 1984). By contrast, if the kelp is removed in summer there is a 4-5 months of time for the growth and expansion of G. chilense without the juveniles of L. nigrescens. Under these circumstances the settlement of L. nigrescens expected to occur in August does not occur due to monopolization of the primary substratum by G. chilense.

2.4 Nutrition and growth

Little is known of the nutritional requirements of the three Chilean species of Gelidium. Experimental studies with other species in the genus have shown that fertilization with ammonium or with nitrate increases pigment concentration and promotes growth. The effect is more pronounced if the additions are made in the presence of phosphorus (see Santelices, 1974 for a review). Some species can simultaneously assimilate ammonium and nitrate. The addition of $NaHCO_3$ to the culture medium has been found to increase productivity still further.

3. LIFE HISTORY

- 3.1 Life cycle
- 3.2 Reproduction

3.1 Life cycle

The species of Gelidium are supposed to have a "Polysiphonia type" of life history with equal proportions of tetrasporic and asexual generations (Kylin, 1923). Indeed/the occurrence of sexual and tetrasporic phases has been confirmed in several species of Gelidium (see Santelices, 1974 for a review). Nevertheless, it is quite common to find field differences in proportions of tetrasporangial to sexual thalli. Tetrasporangial thalli often are several orders of magnitude more frequent or more abundant than sexual thalli. And this is the case both for G. chilense and G. lingulatum from Central Chile, where the biomass of sexual thalli throughout the year amounted to less than 10% of the fertile biomass (Montalva and Santelices, 1981).

Two hypothesis have been advanced to explain the differences in ratio of sexual to tetrasporic thalli. Based on life history studies of British species of Gelidium, Dixon (1961) suggested that local variations in the life history could be considerable and that meiosis may not be occurring in all sporangia of a given sporophyte. Alternatively, based on results reported by Yamasaki and Osugia (1960) from Japan, Santelices (1974) suggested intra-specific competition between tetrasporic and sexual thalli. Increased sensitivity to environmental parameters and reduced competitive ability could be expected to occur in the sexual, haploid phase while increased vigor could be expected to occur in the diploid thalli, leading to the possibility of a gradual replacement of haploid by diploid thalli in the field. More recently, Barilotti (1960) has agreed with this hypothesis although he has stressed that no direct survivorship difference has been found experimentally between the two phases, nor has there been an experimental evaluation of the importance of reproductive effort leading to diploid dominance performed for any species of Gelidium.

3.2 Reproduction

Reproduction has been found to be a seasonal phenomenon in many species of Gelidium and it is generally assumed to be temperature regulated (see Santelices, 1974 for a review). However, the two species of Chilean Gelidium so far studied are an exception to this trend. As discussed previously, tetraspore formation in Gelidium chilense and G. lingulatum is affected by interspecific interference. Cystocarp production in both species occurs during the whole year (Montalva and Santelices, 1981).

Spore germination has also been shown to be influenced by temperature in several species of Gelidium (Santelices, 1974). However, laboratory experiments with the two Chilean middle intertidal species indicate that temperatures ranging from 10 to 20°C, three different photoperiodic regimes and photon-flux densities from 25 to 75 m Em^{-2}S^{-1} do not induce significant differences in germination values of G. lingulatum or G. chilense (Correa et al., 1985).

4. POPULATION STRUCTURE AND MORTALITY

- 4.1 Population structure
- 4.2 Sporophyte - gametophyte and sex composition
- 4.3 Density
- 4.4 Mortality - morbidity

4.1 Population structure

No study has been performed yet trying to understand the population structure of any of the three Chilean species of Gelidium. However a few ideas emerging from studies in other populations of Gelidium elsewhere are perhaps relevant.

Because vegetative propagation is common in the genus, the basalmost portion of the erect axes as well as the creeping axes might be several years old. Therefore, age composition can be studied only in natural populations of erect axes. Yet these axes generally are slow growers and frequently they are either too small or too weak to tolerate tagging for extended periods. Therefore, approximations to population structure of Gelidium communities have been attempted through the study of size distribution of fronds (Silverthorne, 1977). Thus, the continuous range of possible frond lengths was divided into intervals with all the fronds falling in a particular interval being treated as if they were at the mid-point of that interval. In order to identify rational intervals for the size-classes, Silverthorne (1977) determined and accepted the average elongation per quarter (about 2.25 cm) which was then used to define the first size-class. Recruitment was defined as the entry of new fronds into this size class, and biomass was considered as the weight of the frond excluding the first 2.25 cm. Through tagging of plants and study of size classes of the population, loss rates of the population could be estimated and found to be a function of frond length. With these data it was possible to recalculate loss rates for the various size-classes, evaluate the seasonal variations in loss rate and calculate survival rate for each different frond size. Finally, regeneration and recruitment was estimated experimentally. Data suggested a seasonal pattern of recruitment with increased values in winter and fall. Knowing the dry weight biomass per unit of area and the size-class distribution, Silverthorne (1977) could then calculate the average number of recruits in this species (G. robustum). This approximation probably could be used elsewhere in populations of these algal species.

4.2 Sporophyte - gametophyte and sex composition

Hypothesis and data related to the increased abundance of tetrasporangial thalli over sexual plants have been reviewed in Section 3.1

4.3 Density

It is often impossible to distinguish individuals of Gelidium, therefore density measurements are infrequently used in ecological studies of these species.

4.4 Mortality - morbidity

No data exist on mortality rates of natural populations of the economically important species of Gelidium in Chile. As discussed in the previous section, in the Californian population of G. robustum the loss rate of the population (=LR) was a function of frond length (L) under the expression LR = 0.00307L (Silverthorne, 1977).

Mortality factors known for these and other populations of Gelidium are discussed in Section 5.2, below.

5. PRODUCTIVITY OF THE RESOURCE

- 5.1 Standing stock values of wild resources
- 5.2 Factors affecting productivity
- 5.3 Possibilities of genetic improvement
- 5.4 Relative contribution of sexual reproduction and vegetative regeneration to economic harvesting
- 5.5 Possibilities of improvement by environmental enhancement

5.1 Standing stock values of wild resources

Since the species of Gelidium and Pterocladia are often difficult to distinguish under field conditions, standing stock values reported in the literature may include mixtures of these two genera. Indeed, in some areas such as Japan, the materials identified under the name of Gelidium also might include species of Beckerella, Suhria and Yatabella. Those from Indonesia perhaps include Gelidiella acerosa. Annual production of Gelidiaceae ranges **(Table 1)** between a minimum of 15,000 and a maximum of 19,000 dry tons per year. The production from wild stocks throughout Chile is just a minor part of this World Market.

The standing stock values normally found in commercial beds of Gelidium vary widely from a few hundred grams to a maximum of 1.5 Kg m^{-2} In Japan, the fishing fields are classified as excellent if the standing stock is above 1.5 Kg m^{-2} good if the stock is between 1.0 and 1.5 Kg m^{-2}, common or normal if the biomass of Gelidium is between 0.5 and 1.0 Kg m^{-2} and bad if the value is less than 0.5 Kg m^{-2} (Okasaki, 1971). Detailed standing stock measurements are lacking for commercial beds of Gelidium in Chile. Ecological studies (Montalva and Santelices, 1981; Santelices, Montalva & Oliger 1981) have reported stock values of about 0.5 Kg m^{-2} for Gelidium chilense and 0.9-1.0 Kg m^{-2} for G. lingulatum. The extremely wave exposed habitats occupied by G. rex together with its clumpy distribution has prevented accurate stock measurements of that species.

TABLE 1. Annual crops of Gelidium and Pterocladia harvested in different area

Place	Fishing Area N°	Metric Tons (dry)	Harvesting method used
Spain	27	4000 - 5500	Drift, trawling and diving
Japan	61	3000 - 3300	Hand picking, diving
Portugal	27	2500 - 3000	Drift, hand picking
R. Corea	61	2000 - 2500	Hand picking
Mexico	77	1000 - 1500	Diving
Morocco	34	1000 - 1500	Hand picking, drift
Indonesia	71	400 - 500	Hand picking
France	27	300 - 400	Drift
U.S.A.	77	150 - 200	Diving, hand picking
Chile	87	100 - 150	Hand picking
P.R. China	61	100 - 150	Hand picking
Corea DPR	61	80 - 100	Hand picking
New Zealand	81	50 - 100	Hand picking
Formosa	61	50 - 60	Hand picking
Total		14,730 - 18,960	

5.2 Factors affecting productivity

5.2.1 Wild resources

Section 2.3 reviewed the effects of various ecological factors on the growth and production of these Gelidium species. The following factors seemingly affect commercial beds in Chile, as elsewhere, but in general the ecological data to establish quantitative relationships are still lacking.

a) Currents: It is widely recognized that the temperature regime and the nutrient contents of some bodies of water could be important determining distribution and production of species. The general occurrence of upwelling areas along most of the coast of northern and central Chile is suspected to have some effect on the high production rates of these seaweed populations.

b) Extreme low tides: This represents a widespread detrimental interaction of factors significantly reducing intertidal stocks. In central Chile there is a significant biomass reduction of Gelidium lingulatum in the months with extreme low tides during clear daylight hours (Montalva and Santelices, 1981).

c) Water movement: Intense water movement has been observed to extensively destroy wild crops of Gelidium robustum in Baja California, G. sesquipedale in Spain, Pterocladia lucida in New Zealand and P. capillacea in the Azores, New Zealand and Alexandria (see Santelices, 1974 for a review). This effect has not been observed in the normally wave exposed populations of Gelidium along Chile.

d) Grazing: Grazing by invertebrates and fishes is also expected to cause mortality at least of erect axes in commercial beds of Gelidium (Santelices, 1974). In Chile pertinent data quantifying the phenomenon are lacking although it is known that the species of Gelidium are common food items of sea urchins and some herbivorous molluscs (Santelices et al., 1983; Santelices and Correa, 1985). Field studies have experimentally shown that intense grazing by the sea urchin Tetrapygus niger could prevent the establishment and cover increase of Gelidium chilense (Ojeda and Santelices, 1984).

e) Competition: The interference effects between Gelidium chilense and G. lingulatum and between G. chilense and Lessonia nigrescens have been discussed in Section 2.3. These studies justify the suggestion that once established the populations of Gelidium are quite resistant to invasions by other algal species. This is probably due to Gelidium having creeping axes which, especially on substrata with a calcareous crusty can survive and produce new erect fronds after harvesting or grazing. In the rocky intertidal habitats of Central Chile, Codium dimorphum is one of the few species able to overgrow the plants of Gelidium chilense (Santelices, Montalva & Oliger 1981).

f) Epiphytes and parasites: There is no quantitative information for these, or for other species of Gelidium, on the effects that the organisms living on or inside their thalli might have on their productivity. This is in spite of the general observation, for example, that Bryozoa are common epiphytes on Gelidium rex.

g) Harvesting practices: Careless harvesting practices can have serious and long-lasting effects on the productivity of Gelidium. Cutting of erect axes always has resulted in less destruction and faster regrowth of the various species than scraping of the substratum (see Santelices, 1974 for a review). Scraping of the substratum normally destroys the creeping axes allowing for the invasion of other algal species. In central Chile, a mixed stand of Gelidium chilense and G. filicinum could recover in 48 months only 45% of the 100% previously occupied rocky surface when removed by scraping of the rocks (Santelices, Oliger & Montalva 1981).

5.2.2 Cultured stocks

Massive cultivation of Gelidium still is at the experimental stage with but a few laboratory and field attempts having been performed in different areas. Three basic types of culture have been attempted.

Field cultivation has been initiated either from spores or from vegetative tissues. Spore cultivation of Gelidium amansii has been successful in Japan (Suto, 1974). However, the spores take about two years to grow and reach harvestable size. More recently, Correa et al. (1985) were able to define the optimal conditions for increased sporeling growth of G. chilense and G. lingulatum but they have not entered the stage of field cultivation.

Field cultivation of vegetative branches also has been completed in Japan (Suto, 1974). However, the economic cost of the plants used as the seed and the cost of the labour force needed for setting the seed plants to the ropes was so expensive that the whole operation left little for profit. This same type of field culture has been successful in growing Gelidium rex in intertidal channels and rapids in central Chile and daily growth rates of 2.5 to 3% have been obtained.

The attempts to grow these species under free-floating conditions represent an alternative approach. The first such attempt were performed with Hawaiian populations of Pterocladia (Santelices, 1976) and, more recently, species of Gelidium from India and Norway have been maintained in free-floating conditions with growth rates up to 6.5% daily. This type of cultivation has been initiated with the three Chilean species of Gelidium. Gelidium chilense was the species with fastest growth, a doubling time of about 30 days. The capacity of these algae to grow free floating is related to their ability to adopt a globular habit, devoid of holdfasts and with production of a profusion of radially-oriented branches. In G. chilense the thalli become globose after 28 days. Radially branching thalli of G. ligulatum resulted from proliferations appearing on the attachment parts of the thalli while G. rex did not show any growth or any modification of its morphology at all (Santelices, Oliger & Montalva 1981).

5.3 Possibilities of genetic improvement

No attempts seem to have been made to genetically improve the commercial strains of Gelidium.

5.4 Relative contribution of sexual reproduction and vegetative regeneration to economic harvesting

As commented upon in several sections of this report, the commercial harvests of the three species of Gelidium are based on vegetative regeneration and growth after cutting of the erect axes.

5.5 Possibilities of improvement by environmental enhancement

No attempt has been reported to improve production of the Chilean beds of Gelidium through environmental enhancement. In Japan, management of the beds includes regularly adding nitrate and phosphate and expansion of the beds by setting stones in areas of potential growth but otherwise limited by substratum availability.

6. HARVEST METHODS

- 6.1 Annual cycle of operations
- 6.2 Manpower productivity
- 6.3 Alternate employment

6.1 Annual cycle of operations

All the species of Gelidium presently harvested from Chile are gathered from wild beds either by hand picking in intertidal fields or by snorkel collecting in shallow waters. Since all three species of Gelidium occur in habitats exposed to strong water movement and since storminess along the Chilean coast is seasonal, a naturally closed season probably exists in most areas. However, there is no legal enforcement or regulation restricting access to the Gelidium beds of Chile at any time of the year. Such regulations do exist for other economically important Chilean seaweeds such as Gracilaria.

6.2 Manpower productivity

The harvesting operations of species of Gelidium in Chile are so simple that no one has described manpower productivity. In Japan, Gelidium gathering through swimming and diving in shallow waters yields 14-16 Kg day^{-1} per fisherman (Yamada, 1976). In Japan two other collecting methods are used. Hand picking of seaweed at depths of up to 15 m after diving from a boat yields 40-75 Kg day^{-1} per diver (dry matter) while working on a boat and harvesting using woody frames with bamboo teeth can produce 60-115 Kg day^{-1} per man (Cuyvers, 1978).

6.3 Alternate employment

Hand picking of Gelidium in Chile is just a part-time activity for most fishermen involved in the operation. During other times these fishermen work gathering other types of seaweeds or various types of shellfish.

7. EQUIPMENT USED FOR HARVESTING AND CULTURE OF RESOURCES

The commonest and simplest equipment used in harvesting Gelidium in Chile is a float with a net hanging in it in which the collector puts the hand picked thalli. Knives and iron spatulas are sometimes used to help in the plant's removal. In such a simple operation on one has ever evaluated the efficiencies of the tools used, the percentages of the crop left in the field or the manpower requirements.

8. PROTECTION AND MANAGEMENT OF THE CROP

- 8.1 Management of seaweed resources
- 8.2 Regulation of seaweeds

8.1 Management of seaweed resources

The Subsecretaria de Pesca, a part of the Ministerio de Economia, Fomento y Reconstruccion is the national body concerned with the management, development and conservation of marine renewable resources, including the seaweeds. The Servicio Nacional de Pesca (National Fisheries Service), one of the Divisions of the Subsecretaria de Pesca is the national body executing the management and exploitation policies. These services are performed by eleven Regional Fisheries Offices each located in one of the 12 Geographic Regions in which the country is divided.

The specialists of the Subsecretaria de Pesca maintain a flexible relation with fishermen associations. Decisions on exploitation policies are normally made after technical studies performed by experts from the Universities, private consulting companies or from the Instituto de Fomento Pesquero (equivalent to a National Fisheries Institute). Problems to be solved arise either from field visits of experts from Subsecretaria de Pesca, from documents produced by the local scientific and technological community or from the fishermen's associations and cooperatives.

The general regulations governing the harvesting and culture of seaweeds are contained in the Decreto 175 issued on March 24th, 1980. In synthesis, any enterprise, individual or association intending to either harvest or culture seaweeds has to produce a technical proposal which is evaluated by the experts in the corresponding Departments of the National Fisheries Service. They submit their technical evaluations to Subsecretaria de Pesca which makes a decision regarding authorizing the given activity. In the case of leasing of a nearshore or intertidal area, the Subsecretaria de Marina (Navy Under-secretariat) would authorize the leasing only after a positive report from Subsecretaria de Pesca.

8.2 Regulation of seaweeds

At present, there is no special legislation governing the culture and harvesting of seaweeds in Chile for any genera, except Gracilaria. Harvesting of Gracilaria spp. is specifically regulated by a different legal body (Decreto 136 of July 2nd, 1983). Therefore, the only legal bodies regulating harvesting and culture of Gelidium beds in Chile are contained in Decreto 175 referred to above.

9. UTILIZATION

- 9.1 Chemical and nutritional content
- 9.2, 9.3 & 9.4 Human food, animal fodder and manure
- 9.5 Industrial products and processes

9.1 Chemical and nutritional content

According to Zaneveld (1955), various species of Gelidium analyzed by Matsui (1916) yielded, on a dry weight basis, 2.01% nitrogen, 12.5% crude protein, 23.7% galactan, 2.03% pentosan, 23.2% reducing sugar; 0.93% methyl pentosan, 17.89% fiber, 0.52% magnesium, 0.28% lime and 4.23% ash. Later studies on chemical composition of other species of Gelidium have reported high vitamin B_{12} content (Tsuda et al., 1958; Guven et al., 1979b; Guven and Guler, 1979a), cholesterol and a series of sterols (Tsuda et al., 1958; Fattorusso et al., 1975; Chardon-Loriaus et al., 1976), essential oils with antibacterial and antifungal activities (Guven and Guler, 1979b; Ma and Tai, 1984), proteins with lipolytic, hypoglycemic and anticoagulant activities (Guven and Guler, 1979b) and lipid soluble extracts with anti-inflamatory properties (Baker, 1984). No equivalent study has been performed with the Chilean species of Gelidium.

9.2, 9.3 & 9.4 Human food, animal fodder and manure

Human consumption of Gelidium is restricted mainly to G. divaricatum in China and to G. amansii in Japan, Indonesia, China, Borneo and The Celebes Tzaneveld, 1955, 1959; Johnston, 1966; Levring et al., 1969). Nowhere are the species used as animal fodder or manure. In Chile., all the harvested crops are exported as raw materials for agar production.

9.5 Industrial products and processes

Species of Gelidium are among the most important agarophytes in the world (Santelices, 1974; Santelices and Stewart, 1985). About 35 species are harvested in various areas contributing to 40-50% of the world's annual exploitation of agarophytes, estimated at 39,000 tons of dry matter (Whyte and Englar, 1981).

The agar content in the species of Gelidium varies with species (Table 2), season, location and environment. Commercially, 17-25% yield from agarophytes is considered normal (Whyte and Englar, 1981). However, agar concentrations found in several Gelidium species can be far above this **(Table 2).** Among the Chilean species, Gelidium chilense produces the highest agar yield while G. lingulatum yields the least gel (20%). Gelidium rex yields an intermediate amount of gel but it produces the strongest gel (Santelices, Oliger & Montalva 1981). It should be noticed that Gelidium lingulatum has shown significant differences in viscosity and gel strength among karyologically different generations with the tetrasporangial thalli having higher gel strength values (Santelices, Oliger & Montalva 1981).

TABLE 2. Agar content of several species of Gelidium on a dry weight basis

Species	Locality	Fishing Area N°	Amount of Agar	Reference
Gelidium amansii	Japan	61	25 to 30%	Levring et al., 1969
Gelidium chilense (=filicinum)	Chile	87	25 to 31%	Santelices et al., 1981a
Gelidium latifolium	Java	71	25 to 35%	Levring et al., 1969
Gelidium lingulatum	Chile	87	20 to 24%	Santelices et al., 1981a
Gelidium micropterum	India	51	43%	Levring et al., 1969
Gelidium pusillum	Philippines	71	41%	De León &. Domantay, 1974
	India	51	50%	Kaliaperumal & Umamaheswara Rao, 1981
Gelidium purpurascens	California, USA	77	25.4%	Whyte & Englar, 1981
Gelidium rex	Chile	87	27%	Santelices et al., 1981a
Gelidium robustum (=carti lagineum)	California, USA	77	40 to 45%	Barilotti & Silverthorne, 1972
Gelidium sesquipedale	Portugal	27	24%	Da Fonseca, 1966
Gelidium spinolosum	Morocco	34	33%	Levring et al., 1969
Gelidium sp.	Sri Lanka	51	21 to 40%	Arumugam et al., 1981

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The wild harvest and culture of Laminaria longicruris in Eastern Canada

1. IDENTITY
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ABSTRACT

Laminaria longicruris was harvested as a source of alginate through the 1940's. Peak harvests were 5-6000 T/year. Since 1949 the species has been cut sporadically for human consumption with a peak harvest of 300 tons in 1979. The standing crop is at least 1,000,000 tons with a conservative yield estimate of about 300,000 T/year. Determinants of distribution, abundance and production are well studied for this under utilized species.

1. IDENTITY

1.1 Nomenclature
1.2 Taxonomy
1.3 Morphology and Anatomy

1.1 Nomenclature

The species binomial is Laminaris longicruris de la Pylaie (1824). De la Pylaie described the species from specimens collected on the island of Newfoundland. There are no published reports to show that a Type specimen has been designated in de la Pylaie's collection held in Paris (PC [see Stafleu and Cowan, 1976 for herbarium location]).

Recent taxonomic decisions (Chapman, 1974; Kain, 1976) indicate the following binomials may be regarded as synonyms of L. longicruris: L. agardhii Kjell.; L. faeroensis Borgesen.

1.2 Taxonomy

Laminaria longicruris belongs to the family Laminariaceae (order Laminariales, Division Phaeophyta). The genus Laminaria is divided into sections Simplices and Digitatae which have undivided and divided laminae, respectively. L. longicruris belongs to the Simplices.

The North Atlantic species of the section Simplices were revised by Wilce (1965). He distinguished Laminaria longicruris from other members of the section by the presence of a long, hollow stipe. This definition reduces L. faeroensis to conspecificity with L. longicruris.

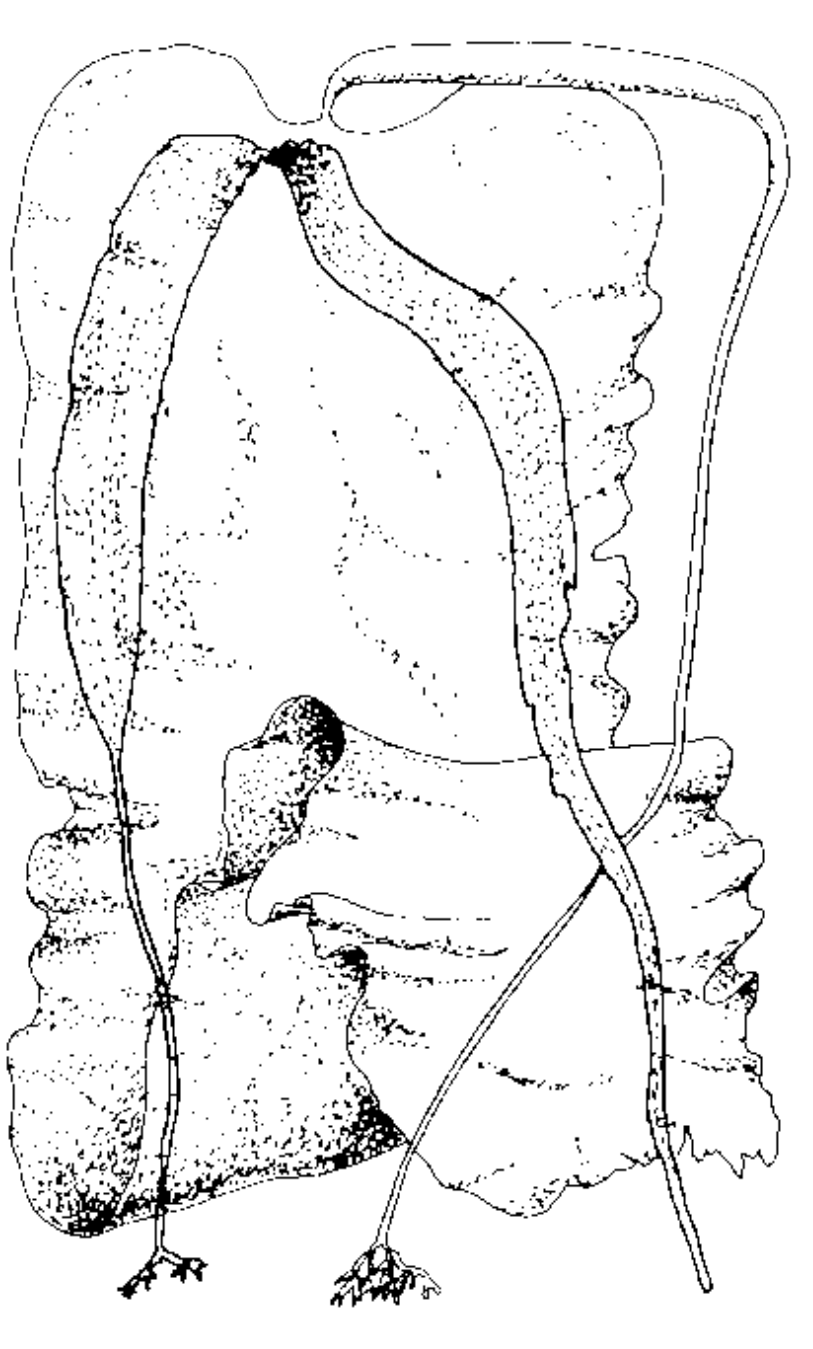
Since Wilce's (1965) revision, Laminaria longicruris has been the subject of a number of descriptive and experimental taxonomic studies which cast some doubt on it's taxonomic identity (Mann, 1971; Chapman, 1973, 1974, 1975; Kain, 1976; Luning et al., 1978; Bolton et al. 1983). In spite of this, the species is listed as a separate entity in the most recent checklist of marine algae of eastern Canada (South, 1984), with a footnote to indicate that L. longicruris may be conspecific with L. saccharina Lamour. According to Wilce (1965), L. longicruris can only be distinguished from L. saccharina on the basis of stipe length and the occurrence of hollowstipes. In Nova Scotia and in the Shetland Islands (to the north of Scotland) populations of plants with long, hollow stipes grade into populations with short, solid stipes (Chapman, 1973; Kain, 1976). There is no morphometric discontinuity. Furthermore, Bolton et al. (1983) were able to show that Nova Scotian populations of L. longicruris are interfertile with European populations of L. saccharina. The F_1 hybrids became fertile in culture and produced healthy F_2 gametophytes.

There is a significant genetic component in the expression of stipe length and hollowness in Nova Scotian populations of Laminaria, section Simplices, (Chapman, 1974) and it may be best to regard the long, hollow stiped members as a separate race of the species L. saccharina. Formal taxonomic decisions with nomenclatural changes have yet to be made and, for convenience, the race is considered here under the name Laminaris longicruris.

1.3 Morphology and Anatomy

The morphological extremes found among the sporophytes of Laminaria longicruris are shown in **Fig. 1.** Very large plants with stipes up to 5 m and blades up to 7 m in length have been recorded from Seal Island off the southwestern shore of Nova Scotia (McPeak, 1980). More typically, populations contain plants with stipes and blades up to 2-3 m in length (Chapman, 1973; Kain, 1976).

Figure 1. Morphological form range in Laminaria longicruris (modified after Taylor, 1957, x 0.14.



The anatomy of Laminaria longicruris is typical for members of the genus as described by Pritsch (1945). The species has not been the subject of detailed fine structural analysis. The only aspect of the anatomy which has received special attention is the presence of mucilage ducts in the superficial tissues of the blade and stipe (Wilce, 1965; Chapman, 1975; Luning et al. 1978). At its southern limit in the NW Atlantic the species lacks mucilage ducts in the blade and in the stipe (Chapman, 1975). At the southern limit of the species in the eastern Atlantic (Shetland Islands, Kain, 1976) the blades have mucilage ducts, but the stipes do not. In more northerly locations in the NW Atlantic all combinations of duct occurrence in the blade and stipe may be found (Chapman, 1975).

2. DISTRIBUTION, ECOLOGY AND METABOLISM

2.1 Geographical extent
2.2 Local vertical and horizontal distribution
2.3 Effects of ecological determinants
2.4 Nutrition and growth

2.1 Geographical extent

The species occurs widely throughout the NW Atlantic and eastern Arctic Oceans (South, 1984; Lee, 1980), mostly within Canadian territorial waters, and along the west coast of Greenland north of 62° N (Rosenvinge, 1899). The species is rare on the east coast of Greenland (Lund, 1959), but has been recorded from Iceland (Jonsson, 1912), the Faeroes (Borgesen, 1902) and as far south as Long Sound on the Shetland Islands at latitude 60°N (Kain, 1976). L. longicruris has not been recorded from the European mainland.

In the NW Atlantic Laminaria longicruris occurs as far south as Long Island Sound to about 41° N (Schneider et al., 1979). The species may occur further south on the New York side of Long Island Sound to Latitude 40°58N (Brinkhuis et al., 1984), but there is no indication that the plants at this site have hollow stipes.

North of New England Laminaria longicruris forms an important component of the sublittoral seaweed flora of the Canadian Maritime provinces (personal observations), Newfoundland and Labrador,(Wilce, 1959). In the eastern Arctic Ocean L. longicruris gives way to L. solidungula J. Ag. as the dominant component of the sublittoral seaweed vegetation (Chapman and Lindley, 1981). Nevertheless, populations of L. longicruris have been recorded to as far north as 82° off Ellesmere Island (Lee, 1980).

2.2 Local vertical and horizontal distribution

Laminaris longicruris is normally restricted to subtidal habitats. Very large plants often reach the surface at low water, but the holdfasts of the species are normally underwater at all times. Exceptions occur at very exposed sites where scattered small individuals may be found in the lower intertidal zone. Plants may also be found in intertidal pools on exposed coasts.

In Nova Scotia the species commonly forms a dense zone, in association with Laminaria digitata, through a depth range of about 4 to 18 m (Mann, 1972a). Members of the genus are commonly bounded by a zone of Chondrus crispus Stackh. at their upper limit and by a zone of the kelp Agarum cribrosum (Mert.) Bory at their lower limit. In very turbid waters (such as the upper reaches of the bay of Fundy) L. longicruris is restricted to shallow waters of less than about 3 m depth (Tremblay and Chapman, 1980).

In the High Arctic site of Turton Bay off Igloolik Island (69°21.9 N) Laminaria longicruris occurs to a depth of 20 m (personal observations).

Local horizontal distribution is determined to a large extent by substratum type and salinity. In very sheltered sites the species can occur on an unstable substratum of gravel and small stones, but it is absent from muddy and sandy bottoms. In exposed sites Laminaria longicruris is restricted to hard rock substrata. The species is absent from sites with salinities of less than about 20‰.

2.3 Effects of ecological determinants

There is little information on the physiological determinants of geographical and vertical distribution of the species. Bolton and Luning (1982) have shown that above 22°C gametophytes of Laminaria longicruris suffer cell damage. All cells die in cultures maintained at 24°C. Bolton and Luning (1982) also tested the effects of temperature on the growth of sporophytes in culture **(Fig. 2).** Plants with parents from Nova Scotia and from Igloolik in the Canadian North-West Territories grew best at 10°C. Growth rate at 0°C was depressed by about 70% in both isolates. All plants disintegrated at 23°C.

There have been few laboratory studies on the effects of varying levels of irradiance on the photosynthesis and growth of Laminaria longicruris. Within the temperature range of 1-15°C photosynthetic saturation of tissue discs cut from adult blades occurs at photon flux densities between 75 and 90 m Em^{-2} s^{-1} **(Fig.** 3). The photosynthetic compensation photon flux density for tissue discs at temperatures between 2 and 5°C is about 4-5 m Em^{-2} s^{-1} (Chapman, unpublished data). Gagn'e and Mann (1981) have shown that in the middle of the depth range of L. longicruris in southwestern Nova Scotia, the average photon flux density in February, 1979, fell to about 7 m Em^{-2}s^{-1}. Presumably light levels were below photosynthetic compensation values at the lower limit of the kelp vegetation, at least during the month of February. The average photon flux density at about 8 m depth during the summer months at the 3 Nova Scotian sites studied by Gagne and Mann (1981) approached saturation.

Figure 2. Relationship between growth rate of juvenile sporangial plants and seawater temperature (modified after Bolton and Luning, 1982). Dashed line shows results for juveniles with parents collected in Nova Scotia, solid line for juveniles with parents collected in the Canadian High Arctic. Means and 95% confidence intervals are given.

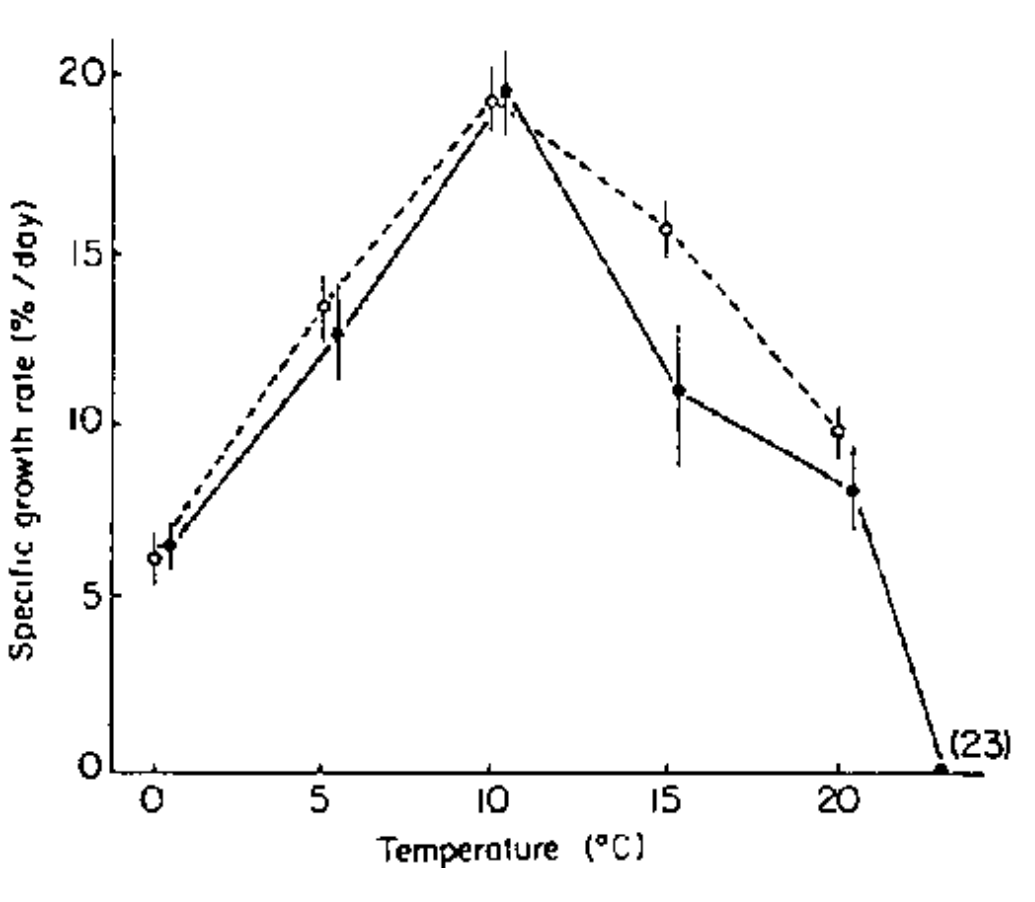


Figure 3. Relationship between gross photosynthetic rate of mature marginal tissue discs and photon flux density. Results obtained at 15°C in August.

The effects of salinity on the development of Laminaria longicruris is known from the work of H. Stegenga (unpublished study, 1973) and seem to explain the absence of this species from low salinity sites in the sea. In Stegenga's study plants were grown from spores in seawater diluted with distilled water. Below about 17 ‰ salinity the fertility of female gametophytes was reduced by nearly 50% in comparison with cultures maintained in full strength seawater. The eggs produced collapsed at salinities below about 17 ‰. The growth of young sporophytes was severely reduced at salinities below about 20 ‰. Maximum growth of sporophytes took place at salinities between 25 and 32 ‰.

2.4 Nutrition and growth

2.4.1 Nutrition

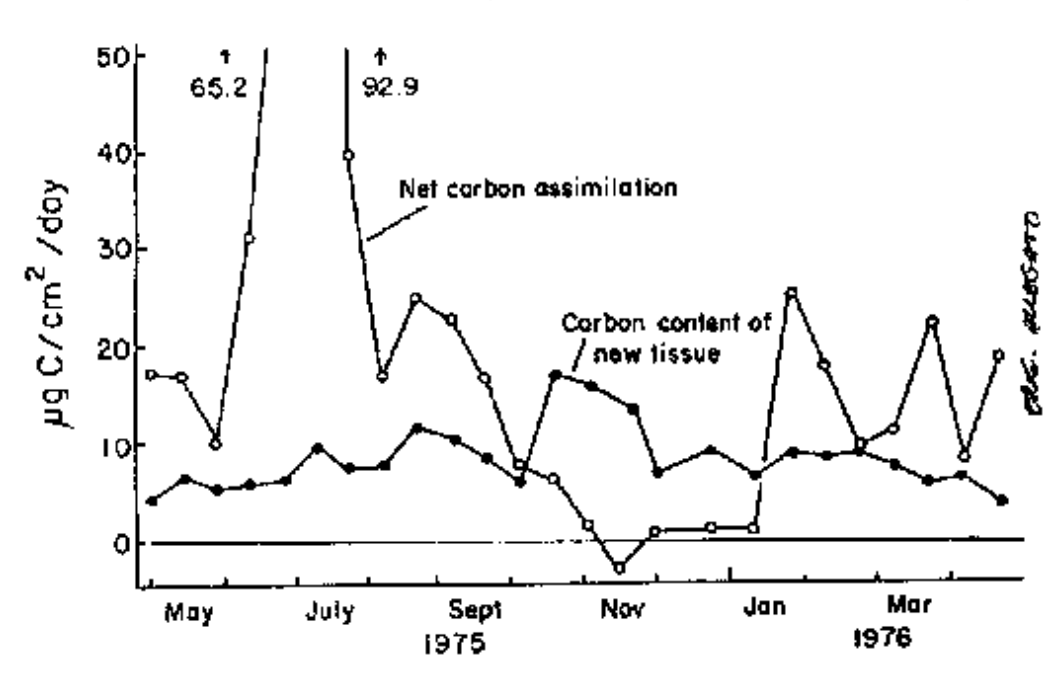
There is information available on the carbon and nitrogen nutrition of Laminaria longicruris. Hatcher et al. (1977) carried out a study of photosynthetic carbon assimilation in a Nova Scotia population of the species. Rates of oxygen evolution by whole plants were measured over a 24 h period once every two weeks through 12 months. The apparatus used to make these in-situ measurements is described by Hatcher (1977). The daily net photosynthetic rates were extrapolated to 1 wk before, and 1 wk after the field measurements by reference to continuously measured, in-situ light measurements. In this way, daily net photosynthesis was estimated for every day of the study year. The weekly integrals of net production of tissue carbon are shown in **Table 1.** The carbon assimilation values were calculated from oxygen evolution rates using the photosynthetic quotients shown in **Table 1.** The photosynthetic quotients were derived from simultaneous in-situ measurements of O_2 evolution and ^{14}C bicarbonate uptake in plant tissue discs.

Hatcher et al. (1977) also calculated carbon accretion in this Laminaria from measurement of growth rates through the year in which photosynthetic assimilation rates were estimated. Increase in blade surface area was converted to carbon accretion by measurements of the total carbon per unit surface area. Net carbon assimilation by photosynthesis and the carbon content of new tissue are compared in **Fig. 4.** More than twice as much carbon was assimilated photosynthetically as was present in newly formed blade tissue. The fate of this excess carbon is unknown.

Table 1. Weekly integrals of (1) photosynthetic net production of carbon and (2) accretion of tissue carbon measured from growth rates in Laminaria longicruris in St. Margaret's Bay, Nova Scotia (modified after Hatcher et al., 1977).

Period	Extrapolated net O_2 production (m g O_2 cm^{-2})	Mean diel net O_2 production (m g O_2 cm^{-2})	Photo-synthetic quotient	Equivalent diel net carbon assimilation (m g C cm^{-2})	Net production of tissue carbon: average of 2 plants in period (m g C cm^{-2} d^{-1})
1975					
May 1-7	311	42	1.03	17	4.3
May 8-21	845	60	1.33	17	6.4
May 22-June 4	491	35	1.33	10	5.2
June 5-18	1191	85	1.03	31	5.6
June 19-July 2	2506	179	1.03	65	6.2
July 3-16	3155	225	0.86	93	9.5
July 17-30	1892	135	1.29	39	7.5
July 31-Aug 13	1000	71	1.50	17	7.5
Aug 14-27	1132	81	1.11	25	11.4
Aug 28-Sept 11	957	68	1.14	23	10.2
Sep 12-25	717	51	1.17	17	8.3
Sep 26-Oct 9	344	25	1.11	8	5.9
Oct 10-23	250	18	1.04	6	17.0
Oct 24-Nov 7	62	4	0.98	2	15.6
Nov 8-21	-122	-9	0.91	-3	13.5
Nov 22-Dec 7	55	3	1.23	1	6.8
Dec 8-28	92	4	1.57	1	9.4
Dec 29-Jan 14	62	4	1.05	1	6.9
1976					
Jan 15-28	987	70	1.05	25	9.0
Jan 29-Feb 11	569	41	0.77	18	8.8
Feb 12-25	370	26	1.06	9	9.2
Feb 26-Mar 11	457	30	1.04	11	8.1
Mar 12-25	853	61	1.01	23	6.3
Mar 22-Apr 8	266	19	0.84	8	7.0
Ap 9-30	889	40	0.67	19	4.2

Figure 4. Mean diel net photosynthetic assimilation by whole plant (open circles) and carbon content of new tissue formed at meristem (black circles), calculated for 2 wk intervals (modified after Hatcher et al., 1977).



Although most photosynthetic carbon fixation occurs during the summer months **(Fig. 4),** the peak of carbon content in new tissue occurs during the winter. In the months between October and December there is insufficient photosynthetic carbon assimilation to support new growth. Chapman and Craigie (1978) have shown that storage carbohydrate reserves are exhausted through the same time period. Presumably the reserves are mobilized, translocated to the meristem and used to support the production of new tissue.

Information on nitrogen assimilation in Laminaria longicruris comes from the studies of Harlin and Craigie (1978) and Espinoza and Chapman (1983). Harlin and Craigie (1978) measured the rates at which tissue discs (2.3 cm diameter) removed nitrate nitrogen from 1 or 2 L of seawater spiked with $NaNO_3$. Uptake rates were measured at various nitrogen concentrations, various temperatures, in light and in dark, in the presence or absence of oxygen, and in the presence or absence of NH4$^{+.}$ The results may be summarized as follows. An apparent Km (Michaelis-Menten half saturation constant) of 4- 6 m M NO_3^- was estimated for winter and summer plants. A maximum uptake rate of 7- 10 m mol h^{-1}g^{-1} dry wt. was recorded at 15°C at an irradiance of ca. 1800 m W cm^{-2}. Uptake rates at 5°C were reduced by about one third, and those at 0°C were reduced by about two thirds of the rate at 15°C. The uptake rate of NO_3^- increased hyperbolically with NO_3^- concentration **(Table 2)**. Finally, Harlin and Craigie (1978) showed that the presence of ammonium did not inhibit nitrate uptake in tissue discs.

Table 2. Rate of nitrate uptake by Laminaria longicruris tissue discs at various substrate concentrations. Results are means (and standard deviations) at 15°C (modified after Harlin and Craigie, 1978).

Nitrate concentration (m M)	Uptake rate (m mol h^{-1} g^{-1}	No. of replicates
1.2	2.1 (0.9)	7
2.9	4.0 (1.3)	7
6.8	6.7 (1.4)	6
10.1	5.6 (1.3)	3
11.7	6.7 (1.8)	4
14.9	8.3 (1.8)	6
17.2	8.2 (0.6)	4

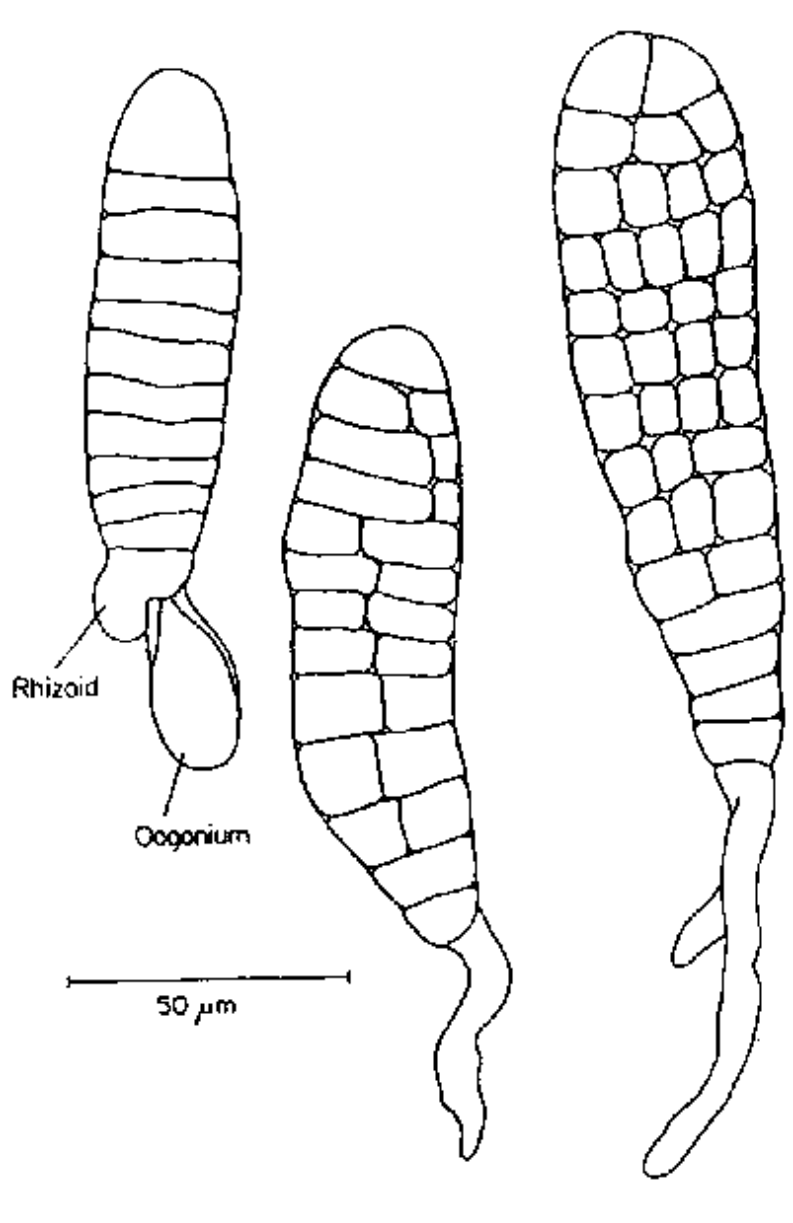
Nitrate uptake is energy demanding. When discs were pre-treated with 15 h of darkness, subsequent uptake rates of nitrate in the dark were between half and one third the rates of discs transferred to the light. Presumably the above dark treated discs were energy deficient. In the absence of oxygen, nitrate uptake in dark treated discs was reduced to zero. The uptake rates of light treated discs (which were presumably photosynthe-sizing) were not reduced in water from which the oxygen had been purged.

Espinoza and Chapman (1983) measured the nitrate uptake rates of small plants of Laminaria longicruris (<10 cm length) in a flow-through system (described by Probyn and Chapman, 1982). Harlin and Craigie (1978) used a batch mode system. In spite of the differences in the methods, the half saturation constants (Km) obtained by the two groups of researchers were quite similar. However, the uptake rates of young plants (measured by Espinoza and Chapman, 1983) were double those found in tissue discs cut from mature blades of plants from the same population (14.6 vs. 7. 0 m mol h^{-1}g^{-1} dry wt.). Presumably the differences in uptake rates between juvenile and mature tissues can be related to their surface area to volume ratios (higher in younger tissues).

2.4.2 Growth

There is no information on the growth of microscopic juveniles of Laminaria longicruris in the sea. Stegenga (unpublished manuscript) has studied growth of juveniles in laboratory culture. Following fertilization the zygote undergoes a number of divisions producing a uniseriate filament of 5- 10 cells surmounting an attaching rhizoid **(Fig. 5)**. Subsequently divisions occur in two planes to produce a monstromatic sheet of cells **(Fig. 5)**. The thallus remains monstromatic until it reaches a surface area of 1- 2 mm². After this more cell layers are formed in the basal region of the plant and growth is gradually confined to a meristem between the base of the blade and the stipe that develop. During the first 28 days of development growth of plants was found to be exponential, with the average surface area doubling every 1.6 days.

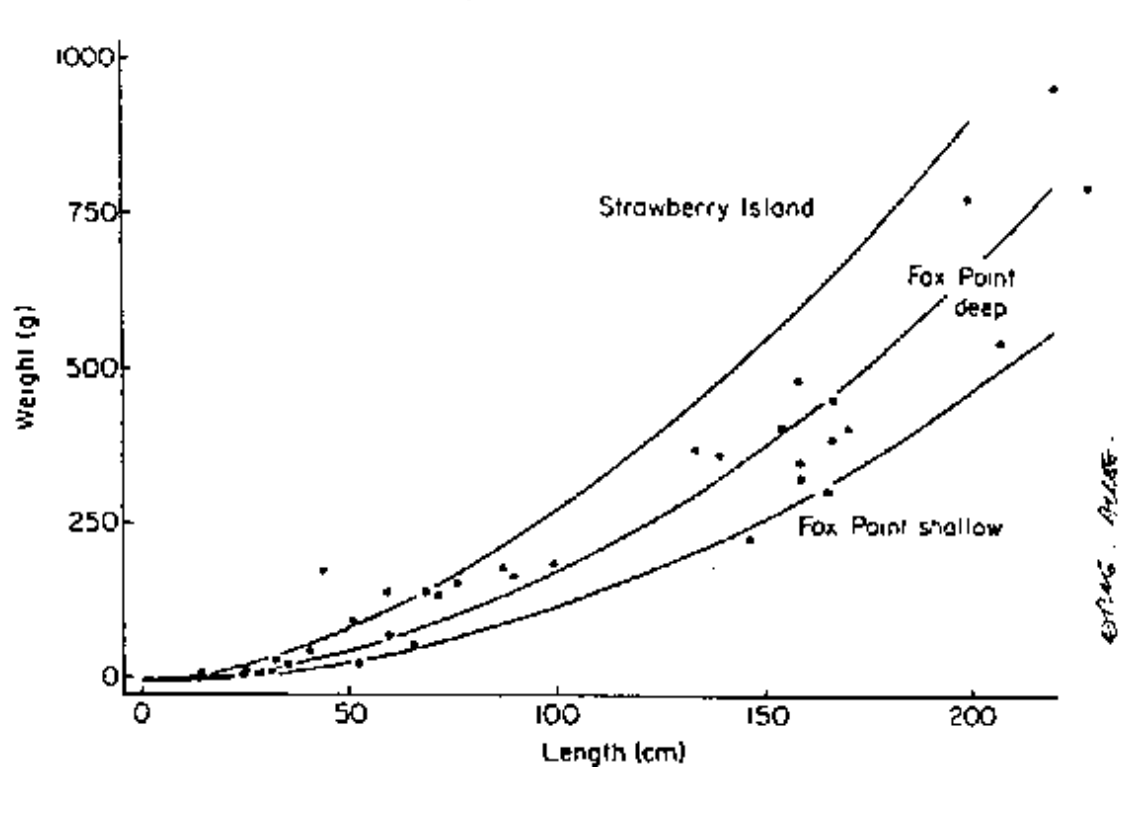
Figure 5. Early stages in sporophyte development (after an unpublished MS by H. Stegenga).



Studies on the growth of Laminaria longicruris in the sea seem to have been restricted to adult sporophytes. Most workers have used the "punched-hole" technique of Parke (1948) to follow the elongation of blades. On the Atlantic coast of Nova Scotia blade elongation rates usually decline from a peak of 0.6 to 1.0 cm d^{-1} in May and June to a minimum of 0.2 to 0.4 cm d^{-1} in the late fall or early winter (Chapman and Craigie, 1977; Gerard and Mann, 1979). In the Bay of Fundy and in the Gulf of St. Lawrence maximum elongation rates are higher (2- 3 cm d^{-1}) and occur later in the summer than on the Atlantic coast (Chapman and Gagne, 1980; Gagne and Mann, 1981; Anderson et al., 1982).

Mann (1972b) expressed monthly elongation rates as instan-taneous growth coefficients ($\log_e$length$_2$-$\log_2$length$_1$) for populations he studied on the Atlantic coast of Nova Scotia. The annual average in 1968/69 was 2.64 yr^{-1} (standard deviation = 1.2). In 1969/70 the annual average was 2.76 yr^{-1} (standard deviation = 0.84). The length increases were used to calculate biomass increases. To do these calculations, regressions of plant weights on plant lengths (power curve fits) were obtained **(Fig. 6).** It was found that in larger plants (>400 g initial weight) the annual biomass turnover was in the range of 5- 10 times. In smaller plants (<100 g initial weight) the annual turnover in weight approached 100 times in some populations. In the population at 10 m depth off Luke Island in St. Margaret's Bay a plant of 100 g increased it's biomass about 5 kg in one year, a 500 g plant about 10 kg, and a 2000 g plant about 20 kg.

Figure 6. Relationship between plant weight and plant length in 3 populations in St. Margaret's Bay, Nova Scotia (after Mann, 1972b). Regression lines are fitted power curves.



3. LIFE HISTORY

3.1 Life cycle and reproduction

3.1 Life cycle and reproduction

Laminaria longicruris has a life cycle that is typical of the order Laminariales. The large kelp plants found in the sea are sporangial and give rise to microscopic gametangial plants. Sporangial plants that are fertile may be recognized by the presence of sori on the distal median portions of the blade. A sorus is a dense aggregation of unilocular sporangia and associated sterile hairs (paraphyses) that form on the surfaces of the blade. There are between 2.8 and 4.4 x 10^{5} sporangia cm^{-2} of sorus (Chapman, 1984). Sporangia are assumed to contain 32 spores each.

The spores released are biflagellate and about 5.5 m m in diameter. After a period in the plankton they settle and form germination tubes **(Fig. 7)** into which the cell contents move. The spore case remains empty. During further development male and female gametangial plants become distinguishable. Male plants are compact structures with cell dimensions that are not much different from those of the original spore. The narrow cells of the males are lightly pigmented. Conical antheridia may be formed **(Fig.7)** at the one-celled stage. After release of the sperm these plants usually die.

Female plants enlarge to diameters that are 2- 3 times those of the male cells. Females are also more darkly pigmented. Most one-celled plants transform directly into oogonia **(Fig. 7)** and form an egg which, in culture, remains seated on the top of the oogonium after extension. The egg cells reach diameters of about 25 m m. Fertilization has not been reported, but presumably occurs while the eggs are still attached to the oogonia. Young sporangial plants begin their development in the same position. The complete sequence from spore settlement to zygote formation occurs in less than 14 days under ideal culture conditions.

4. POPULATION STRUCTURE AND MORTALITY

4.1 Age, weight and size composition
4.2 Sporophyte-gametophyte and sex composition

4.1 Age, weight and size composition

It is not possible to determine the age of individual plants in wild populations. Population age class structures are therefore unknown. Cohort analysis has shown that there is considerable variation in plant size at any given age (Chapman, unpublished observations). It is not possible to determine population age class structures from size class frequencies.

The weight and length class frequencies in 4 sample of Laminaria longicruris collected from Abbott Harbour (southwestern Nova Scotia) in August, 1981 are shown in **Fig. 8.**

Figure 7. Development of microscopic male and female gametangial phases from haploid spores. The final stage shown is a 3 celled sporangial plant growing attached to an empty oogonium (after an unpublished MS by H. Stegenga).

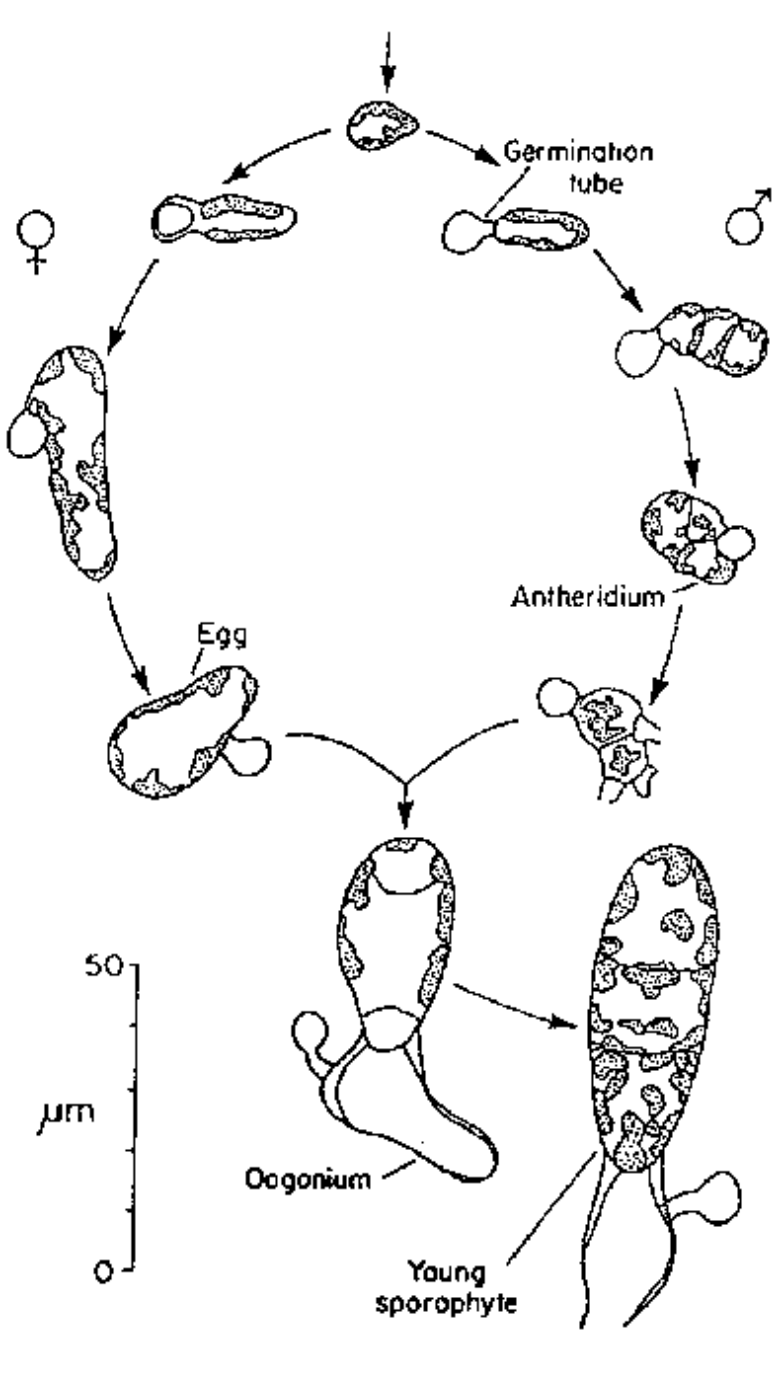
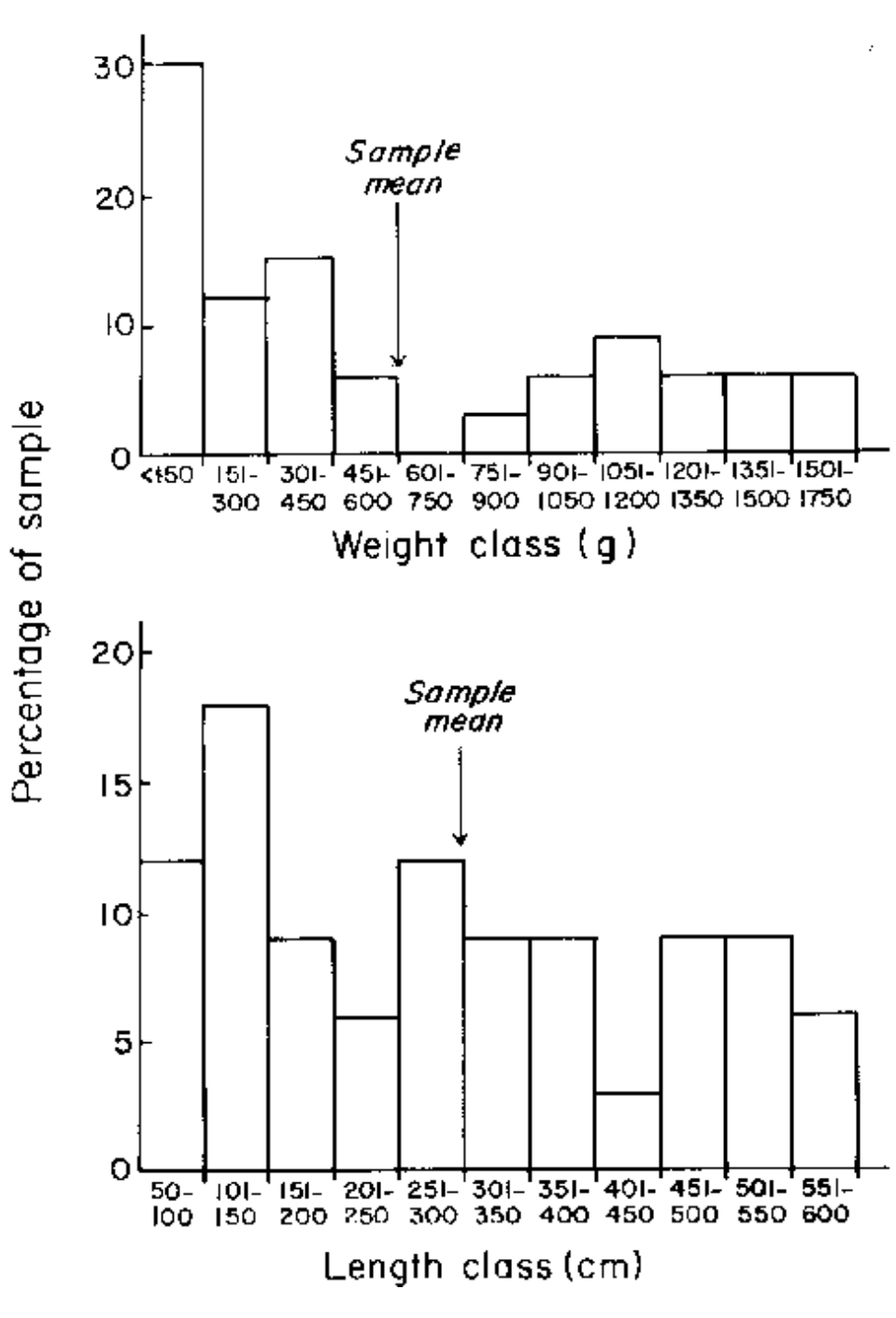


Figure 8. Size class frequency distributions for weight and plant length in a sample collected from Abbott Harbour in southwestern Nova Scotia.



On the shores of Nova Scotia closer to Halifax, Gerard and Mann (1979) showed that mean plant length varied with exposure to wave action. At an exposed site mean plant length (150 cm) was considerably shorter than in a nearby sheltered site (200.8 cm). The shorter stature of plants at exposed sites was seen as an adaptation to reducing form drag. In general, the populations of southwestern Nova Scotia are made up of longer individuals than those found in the eastern part of the province. The determining factors in this inter-population variability have not been identified. There is some evidence for genetic differentiation in total stipe length among sheltered and exposed coast populations (Chapman, 1974).

There are very few published data on population size class distributions in terms of plant mass. Some sample data are shown in **Fig. 8** for a population in southwestern Nova Scotia. McPeak (1980) has reported that in 4 other populations sampled in that same general area the average weight of large (undefined) Laminaria longicruris plants varied between 1910 g and 550 g (mean = 670 g). The average weight of small plants (again undefined) varied between 60 and 160 g (mean = 70 g). Although it is difficult to interpret McPeak's data, since his "small" and "large" plant classes are undefined, it is clear that the population sample in **Fig. 8** has a similar average plant mass (about 600 g) to those population sampled by McPeak. Average plant weights in sheltered and exposed sites close to Halifax were 549.0 and 228.5 g respectively (Gerard and Mann, 1979).

There is considerable variation in the densities of the Laminaria longicruris populations in Nova Scotia. These variations are not clearly related to the size class composition of the populations. In a population (close to Halifax) with the highest density recorded (24.0 m^{-2} SE = 4.0) the average plant mass was relatively low (228.5 g SE = 20.8, Gerard and Mann, 1979). In southwestern Nova Scotia, where average plant mass is higher, densities tend to be lower (McPeak, 1980; Sharp et al., 1981; Chapman, 1984). However, McPeak (1980) did not demonstrate any clear relationship between variations in plant density and average plant mass in 5 sites examined off the southwestern shore of the province.

Off Bon Portage Island on the southwestern shore of Nova Scotia densities of Laminaria longicruris varied between 3.8 and 14.2 m along a gradient of increasing shelter to wave action (Sharp et al., 1981). Through the same populations average plant mass varied very little (0.35 kg - 0.5 kg). The lack of any clear relationship between average plant mass and plant density might be expected in wild communities which contain several interacting species.

It seems likely that interactions with herbivores and competing plant species are major determinants of density variations in Laminaria longicruris populations (see Section 5.2 below). In addition, Sharp et al. (1981) have shown that density varies with depth and with exposure to wave action **(Fig. 9, Table** 3). At Bon Portage Island off southwestern Nova Scotia the maximum densities occurred in waters of about 5 m depth. Densities were inversely related to wave action.

Figure 9. Relationship between plant density and depth at a site in southwestern Nova Scotia (after Sharp et al., 1981).

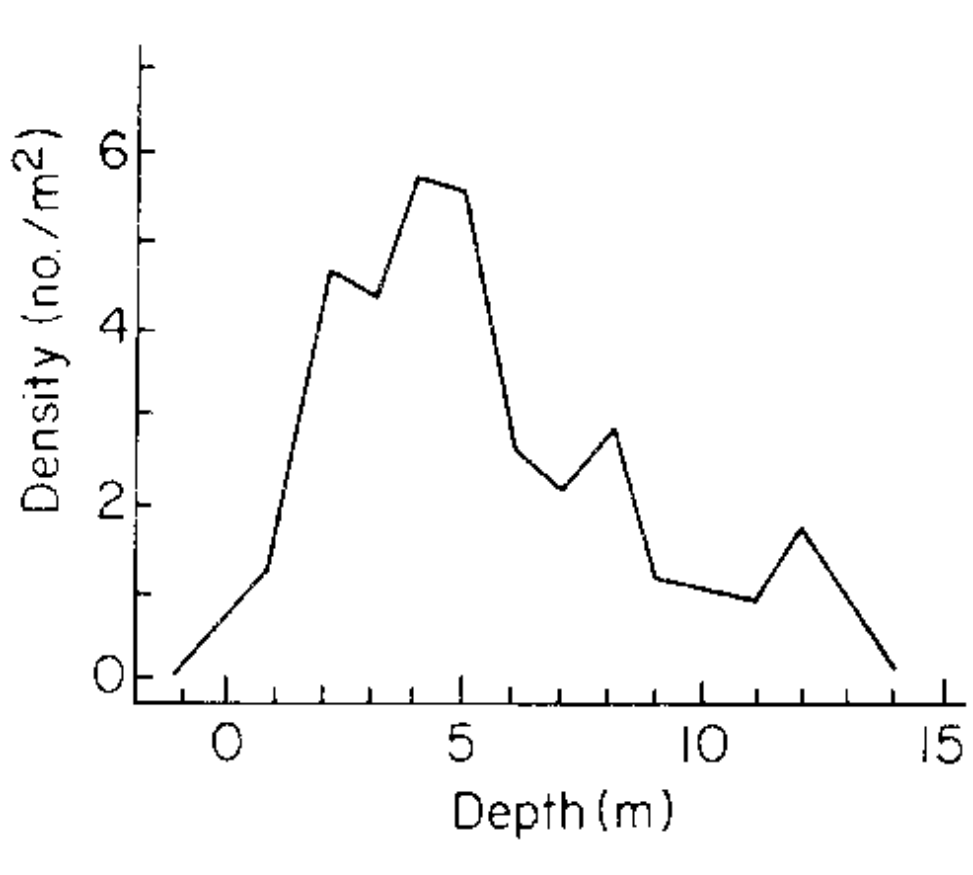


Table 3. Relationship between plant density (no./m²) and exposure to wave action. The wave exposure index is subjective and arranged from 2 (sheltered) to 6 (exposed). Data for plants of <1m length are displayed separately (modified after Sharp et al., 1981).

Exposure index		Plant density
	< 1 m long	> 1 m long
2	4.6	9.6
3	1.7	3.7
5	1.3	3.6
6	2.3	2.5

4.2 Sporophyte-gametophyte and sex composition

Populations of Laminaria longicruris are made up of macroscopic sporangial plants (visible) and microscopic gametangial plants that are not visible and have never been identified in the wild (see Section 3.2). Chapman (1984) has used an indirect method to estimate the proportion of macroscopic to microscopic plants in a kelp bed off Abbott Harbour (southwestern Nova Scotia). The density of sporangial plants was counted directly by field observation and estimated at 1.24 m^{-2}. Artificial ceramic surfaces were placed on the floor of the kelp beds at one month intervals through one year. Each set of ceramic surfaces was exposed for one month to spores descending from the plankton. At the end of each month the exposed surfaces were collected and transferred to showers of running seawater under enhanced light conditions. Microscopic stages that had been trapped in the field grew to a size that could be identified with a dissecting microscope within 6 weeks. The numbers of recruits collected in this way are shown in **Table 4.** Through one year almost ten million microscopic plants were recruited per meter squared.

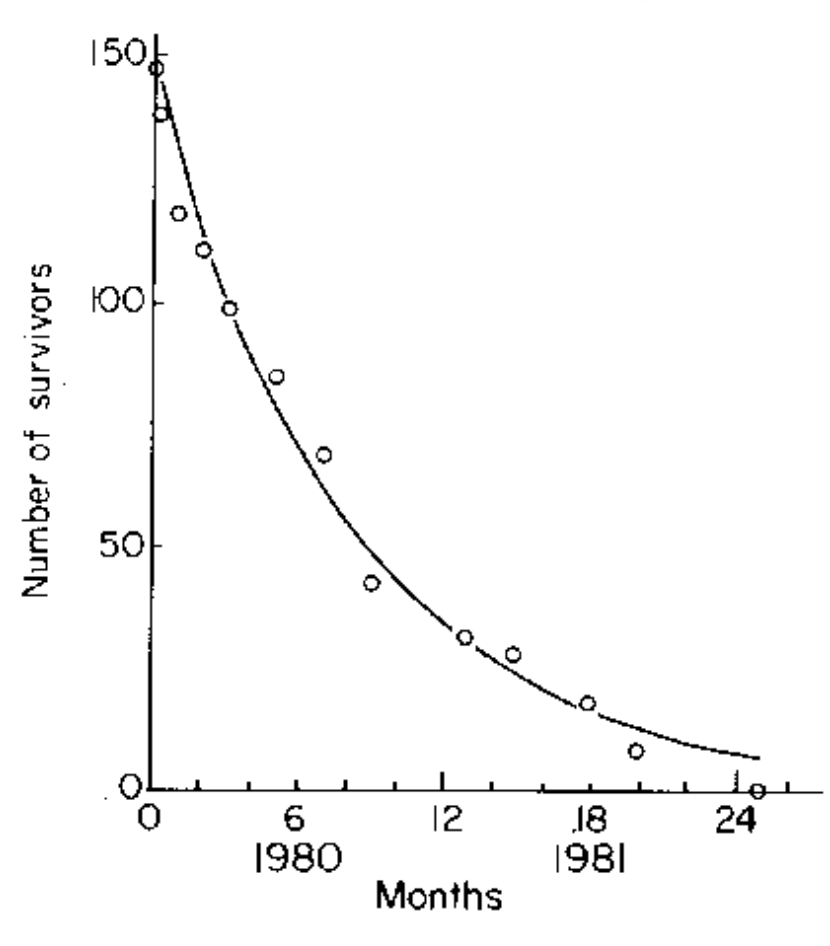
Table 4. Benthic recruitment rate of microscopic stages of Laminaria longicruris (modified after Chapman, 1984).

Time period	Number of recruits (no./m²[SE])
1981	
Oct 6-Nov 5	5.11x10^{5} [0.92x10^{5}]
Nov 5-Jan 9	6.60x10^{5} [0.59x10^{5}]
1982	
Jan 9-Feb 9	1.42x106[0.67x105]
Feb 9-Mar 9	20.02x10^{3} [5.84x10^{3}]
Mar 9-28 April	75.40x10^{3} [18.28x10^{3}]
April 28-May 18	1.62x10^{5} [0.36x10^{5}]
May 18-July 6	1.25x103[0.23x10^{3}]
July 6-Aug 6	1.83x104[1.13x10^{4}]
Aug 6-Sept 13	4.47x10^{4} [2.59x10^{4}]
Sept 13-Oct 13	3.48x10^{4} [8.87x10^{3}]

These microscopic sporangial plants were produced from female gametophytes. Normally, in culture, one zygote is produced from each female, and females comprise half of the gametangial population (Stegenga, unpublished data). Luning (1980) has shown directly that females of 3 European species of Laminaria (not including L. longicruris) produce only one egg each in the sea. It may be estimated, therefore, that about 20 million gametangial plants (male + female) develop per meter squared per year on the kelp forest floor at the site studied. The highest standing crop occurs in the winter months (November - January) with close to 13 million gametangial plants per meter squared. During these winter months there are at least 10 million gametangial plants per sporangial plant. Production of spores is minimal during the summer and this ratio falls to about 250/000:1.

Chapman (1984) has studied some of the components of mortality in the kelp population at Abbott Harbour. A depletion curve for Laminaria longicruris is shown in **Fig. 10.** The individuals included were macrobenthic sporangial plants of mixed age and size classes. About 76% of the population was lost in a 12 month period. Since the population density remained stable during the same time period, the replacement rate was about 1m^{-2} yr-1. The decline in the numbers of tagged individuals was exponential with time and all plants were lost within 24 months. In a concurrent study of survivorship among a cohort of individuals recruited in 1980, sporangial plants were found to survive to a maximum age of 4 years (unpublished data).

Fig. 10. "Depletion" curve showing survivorship of a sample of plants of mixed age and size classes at Abbott Harbour, Nova Scotia. The curve is an exponential fit (r2=0.96). Modified after Chapman, 1984.



Replacement of lost individuals in the population studied by Chapman took place by spore production only (no vegetative regeneration). The number of spores produced by the population was estimated at 8.9 x 109 yr^{-1} of which half were assumed to produce one female gametangial plant and one zygote each. Since the rate of microbenthic recruitment was estimated (see above), the chances of a female spore surviving through the planktonic phase can be calculated as about one in 500. The chances of surviving the microbenthic to macrobenthic transition were much smaller (~ 1 in 9 x 10^{6}). The least risky phase of life was in the macrobenthos (chances of surviving one year ~ 1 in 4).

5. PRODUCTIVITY OF THE RESOURCE

5.1 Standing Stocks and Harvestable Yields
5.2 Physical and biological determinants of productivity, growth and mortality
5.3 Potential for genetic improvement of stocks
5.4 Relative contributions of sexual and vegetative reproduction
5.5 Potential for environmental enhancement

5.1 Standing Stocks and Harvestable Yields

The best estimates of standing stocks and harvestable yields are to be found in the review by Smith and Loucks (1980). In their work Smith and Loucks estimated **K** (the maximum total standing crop in the absence of harvesting) and **ms^{Y}** (maximum sustainable yield). These two parameters were calculated as follows. K (tonnes) was estimated from data on standing biomass (kg m^{-2}) and areas of seaweed beds (ha). ms^{Y} is equal to R.K/4 where R is the instantaneous growth coefficient at low plant density. Smith and Loucks also provided a "conservative yield estimate" for the resource which is ms$^{Y/2}$. The data available (Atlantic coast of Canada only) are presented in **Table 5.** The highest estimates of K are for the southwestern shore of Nova Scotia with 833,000 tonnes and a conservative yield estimate of 36,500 dry tonnes per year.

Table 5. Resource estimates for Laminaria longicruris in Atlantic Canada (modified after Smith and Loucks, 1980). K is the standing crop in the absence of harvesting, Y is the -conservative yield estimate". See Section 5.1 for calculation procedures.

Marine Plant District	Standing crop bio-mass (kg m^{-2})	Area of seaweed beds (ha)	K (tonnes)	y[a] (tonnes fresh)	Y[a] (tonnes dry)
New Brunswick	0.7[b]	1700[b]			
(Bay of Fundy)	4.9[c]	34[c]	25800	9000	1100
Nova Scotia	17.0	4860	833000	291400	36500
(Chebogue-Cape Sable)					
Newfoundland			17800	6250	780

[a] Assumes an instantaneous growth coefficient of 2.8 yr-^{1}
[b] Hide frond population
[c] Narrow frond population

It should be pointed out that the kelp resource estimates of the southwestern shore of Nova Scotia of Smith and Loucks (1980) were based on standing crop and kelp bed area measurements of MacFarlane (1952). In 1977 McPeak (1980) resurveyed three of the sites examined by MacFarlane. McPeak found that, on the average; biomass (kg m^{-2}) and kelp bed area (ha) were less than half of MacFarlane's earlier estimates. Accordingly, McPeak (1980) estimates that the total standing stock (K) for the 3 sites is only one quarter to one half of the earlier estimate. On this basis alone, it seems likely that the calculations of K and Y for Nova Scotia kelp beds (Smith and Loucks, 1980) are overestimates.

Biomass (kg m^{-2}) has been estimated in several Nova Scotia kelp beds other than those examined by MacFarlane (1952) and McPeak (1980). In most recent studies (Neish, 1973; Gerard and Mann, 1979; Pringle and Sharp, 1980; Sharp et al. 1981; Chapman, 1981) the estimated biomass has consistently been within the range of 3.5 - 5.5 kg fresh weight/m² in stands that are dominated by Laminaria longicruris. An exception is found in the estimates of Mann (1972b) for St.Margaret's Bay on the Atlantic coast of the province (11.5 kg^{-2} m SE = 1.2).

At an arctic site (69°21.9'N 81°46.2'W) examined by Chapman and Lindley (1981) the biomass of Laminaria longicruris was only 0.097 kg m^{-2}. At this site the kelp vegetation was dominated by the arctic species L. solidungula (0.87 kg m^{-2}).

The productivity of Laminaria longicruris has been estimated several times since Mann's (1972b) pioneering study. According to Mann (1972b), the productivity of the species may reach 2000 g C m^{-2}yr^{-1} in St. Margaret's Bay. This estimate was obtained from measurements of growth and biomass of plants in all size classes. In a later study of photosynthetic production of mature plants, Hatcher et al. (1977) estimated productivity as 143-428 gC m^{-2} yr^{-1} in the same bay. Using growth measurements and biomass data, Gerard and Mann estimated productivity as 540 g C m^{-2}yr^{-1} for a sheltered site close to St. Margaret's Bay and 270g m^{-2}yr^{-1} at an exposed site. The reasons for the discrepancies among these estimates are unknown.

The only information on harvested yield per unit area of a Laminaria longicruris forest comes from the work of Pringle and Sharp (1980). In 1979 a commercial dragrake was operated in southwestern Nova Scotia. The standing crop before harvesting was 4.0 kg m^{-2}. The harvest removed 2.4 kg m^{-2}. Assuming an instantaneous growth coefficient of 2.8 yr^{-1}, a maximum sustain-able yield (ms^{Y}) of 2.8 kg m^{-2}, and a "conservative yield estimate" of 1.4 kg m^{-2} can be calculated. Within the swath of the dragrake the harvested yield is clearly close to the maximum sustainable yield. However, it should be pointed out that over the boulder terrain on which kelps grow substantial portions of the forest would remain unharvested.

5.2 Physical and biological determinants of productivity, growth and mortality

5.2.1 Physical determinants

Nearly all information of the effects of physico-chemical determinants comes from studies in eastern Canada (especially Nova Scotia). Only two of these studies (Hatcher et al., 1977; Gerard and Mann, 1979) examined variations in productivity. Most other publications have been concerned with variations in linear growth rates.

During the year in which Hatcher et al. (1977) estimated the photosynthetic assimilation of whole mature plants of Laminaria longicruris, continuous measurements of photon flux density and temperature were also made. The data were subjected to multiple regression analysis **(Table 6).** Sixty percent of the variance in diel net photosynthesis was accounted for by variations in photon flux density. Twenty-seven percent of the variance in diel respiration rates were accounted for by temperature variations. The effect was significant (P<0.01) but hardly accounts for most of the variance in respiration rate.

Gerard and Mann (1979) examined the relationship between the rate of water movement (wave generated) and productivity of the species. At an exposed site the rate of diffusion of Plaster of Paris balls by water movement was 1.5 to 5 times greater than at a nearby sheltered site. Nutrient supply, temperature and irradiance were similar at the two sites. Biomass estimates were also similar at the two sites. Productivity at the sheltered site (1.8 kg dry wt m^{-2}yr^{-1}) was twice that at the exposed site (0.9 kg dry wt. m^{-2}yr^{-1}). Gerard and Mann (1979) suggest that the differences in productivity among the two sites may be related to differences in plant morphology. At the exposed site the laminae of the plants were narrow and thickened. At the sheltered site the blades were wider and thinner. These relationships mean that the surface area to volume ratios of plants in the sheltered site were higher than those at the exposed site. The consequences in respect to nutrient absorption rates are self evident.

Table 6. Multiple regression analysis of the relationship between (a) diel net photosynthesis and environmental variables (photon flux density and temperature), (b) diel respiration and environmental variables (modified after Hatcher et al., 1977).

Percent of variance accounted for			
Variables	Photon flux density	Temperature	Both
Diel net Photosynthesis	61**	6 ns	63**
Diel Respiration	2 ns	27**	28*

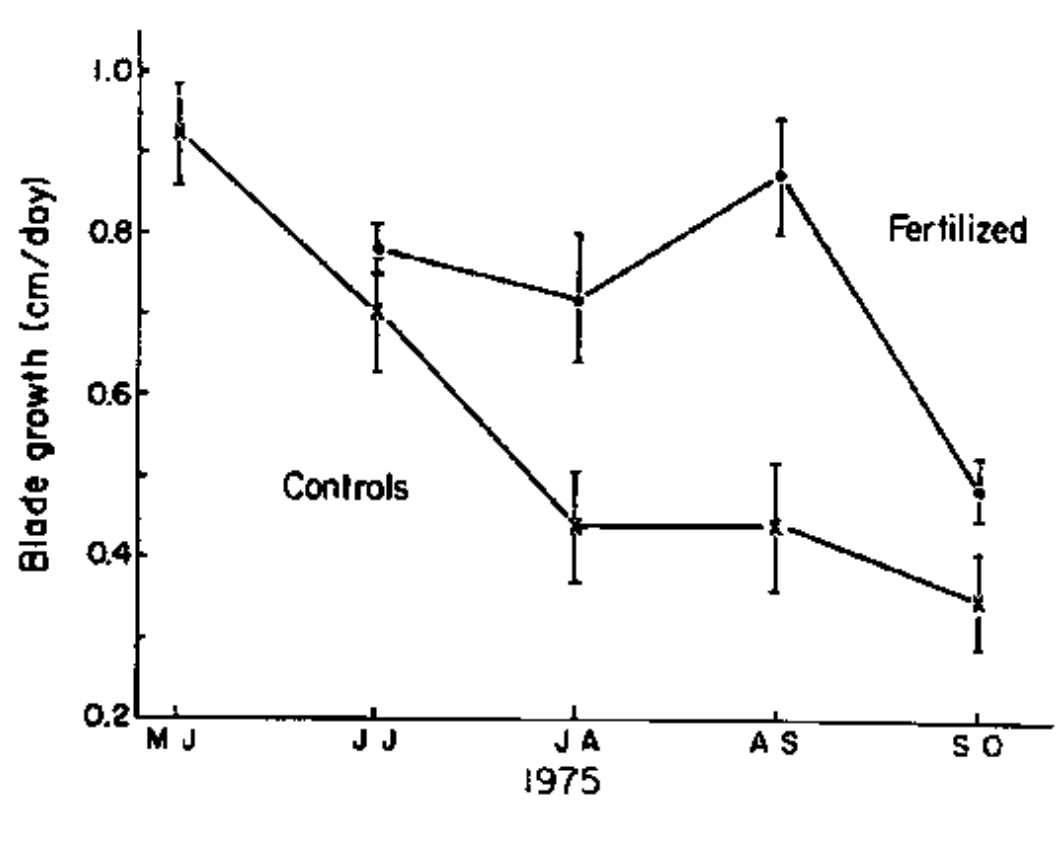
** Significant, P<0.01
* Significant, P<0.05
ns- Not significant

Experimental analyses of the relationships between linear growth rates and seawater nitrate concentration have been carried out by Chapman and Craigie (1977) and Espinoza and Chapman (1983). During the year 1974-75, Chapman and Craigie (1977) observed a declining rate of linear growth through the summer (Fig. 11) when there were very low nitrate concentrations.

Figure 11. Composite graph showing seasonal changes in growth rate, seawater nitrate concentration and tissue nitrate concentration in plants at the 9 m depth in St. Margaret's Bay, Nova Scotia (after Chapman and Craigie, 1977).

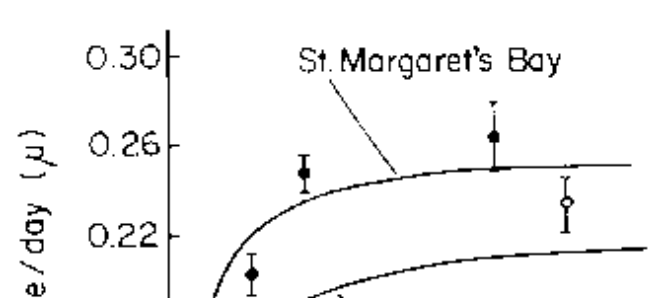
Growth rates increased again in December as nitrate concentrations increased from undetectable levels to about 6 m M. During the winter internal tissue concentrations of nitrate increased to maximum values of about 150 m moles g^{-1} fresh wt. (~ 28,000 times ambient seawater concentrations). During the summer months tissue concentrations of nitrate fell to undetectable levels. To test the relationship between linear growth and seawater nitrate concentration, a portion of the kelp forest was fertilized with sodium nitrate at least once a week through the summer of 1975. Tissue nitrate concentrations were raised up to 20 fold in the experimental group of plants and linear growth rates increased back to maximum winter rates of about 1 cm d^{-1} **(Fig. 12).**

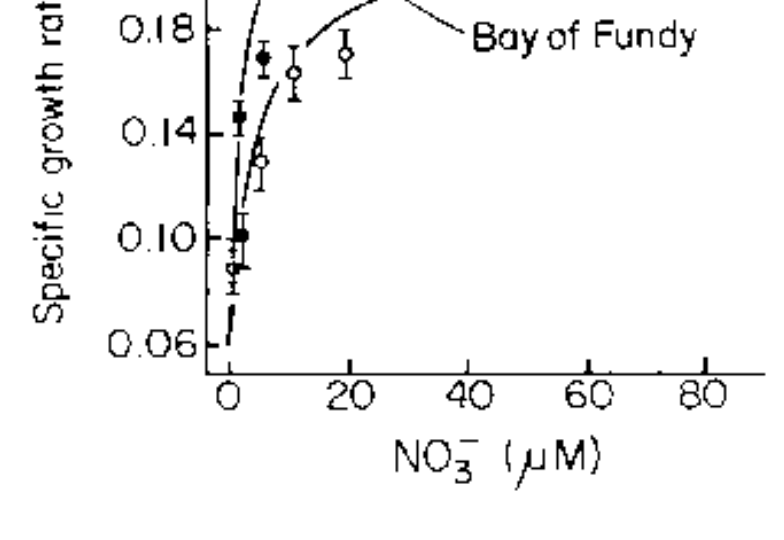
Figure 12. Effect of nitrate fertilization on the linear growth rate of plants through one summer. Means and standard errors are shown for treatment and control groups of 20 plants (after Chapman and Craigie, 1977).



Espinoza and Chapman (1983) measured the linear growth rates and weight increases of small (2 cm long) plants in a flow-through culture system at various nitrate concentrations. They showed a hyperbolic relationship between specific growth rate (m) and substrate concentration **(Fig. 13).** The half saturation constant (K_S = S at one half m $_{max}$) at 9°C was 1.1 m M nitrate for linear growth and 1.8 m M nitrate for growth in fresh weight. Growth saturation occurred above 20 m M nitrate, which explains why the growth of the species is so limited during the summer months on the Atlantic coast of Nova Scotia.

Figure 13. Relationship between growth rate (weight increase) and nitrate concentration in juvenile sporangial plants collected from 2 sites in Nova Scotia. Means and 95% confidence limits are given. Curves fitted to the Monod equation (after Espinoza and Chapman, 1983).





The major effect of a summer depletion of available nitrogen in seawater is to uncouple seasonal growth patterns from seasonal variations in light availability and photosynthetic assimilatory rates (see Hatcher et al., 1977; **Fig. 4).** Anderson et al. (1981), Gagne and Mann (1981) and Gagne et al. (1982) have examined seasonal growth patterns at sites in eastern Canada that do not experience a major summer depletion of the nitrogen resource. It was shown in all cases that seasonal patterns of linear growth track seasonal variations in light availability when nitrogen supply is elevated during the summer months.

In populations which never experience a summer nitrogen depletion, winter growth rates are depressed in relation to populations that are nitrogen starved during the summer (Gagne and Mann, 1981; Gagne et al., 1982). The difference in winter growth rates may be attributed to differential carbohydrate reserve accumulation. In nitrogen depleted populations part of the photosynthetic assimilatory surplus that is built up during the summer is converted into reserves of laminaran (Chapman and Craigie, 1978; Gagne and Mann, 1981; Gagne et al., 1982). Laminaran was undetectable in the tissues of plants collected from the Bay of Fundy which has elevated nitrogen resources during the summer months. Carbohydrate reserves are used to support growth in late fall and early winter when the carbon demand for growth exceeds photosynthetic production (Hatcher et al., 1977; Chapman and Craigie, 1978).

It is interesting to note that, in one of two sites that experience a marked summer depletion of nitrogen, Gerard and Mann (1979) did not observe a corresponding decline in linear growth rates. In the second population, which was located at a site more exposed to wave action, the effects of the summer depletion of the nitrogen resource were clearly evident. Gerard and Mann (1979) had no obvious explanation for the growth rate difference among the two sites during the summer months.

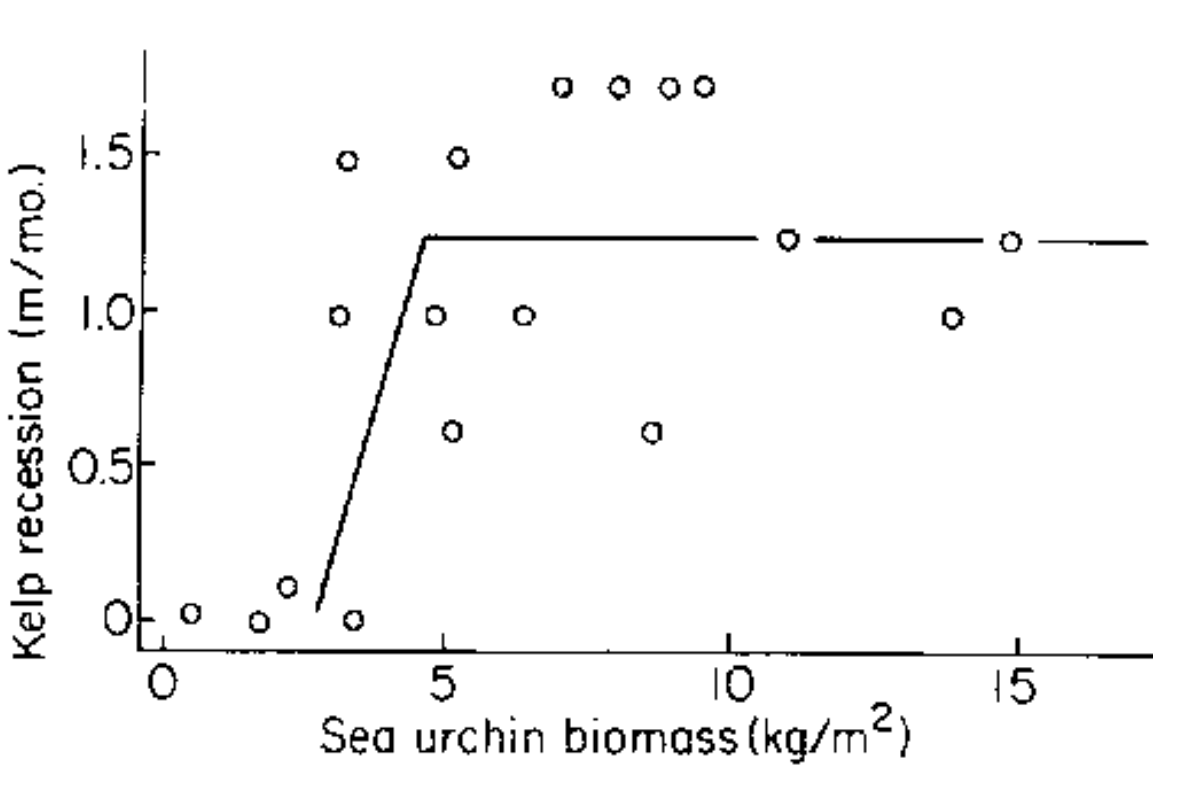
5.2.2 Biological determinants

The standing stocks (and hence productivity) of Laminaria longicruris forests are regulated by a complex suite of biological interactions. Herbivory, carnivory and parasitism are all important structuring agents. Most of the experimental information available comes from work on the Atlantic shores of Nova Scotia (especially at St. Margaret's Bay).

The importance of herbivory to the maintenance of standing stocks of kelps was not apparent in an early study of energy flow through the marine benthos of St. Margaret's Bay (Miller et al., 1971). It was estimated that seaweed annual production exceeded the annual consumption by herbivores by a factor of >10. Furthermore, in a survey of the subtidal seaweed zone in 1968 sea urchins (Strongylocentrotus droebachiensis) were found in abundance in only 7 of 25 sites (Mann,1972a). Through the 1970s the patches of sea urchins expanded in area and eliminated the great bulk of the seaweed biomass (Breen and Mann, 1976a; Chapman, 1981). By the end of the decade about 90% of the kelp forest area had been removed by grazing (Chapman, 1981). Benthic primary production was reduced by about 2 orders of magnitude. After kelp bed destruction sea urchins were able to prevent the regrowth of perennial foliose macrophytes. The herbivore populations were maintained by a diet of microalgae and drift from the intertidal zone.

The relationship between kelp bed recession rate and sea urchin biomass was examined by Breen and Mann (1976a). The destruction of kelp appeared to be a threshold event **(Fig. 14).** Above a biomass of about 2 kg m sea urchins were able to effect kelp bed recession. Below this threshold kelp bed recession did not occur. However, once kelps had been removed, reforestation was prevented at sea urchin biomasses of only 150 g m^{-2}.

Figure 14. Relationship between the rate at which a surveyed kelp bed receded and the biomass of sea urchins. Curve fitted by eye (after Breen and Mann, 1976b).



Experimental removal of sea urchins leads to reforestation by kelps (Breen and Mann, 1976a); Chapman, 1981). When Laminaria longicruris is rare in areas adjacent to experimental sea urchin removal areas, other kelp species may come to dominate the benthos (Himmelman et al., 1983; Keats et al., 1982).

Beginning in 1980, sea urchin populations of Atlantic Nova Scotia have been decimated each fall by a disease that has led to the loss of >99% of their biomass over nearly 1000 km of coastline (Miller and Colodey, 1983; Scheibling and Stephenson, 1984). Jones et al. (in press) have demonstrated that the pathogenic agent in this disease is closely similar to the genus Paramoeba. In absence of sea urchins the subtidal benthos has converted once more to a system dominated by foliose seaweeds (Johnson, 1984). At sites exposed to strong wave action Laminaria longicruris became the dominant component of the vegetation within 3 years (Scheibling, personal communication). In sheltered sites the benthos remains dominated by diminutive species of fleshy seaweeds more than 4 years after the destruction of the sea urchins (personal observation; Johnson, 1984).

The importance of sea urchins and their amoeboid disease causing agent as determinants of standing stocks of kelps is self evident. The reasons for the expansion of urchin populations are less fully understood. Breen and Mann (1976b) put forward evidence in support of the contention that a reduction of lobster (Homarus americanus) stocks led to an increase in sea urchin population densities. The evidence is as follows: (a) lobsters appear likely as key predators of sea urchins, (b) lobsters have declined in abundance and (c) sea urchins have increased in number and destroyed kelp beds at a high rate. Pringle et al. (1982) have difficulty in accepting the hypothesis that the lobster is a keystone predator of the kelp bed ecosystem and that overfishing of lobsters has caused Laminaria densities to decline. It is difficult to manipulate the densities of benthic and pelagic carnivores in order to observe their effects on community structure at lower trophic levels. In this respect the predation hypothesis of Breen and Mann (1976b) remains untested, but it needs to be pointed out there is no evidence in support of its rejection.

In a more recent graphical model (Fig. 15) of the predation hypothesis of benthic community organization Wharton and Mann (1981) have incorporated the effects of fishfish (plaice, wolffish etc.) along with the effects of lobsters. The model also takes into account the behavioural responses of urchins to their predators. The key to kelp bed destruction is the development of urchin biomasses of >2 kg m^{-2}. Bernstein et al. (1981, 1983) believe that when urchin densities exceed 10 m^{-2} the presence of lobsters leads to the formation of aggregations which can overgraze kelp beds.

Figure 15. Graphical model of feedback relationship between kelp bed destruction and declining lobster stocks in the northwest Atlantic (after Wharton and Mann, 1981).

Johnson (1984) has studied the biological determinants that influenced the development of kelp stands following the disappearance of major sea urchin populations in St. Margaret's Bay. The interactions of major importance are (a) antifouling properties of crustose coralline algae and (b) grazing by the gastropod Lacuna vincta. At 2 sites in St. Margaret's Bay crustose corallines covered >90% of available primary rock substratum. The dominant genus in terms of cover was Phymatolithon. Johnson (1984) was able to demonstrate experimentally that the standing stock development of seaweeds growing on Phymatolithon was reduced by 46% in comparison with standing stock development on bare rock. The antifouling effect was not species specific; all seaweeds were equally affected.

The major grazer of Laminaria longicruris in the absence of sea urchins is Lacuna vincta (Johnson, 1984). Between February and September of 1980 the snails consumed only 0.05% of the blade biomass available to them. The major effect of snail grazing is to increase the ripping and loss of parts of the blade canopy. Johnson (1984) estimated that the standing biomass of L. longicruris in the bed he studied would have been about 28% higher in the absence of snails.

Chapman (1984) showed that in the kelp beds of the southwestern part of Nova Scotia, where sea urchins have never been recorded in high densities, interactions with perennial turf-forming red algal species are the major determinants of kelp density. Experimental removal of the red algal turf species (mostly Chondrus crispus, Phyllophora truncata and Ceramium rubrum) led to a ten fold increase in Laminaria recruitment.

5.3 Potential for genetic improvement of stocks

There has been only one genetic study of a trait of commercial importance in Laminaria longicruris (Chapman and Doyle, 1979). Within a sample of 80 sporangial plants collected from a single population in St. Margaret's Bay, Nova Scotia there was found to be a three fold variation in percentage alginate of dry weight. Alginate is a structural cell wall carbohydrate of commercial value. Chapman and Doyle (1979) used a selective breeding program to quantify the genetic component of phenotypic variance in alginate content. The mean alginate content of the 80 plants tested was 23.8% of alcohol extracted dry weight (SE= 0.47). Five plants with a high alginate content (mean=30.1%) were allowed to interbreed. A second set of parents with a low alginate content (mean=14.4%) was also interbred. The alginate contents of the offspring off the 2 groups of families are shown in **Table 7.** After 6 months growth in the sea the alginate content of the two groups of offspring were not significantly different from one another or from the original 80 plants tested. Consequently the realized heritability values are very low. This result was confirmed in a separate breeding plan (offspring on mid-parent regression breeding scheme).

The work of Chapman and Doyle (1979) suggests that simple mass selection breeding for increased alginate content is unlikely to work. It should be pointed out, however, that in the People's Republic of China there has been considerable success in the production of strains of Laminaria japonica that are better suited to aquaculture than wild plants (Fang et al., 1962; Fang et al., 1963; Fang et al., 1978). The breeding program used involves selection of suitable phenotypes (with appropriate temperature tolerances, growth rates; etc.) followed by intensive inbreeding in which the gametangial plants from single parents are mated with one another. Fang et al. (1962) found considerable phenotypic variability within inbred lines indicating that a high degree of homozygosity had not been achieved. Complete homozygosity was achieved in later work (Fang et al. 1978) when sporangial plants were produced parthenogenetically from isolated female gametangial plants. Surprisingly, the partheno-sporophytes developed normally. Luning et al. (1978) showed that parthenosporophytes of L. longicruris were extremely stunted. However completely homozygous lines can be produced by isolating gametangiail plants and growing them vegetatively whilst preventing gamete formation through the use of red light (Luning and Dring, 1975). Large filamentous gametangial plants will become fertile on transfer to white light. Crosses of single large males and females in this way will lead to the production of hundreds of genetically identical offspring.

Table 7. Response of Laminaria longicruris to artificial selection. Results are means (standard errors) for % alginate of alcohol extracted dry weight.

	Offspring	
	Laboratory grown	**Field grown**
Mean of parent population = 23.8(0.47)		
Mean of 5 selected parents = 30.1	20.7(1.0)	23.0(2.7)
Mean of 5 selected parents = 14.4	26.6(1.25)	25.6(1.0)

5.4 Relative contributions of sexual and vegetative reproduction

Population replacement takes place entirely through the sexual life history of the species (Pringle and Sharp, 1980; Chapman, 1984).

5.5 Potential for environmental enhancement

There have been two experimental attempts at environmental enhancement of the kelp habitat by sea urchin removal (Bernstein and Welsford, 1982; Miller, 1985). Bernstein and Welsford used a diver to apply a quicklime slurry to reduce sea urchin densities. They found that an application of 1.02 kg of lime/m² resulted in a 73% reduction in urchin densities. There were no apparent ill effects on other organisms. Bernstein and Welsford estimated that liming 4 ha would require ca 40 t of lime (at CAN$60/t) and 60 man days of work.

Miller (1985) explored the possibility for biological control of sea urchins using a pathogenic disease (see Section 5.2). In the summer of 1983, 580 sea urchins exposed to the disease (and presumably infected) were transplanted into a natural population of urchins. A control group of uninfected animals was transplanted to another site. By October, 1983, diseased animals were found 50 m from the release site. The disease was not evident at the control site. There is therefore a potential for biological control of sea urchin densities by the virulent pathogen that occurs naturally in Nova Scotia.

6. METHOD OF HARVESTING AND HARVESTING CYCLE

6.1 Annual cycle of operations
6.2 Manpower productivity
6.3 Alternate employment

6.1 Annual cycle of operations

Laminaria longicruris was harvested in southwestern Nova Scotia between 1940 and 1949 (Sharp, 1980). Harvesting since 1949 has been sporadic and without any consistent annual cycle of operations. During the 1940s the main harvest began in the early summer and continued for many months into the early winter. At Clarks Harbour the operational period was 6 months/year through the first half of the decade declining to 3 months/year in the period 1946-49 (Sharp, 1980).

The annual cycle of harvesting operations was related to biological and environmental conditions in only one respect. During the early part of the 1940s a significant portion of the harvest came from beach cast kelp. The volume of beach cast increases during the stormy winter months and is related to the loss rate of larger plants. This portion of the harvest was clearly related to environmental conditions.

6.2 Manpower productivity

The only data available are for the Clarks Harbour operation during the 1940s. According to Sharp (1980) 20 - 30 boats each with a 2 man crew worked on the harvest operations around Clarks Harbour. MacFarlane (1952) estimated the total area of kelp beds on the Cape Sable Island ledges around Clarks Harbour as 11,700 ha. The manpower requirements to maintain the operation were therefore 0.0034 - 0.0051 men/ha. The seasonal variation in manpower requirements is unknown.

In an experimental harvest using a dragrake method (see Section 7.1 below) Pringle and Sharp (1980) demonstrated an economic CPUE (catch/unit effort) limit of 1.2 t h^{-1}.

6.3 Alternate employment

During the 1940's kelp harvesting was done from lobster fishing boats. The lobster fishing season in southwestern Nova Scotia extends through the winter months and provides alternate seasonal employment for the fishermen. After 1945 the Irish Moss (Chondrus crispus) harvesting industry developed into a major alternate form of employment. The dominant seaweed industry in eastern Canada is now based on Irish Moss.

7. EQUIPMENT USED FOR HARVESTING OF SEAWEED RESOURCES

7.1 The wild resource
7.2 Seaweed culture
7.3 Sources of credit and insurance of the crop

7.1 The wild resource

The equipment used to harvest Laminaria longicruris has been described by Sharp (1980). During the first 3 years of commercial harvesting plants were cut with sickles or scythes at low tide, using grapnels and gathering storm tossed drift. The kelp buyer improved harvest technology by the introduction of a large dragrake **(Fig.** 16) with which deeper water populations could be accessed. The rake consisted of a 1.5 - 1.8 m length of oak furnished with steel rods 30 - 45 cm long, spaced 7.5 - 12.5 cm apart as tines. This equipment was draggad behind a wooden lobster boat (9.2 - 12.3 m in length). Two men handled the equipment.

Harvested kelp was taken by boat to two holding tanks at Clarks Harbour and at Dog Island in the Tusket Islands. The holding tanks had dimensions of 4.6 x 4.6 x 1.2 m and could hold 40 - 60 t of kelp. During the harvest season the kelp was transported from the holding tanks to Rockland, Maine (for processing) twice a week in a 29 m boat.

Each of the harvest boats could hold 10 - 12 t of kelp and some harvesters made two collecting trips a day. The harvesting rate was therefore about 10 t per man per day. The price paid by the buyer peaked at CAN$8.00/t. Therefore the gross income was about CAN$80.00 per man per day. During the peak years of harvesting 5-6000 t of kelp were cut each year in southwestern Nova Scotia.

Pringle and Sharp (1980) reported on an experimental harvest of kelp with dragrakes identical to those used in the 1940s. Ninety eight per cent of the harvest was Laminaria longicruris. The plants were mostly whole so that regrowth from intact meri-stems was precluded. In 1946 a mechanical harvester was developed **(Fig. 17).** There were numerous problems with this mowing device, but it is interesting to note that kelp bed regrowth was judged to be faster than after dragraking.

Figure 16. Kelp dragrake used in southwestern Nova Scotia. a- towing point (flat steel bar), b- rake tines (mild steel rod), c- main beam (hardwood), d- trip point (after Sharp, 1980).

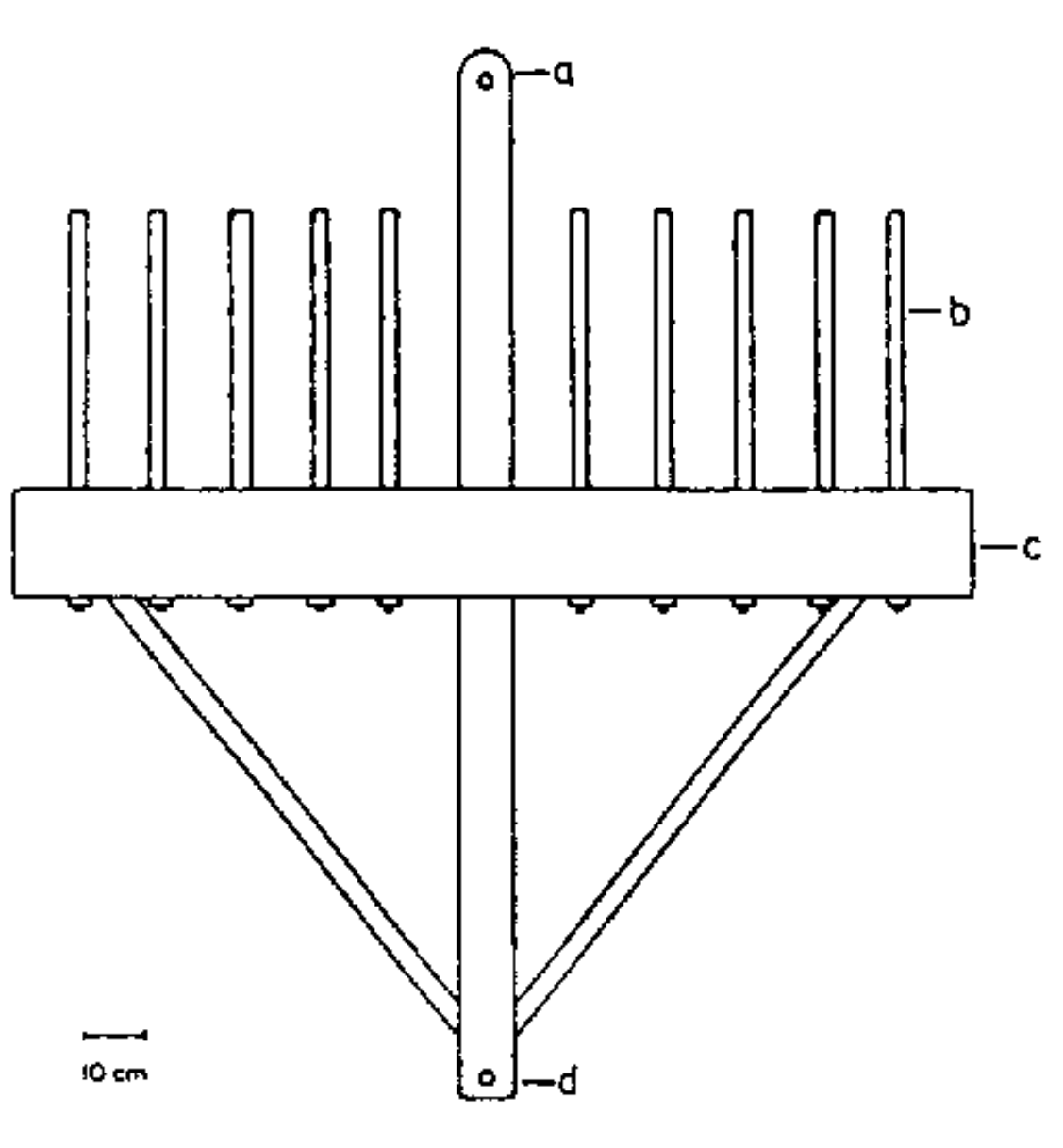
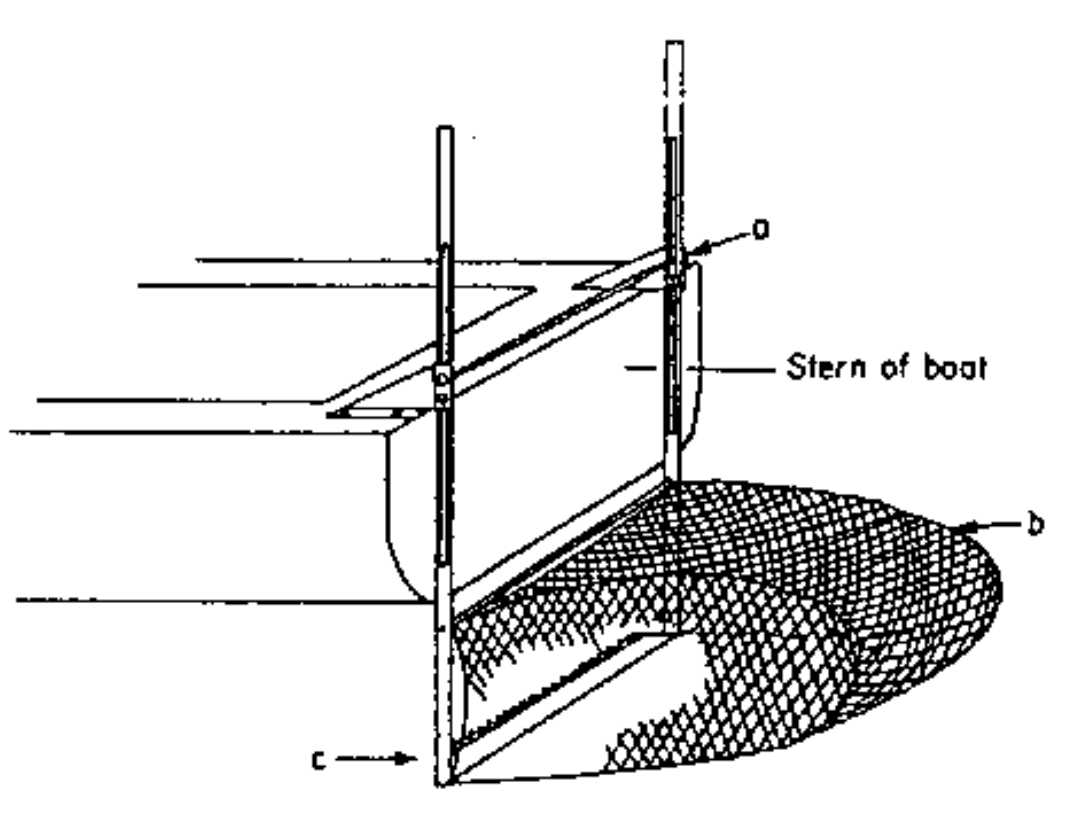


Figure 17. Mechanical harvester under development in 1946. a- spring loaded lifting device, b- removable net bag, c- mower blade chain driven from main engine (after Sharp, 1980).



The detailed economics of the 1940s kelp harvesting operation are unknown. According to Smith and Loucks (1980) the caloric advantage (caloric output [in cal/day]/caloric input [in cal/day]) of dragraking is 3 to 5. The caloric advantage of other harvesting methods are unknown, but cutting with sickles and scythes and collecting storm tossed drift are assumed to have high caloric advantages.

The plants harvested in the period 1940-49 were processed for alginate extraction in Rockland. Since 1949 there have been only minor harvests of 20 - 300 t per year and the product has been used mostly in the health food industry (kelp pills, kelp powder etc.). The technology of the later harvests was identical to that of the 1940s with similar catches per unit effort.

7.2 Seaweed culture

There is no aquaculture industry for Laminaria longicruris.

7.3 Sources of credit and insurance of the crop

Within Nova Scotia the major source of credit for the industry is through the provincial Fishermen's Loan Board. Insurance for boats only is provided by an insurance program operated by the Canadian Federal Department of Fisheries and Oceans (a division of Environment Canada). This insurance program is to be discontinued in 1986.

8. PROTECTION AND MANAGEMENT OF THE RESOURCE

8.1 Management of seaweed resources
8.2 Regulation of the harvest

8.1 Management of seaweed resources

Harvesting of Laminaria longicruris is restricted to two Canadian provinces, Nova Scotia and New Brunswick. The seaweed resource is managed in both provinces by the Department of Fisheries and Oceans, Environment Canada. This is the department of the Canadian federal government that is responsible for all marine biological resources. In addition to setting regulations of catch limits and techniques, the department conducts a research program into the effects of harvesting, not only on the seaweed resource, but also on associated fisheries (Pringle and Sharp, 1980)

The Canadian Department of Fisheries and Oceans interacts with the harvesting industry through a Marine Plants Advisory Committee. This committee has representatives from the industry, government and the academic communities. Members of the Department of Fisheries and Oceans also consult directly with the fishermen at local meetings arranged within the fishing communi-t ies.

8.2 Regulation of the harvest

The kelp harvest industry of 1940-49 was completely unregulated. Under present circumstances permits for harvesting are issued through the Canadian Department of Fisheries and Oceans. Because there is no viable ongoing kelp harvesting industry, permits are issued on an individual basis only. In 1979 the department issued an experimental permit for one boat with three crew members to harvest 1000 t of kelp using dragrakes.

All fisheries regulations governing marine resources of Canada are enforced by fisheries officers of the Department of Fisheries and Oceans. The officers may confiscate catches and equipment that contravene regulations.

9. UTILIZATION

9.1 Chemical and nutritional content
9.2 Human food
9.3 Animal fodder
9.4 Manure
9.5 Industrial products and processes

9.1 Chemical and nutritional content

There is information available on the carbohydrate composition/amino acid composition, polyphenolic content and total organic nitrogen content of the species.

The annual variations in laminaran and mannitol contents in a range of plant portions in various depths of water in St. Margaret's Bay are shown in **Fig. 18** (from Chapman and Craigie, 1978). The seasonal pattern for laminaran for this site was confirmed by Gagne and Mann (1981). In sites with enhanced seawater nitrate availability the laminaran content is reduced. At Centreville in the Bay of Fundy laminaran is undetectable throughout the year in L. longicruris (Gagne and Mann, 1981).

The annual variations in alginic acid and cellulose contents in a range of plant portions collected from St. Margaret's Bay are shown in **Fig. 19** (from unpublished data of A.R.O. Chapman). The data are given as per cent of alcohol extracted dry weight. Variations in total organic nitrogen of extracted dry weight for the same site are given in **Fig. 20** (from Chapman and Craigie, 1977). Fong (1978) measured seasonal variation in the amino acid composition of the species at Fox Point in the same Bay **(Table 8).**

In a study of anti-herbivore defenses in Laminaria longicruris Johnson (1984) measured the polyphenolic content of various tissue portions **(Fig. 21).** The highest concentration of polyphenols occurred in the meristem region in the transition zone between blade and stipe. This zone is the least subject to grazing by Lacuna vincta.

Figure 18. Seasonal variation in laminaran and mannitol content in 5 tissue sections from plants collected at 6, 9 and 18 m depth in Nova Scotia. Means for 5 plants are given (after Chapman and Craigie, 1978).

9.2 Human food

Since 1949 most of the kelp harvest in southwestern Nova Scotia has been used for human consumption. The largest recent harvest (1979) of about 300 t was sold as kombu for consumption in Korea. In addition, a small amount of material is used for the production of health food products (kelp pills, kelp powder).

9.3 Animal fodder

The harvest is not used for animal fodder.

Figure 19. Seasonal variation in alginate and cellulose content in various tissue portions of plants collected from St. Margaret's Bay, Nova Scotia. Means for 5 plants are given. From unpublished data of A.R.O. Chapman drafted by Johnson, 1984.

9.4 Manure

The harvest is not used for commercial crop plant fertilizer although tests on its usefulness in this role were done during the late 1970s (P. Brock, personal communication).

9.5 Industrial products and processes

The harvest of L. longicruris during the 1940s was organized by the Algin Corporation of America for the production of alginate (a cell wall carbohydrate). Alginate is used in a wide variety of industrial products. In the food industry it is used to increase viscosity or to stabilize emulsions (as in ice creams, canned soups etc.). In the textile industry it is used as a sizing agent. In addition, the product is used in the dental and pharmaceutical industries and in the production of coatings for high quality paper products.

Figure 20. Seasonal variations in total organic nitrogen content of 3 blade tissue portions in plants collected from St. Margaret's Bay. Means are from 5 plants (after Chapman and Craigie, 1977).

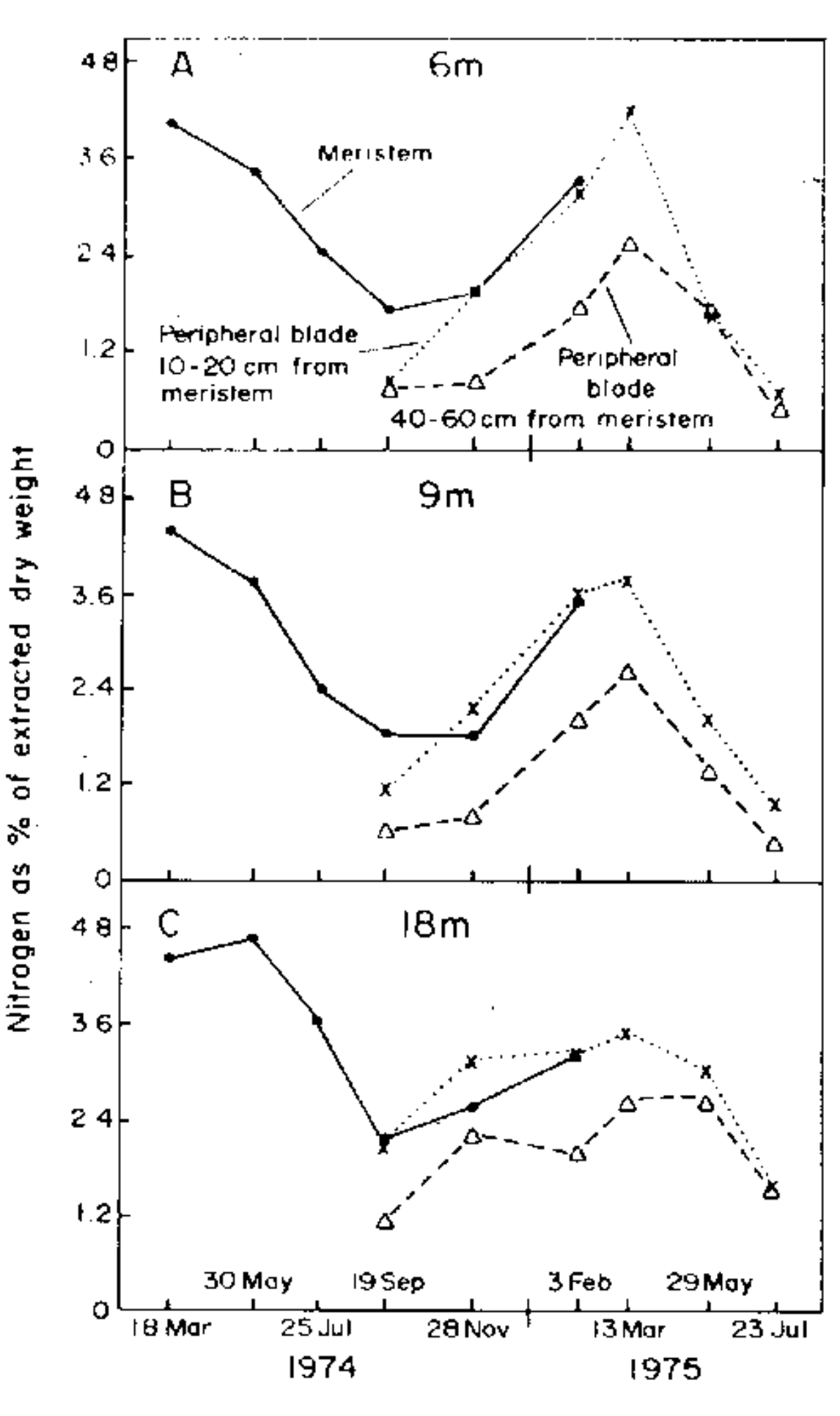
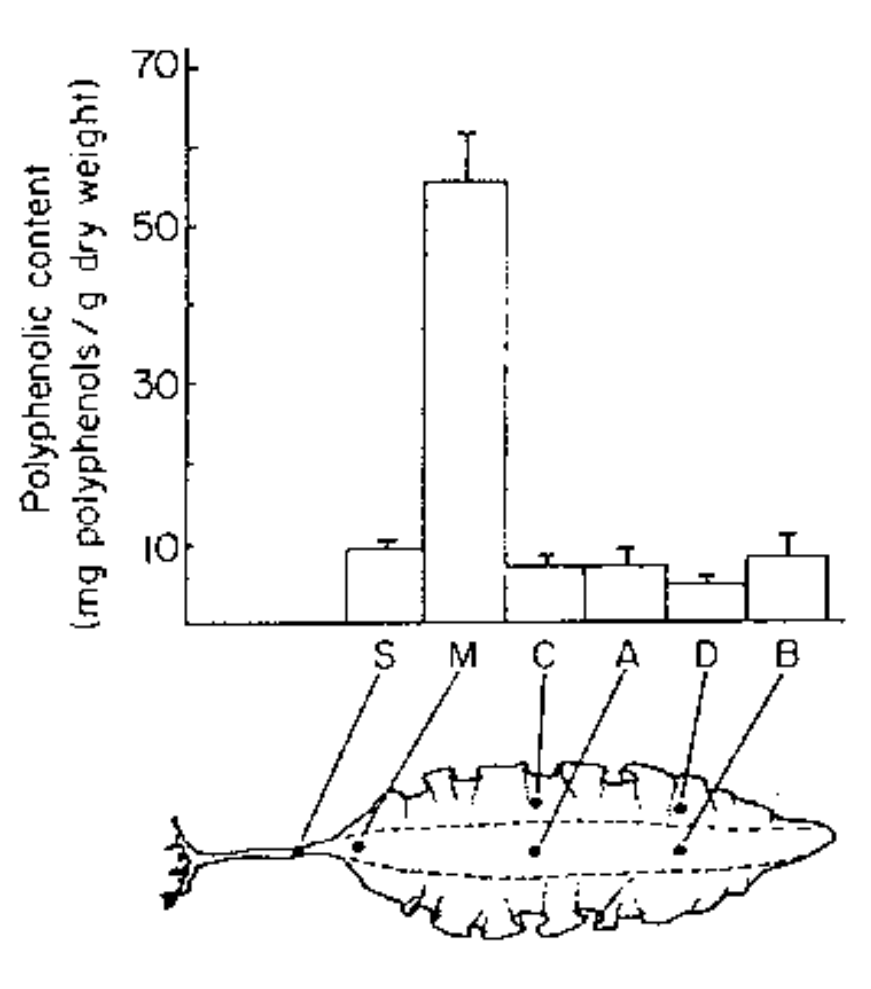


Table 8. Amino acid composition of Laminaria longicruris from St. Margaret's Bay, Nova Scotia. Values are means for 3 plants expressed as per cent by weight of total amino acid composition (after Fong, 1978).

Amino acid	April 1977	June 1977	August 1977	October 1977	December 1977	February 1978
ASP	10.07	12.99	10.39	10.44	11.01	12.95
THR	4.44	4.38	3.86	4.33	4.68	4.96
SER	3.05	2.45	2.40	2.53	3.03	3.14
GLU	24.86	30.23	27.66	32.17	27.16	20.51
PRO	9.90	9.22	5.95	4.52	5.78	6.20
GLY	3.25	4.68	5.06	5.40	4.69	4.48
ALA	19.54	9.49	7.28	9.91	13.48	16.15
VAL	2.92	3.05	3.42	4.11	3.81	4.06
MET	0.56	0.68	1.18	0.76	0.93	0.69
ILE	1.94	2.97	3.93	3.36	3.72	3.84
LEU	3.68	4.39	8.33	6.25	6.51	6.18
TYR	1.72	2.37	3.96	3.12	3.18	2.79
PHE	2.71	2.77	5.69	4.07	3.53	4.34
LYS	5.69	5.08	5.21	4.01	4.03	4.81
HIS	0.12	0.11	0.16	0.29	0.14	0.13
ARG	5.37	5.16	5.54	4.74	4.33	4.77

Figure 21. Polyphenolic content of various plant portions (after Johnson, 1984).



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Laminaria mariculture in China

1. IDENTITY
2. LIFE HISTORY
3. MARICULTURAL PRACTICE
4. GENETIC IMPROVEMENT AND BREEDING OF NEW STRAINS
5. HARVESTING, PROCESSING AND PRODUCTION
6. UTILIZATION AND MARKETING OF THE CROP
7. REFERENCES

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ABSTRACT

Laminaria is not a native of Chinese shores though it has been a well-known food commodity on the Chinese market for more than one thousand years. It was first imported to China from Korea and later from Japan in large quantities (Tseng 1958, 1981a,b). In 1927 Laminaria was accidentally introduced to Dalian (Dairen), Liaoning Province, in the North Huanghai Sea. From then until 1952, wild and semi-wild Laminaria growing on natural rocks was harvested commercially with the largest annual output being 40.3 tons of the dry product in 1949 (Tseng, 1981a,b). Mariculture of Laminaria on artificial floating rafts started in 1952 and commercial production increased steadily until 1980 when the peak production of 252,907 tons of the dry product was produced (Tseng, 1981a,b; Zeng [=Tseng], 1984).

1. IDENTITY

1.1 Crop history and nomenclature
1.2 Taxonomy
1.3 Morphology and anatomy

1.1 Crop history and nomenclature

Laminaria has been known in China, first, as kunbu (meaning "large cloth") and, more recently, as haidai (meaning "sea ribbon"). According to Chinese literature, more than one thousand years ago, Chinese herbal doctors found that a seaweed under the name kunbu growing on the East China Sea coast had a curative effect on goiter. This has been shown by Tseng and Chang (1961) to have been Ecklonia kurome. It was later discovered that another seaweed, a Laminaria growing on the eastern Korean coast, also had a similar function, and so a large quantity of the dried seaweed was imported to China from Korea under the same name, kunbu. This name was evidently broadly employed for large brown seaweeds having the property of curing goiter. Later it was found that Laminaria grows in even much larger quantities in Japan, which eventually became the most important exporter of kunbu, called kombu by the Japanese (Tseng and Chang, 1961).

A few hundred years ago the name haidai was introduced to refer to this seaweed which the Chinese imported from Japan and Korea. Nowadays, this Laminaria is popularly known in China as haidai and this name has been adopted as the official commercial name for this seaweed. The name kunbu, used for many hundreds of years for both Ecklonia and Laminaria, is no longer employed for Laminaria, but rather is restricted to Ecklonia, at least, in Fujian Province (Tseng and Chang, 1961).

Thus Laminaria has come to be known in China as haidai and in Japan as kombu. Internationally, "kelp" is a widely used name for Laminaria. The term "kelp" was applied originally a few hundred years ago to the ash of laminariaceous algae used for the extraction of soda and potash. In the early part of the present century, American scientists seeking sources of potash began to call other seaweeds belonging to the Laminaria group, including Macrocystis pyrifera, kelps. Nowadays, Macrocystis is well known as "giant kelp", Nereocystis as "bladder kelp" and Laminaria as "kelps". For the different species of commercial Laminaria, the use of an adjective before the word "kelp" is suggested, for instance, "Japanese kelp" for Laminaria japonica and "sugar kelp" for L. succharina, etc.

1.2 Taxonomy

In and before the early fifties, when large quantities of Laminaria were still imported into China from Japan, the haidai or Japanese kelp on Chinese markets was principally Laminaria japonica mixed with various other species of Laminaria. In the early fifties we analyzed haidai on the markets in different places in China and, besides L. japonica, found a significant admixture of L. angustata. There has been quite a controversy among Japanese phycologists on the taxonomy of the Japanese Laminaria, especially concerning L. japonica and the related species L. ochotensis, L. diabolica and L. fragilis. These are treated as independent species by Miyabe (1957). The group of phycologists headed by Hasegawa (1963) considered them to be merely varieties of the same species under the first name applied, L. japonica, as follows:

L. japonica var. japonica (L. japonica and L. fragilis)
L. japonica var. ochotensis (L. ochotensis)
L. japonica var. diabolica (L. diabolica)

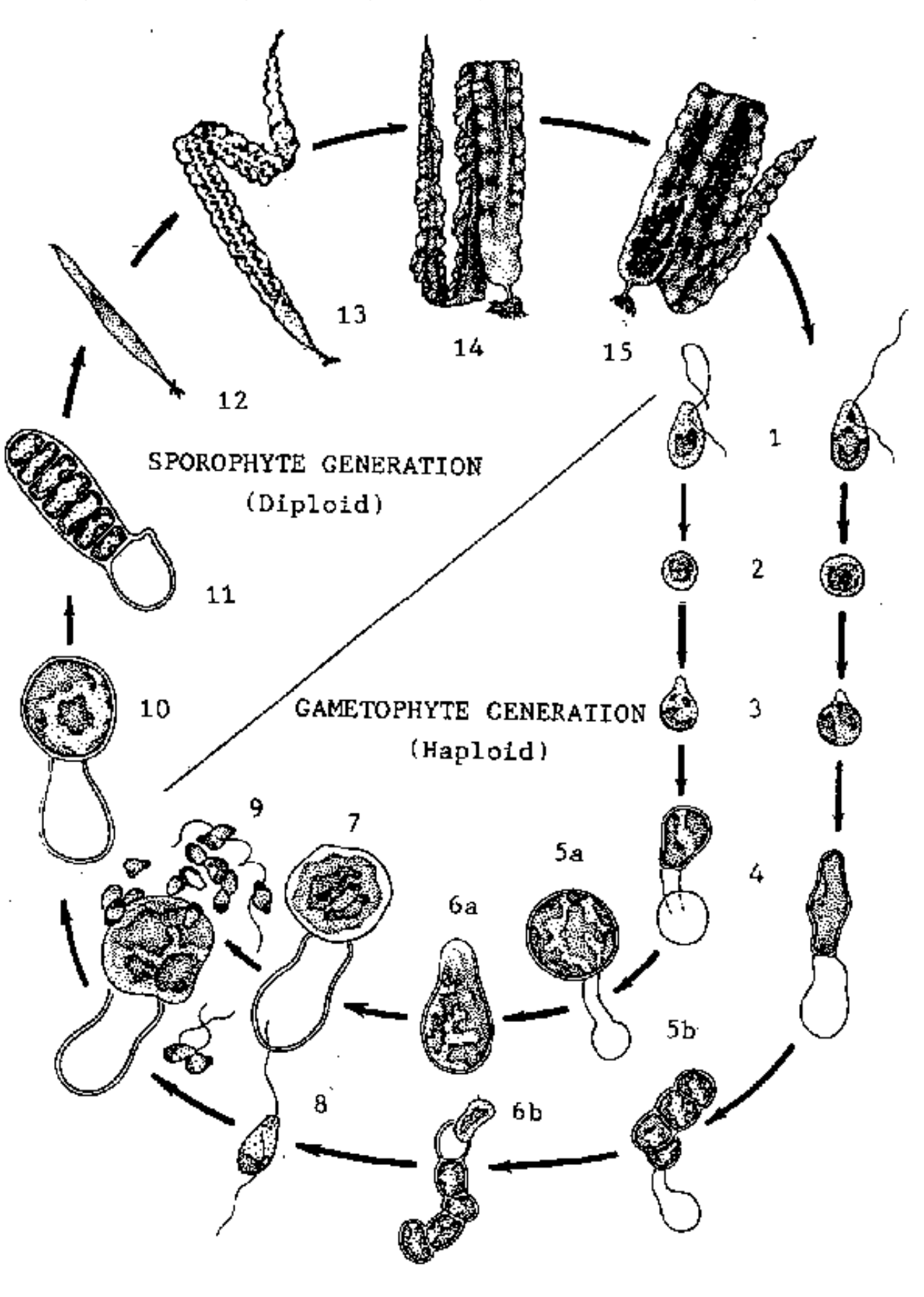
Even L. religiosa may belong to the same species complex. The more we work with the haidai in China, which was transplanted to China from Japan more than half a century ago, the more we come to believe that these "species" are nothing but variants of the same taxon growing under different ecological conditions. It may perhaps be better to treat them as ecological variants. The Chinese haidai now under cultivation is closer to L. japonica var. japonica, but in earlier stages of development it resembles more closely L. japonica var. ochotensis with forms resembling L. japonica var. diabolica also occasionally being found (Tseng and Wu, 1962; Zeng [=Tseng], 1984).

1.3 Morphology and anatomy

The Chinese haidai is a typical laminariaceous seaweed consisting of an elongated simple broad rich-brown, strap-like frond provided with a cylindrical or subcylindrical stipe attached to the substratum by a profusely branched rhizoidal holdfast. The strap-like frond is generally called the "blade". There are two shallow channels in the central parts of the blade forming a central strap portion. This is especially clear-cut in the first year. The concave surface faces outward toward the light and the convex surface inward. The central portion is thicker, and the lateral part thinner, appearing somewhat wavy. When young, this Laminaria has a leafy frond with a strongly cuneate base reminding one of Laminaria ochotensis. When mature, the leafy frond attains a length of 2-6 m, varying from 2 m or less in the Xiamen region in the south to 6 m or more in the Dalian region in the north, and a breadth of 35-50 centimeters. The thallus has a stipe 5-6 cm long and the broad base typical of L. japonica. In its original habitat in Hokkaido, the typical life span of this Laminaria is three years, but in the cultivated forms it is only two years. However under farmed conditions it is actually grown in the sea for only 8 months (Hasegawa, 1963; Miyabe, 1957; Tseng, 1958, 1981a,b).

Morphologically, as seen in the field or by the unaided eye, four different stages may be differentiated: (1) the sporeling stage, (2) the young sporophyte stage, (3) the robust sporophyte stage and (4) the mature sporophyte stage **(Fig. 1: 12-15).**

Figure 1. Life history of Laminaria japonica under cultivation. 1. Zoospore; 2. Embryospore; 3. Germination of embryospore; 4. Gametophyte just formed; 5a. Female gameto-phyte; 5b. Male gametophyte; 6a. Mature oogonium; 6b. Discharging spermatozoid; 7. Egg on empty oogonium; 8. Sperma-tozoid; 9. Fertilization; 10. Zygote; 11. 7-celled spore-ling; 12. Sporeling; 13. Young sporophyte; 14. Robust sporo-phyte, and 15. Mature sporophyte with sporangial sori.



The first stage, the young sporeling stage, includes the time from the germination of the zygotes to sporelings of 5-10 centimeters. The sporelings are at first monostromatic but before reaching about 1 mm in length they become multistromatic, with all cells remaining meristematic, though later differentiating into blade and stipe. Further differentiation results in the formation of a meristematic growth region between the stipe and the blade. This takes place when the sporelings are about 5 or more cm long.

In the present system of cultivation in China, the first or sporeling stage is grown in two totally different environments. The state from the zygote to sporelings of a few mm to 2-3 cm long or even more are reared in a sporeling-culture house (a "glasshouse" or "greenhouse") with the culture solution cooled to about 8-10°C **(Fig. 1:11,12).** In mid-October when the seawater temperature (in Qingdao) drops to about 20°C, the strings on which the sporelings are growing are taken outdoors and cultivated in the sea under natural conditions **(Fig. 1:12).**

The differentiation of the basal meristem of the frond marks the beginning of the second stage, the young sporophyte stage, characterized morphologically by the cuneate bases of the strongly bullate fronds, which are rather thin and brittle. They grow very rapidly in length and fresh weight. In November-December the Chinese transplant the young sporophytes with the meristematic region well differentiated to regular cultivation rafts. Within a few months, by early spring in the Qingdao region, they may reach a length of 3 or more meters. The bulla-tions of the blade gradually disappear as growth advances. This stage occurs during the period when the water temperature gradually drops from about 15°C to the winter minimum of 1-2°C in February and rises to about 13°C in mid to late spring, a period of about 5 months **(Fig. 1:13).**

When the bullations of the blades have entirely disappeared and the blades have become smooth, flat on the surface, and leathery in substance, with the base of the fronds being roundish instead of cuneate in shape, the sporophytes have reached the robust sporophyte stage, the third stage of their growth and development. In this stage growth of the sporophytes in length practically stops; there may even be a decrease in length due to natural shedding of the tips, but growth in thickness and in dry weight continues **(Fig. 1:14).**

With further growth of the sporophytes in the robust stage, the blades become increasingly thicker, their bases more broadly roundish, their substance more leathery and, in May to June, depending upon the light conditions, sporangial sori in small roundish patches begin to appear in the upper part of the frond. Thus the sporophytes have arrived at the fourth stage, the mature sporophyte or sporulating mature stage. In late June to early July when the seawater temperature reaches 20°C and higher, the formation of sporangial sori stops.

Anatomically the blade is composed of three basic structures, the epidermis, the dermal tissue and the pith. The epidermis constitutes the outermost tissue of small epidermal cells arranged in a palisade, squarish in transverse section and elongated in longitudinal section, and with ellipsoidal chromato-phores concentrating in the outer portion. Inside the epidermis is a layer of dermal tissue which may be differentiated into two sub-tissues, an ectodermis of comparatively smaller cells and an endodermis of larger ones. Both sub-tissues are composed of elongated subcylindrical cells, and those of the former are more regularly arranged. The pith is composed of pith cells and trumpet cells, both remarkably smaller than the cells of the endodermis **(Fig. 2: A1-4).** Pith cells are ordinary cylindrical cells but trumpet cells are very much elongated, attaching to each other terminally with their apposed end walls a large circular dish, the sieve plate **(Fig. 2:B5),** bearing numerous punctate holes. Muscilage glands are distributed here and there in the endodermis, stipes and holdfasts **(Fig. 2:C).**

2. LIFE HISTORY

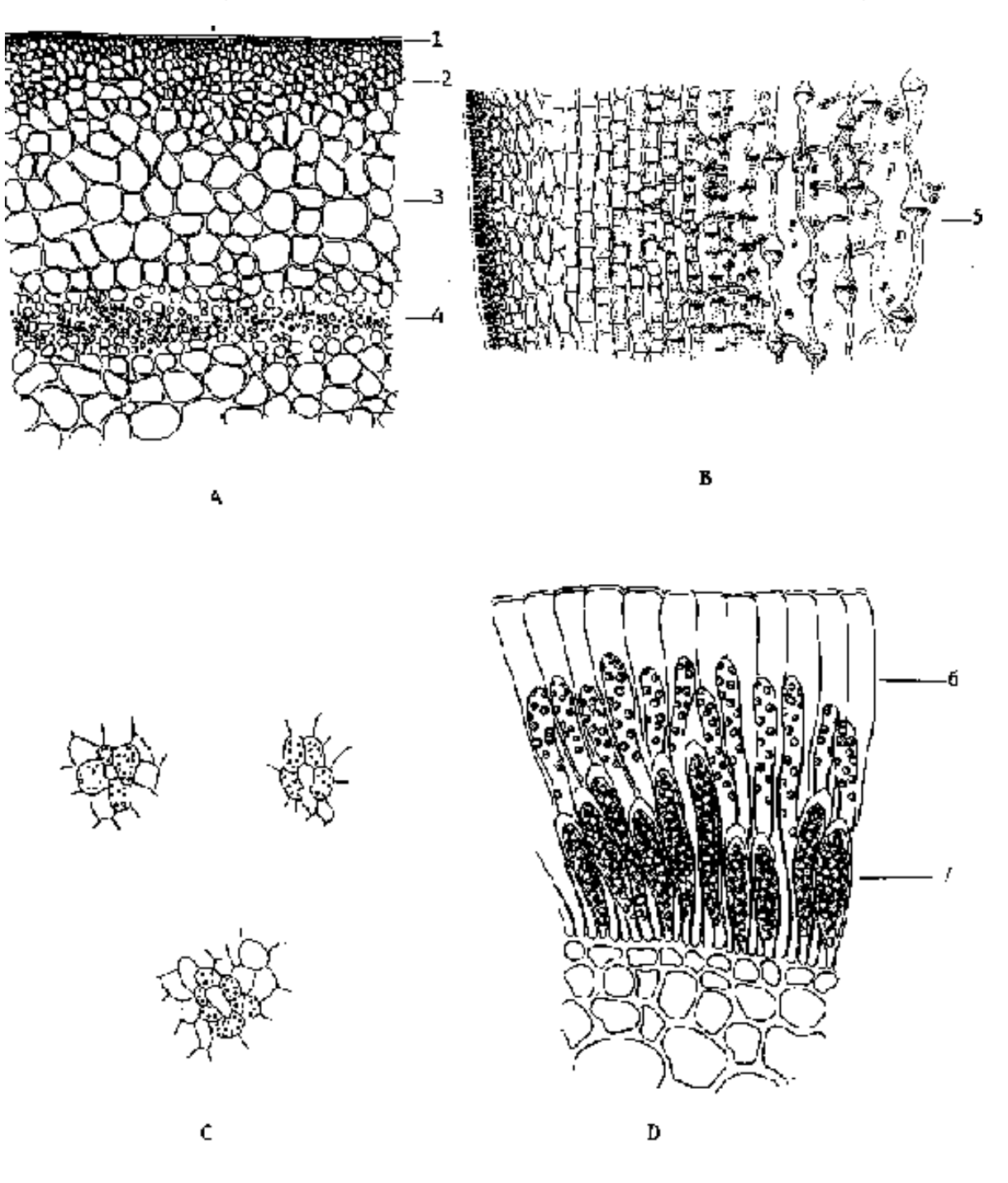
2.1 The sporophyte generation
2.2 The gametophyte generation

Many reports on the life history (See **Fig. 1)** of Laminaria have been published. Although in general they are similar, they differ in detail, especially in the relationship with environmental factors such as temperature. In our investigation of Laminaria japonica under commercial cultivation in China, we have noted differences from previously published reports and have found certain characteristics peculiar to the Chinese strain. Evidently Laminaria japonica, transplanted from Hokkaido and northern Honshu to Dalian several times since 1927, has undergone continuous hybridization and adaptation to its new environment in Dalian, and has formed a new strain genetically different in some respects from the Japanese stock.

2.1 The sporophyte generation

As mentioned above, the sporophyte generation may be subdivided into four different morphological stages. In the mature stage, sporangial sori are found in the terminal portions of the fronds. A cross section of a mature frond shows that the sporangia grow outward from the endodermis and are scattered among paraphyses having gelatinous sheaths **(Fig. 2:D).** Reduction division occurs in the first division of the spore mother cell divisions, and altogether 32 zoospores are produced per sporangium. For the morphology and anatomy of the sporophyte, please refer to Section 1.3.

Figure 2. Sections of fronds. A. Transverse section of blade, showing (1) epidermis, (2) ectodermis, (3) endodermis and (4) pith. B. Longitudinal section of blade, showing (5) trumpet cells. C. Three gland cells. D. Transverse section of blade showing (6) paraphyses and (7) sporangia.



2.2 The gametophyte generation

The haploid zoospores are pear-shaped, about 6-8 urn long and 4-6 m m broad with two lateral unequal flagella, the longer one about 18-20 m m long, directed forward and the shorter one 7-8 m m long **(Fig. 1:1).** Within about 2 hours after liberation from the zoosporangia, most of the zoospores adhere to the substrate. The time needed for the zoospores to adhere depends, however, on the temperature. At 15-20°C, zoospores will adhere in 5-10 minutes, while at 5°C, they may continue swimming actively for 48 hours before adherence. Soon afterwards the zoospores are transformed into embryo-spores which remain naked with only a cytoplasmic membrane **(Fig. 1:2).** In about 4 hours, the embryospores give rise each to a germination tube 19-33 m m long **(Pig. 1:3),** and within 2-3 days the entire cell content flows to its apex, which becomes spherical with a cell wall, thus becoming the initial cell of the gametophyte **(Fig. 1:4).**

The initial cells of the gametophytes are similar to or slightly smaller than the zoospores; otherwise there is practically no difference between the cells of the male and of the female gametophytes. Soon, however, the difference begins to appear. In the case of some gametophytes, cells start to lengthen and divide, and in the case of others there is no such vegetative division. The former become multicellular, eventually with 7 or 8 to as many as 17 or 18 cells in about 6 days. These cells remain similar in size to the initial cells, i.e., 4-8 m m in diameter. These are the male gametophytes **(Fig. 1:5b).** Those spores that remain unicellular grow to 11-22 m m in diameter and are female gametophytes **(Fig. 1:5a).** Vegetative growth of both kinds of gametophytes takes place in about 6 days under the culture conditions normally used.

Development of the gametophytes takes place during the following 2-3 days. In the male gametophytes, each of the apical cells forms a small protrusion with a thinner cell wall and becomes a spermatangium **(Fig. 1:6b).** The single cell of the female gametophyte is directly transformed into an oogonium **(Fig. 1:6a).** Our experiments showed that, for the liberation of the male and female gametes as well as fertilization, a short period of darkness is necessary (Tseng, Ren and Wu, 1959). The egg will first protrude from the oogonium and sit on the empty oogonial cell wall **(Fig. 1:7).** Very soon afterwards spermatozoids in the vicinity break through the thin-walled spermatangium and each spermatangium liberates one spermatozoid **(Fig. 1:8).** Numerous spermatozoids are attracted to any protruded egg **(Fig 1:9),** and soon swim to and surround it. Eventually one of the spermatozoids succeeds in entering the naked egg, which immediately forms a cell wall over its surface. Fusion of the male and female nuclei results in the formation of the zygote. Thus, under the most favourable conditions, it takes only 10-12 days for the gametophyte generation to pass through three stages of growth and development from the liberation of the zoospores to the formation of zygotes. This includes 2-3 days for the stage of gametophyte formation, 6 days for its vegetative growth stage and 2-3 days for its differentiation stage and the resulting zygotes, the latter starting the diploid sporophyte generation of the life cycle **(Fig. 1:10).**

In the present system of Japanese kelp cultivation in China, the entire process from the adherence of the liberated zoospores to the sporeling cords to the formation of the zygotes, all takes place in a sporeling- culture house with controlled environment.

Under natural conditions, it will take twice or even three times the time for the completion of the entire process, namely, from zoospore to zygote.

3. MARICULTURAL PRACTICE

3.1 Floating raft mariculture
3.2 Culture of summer sporelings
3.3 Fertilizing kelps in the open sea
3.4 Southward extension of commercial cultivation
3.5 The tip-cutting practice
3.6 Environmental and pathogenic diseases

3.1 Floating raft mariculture

Development of the kelp production from the maximal pre-1950 annual output of 40.3 tons (dry) in 1949 to 6253.3 tons in 1958 shows **(Table 1)** an increase of 155 times within a few years. The large increase in production was made possible by the introduction of artificial substrata constructed of floated lines in raft form for the growth of the kelp. Perhaps for historical reasons these floated line systems are referred to as rafts.

Table 1. Comparison between natural substratum (rock) and artificial substratum (palm rope) production of the kelp (Laminaria japonica) in China, 1946-1958 (in tons dry wt.)*

Year	Production on sub- substratum (sub tidal rocks)	Production on artificial substratum (Palm ropes)	Total	Artificial sub-stratum culture as percentage of total production
1946	24.5			
1947	17.3			
1948	20.0			
1949	40.3			
1950	0.7			
1951	-			
1952	12.0	10.3	22. 3	46.4
1953	86.5	28.2	114. 7	24.5
1954	251.2	78.7	254.8	30.9
1955	321.8	206.0	527.8	39.0
1956	167.7	391.7	559.3	70.0
1957	580.8	1439.3	2020.2	71.3
1958	986.2	5267.3	6253.3	84.2

*Based on data in Zeng (Tseng) 1984, original figures in fresh weight converted to dry weight by a factor of 1/6.

The floating rafts now in use in China evolved from simple square bamboo frameworks with one piece of bamboo about one meter or less in length on each side, tied together with ropes. Inside the framework two ropes were diagonally tied to the frame. The raft was then anchored to the sea bottom by two anchor ropes and was intended originally as a means of preserving seaweeds following harvest.

The first successful raft cultivation experiment used floating rafts made of palm ropes as the artificial substratum for the growth of the kelp, palm rope in the beginning but nowadays synthetic rope. Thus, natural substrata such as rocks are no longer necessary and cultivation can be effected anywhere even in places without rocks but with a mud-sand bottom.

The method is characterized by four important processes. The first is collecting of the zoospores on rope, which is equivalent to the sowing of the seeds in land crop farming. To do this a Laminaria frond with mature sporangial sori is subjected to partial drying in the air and then placed in a small body of sea water in a container. The liberated zoospores will soon attach themselves to the substratum, the seeding cords, which are placed in the water beforehand. The second process is the setting up of the sporeling floating raft **(Figure 3)** for the cultivation with the seeding cords hanging beneath the floating ropes in the sea. The third process is sporeling transplantation, which is equivalent to the transplanting of rice seedlings in rice farming. This is a crucial process ensuring appropriate density for the growth of the kelp fronds. In the spore collection process, the zoospores attach to the seeding cords randomly and generally in great density, and if the resulting sporelings are allowed to grow in this manner, the growth would be too dense, and the resulting plants small and thin. Therefore when the sporelings reach 10-15 cm in height, it is necessary to detach them from the seeding cords and twist them onto coarser cultivation ropes, the kelp ropes. The fourth process is the cultivation and tending of the sporelings in normal rafts beneath the floating ropes. The floats were formerly elongated bamboo, but now are mostly glass balls (Tseng, 1958, 1981a, 1981b, 1982).

At first autumn sporelings were used but later summer sporelings/a discussion of this point will follow. The four processes together form the culturing program of a kelp farmer.

The employment of floating raft cultivation technique has been a major key to the success and development of the Chinese kelp industry. When the floating raft method was first introduced/many mariculturists were still in favour of the so-called sea-bottom cultivation on natural rocks and stones. The first time in the history of mariculture that kelp was commercially cultivated and harvested on artificial substrata in the form of floating rafts about 10 tons of dry kelp was harvested. Up to 1955 production on sea-bottom rocks was still leading, being 3,218 tons against 206 tons for the raft culture. In 1956 raft culture production began to lead, being 319.7 tons against 167.7 tons produced by sea bottom growth, and in 1958 raft culture produced 5267.3 tons against 986.2 tons by sea bottom culture **(Table 1),** thus proving definitely the superiority of raft culture as a mariculture method. Since then cultivation on natural rocks on the sea bottom has been abandoned as a method for commercial seaweed cultivation. Nowadays, the floating line systems for commercial cultivation of kelps and other organisms have become elaborate structures. Many kinds are now in use; almost every locality has its own special type to fit its particular environmental conditions.

I. Hanging Kelp Rope Cultivation Method

Figure 3a. Two basic floated line, or raft, kelp cultivation methods, I and II. - a) Single line hanging kelp rope cultivation method.

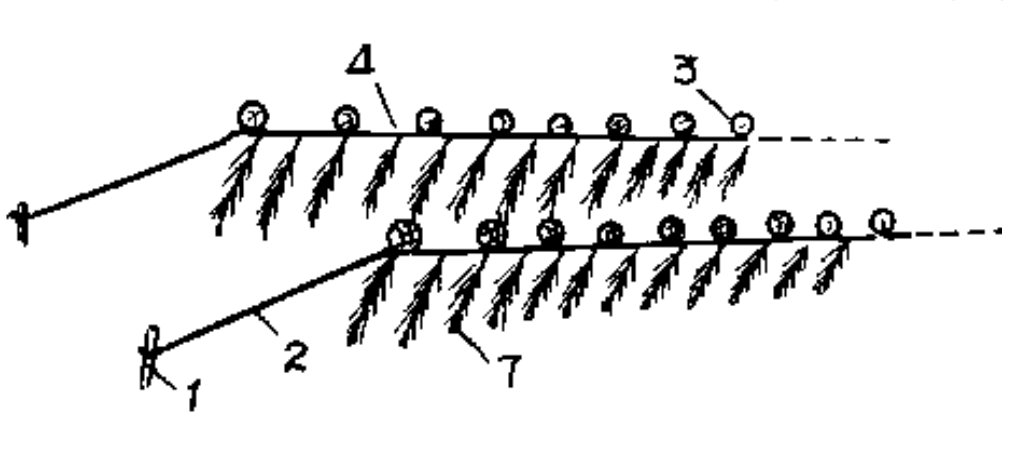
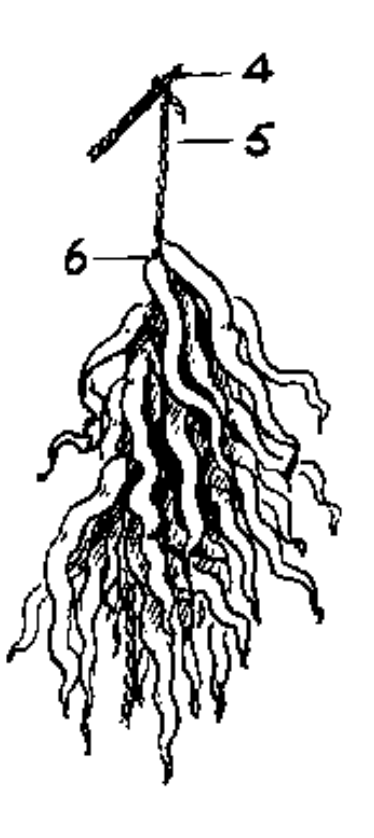


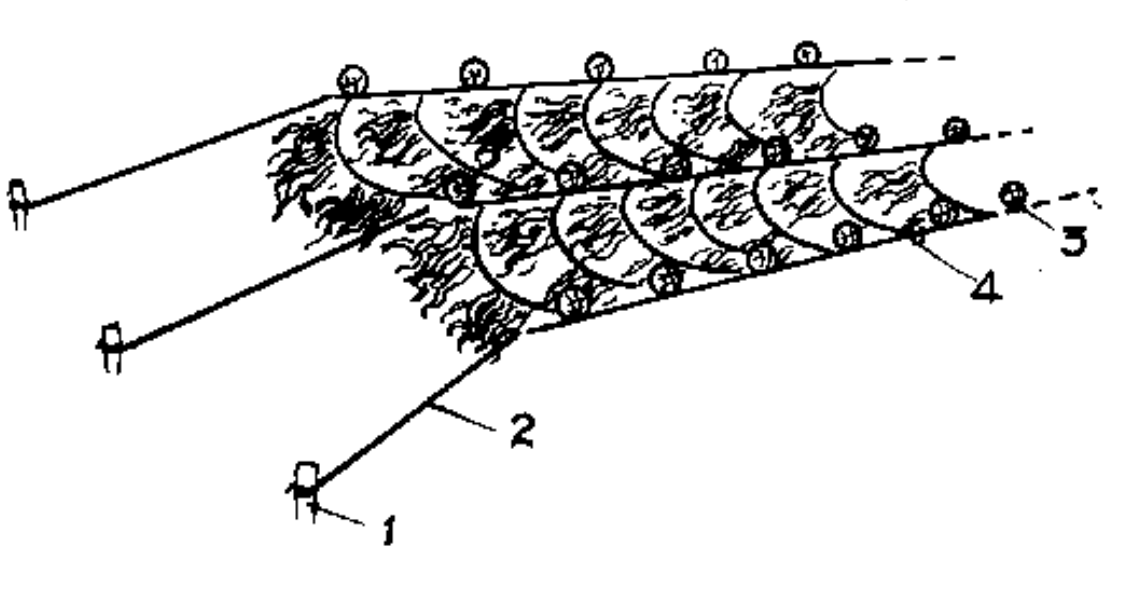
Figure 3b. Two basic floated line, or raft, kelp cultivation methods, I and II. - b) A hanging kelp rope with kelps.



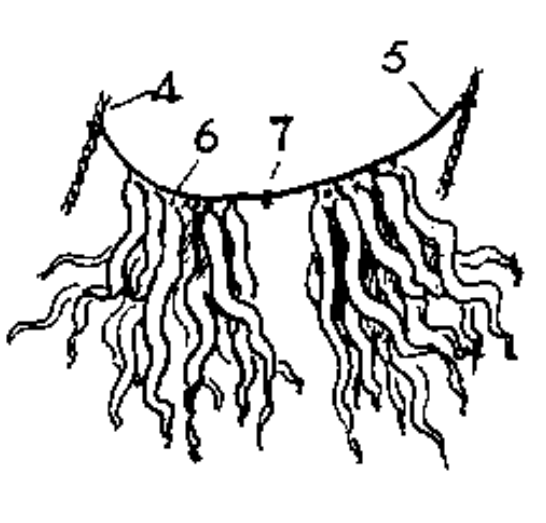
1. Wooden peg (anchor) 2. Anchor line
3. Float (glass) 4. Floating line
5. Kelp rope 6. Kelp 7. Weight

II. Horizontal Kelp Rope Cultivation Method

a) Figure 3c. Two basic floated line, or raft, kelp cultivation methods, I and II. - "Double line" floating rafts for the horizontal kelp rope cultivation method.



b) Figure 3d. Two basic floated line, or raft, kelp cultivation methods, I and II. - A pair of horizontally-linked kelp ropes with kelps.



1. Wooden peg (anchor) 2. Anchor line 3. Float (glass)
4. Floating line 5. Connected kelp ropes 6. Kelp
7. Link or knot

There are at present two basic variations in the floating rafts, the hanging rope and the horizontal rope forms I and II, respectively, in **Figure 3.** The former is characterized by its solitary lines, generally abbreviated as "single-raft" type; the latter is generally referred to as the "double-raft" type though sometimes even three or more rafts are tied together.

The "single-rope" or "hanging kelp rope" cultivation method has a large-diameter, more or less horizontal, line about 60 meters long floated at the surface **(Figure 3-Ia)** by buoys generally made of glass and anchored terminally by anchoring lines tied to wooden pegs driven into the sea bottom. The line is a large diameter rope. Hanging down from such floating lines are numerous kelp ropes, each about 50 cm long and weighted down by a small piece of stone or some other weighting material. To each kelp rope, in turn, are fastened the kelp. Each kelp rope in the Qingdao region has about thirty kelps twisted in it and is about 2 meters in length **(Fig. 3-Ib).**

The "double-raft" or "horizontal line" cultivation method has parallel pairs of kelp ropes **(Fig. 3-II)** instead of the solitary pendent kelp ropes of the "single-raft". The only difference being that the kelp ropes opposite each other in position on the parallel lines are linked or tied to each other, each pair of kelp ropes thus forming one horizontally placed floating kelp rope **(Fig. 3-IIb)** double the length of one of the solitary hanging kelp ropes. To keep the kelp ropes relatively near the surface, the long floating lines should be kept at least 5 meters apart. In order to economize on such floating lines, one may use three lines to support two rows of horizontally placed double length kelp ropes and in this case **(Fig. 3-IIa)** the middle line serves the function of two single lines.

The hanging kelp rope method has the advantage of better water movement and better utilization of the sea but has the defect of uneven growth of the kelps, since the uppermost kelps receive more and the lowermost kelps less light. The "double-raft" method has the benefit of more even growth of the kelps which, growing more or less in the same plane, receive similar light intensities. However, it has the defect of being more resistant to water motion and thus decreases it. Generally speaking, the "single-raft" method is better adapted to comparatively clearer water regions, and the "double-raft" method to turbid regions with lower water transparency; such as the Zhejiang coast near the Changjiang estuaries.

The floating raft method of kelp mariculture is one of the important reasons for the success of the kelp cultivation industry in China. The superiority of the method lies in the fact that it maintains the cultivated kelp at the water level selected as best suited for the growth of the kelp at each specific stage of growth and development. For instance in the Huanghai Sea coastal region; seawater is not as clear as in the original "home" of the Laminaria in Hokkaido and northern Honshu; therefore a series of experiments was carried on to determine which water level would be most suitable for the growth of this Japanese kelp. In the Qingdao region it was found that the kelp grows best two to three meters below the sea surface. When branchlets of the Kuroshio current approach this area and the sea water becomes much clearer in late spring, the kelp ropes are lowered half a meter to one meter to avoid the too strong light. On the East China coast, the sea water is very turbid and the water transparency very low; and the kelp has to be kept practically at the water surface to obtain optimal growth.

3.2 Culture of summer sporelings

There are two seasons for the production of sporangial sori, early summer and mid autumn. For the first few years up to 1956, the kelp spores were collected on sporeling cords in the autumn (mid-October in Qingdao) when the water temperature got down to about 26 degrees Centigrade. The kelp fronds therefore over-summered between July and October, since summer water temperature in the Huanghai Sea got to about 27°C which is intolerable for the Japanese kelp. For oversummering the kelp, fronds had to be moved to deeper waters, i.e., 10 or more meters below the surface. During the summer, typhoons occasionally come to Qingdao, and when they do, most of the submerged rafts with the kelps are destroyed. Loss may amount to about 90 percent. Besides, summer is the time that animals and plants, especially the barnacles, grow luxuriantly and before spores could be collected in autumn the barnacles had to be scraped away mechanically. Moreover, autumn is the season when Ectocarpus, Enteromorpha and other wild seaweeds shed their spores, and as soon as the seedling cords with collected spores were lowered in the sea, the spores of wild seaweeds would attach to them, germinate and grow readily and eventually cover the seedling cords entirely. The collected spores of the kelp generally need about 20 days to develop to seedlings of a few cells and since they had no light, they were unable to grow until about two months later when the wild weeds became mature, set off spores and died. Thus there would be a delay of about two months. The seedlings would not be large enough until late January to early February, which is the coldest season in the year. Then the seawater temperature is about 1°C and transplantation is very difficult work.

In working with summer sporelings, the difficulty is the high water temperature of those months, but by providing seawater artificially cooled down to 8-10°C, the collected spores would have a healthy environment in which to germinate and grow without the interference of wild weeds. Experiments proved the superiority of this method, with an increase of production by 30-50 percent. Labor conditions were greatly improved by transplanting the sporelings in late November or early December, when the seawater temperature was about 10°C (Tseng, Sun and Wu, 1956: Tseng, 1981b, Zeng, 1984). In the initial stage of the development of summer sporeling culturing, fluorescent lamps were used for lighting and the room was cooled to 8-10°C (Tseng, Sun and Wu, 1955a). In later improved systems a glass house ("greenhouse") was employed with natural light and fertilized sea water similarly cooled to 8-10° Centigrade.

The summer sporeling culture glass house is a standard glass house. Other than the water being cooled, if there is anything special it is perhaps in the construction of a series of shallow concrete tanks within it. In one case the paired tanks are about 12 m long, 2.4 m broad and 20-30 cm in depth, with one 20-30 cm higher than the other so that sea water can flow from one tank to the other under gravity.

In the Chinese method of kelp cultivation, collection of the zoospores on the sporeling cords should be effected at a temperature below 20°C., and the sporeling cords should be cultured in fertilized seawater cooled down to 8-10° Centigrade.

Sporeling cords are intertwined into a sort of framework for collecting the spores. After spore collection the frames with their collected spores are placed in a tank in the glass house with running cooled water enriched with nitrogen and phosphate fertilizers. The frames and the tanks differ from place to place but the principle is the same. In one case the sporeling frames are made of repeatedly intertwined palm cords. The sporeling frames are about 1.2 m long and 50 cm broad, so that two rows each with 30 frames can be placed in one tank. In each of the tanks there are four supporting ropes strung under water and parallel to the long axis of the tank. These are for supporting the submerged sporeling frames. In one to two months the sporeling cords on the frames will be crowded with sporelings one or more mm high. (See Section 5, below, for more detail.) When the temperature of the sea water drops to about 20°C these sporeling cords on the frames will be loosened and hung in sea water, and in one to two months the sporelings will grow to be 10-15 cm long. They are then ready for transplantation to the commercial rafts in the field.

3.3 Fertilizing kelps in the open sea

It has been experimentally proved that the inability of the vast Huanghai Sea region to support growth of Laminaria is due to the low nitrogen fertilizer content of the sea water. Water analysis of the so-called outer region of the Huanghai Sea showed that nitrate-nitrogen is only about 2-3 mg/cubic meter. It was also proved that Laminaria kelp needs a rather high gradient for effecting absorption of the nitrogen salts, generally over 20 mg m^{-3} in terms of nitrate-nitrogen. Experiments further proved that if the sea in this region is not fertilized with nitrogen fertilizers, it will not be able to support commercial production of the kelp. In 1956, small-scale experimental fertilization was conducted on kelp farms. In that year 2350 tons of fresh kelp were produced (Tseng, Sun and Wu, 1955b). In the following two years a large scale program of fertilizing kelp farms in the open sea was carried out, and in 1958, 31,604 tons of fresh kelp were produced, achieving a major increase of production of 1245% within two years. The increase was primarily due to fertilizing, making it possible for kelp mariculture activities to be extended to various coastal districts not previously engaged in kelp cultivation.

Since 1956, kelp farm fertilizer application methods have undergone three stages of development. In the first stage a non-glazed clay-bottle method of fertilizing was the sole method employed. The principle of this method is to utilize the minute porosity of non-glazed clay bottles to disperse and concurrently limit the outward diffusion of the fertilizer solution placed inside each bottle. This assured that the kelps in the vicinity received the necessary fertilizer and at the same time it minimized the loss of the fertilizer due to water currents. In the late fifties and early sixties, an extention of this method of fertilizer application made it possible to cultivate kelp commercially along the vast coast of the Huanghai Sea.

The second stage of the development of a fertilization method for kelp farms took place in the early sixties by simplifying the original clay-bottle method. The same principle of fertilizing by diffusion through porous bottles was employed, but measures to increase the efficiency and lower the cost of operation were taken. In the original method the clay bottles employed were rather heavy and clumsy, their cost was quite high, and much labor was involved in hanging the bottles and in changing their fertilizer solutions. Therefore various improvements were made, for instance, employing plastic bags with a few very minute holes punched in them. Methods for minimizing fertilizer loss and increasing fertilizing efficiency, such as intermittent fertilization, soaking juvenile sporophytes in fertilizer solution and refraining from fertilizing the mature sporophytes, have been suggested and partially applied.

A third stage of development also occurred in the sixties. With the further advancement of the cultivation techniques, the cost of kelp production continued to drop, and the profit obtained from kelp cultivation increased, so that kelp farming became an attractive means of improving the livelihoods of many coastal farmers and fishermen. More kelp farms were organized, and kelp farms became larger; some farms grew from a few acres to tens or even hundreds of acres. In places where fertilization was necessary, it became more and more difficult to apply the methods based on the diffusion of fertilizer through porous materials. By the early sixties, sufficient knowledge had been obtained to indicate that kelps, especially nitrogen-starved kelps, are able to absorb nitrogen fertilizer very quickly in large quantities and satisfy their needs for several days to come. Therefore fertilization by spraying has been popularly employed. This is done by providing a kelp farm with a motor boat equipped with a tank for holding fertilizer solution and a spray gun for applying it. Spraying sessions rotate from one part of the farm to another. It has become evident, because of the large area of the kelp farms, that the loss of the fertilizer due to currents is very small.

3.4 Southward extension of commercial cultivation

China's coastal regions of the East China Sea, south of the Changjiang (Yangtze) River are very fertile. According to our investigation in 1956, the nitrate-nitrogen content of the sea-water in the Zhoushan region of Zhejiang Province was 88-227 mg m^{-3} and that in the Xiapu region of the Fujian, Province 88-123 mg/cubic meter. These are respectively 11 times and 6 times more than for a fertile region in the Qingdao region. Cultivation of Laminaria in these two provinces, if otherwise possible, would not need the application of fertilizer, thus decreasing greatly the cost of production and broadening the area of cultivation. The turbidity of the sea water in these regions will not be a serious problem for the commercial cultivation of the kelp, since with the floating raft method, the elevation of the plantings and, thus, the light, may be regulated at will. The difficulty lies undoubtedly in the relatively long period of high sea water temperatures there. Therefore an experiment was conducted on the growth of the Laminaria in relation to water temperature. The results of the experiment showed that, although the optimal temperature for the Laminaria growth was 5-10°C, growth was still good enough at 13°C; even at as high as 20°C, a Laminaria frond of 1-2 m was still able to effect some growth. An investigation of the sea water temperature characteristics of Zhejiang and Fujian Province led us to believe the Japanese kelp would grow to commercial standards in these provinces south of the Changjiang River (Tseng, Wu and Ren, 1962).

On the basis of the above experiment and investigations, an experiment was conducted in 1956 on the cultivation of Laminaria at Gouji Island, Zhejiang Province. The results of the experiment fully confirmed our postulation that this Japanese kelp could be cultivated satisfactorily in the region south of the Changjiang River, and thus the groundwork was laid for a large-scale southward extension of its cultivation industry. At present, this extension accounts for about one third of China's total kelp production.

3.5 The tip-cutting practice

Natural shedding of the distal part of the blade is a common phenomenon with Laminaria in late spring. This loss amounts to as much as 25% of the total harvest. Moreover, nutrient matter is transported from the upper parts downward. The accumulation of the nutrient matter is greatest in the basal part of the frond and less near the apex. Experiments employing P^{32} as a tracer showed that phosporus moves from the apex to the basal part of the frond through the trumpet tissues, then to the stipe and finally to the holdfast. There is no indication whatsoever of a movement of phosphorus in the reverse direction.

On the basis of the downward movement of nutrient matter in the Laminaria fronds, and the phenomenon of natural shedding of the distal parts of the fronds, "tip-cutting methods" have been proposed to increase production. By this method, cutting off and removing the distal part of the frond take place between late April and early May. The cut parts, gathered and dried, have amounted to 12 to 15% of the production and in some cases about 6.75 tons per hectare in northern Shandong. This is in dry weight. Tip-cutting also helps to promote the quality and quantity of the crop because of the improvement of both light penetration and water flow. Besides, for the same reasons it helps also to minimize the occurrence of diseases and improve the environment.

3.6 Environmental and pathogenic diseases

Among the more important diseases in Laminaria cultivation, three are caused by adverse environments. They are the green rot disease, the white rot disease and the blister disease. In addition there are two diseases caused by pathogenic organisms, namely, the malformation disease of summer sporelings and the swollen stipe/twisted frond disease.

The green rot disease is characterized by the apical part of the frond turning greenish and becoming soft. The symptoms gradually spread to the lower part, resulting in the loss of the entire plant. This is due to insufficient light, and it generally occurs on the lowest part of a hanging cultivation rope. To stop the spread of the disease, the light conditions must be improved, for instance, by bringing the kelp ropes up to shallower levels or by inverting the kelp rope so that the lower kelps will receive more light.

The white rot disease is characterized by the kelp fronds turning from brown to yellowish and finally to white; the disease spreads from the tip to the lower part of the frond. Eventually the whole frond decays and drops from the cord. This usually happens in April or May and occurs in places where the transparency of sea water suddenly increases and the nitrogen fertilizer content in the sea water is insufficient to meet the demands of the kelp. In this case, more nitrogen fertilizer has to be applied and the kelp ropes lowered to reduce the light.

The blister disease is characterized by the presence of blisters on different parts of the frond, and decay spots resulting from disruption of the blisters. This is due to the influence of large quantities of fresh water following heavy rainfall. It generally occurs in shallow bays. To stop further spread of this disease; the kelp ropes should be lowered below the fresh water which floats at the surface.

The malformation disease of the summer sporelings is characterized by abnormal cell division of the zygote and in the early stages of the sporeling. The resulting malformed sporelings consequently die and drop off the nursery cords. It has been shown that the presence of hydrogen sulphide resulting from the growth of sulphate-reducing bacteria, such as Micrococcus, causes such abnormal cell division of the zygote and malformation of the sporelings. It has also been shown that mature sporophytes used for production of zoospores for commercial purposes harbour numerous kinds of bacteria, including sulphate-reducing bacteria. It is therefore believed that during the processes of spore collecting, the nursery will be contaminated with these bacteria which, if they multiply and grow in the nursery tanks, cause the disease. Sulphate-reducing bacteria are also found in quantities in old iron pipe systems. Preventive measures have therefore been taken by separating the sporeling culture system from the mature sporophytes employed in spore collecting, and by sterilizing the sporeling culture water system with bleaching powder before the seeding season.

The other disease caused by pathogenic organisms is the swollen stipe and twisted frond disease, usually abbreviated as "frond twist disease". It has a combination of three characteristic symptoms, namely, coarsened and hollowed stipes, twisted fronds and withered or shortened rhizoidal holdfasts. This is a very characteristic disease. It was prevalent in the Dalian region in 1973, causing serious damage to the kelp industry. It became less serious during the following two years. The disease has not recurred during the last ten years. The contagious and biotic nature of this disease has been experimentally proved, and the latent period found to be quite long, 60-70 days. Electron microscope examination revealed the presence of numerous polymorphic mycoplasm-like organisms, mostly coccoid and some ovoid, dumbbell and amoeboid in shape. Experiments also showed that tetracycline antibiotics were effective in controlling the disease. Measures were also taken to increase the disease-resisting ability of the kelps by improving the cultivation techniques.

4. GENETIC IMPROVEMENT AND BREEDING OF NEW STRAINS

Genetic studies of the natural stock of Laminaria japonica, the Japanese kelp now under cultivation in China, showed its hybrid nature. This conclusion was derived from the following experimental evidence: (1) Under the same environmental conditions gametophytes can have somewhat different morphologies and growth rates; (2) different female gametophytes react differently under x-ray treatment; (3) different gametophytes react differently to the temperature parameter, and (4) partheno-sporophytes have different morphologies and growth rates. It has also been proved that frond length, frond thickness, stipe length and even iodine content of the kelp under cultivation are all quantitative characteristics controlled by both environmental factors and poly-genes.

The above evidence forms the basis for selection work. Since the Japanese kelp is a hybrid, it can be subjected to selection and x-ray treatment during breeding to develop more desirable strains. It has also been pointed out that the harmful effect of continual inbreeding is relative and conditional; in some inbred lines there are harmful effects, while in others no harmful effects are found. It is these latter which eventually form strains with useful characteristics. Therefore the Chinese genetists have employed methods of continual inbreeding and selection in developing new strains. In the inbreeding process, single fronds of the kelps are used to produce the zoospores instead of several fronds as in the commercial production of the summer sporelings. In this way, the gametophytes and the resulting sporophytes all come from one single kelp frond (Pang, 1983).

In the sixties, three strains of kelp were selected, one with broad fronds, one with long fronds and one with thick fronds. In the seventies, two strains with both high production and high iodine content were selected. The selection of the high iodine content characteristic was effected by the so-called half-frond method. In 1970 the Chinese phycologists conducted large scale selection work in the nine cultivation regions of the five coastal provinces. They selected many mature fronds, cutting half of the frond for iodine analysis and found 19 plants with high production and high iodine content. The other half of each of these plants was left to mature further and zoospores were collected from them. Breeding was carried out by repeated inbreeding and selection and then offspring of a single frond were treated by x-radiation. After a few years of cultivation and examination of genetic characteristics, two new strains with high production and high iodine content were successfully produced. These answered better the demands of the industry and are now under cultivation in large areas where they have won the approval of the kelp farmers. Recently a hybrid between these two strains has been successfully bred; it shows even higher production rates and higher iodine content (Fang, 1983).

Recent studies show that kelp parthenosporophytes can complete their own life-cycles without the help of any male gametophyte. It is therefore suggested that the monoecious sporophyte of Laminaria are really dioecious in nature. It is also suggested that there might be a sex chromosome in the gametophytic cells. No high percentage of natural doubling of chromosome number from haploid to diploid has been observed in any higher plant. The success in monocloning the haploid phases, i.e., the gametophytes, makes Laminaria desirable for further biological genetic investigations (Fang, 1983).

5. HARVESTING, PROCESSING AND PRODUCTION

Harvesting takes place when the fronds are mature **(Figure 1:15).** Selecting the optimal time of year and frond condition are very important subjects.

The time for harvesting the crop is important to kelp farmers, since harvesting too early will affect the quantity and quality of the product and, if the harvest takes place too late, there is a chance that a significant part of the crop may be swept away by a typhoon. Since the Chinese haidai is sold on the market on the basis of dry weight, and since the wet weight to dry weight ratio changes from month to month, and the quality of the product is higher with a lower wet-to-dry ratio, the criterion for selecting harvest time should take into consideration the highest per-unit area production rate plus the lowest wet-to-dry ratio.

Table 2, which follows, shows the results of an experiment conducted on the quantity and quality of the production on kelp rope at different dates. From the table it is readily seen that mid to late June is the best time for harvesting. The harvest on June 11 was the highest while that on June 29 was slightly lower in production but the quality was better. On July 14 production was still lower, but the quality was still better. It is there- fore recommended harvesting begin in mid June and continue until late June or early July in North China.

Table 2. Production quality and quantity per kelp cord at different dates.

Harvest time month/day	Production in wet wt. kg.	Production in dry wt. kg.	Wet Weight Dry weight Ratio
4/25	21.8	2.2	10:1
5/10	24.4	2.7	9:1
5/26	24.6	3.1	7.9:1
6/11	22.0	3.3	6.6:1
6/29	17.6	3.1	5.7:1
7/14	14.5	2.9	5:1

In harvesting the crop, the kelp ropes are detached from the floating ropes, and collected in small boats, many of which are towed in a long line by a motor boat. In Dalian, when the boats reach the wharf, the harvested kelp is taken up onto the wharf along a wire-rope between two posts, one at the wharf and the other in the sea. The motor boat is also employed in seed-scallop or other work. Actually, therefore, the boats and glass house serve kelp sporeling production only about 50% of the time.

Kelp farms vary greatly in size, but are generally large enough for fertilizer application by spraying in north China. The shore facilities are simple, consisting of a warehouse, working space for transplanting sporelings, space for preparing the floating rafts, an area offshore for their anchorage and, of course, offices for farm management. Each kelp farm in North China uses a fertilizing boat with a fertilizer spraying gun. For tending the kelps, small manually operated boats are provided.

Generally two kinds of workers are employed, skilled and unskilled. The kelp farmers are skilled laborers with experience in tending kelps. Generally about 2 farmers operate one hectare of kelp farm. They are busy for most of the year, since before the cultivation season they have to do a great deal of preparatory work in setting up the floating rafts, including preparation of the various kinds of lines and ropes together with production of a large quantity of floats and anchoring materials, including cement and wooden-peg anchors. Besides the skilled workers employed on a permanent basis, there are temporary unskilled workers for such work as inserting sporelings into the twisted kelp ropes.

After the kelp farms have purchased the necessary number of kelp sporeling culture cords, the latter have to be put in the sea where the water temperature has already dropped to about 20° Centigrade. In a month or so the sporelings of a few millimeters in length will have grown to juveniles of 10-15 or more centimeters long. These juvenile sporophytes have to be brought to the transplanting room and placed in tanks filled with seawater. Since they grow on the cords so thickly that they would crowd each other, resulting in slow and poor growth, they have to be thinned. The best way in our experience is to remove them from the original sporeling cord and insert them in the twists of the kelp ropes in a systematic and orderly fashion generally with about 30 juveniles to each rope. This type of work is important but can be effected by non-skilled workers after a very short period of training. Temporary workers are also employed for drying the harvested kelp.

Production of the kelp per unit area differs from place to place. In the Qingdao region there are in general about 30 kelp plants per kelp rope and these, when dried, weigh about 3 kg,i.e., on the average, about 100 gm for each dry kelp plant. As to the production per hectare (10,000 m^2), there are about 12,000 kelp plants per mow (1/15 of a hectare) or 180,000 kelp plants per hectare so that production amounts to 18 tons of dry kelp per hectare in the north. South of the Changjiang estuaries the per unit production of the kelp is lower because of the shorter growth season; per hectare production may be about 13-15 tons. In the south the seawater is very fertile, and no fertilizer application is involved. Thus, production costs are lowered and kelp cultivation is still a profitable industry.

6. UTILIZATION AND MARKETING OF THE CROP

Most of the Laminaria japonica produced in China is used for food. According to an official analysis made in the early fifties of the imports of Japanese kelp by the Chinese Ministry of Health, haidai on the market has the following composition per 100 grams: 0.75 mg carotene; 0.69 mg vitamin B1; 0.36 mg vitamin B2; 1.6 mg nicotinic acid; 8.2 gm crude protein; 57 gm carbohydrate; 9.8 gm crude fiber, and 12.9 gm inorganic salts, including 2.25 gm calcium and 0.15 gm iron, yielding 262 kilo-calories. Our analysis of the samples of the kelp produced in China from different periods of the year showed that 100 gm of the dry kelp contained 17.1-32.0 gm alginic acid, 8.46-28.48 gm mannitol, 5.97-18.99 gm crude protein, and 19.35-45.29 gm ash, including 0.13-0.69 gm iodine and 4.35-12.65 gm potassium. Chemical analysis of the kelp shows that it may be regarded as a "health food", especially desirable in the winter season in the north when green vegetables are comparatively scarce.

Beside its role as a "health" vegetable, in China haidai is also important as raw material to be processed for its algin, mannitol and iodine content in a special program for the comprehensive utilization of Laminaria. The uses of the algin, mannitol and iodine are well known and beyond the scope of the present paper. Recently the kelp produced in China has also been employed in the processing of synthetic feed used in mariculture. Formerly the kelp was sold on the market only in the crude dried form, but recently small packages of shredded and seasoned forms with different flavours have appeared on the market and are very well accepted by the people.

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Biology of the Macrocystis resource in North America

1. IDENTITY
2. DISTRIBUTION, ECOLOGY AND METABOLISM
3. LIFE HISTORY
4. POPULATION STRUCTURE AND MORTALITY
5. PRODUCTIVITY OF THE RESOURCE
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ABSTRACT

The major North American source of alginate is Macrocystis from California. The area, standing crop and yield in California have varied greatly, e.g., from a maximum of 358,425 wet tons from 13,171 ha in 1918 to a minimum of 236 T from 13,171 ha in 1931 to recent tonnages of about 100,000 to, in 1984, 47,320 T from 4,765 hectares. To some extent variations in the southern sea level index and appearance of the El Nino current off the west coast of South America are related: a complex of grazer and other phenomena have been implicated.. A large amount of experimental physiological and population work is reviewed.

1. IDENTITY

1.1 Nomenclature
1.2 Taxonomy
1.3 Morphology and anatomy

1.1 Nomenclature

The genus Macrocystis (Macro = large, Kystis = bladder) is presently recognized as containing three species[1] M. pyrifera, (refers to the pear-shaped or pyriform bladders), M. angustifolia (narrow leaves), and M. integrifolia (complete leaves). There were formerly many more species recognized, based on frond morphology. Further study revealed that frond morphology could be profoundly affected by environmental factors. Later workers consequently chose holdfast morphology as a basis for species separation (Womersley, 1954). The holdfast of M. pyrifera is terete with an upright axis usually conical for plants a year or more old. Holdfasts of M. integrifolia are more or less prostrate with fronds developing from a creeping rhizome with a flattened axis. Holdfasts of M. angustifolia are intermediate between M. pyrifera and M. integrifolia. Neushul and coworkers have obtained viable crosses between all three species.

[1] Note added in proof, a fourth species, M. laevis, has just been proposed by C.H. Hay (Phycologia, Vol. 25, 1986, pp. 241-252.

1.2 Taxonomy

Macrocystis belongs to the Order Laminariales, which includes those Phaeophyta growing by means of an intercalary meristem as well as a superficial meristoderm and has oogamous reproduction by microscopic dioecious gametophytes. Macrocystis above the holdfast is differentiated into a blade and stipe, with the blade being split forming several intercalary meristems during early sporophytic development. This places it in the Family Lessoniaceae.

1.3 Morphology and anatomy

Microscopic stages in the Macrocystis life cycle (i.e. gametophytes and embryonic sporophytes) resemble those of other members of the Lessoniaceae (see below) and they cannot be distinguished from one another. The morphologies of the macroscopic adult sporophytes differ widely in this family and constitute the basis for separation into genera and species. The typical Macrocystis adult sporophyte **(Figure** 1A) consists of numerous blade-bearing fronds that arise from a basal branching system of stipes. Lower portions of the basal stipe system also produce root-like haptera that grow downwards, wrapping around and forming attachment to irregularities in solid substrata. Uniquely the haptera of M. angustifolia can also attach to sedimentary bottoms (See Section 2. 3). The mass of haptera constitutes the holdfast.

Figure 1A. Diagram of the Macrocystis life cycle showing (left side) development of the young diploid sporophyte, increasing frond numbers through production of basal and apical meristematic blades; (.right side) growth habit of an adult diploid sporophyte ca two years old, standing in 10 m of water depth, and liberating haploid zoospores; (below center) development of haploid gametophytes from settled zoospores, proceeding to gametogenesis, and fertilization yielding the zygote and, thence, a diploid embryonic sporophyte.

New young fronds arise **(Figure 1A)** from longitudinal splits in meristematic blades located on the basal branches just above the holdfast (the basal meristems, **Figure 1A).** The outer blade of the two produced by the splitting becomes an apical frond initial while the inner portion remains as a basal meristem that will give rise to yet further new frond and basal meristem initials.

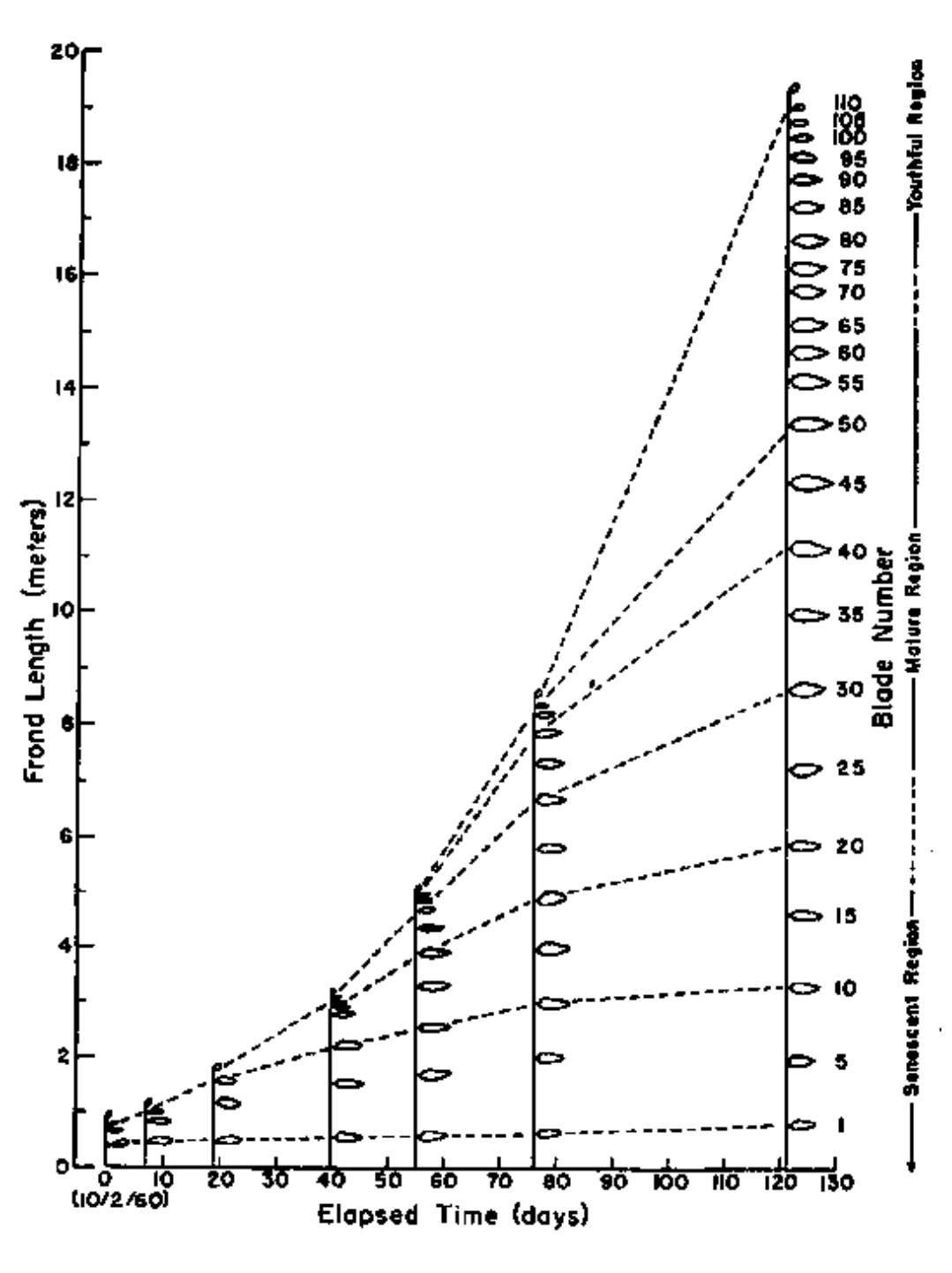
Splits appear near the base of the outer (apical) frond initial of a young frond, and developing longitudinally toward the blade edge, subdivide the original lamina into lanceolate strips each of which becomes one blade on the young frond. Elongation occurs in that part of the blade base where the splits arise, yielding the stipe of the young frond and causing separation of the newly forming blades. Further stipe growth and splitting produces an apical scimitar-shaped blade distinct from the remaining blades. This is the apical meristem which generates additional blades and stipes as the frond continues to develop. The lowermost 2 or 3 blades lack pneumatocysts (bladders) but thereafter all upper blades carry these pyriform flotation devices joining the laminae to the stipe. Continued elongation in the stipe plus production of new blades by the apical meristem results **(Figure 1B)** in elongation of the frond and increase in the numbers of blades. Eventually the apical meristem reaches the water surface and then is pushed horizontally in the canopy by continued growth throughout the stipe length. Finally, meristematic activity ceases in the apical blade and a terminal blade is formed. A fully grown frond may display **(Figure 1B)** 100 to 200 or more blades.

A mature frond thus ultimately consists **(Figure 1B)** of a basal senescent, a central mature and a terminal youthful region as sections of differing ages. The oldest blades occur near the base with a gradient extending upwards to the youngest blades at the apex. Senile deterioration often occurs among the lowest blades of a mature frond even while new youthful blades are developing in the upper regions. The lifespan of an entire frond is about six months but may be somewhat longer or shorter, depending on environmental conditions in the surrounding water. Senile, deteriorating fronds are replaced by young new fronds constantly arising from the basal meristems just above the holdfast. If an apical meristematic blade is severed from a growing frond, further blade production ceases. The remaining basal portion of this frond survives until it is overcome by senility near the end of its normal lifespan.

Harvesting a Macrocystis canopy removes all apical meristems lying above the cutting depth. Canopy regeneration is accomplished by growth from fronds whose apical meristems all lie beneath the cutting depth. The lowermost two to six laminae (called sporophylls **[Figure 1A])** at the base of a frond develop reproductive sporangia. These sporangia are densely packed in certain areas, called sori, on the sporophyll blade surfaces. Each saclike sporangium at maturity releases numerous biflagellated zoospores which develop into gametophytes if they attach to a suitable substratum (see below). The chromosome numbers for a haploid M. integrifolia cell are 14 to 16 (Cole, 1968).

Adult Macrocystis sporophytes generally display increased numbers of fronds as they age. Very large plants in protected waters may bear several hundred fronds and may be many years old. In exposed locations, however, storms rip holdfasts loose from their attachments and such plants do not usually survive longer than 2 to 3 years. The largest plants under such circumstances may bear 40 to 60 fronds. Fronds growing from holdfasts in deep water do not produce substantially more blades than are found on comparable fronds growing in shallow water. Fronds compensate for greater water depth by increasing internodal distances (lengths of the stipe sections between adjacent pneumatocysts), not by increasing the total blade numbers.

Figure 1B. Time scale frond development illustrated from consecutive observations of one frond of an adult Macrocystis plant standing in a water depth of 20 m off La Jolla California. The senescent; mature, and youthful regions of the frond are shown but only some of the blades (from North, 1979a).



2. DISTRIBUTION, ECOLOGY AND METABOLISM

2.1 Geographical extent
2.2 Local vertical and horizontal distribution
2.3 Effects of ecological determinants
2.4 Nutrition and growth

2.1 Geographical extent

The genus Macrocystis occurs naturally around every major land mass in the Southern Hemisphere except for Antarctica (i.e. South America, South Africa, Australia, New Zealand), and also along the eastern Pacific coast in the Northern Hemisphere. Presumably a cold water bridge that formed across the Gulf of Panama on the Pacific side of Latin America permitted transport of Macrocystis from South America northward to Mexico, United States and Canada. Macrocystis pyrifera was introduced to Asiatic waters in 1978 by scientists from the People's Republic of China (Liu et al., 1984). The species has also been successfully cultured in North Atlantic waters on at least three separate occasions. Thus it appears that Macrocystis will survive and grow in any of the temperate oceanic waters of our planet. It has not been able to colonize in either tropical or high arctic climates. M. pyrifera and M. integrifolia occur in both Hemispheres. M. angustifolia was described from Australia (Womersley, 1954). Neushul (1971) identified the Macrocystis growing near Santa Barbara, California, as M. angustifolia, based on Womersley's description.

2.2 Local vertical and horizontal distribution

Vertical distribution of Macrocystis is apparently affected more by local conditions than by preferences or a specific range of depths. For example, given year-round suitably low water temperatures, ample nutrients, and protection from wave action, both M. pyrifera and M. integrifolia can colonize low intertidal pools. On exposed coasts, however, the inner limit of large Macrocystis beds is usually at 7 to 10 m depths and is apparently controlled by wave action. The outer limit of Macrocystis beds in California coastal waters usually occurs at depths of 10 - 20 m. The depth range may increase to 25 - 30 m in very clear waters around offshore islands. Presumably the lower depth limit is governed by the bottom illumination required to sustain development of the microscopic gametophytes and small sporophytes. The deepest adult plant ever observed by the author was 40.2 m beneath the surface at Punta Banda, Mexico, an area of extremely clear water.

Local horizontal distributions are most frequently controlled by the availability of rocky substrata. Holdfasts of M. pyrifera or M. integrifolia require solid substrata for firm attachment. Macrocystis angustifolia does occur on sedimentary bottoms. (See Section below.)

2.3 Effects of ecological determinants

The primary ecological factors affecting success and survival of Macrocystis populations in the United States and Mexico (and probably elsewhere in the world) are water motion, nutrient availability, water temperature, competition, grazing organisms, bottom illumination and sedimentation, more or less in that order of importance. We discuss nutrients and grazing below, so primary emphasis here will be on wave action, water temperature and illumination.

Importance of wave action as a disruptive factor is demonstrated by the distribution of Macrocystis in southern California, comparing the well-protected Santa Barbara coastline with the remaining exposed habitat. Harger (1983) reported that the coastline from Santa Barbara to Point Conception (including San Miguel Island) contained 65 percent of all kelp bed areas in southern California along only 18 percent of the entire shoreline. Variation of canopy coverage was smallest for the Santa Barbara region. These statistics suggest that some degree of protection against wave action is very beneficial for increasing area of coverage and stability of kelp beds.

Studies of plant mortality in exposed kelp beds clearly indicate that maximum life span of adult plants is short, usually around two to three years for most of the population (North, 1971a; Rosenthal et al., 1974; Dayton et al., 1984). Juvenile recruitment thus is necessary to assure continuation of the population. While wave action can be destructive, water motion is also necessary for nutrient renewal. Back and forth motion such as caused by waves creates a scrubbing action across blade surfaces enhancing nutrient exchange (W.N. Wheeler, 1982; Gerard, 1982a). Longer period motion resulting from tidal cycles, internal waves, and alongshore current replenishes dissolved nutrients within beds and transports food and waste products for the associated fauna. Resistance to flow reduces current velocities within the kelp beds and causes deviation of flow around kelp stands (Jackson and Winant, 1983).

Nutrient availability is negatively correlated with water temperature for values greater than 15.5°C (Zimmerman, 1983). Consequently, the many reported observations of summertime deterioration by Macrocystis attributed to high temperature, probably represent combined effects from elevated water temperatures and low nutrients (Jackson, 1977; Zimmerman and Kremer, 1984). North and Zimmerman (1984) showed that fertilizing an experimental group of kelp plants resulted in substantial canopy preservation during summertime compared to an unfertilized group of control plants. In natural beds, stratification in the water column during summer results in a warm, nutrient-poor environment above the thermocline and a cool, nutrient-enhanced milieu below. Consequently, kelp deterioration is greatest in the surface layers while basal portions may survive with little, if any, damage. When sea surface temperatures fall during autumn, basal portions may regenerate the canopies in a few weeks or months.

Summertime deterioration is typically accompanied by a number of symptoms or signs which may conveniently be grouped into a single term we shall call "summer syndrome". Most of these symptoms can be seen within kelp beds at other times of the year as well but less frequently. Prevalence may simply increase sharply during warm summers. Summer syndrome includes loss of coloration in kelp tissues, lesions in the blades, tissues may become brittle and break easily or they may become soft and slough away, coverage by encrusting animals may increase, bladders become perforated or may simply fill with liquid so that fronds lose buoyancy and sink, apical blades become scarce and roost fronds display terminal blades. At a physiological level, photosynthetic capacity declines (Gerard, 1984a). Some of these symptoms undoubtedly arise from nutrient insufficiency (i.e. loss of color). Others may be indirect effects of increased temperature (e.g. lesions and sloughing, caused by enhanced microbial activity). Clendenning (1971) reported that light-saturated photosynthesis was always highest over the range of 20° to 25°C among all kelp tissues he studied (except for kelp from central Baja California which peaked in the range 25° to 30°C) during short term exposures. Summer syndrome, however, usually develops at around 20°C. Appearance of summer syndrome apparently involves relationships between duration of a period of elevated temperature and the level to which temperature rises. Thus a temperature of 20° may be tolerated for 2 or 3 months while 23°C or more for a month will result in rapid deterioration.

The microscopic stages of Macrocystis may be more sensitive than adult plants to elevated water temperatures. Dean and Deysher (1983) reported that the upper limit for sporophyte production from gametophytes they outplanted to a natural kelp bed was 16.3°C.

Competition from other algal species takes several forms including shading of juvenile Macrocystis (i.e. competition for light), competition for space, substratum, and possibly competition for nutrients. There may also be poorly understood competitive mechanisms. For example, small Macrocystis and other lami-narian sporophytes appear to recruit poorly on substrata thickly covered by encrustations of coralline algae and animals when compared to non-encrusted surfaces. On the other hand, remains of old decaying Macrocystis holdfasts sometimes support numbers of young sporophytes while none occurs on the surrounding bottom. These observations suggest that chemical mechanisms may exist which affect suitability of a substratum for colonization by kelp spores. Barren rocky bottoms severely and constantly grazed by sea urchins are usually excellent substratum for colonization by Macrocystis and other brown algae after the urchins are eliminated; provided, of course, that fertile adult plants are close by enough to serve as spore sources. When territory dominated by Macrocystis is lost due to some catastrophic effect, other seaweed species may colonize the area and prevent Macrocystis from reestablishing. Persistence, resistance to invasion, and resilience or recoverability after loss of territory are discussed by Dayton and Tegner (1984) and by Dayton et al. (1984). Physical abrasion from nearby blades of tough species such as Laminaria and Agarum may damage small Macrocystis sporophytes, (R. McPeak, pers. comm.).

Significant grazing damage can be inflicted on Macrocystis plants by several herbivores including sea urchins, crustaceans, mollusks and fishes. Probably the most damaging grazers in California waters are the sea urchins, Strongylocentrotus franciscanus, S. purpuratus and Lytechinus anamesus. These echinoids can occur in enormous populations at concentrations well above 10/m^2. The animals migrate slowly across the sea floor, consuming all plant life except for crustose corallines, as well as many sessile invertebrates such as sponges, tunicates, and bryozoans. Under some conditions, urchin populations persist indefinitely at high concentrations, preventing vegetation from reestablishing and creating "urchin barrens" (Dean et al., 1984). Urchin barrens have been observed in many shallow benthic areas other than California. Disappearances or significant reductions of predators that control urchin numbers permit development of huge urchin populations. Urchin predators include lobster, fishes, sea otters, and asteroids (Tegner and Levin, 1983; Dayton et al., 1980; Estes and Palmisano, 1974). Human exploitation of urchins as food may also act as a significant control, (Wilson and North, 1983). Very severe storms may even remove urchins from kelp bed depths (Ebling et al., 1984). Techniques for artificially controlling urchin populations are described below.

Herbivorous fishes are not usually sources of significant damage to Macrocystis populations in dense healthy kelp forests because the amounts of plant tissue consumed are small in relation to total productivity. Fish grazing may assume importance when productivity declines as, for example, in a kelp bed under stressful conditions or where small plants colonize the sea floor after the adult Macrocystis plants were destroyed by some catastrophe. Two herbivorous fishes in California waters, Girella nigricans and Medialuna californiensis, preferentially feed on youthful kelp tissues such as the apical meristems and the blades of very young sporophytes (Harris et al., 1984). A third fish species, Oxyjulis californiensis adventitiously removes chunks of kelp tissue when feeding on encrusting bryozoans (Berstein, 1977), sometimes damaging blades significantly. For grazing of small sporophytes or apical meristems, the damage inflicted may be far out of proportion to actual amounts of tissue consumed. Effects from fish grazing may be especially significant when small young Macrocystis plants are first reestablished in an area where a catastrophe has eliminated all the adults.

Leighton (1971) studied food preferences of eleven invertebrate herbivores common in California kelp beds. All eleven showed preferences for Macrocystis tissues. He did not include herbivorous fishes in his studies but our field observations suggest that Macrocystis is strongly preferred by Girella and Medialuna. We frequently record instances where extensive damage from fish grazing occurs on blades of small Macrocystis plants but none is seen on other recruiting kelp species such as Eisenia, Egregia, Pterygophora, and Laminaria. Fish grazing undoubtedly enhances competition from other kelp species on such occasions. Grazing fishes can be a serious problem when we undertake to develop Macrocystis stands by transplantation techniques (see below).

Grazing by crustaceans and gastropods infrequently may cause significant damage to Macrocystis populations. Numbers of these herbivorous species are usually so small that their activities only result in trivial losses of kelp tissue. Very occasionally, however, dense concentrations of a species may appear so that grazing effects reach destructive proportions. We have observed significantly destructive grazing on Macrocystis by large numbers of kelp crabs (Pugettia), abalone (Haliotis), dove snails (Mitrella), and microcrustaceans (primarily Ampithoe) and Idothea).

Adequate sunlight is, of course, a requirement for all plants, but effects of cloudy days or turbid water are less for adult Macrocystis than for short-statured algae because of the extensive canopies which extend just beneath the surface where submarine illumination is maximal (cloudy days may affect kelp productivity but not survival of adult plants). The primary influence on Macrocystis populations by attenuation of submarine light is the effect on microscopic plants and recruitment of small plants. Dean and Deysher (1983) outplanted gametophytes to a natural kelp bed at San Onofre, California, and after six weeks recorded densities of resulting sporophytes on their artificial substrata. They found that no sporophytes were produced at irradiances below 0.4 E/m^2/d. They also noted an interactive effect between water temperature and irradiance. As temperatures approached 16°C, about 1E/m^2/d was required for moderate sporo-phyte production. These authors also measured daily irradiance on the bottom in clear areas within the San Onofre kelp bed for 3 1/2 years (July, 1978 to January, 1982). Favorable irradiances over 2-week intervals combined with suitable bottom temperatures occurred only eight times during the 3 1/2 year interval and each recruitment was traceable to a period of favorable light and temperature as defined by Dean and Deysher's measurements. These authors postulated that "windows" of environmental conditions favoring recruitment occurred only occasionally and were critical to persistence of this kelp bed. Photosynthesis by Macrocystis gametophytes and embryonic sporophytes became light saturated at 70 m E/m^2/s (Fain and Murray, 1982). Compensation irradiance for embryonic sporophytes was 2.8 m E/m^2/s. Luning and Neushul (1978) estimated that 20 m E/m^2/s was adequate for saturation of vegetative growth in M. pyrifera and M. integrifolia gametophytes but 2 to 3 times this irradiance was necessary to induce gametogenesis.

Sedimentary deposits can affect M. pyrifera in several ways. Even very light sedimentary films may interfere with spore settling under laboratory conditions (Devinny and Volse, 1978). An approximately tenfold increase in sedimentary load caused burial of already settled spores and interfered with their survival. Presumably due to sediment scouring, water motion in the presence of fine sediment further reduced survival. Dean and Deysher (1983) noted a substantial influence from sedimentation on sporophyte production by their gametophyte outplants to the San Onofre kelp beds (in their regression analysis, sedimentation accounted for 11% of the variance observed, temperature 25%, light 10%, nitrogen 0%). The thin sedimentary deposits that may bury microscopic stages of Macrocystis are, of course, ineffective against larger plants. Major sedimentary shifts have been noted, however, damaging young and even adult sporophytes (Neu-shul, 1959; North, numerous observations, unpub.).

Partial burial of holdfasts does not appear to affect haptera adversely, e.g., the haptera of M. angustifolia actively growing downward into the sedimentary bottom. The haptera penetrate deeply into the sediments, and interstices within that part of the holdfast above the bottom become filled with sand or mud. This plant produces holdfasts that may be 3 to 5 m in diameter but less than one meter tall (i.e., low mounds). By trapping and penetrating the sediment, it creates a heavy mass that withstands displacement by wave action.

Burial of the primary or secondary stipes at the holdfast apex is not tolerated well. Stipe tissues rot in a few days if they are not freely exposed to surrounding water. Blades also are intolerant of even light sedimentary deposits and may disintegrate after a few weeks of coverage. This type of damage is common among Macrocystis plants growing in quiet waters of bays and inlets where scrubbing action by wave surge is lacking. The Santa Barbara region, however, is protected from long period waves by offshore islands and orientation of the mainland.

Ecological determinants of lesser importance affect Macrocystis from time to time. Aggregations of encrusting animals may appear on Macrocystis blades so densely as to cause loss of buoyancy and sinking of fronds. Encrustation of kelp by the Bryozoan, Membranipora, enhances blade loss by reducing flexibility and by encouraging fish grazing on the Bryozoan colonies (Dixon et al., 1981; Kirkwood, 1977). Compensating light intensity was about 50% higher for Membranipora encrusted than for clean Macrocystis blades (Wing and Clendenning, 1971). Isolated plants and those near the edges of kelp beds are more susceptible to colonization by Membranipora (Bernstein and Jung, 1979).

Salinity remains sufficiently constant along open coastlines so that distribution of Macrocystis populations is rarely, if ever, affected in California. Lowering of salinity in bays and estuaries may regulate Macrocystis distribution in these habitats, especially north of southern California where rainfall increases. According to Druehl (1979), beds of M. integrifolia are able to grow at Nootka, Vancouver Island, where the yearly salinity range was from about 23 ‰ to 30 ‰. Druehl indicated that high temperatures (i.e. 14° - 18°C) during periods of low salinity were associated with absence of Macrocystis and that the season of low salinity at Nootka coincided with a time of low temperatures (8° - 12°C). North (unpub.) grew gametophytes of M. pyrifera in serial dilutions of open ocean seawater and distilled water. Gametophytes did not survive at dilutions greater than 3 to 1 (i.e. just below 25 ‰ salinity if we assume the salinity of the undiluted seawater was 33 ‰. This conclusion was in rough agreement with Druehl's (1979) observations.

2.4 Nutrition and growth

Kelp growth is probably rarely, if ever, limited by availability of micronutrients in surface seawater. Kuwabara and North (1980) demonstrated nine elemental requirements by Macrocystis including the macronutrients nitrogen and phosphorus as well as the micronutrients copper, zinc, cobalt, manganese, iron, molybdenum and iodine. Kuwabara (1982) found indications that sea-water from 300 m depths in southern California was somewhat deficient in manganese and cobalt for growth by Macrocystis gametophytes.

Nitrogen may at times be a limiting element in surface water and very occasionally phosphorus (Manley and North, 1984). Luxury uptake of nitrogen and phosphorus occurs in Macrocystis during times when these elements are plentiful and reserves are utilized when external supplies are inadequate (Gerard, 1982b; Manley and North, 1984). These authors indicated that values of critical tissue levels (where the element is neither in excess nor in short supply) for Macrocystis were 0.2% dry wt. for Phosphorus and 1.0% dry wt. for Nitrogen in blade tissues. P.A. Wheeler and North (1980) found that blade N-contents of juvenile sporophytes reached a maximal value of 3% dry weight when external nitrate concentration in a flowing water culturing system was at 13 m M. Gerard (1982b) transplanted large adult sporophytes with laminar tissues initially containing 2.2 to 3.5% dry wt. Nitrogen from a coastal kelp forest to an offshore island site where ambient external Nitrogen was well below m M (as indicated by continual temperature measurements). Growth rates stayed at relatively high levels for two weeks, then declined sharply. Ambient Nitrogen rose during the fourth week and growth rates recovered somewhat. The Nitrogen contents of laminae declined steadily during the initial 3 weeks of starvation, then remained constant or rose slightly thereafter. Holdfast Nitrogen remained constant throughout. Gerard (1982c) further proposed a mathematical model for nitrate uptake by whole plants. Zimmerman and Kremer (1984) demonstrated a relationship between estimated nitrate concentration and frond growth rate. Growth rates fell for nitrate concentrations below 1 m g-at/1.

Haines and P.A. Wheeler (1978) listed values of K_S=13.1 m q-at N/1, V_{max}=3.05 m g-at N/wet g/h for NO_3 uptake by juvenile Macrocystis and K_S= 5.3 m g-at N/1, V_{max}=2.38 m g-at N/wet g/h for NH_4 for concentrations below 22 m g-at/1. W.N. Wheeler (1978) reported maximum uptake rates by tissue discs cut from blades on an adult frond as 75 m m/cm^2/h for NO_3, 275 nM/cm^2/h for NH_4, and 3.8 nM/cm^2/h for PO_4 under saturating water motion. All workers reported that nitrate and ammonium were taken up simultaneously without any effects on uptake rates by presence of another form of nitrogen. Manley (1985) found values of KS= 3.51 m M and Vmax= 5.29 nM/cm^2/h for PO_4 uptake by blade tissue discs from adult sporophytes. Manley suggested that differences between his results and those of W.N. Wheeler might arise from differences in tissue Phosphorus levels. Gerard (1982c), using whole blades attached to adult plants, showed that NO_3 uptake rates differed substantially for tissues from different parts of the plant and similar findings have been shown for PO_4 uptake (Manley, 1985; Schmitz and Srivastava, 1979) and for NO_3 uptake by M. integrifolia (W.N. Wheeler and Srivastava, 1984). Uptake of NO_3 and PO_4 was more rapid in light than in darkness or under shaded conditions (W.N. Wheeler, 1982; Gerard, 1982a; Manley, 1985). Culturing tissues in water high in NO_3 or PO_4 reduces uptake of these nutrients and Gerard (1982b) found an inverse relation between depth and NO_3 uptake. W.N. Wheeler (1978, 1980a, 1982) found that water motion affected carbon and nutrient uptake rates with uptake saturating in the range of 3 to 5 cm/sec current velocity. Gerard (1982c) concluded that NO_3 uptake regardless of concentration, became saturated at a water flow of 3 cm/sec. She found that water motion under field conditions exceeds this critical value even inside dense canopies during calm seas. W.N. Wheeler (1980a) reported that transport rate of inorganic carbon through the boundary layer on Macrocystis blades saturated at flow velocities of 4 cm/sec.

Uptake rates of the micronutrients I, Fe, Zn, Co, and Mn as a function of external concentration were presented by Manley and North (1981), using an artificial seawater. Manley (1984) showed that these elements as well as Mo and Ni were concentrated in sieve tube sap. He calculated that adult plants sometimes might not be able to fulfill their requirements for Mn and Co, resulting in growth limitation by availability of these elements. Manley (1981) showed that Fe uptake is light independent and energy dependent. Manley (1.c.) and Anderson (1984) both showed that iron is reduced from Fe^{3+} to Fe^{2+} during uptake.

Ability to translocate inorganic and organic ions and compounds is an important feature of nutrition in the Laminariales. Structural elements of the translocation system are maximally developed in the tree-like kelps such as Macrocystis. Translocation processes nourish portions of adult plants growing under low illumination near the bottom by photosynthate created in the upper well-lit parts of the water column. The translocation capability allows Macrocystis plants to grow in dense aggregates with over-lapping canopies which effectively shade out competitors on the bottom, yet supports rapid growth by young fronds, sporophylls, haptera and other tissues near bases of the plants. The sieve tubes occurring around the periphery of medullary tissue centrally within blades and stipes, are the conducting pathways supporting translocation. The sieve tubes are enclosed by cellular membranes. Osmotic pressure is believed to be the driving force causing movement of fluid through the sieve tubes (Schmitz, 1982). Synthesis of organics and rapid uptake of inorganics in the "source" region of a frond creates high concentrations of solutes there, creating a tendency for intake of water from outside and movement of water plus solutes through the sieve tubes towards more diluted solutions in the "sink" regions. Accommodation of the flow is accomplished by loss of water in the sink region. Flow can be bidirectional within a single mature frond (i.e. from the center toward both ends). Thus, both apical meristems in the upper parts of the water columns and newly developing fronds at the plant base receive photosynthate and nutrients from mature blades located in the central part of a long frond.

Lobban (1978a) showed that newly developing fronds of M. pyrifera act as sinks until they are approximately three meters long. Loss or disappearance of an apical meristem caused all translocation to occur toward the base. Translocation in M. integrifolia differed from that in M. pyrifera in terms of seasonal changes in direction of translocation and in distances from the apices where changes occur (Lobban, 1978b). Manley (1984) postulated that young short fronds probably depend on translocation of Mn, Co and Fe to meet growth requirements because their small total blade areas provided insufficient uptake capacities.

Translocation velocities of 25 to 45 cm/hr were measured using radioactive 32p compounds as tracers in M. integrifolia (Schmitz and Srivastava, 1979). These velocities were comparable to velocities shown for 14C compounds. Translocation velocities in M. pyrifera blades were only 6 to 22 cm/hr., possibly because of small diameter pores in sieve plates forming the interconnections between adjacent sieve tube cells (Buggeln et al., 1985).

Phosphorous is assimilated from the exterior in inorganic form but is primarily incorporated into organic compounds during translocation in the sieve tube sap. Similarly, organic forms of nitrogen are taken up very slowly or not at all by M. pyrifera (P.A. Wheeler, 1979), yet nitrogen in sieve tube sap occurs almost entirely as amino acids (Jackson, 1976). Jackson (1977) calculated that the flux of nitrogen due to translocation in Macrocystis stipes amounted to 0.2mM/hr, while that of carbon was 2mM/hr. The principal amino acid in M. pyrifera was alanine.

The initial product of photosynthesis in Macrocystis is mannitol (Vaughn, 1959) and the primary low molecular weight carbohydrate was mannitol in both M. pyrifera and M. integrifolia (Jackson, 1.c., Schmitz and Srivastava, 1979).

The basis of growth and productivity in Macrocystis, as in all plants, is photosynthesis. Photosynthesis in an adult Macrocystis sporophyte is affected by a number of factors, resulting in an extremely complex situation. Different tissue types (i.e. blades, stipes, sporophylls, haptera) display different photo-synthetic capacities (Arnold and Manley, 1985). Gradients in photosynthetic capacities exist from base to tip within blades and between blades along the frond length (Arnold and Manley, 1.c.; W.N. Wheeler, 1980b; Clendenning, 1963). The blades account for nearly all the photosynthetic activity of Macrocystis sporophytes in nature). The submarine light field that drives photosynthesis is extremely variable and complex in kelp beds as a consequence of canopy absorption, refraction by ripples and waves, and constant movement by blades resulting in flashing light patterns in the upper part of the water column (Gerard, 1984b). Vertical distribution of blade area is not uniform (Jackson et al., 1985) with 50% or more of the total area occurring near the surface in adult plants displaying full canopies. Very substantial seasonal changes in photosynthetic capacity may occur for both M. pyrifera (Clendenning 1971) and M. integrifolia (Smith et al., 1983) due to changes in water temperature, availability of micronutrients and general healthiness of the blades. Jackson (personal communication) is developing a computer-based mathematical model of kelp bed photosynthesis and productivity that takes account of the many factors affecting photosynthesis in Macrocyst is. The model is still in a preliminary state of development, but in its present state has yielded interesting predictions as to effects of planting density, changes in latitude, and seasonal changes in plant size (the seasonal changes in plant size predictions were confirmed by measurements conducted by Kirkwood, 1977, in a Macoystys bed at Palos Verdes, California).

Growth in Macrocystis, on a short term basis, consists of development by individual fronds and haptera and, over the longer term, increase in holdfast size and total numbers of fronds per plant. The short term growth parameters can be easily determined through in situ measurements of hapteral and frond lengths by divers. Long term results of growth can also be estimated in situ (measuring holdfast dimensions, counting numbers of fronds), or by removing plants from the water and weighing them (Neushul and Harger, 1983; the latter technique requires correction for added weights from extraneous factors such as entrapped water and sediment as well as encrusting organisms). Gerard (personal communication) developed a technique for estimating changes in frond biomass based on in situ measurements. First, a relationship is determined for frond length vs frond weight by sampling fronds from a target population. Then the frond size distribution pattern is determined by measuring overall lengths of a large number of randomly selected fronds from the population in situ. Concurrently, frond density is estimated in situ by counting all fronds within randomly positioned quadrats of known areas. Biomass per unit area is then estimated as the sum of the mean weights of the various size classes of fronds, adjusted for the frequency of occurrence of each size class in the total frond population, multiplied by the density of fronds per unit area. The determinations are repeated at a later date and the difference between the two sets of measurements provides an estimate of biomass change during the interval. The productivity of each frond size class can be assessed by measuring elongations of fronds in the population over a given time period and calculating the resulting weight increment from the length-weight relationship. Summing productivities of each frond size class (adjusted for frequency of each size class) yields productivity by the entire frond population.

Methods for assessing frond growth have been variously proposed (North, 1971b; Kain, 1982; Gerard, 1982b; Grua, 1964; Manley, 1984). Changes in mean frond growth rates are useful for assessing healthiness of Macrocystis populations. Frond growth rates, measured either as length or weight changes, are hot uniform with time, but change as the frond ages. It is thus necessary that measurements either be made on a sample of fronds all of similar ages or that corrections for the age factor be introduced if the sample includes fronds of various ages.

3. LIFE HISTORY

3.1 Life cycle and reproduction

3.1 Life cycle and reproduction

The Macrocystis life cycle **(Figure 1A)** consists of a dimorphic alternation of generations between a macroscopic diploid sporophyte and microscopic haploid gametophytes. Biflagellated zoospore production begins after the sporophytes are 6 to 12 months old. Spores are transported away from the parent plant primarily by natural water movements and secondarily by their own swimming activity. Those settling on suitable substrata produce germ tubes in a few hours. The spore content migrates down the germ tube in producing the first cell of the gametophyte (a few gametophytes apparently do grow directly from the spore without intervention of a germ tube). The initial gametophytic cell grows and divides into one or two cells (females) or several cells (males) in a week or two.

Male and female gametophytes can be differentiated after about a week in laboratory cultures by color and shape. Males are pale or bluish, the cells are small, and the overall shape is often filamentous. Females are yellow-green, gold, or brown with round or ovoid shapes. Gametogenesis may begin in 7 to 10 days. Antheridia on males liberate biflagellated sperm. The entire gametophyte in single celled females may form the deeply pig-mented ovum, or only one cell may become an ovum in multicellular females. All cells, however, may eventually develop into ova.

The ovum is extruded from the oogonium and becomes fertilized. Extrusion may or may not rupture attachment of the ovum to the oogonium. If detached, the ovum or zygote is capable of settling elsewhere and forming a new attachment. Rapid cell division in the zygote produces the embryonic sporophyte. Within a few weeks, growth yields tiny blades just visible to the naked eye.

The single blade stage in Macrocystis closely resembles that of other Laminariales. Positive identification as Macrocystis can be made when traces of the first or primary split occurs immediately at the junction of blade and stipe which eventually creates two separate blades or basal meristems **(See Figure 1A).** Further splitting and appearance of frond initials leads to development of the adult morphology in the young plant.

Although spore production is enormous (Neushul, 1959, estimated there were 10,000 sporangia/cm^2 in Macrocystis sporo-phylis), probably only a small fraction ever settle on suitable substrata and vastly smaller numbers survive through the microscopic phases of the life cycle (Anderson and North, 1966; Deysher, 1984).

Young sporophytes normally appear at only distances of a few meters to ca 100 m from attached plants. Drifting adult sporophytes, however, may disperse spores in areas lacking attached Macrocystis, possibly providing opportunities for establishing the species.

4. POPULATION STRUCTURE AND MORTALITY

4.1 Age, weight or size composition
4.2 Sporophyte - gametophyte sex composition
4.3 Mortality, morbidity

4.1 Age, weight or size composition

Natural Macrocystis populations vary widely in their population structures. Sometimes nearly all plants will be of similar sizes and ages while in other cases plants of varying ages and sizes occur intermixed. The former type of age-size structure sometimes arises after a major catastrophe such as an exceptional storm destroys almost all Macrocystis throughout a large area. Normally, the bottom in such an area would be well seeded with microscopic spores and, thus, gametophytes. Removal of most adult plants would increase bottom illumination dramatically, stimulating garoetophytic growth and production of embryonic sporophytes. Assuming good survival, a population of adult sporophytes of uniform age would eventually develop. Once a canopy is formed, further recruitment of juvenile plants ceases and only the oldest plants with fronds in the canopy receive enough sunlight to survive. The shorter plants perish for lack of sunlight, leaving a population of uniform age and size. If a few of these survivors perish more or less randomly as time passes, canopies of the remaining plants will still prevent recruitment of juveniles. Random attrition and continued growth by the survivors produces a population of scattered old plants with large holdfasts, each supporting many fronds.

Populations of variously sized plants occur where forces of attrition are high so that mortalities occur frequently. Patches of open water can appear between adult plants, allowing enough sunlight into the water column to support areas of juvenile recruitment during periods of clear water. Thus, plants of all sizes and ages coexist (for harvesting effects, cf. Kimura, 1980).

One of the major agents of attrition in Macrocystis forests is dislodgement of plants by storm-generated waves. Storm-attrition is greater the shallower the water. Consequently, the offshore edges of kelp beds experience less storm attrition than inshore edges. We frequently observe uniformly large and widely spaced old plants along the offshore borders of Macrocystis beds, while inshore portions of the beds support mixed sizes of fairly young plants, often in dense aggregates.

A unit commonly employed for assessing size among adult Macrocystis plants is the number of fronds. The typical adult Macrocystis is composed of fronds of varying lengths ranging from initials a few cm long to fully mature fronds with 5 to 10 m or more of their length stretching horizontally in the canopy (the longest frond I ever measured was 44.8 m and probably 3 m was missing from the distal end). Although frond lengths on a given plant vary, frond size distribution per plant stays within narrower limits (North, 1968), particularly for populations growing at a given depth. The average weight of all fronds in a population thus tends to be similar, increasing slightly with depth. Thus the mean wet weight of all fronds from plants growing at depths of 10-20 m is slightly more than 1 kg, while for plants growing at 20-25 m depths, the mean wet weight is ca 1.5 kg (North, 1958). Total biomass in a population can be estimated by multiplying frond density (obtained by counting all fronds at the plant bases occurring within several randomly-located quadrats in the bed) by the mean wet weight of a frond (i.e. ca 1 kg). For natural kelp beds with coherent canopies, a range of biomasses of 3 to 22 kg/m^2 was reported by North (1971a).

4.2 Sporophyte - gametophyte sex composition

Nothing is known about proportions of Macrocystis sporophytes to gametophytes in natural populations, or of the sex composition of gametophytes. The microscopic dimensions of gametophytes make them difficult to detect on natural substrates such as rock or hard organic material. Fates of gametophytes and sporophytes have been followed on outplanted artificial substrates (Dean and Deysher, 1983), and recruitment has been monitored on concrete blocks (Foster 1975a, 1975b). Outplanted Macrocystis gametophytes survived only 40 to 45 days off San Onofre, California (probably a fairly hostile environment). In laboratory cultures, approximately equal numbers of male vs female gametophytes develop from settled spores.

4.3 Mortality, morbidity

Rosenthal et al., (1974) monitored tagged adult Macrocystis in a bed off Del Mar, California for 5.7 years and reported that the primary causes of mortality were: storms, entanglement between drifting and attached plants, and kelp harvesting (holdfasts were presumably pulled loose during cutting). North (1971a) studied Macrocystis mortality by tagging plants and following their disappearances over a few months, computing half-lives by assuming that mortality remained fairly constant (a half-life is the time required for 50% of a tagged population to disappear). Half-lives ranged from two months for very exposed populations during winter, to several years for well-protected plants off Santa Barbara, California. Similar results were reported by Dayton et al. (1984).

Gametophyte mortalities are probably much greater. Deysher (1984) found that Macrocystis gametophytes outplanted on rope substrata, survived only 40 to 45 days off San Onofre (as judged by cessation of sporophyte production on the ropes). San Onofre is believed to be a somewhat hostile environment for gametophytes because of sedimentation (Devinney and Volse, 1978, showed that even light sedimentary deposits were very harmful towards Macrocystis gametophytes).

5. PRODUCTIVITY OF THE RESOURCE

5.1 Productivity and harvesting yield
5.2 Principal factors affecting productivity
5.3 Genetic studies and breeding studies
5.4 Relative contributions from vegetative & sexual reproduction to the harvest
5.5 Environmental enhancement

5.1 Productivity and harvesting yield

Biomass production by plants depends on availability of sunlight and nutrients. Most of the photon flux through the water surface is presumably utilized when plant biomass is distributed so as to completely cover the surface, as in dense Macrocystis canopies. Nutrient availability is influenced not only by concentrations of nutrients in the surrounding waters, but also, by water motion and amounts of plant surfaces exposed for taking up nutrients. Ryther and coworkers have shown that approximately parabolic relationships exist between production and density of biomass when aquatic plants and seaweeds are grown under light limiting conditions (i.e. water motion and nutrients are not growth-limiting). That is, there is an optimum density of plant tissue at which biomass production and yield are maximal. The optimum tissue density is different for differing kinds of plants (e.g. 0.02 kg dry/m^2 for Lemna minor, 0.5 to 1 dry kg/m^2 for Eichornia crassipes, Ryther et al., 1979) and is affected somewhat by season (Ryther et al., 1977).

Neushul and coworkers attempted to determine the optimal biomass density for maximizing yield from Macrocystis angusti-folia by growing adult transplants at three biomass densities (initial values 1.7, 6.4 and 24.3 fronds/m^2, representing 0.0625 to 0.25 and 1 plant/m^2) on test plots. Half of the plots were fertilized with ammonium sulfate, half were unfertilized. Harvested yields varied seasonally and were highest for the period May-July for all three planting densities (Neushul and Harger, 1983). Projected yields (i.e. assumes that no frond was lost and that all fronds produced were eventually harvested) from five harvests the yields averaged 5.6, 13.9 and 24.8 DAFMT/ha/yr (dry, ash-free metric tons per hectare per year; presumes that one DAFMT =1.786 dry ton = 14.286 wet ton) from the three densities respectively. Total yields from the fertilized plots were slightly higher than from the unfertilized areas for the two highest densities, but yields from the fertilized plots for all three densities were substantially higher for the July-September period, a time when ambient nutrients were low (Neushul and Harger, 1983). The study thus indicated that the optimal biomass density for Macrocystis lies above 24.3 fronds/m^2. Although I have measured a density of 30 fronds/m^2 in a natural Macrocystis bed, it seems likely that such very high densities cannot be sustained for long. During the course of this 15 month study, Neushul and Harger (1.c.) reported that plants in their high density plots decreased in size so that the overall frond density declined by a half during the study. North (1971a) found a range of 2 to 15/fronds/m^2 for large size samples from Macrocystis beds in California and Mexico. Most populations fall in the range of 3 to 6 fronds/m^2.

Gerard and North (1984) measured production and harvested yield on a group of 63 adult M. pyrifera held for 2 1/2 months in an enclosure with intermittent fertilizing (9-13 uM NO_3 and 1 uM PO_4). Deterioration in the basal portions of the plants occurred, probably from lack of water motion due to the enclosure. In spite of these difficulties, they estimated that 50% of the total productivity was recovered as harvested yield.

Considerable data are gathered by the California Department of Fish & Game as to fresh weights of Macrocystis harvested from beds within the State. In most cases, kelp bed areas involved in the harvesting were not distinguished. Neushul et al., (1982) conducted a special study in cooperation with a kelp harvesting concern in which both the weight of kelp and the area harvested were determined for a kelp bed off Goleta, California. They obtained a yield of 8.3 DAFMT/ha/yr. A similar one year study by North et. al., (1982) for a fertilized bed off Leucadia, California/gave a yield of 12.3 to 14.8 DAFMT/ha/yr. Barilotti (pers. comm.) reported that yields from the kelp bed off Pt. Loma, California, ranged from 1.2 to 4.9 DAFMT/ha/yr.

The total annual harvest of kelp (primarily Macrocystis) from California waters shows considerable year to year variation resulting from interactions of both environmental, economic, and other factors **(Table 1).** Data from Neushul (1981a) suggest that areas of canopies have varied substantially, probably accounting for some of the variations in total harvest. (Examples of canopy variation are shown in **Figures 2 and 3** below). Macrocystis was harvested maximally from 1916 to 1918 and from at least 1955 onward because of favorable economics. Kelp was used as a source of potash during World War I, but the demand collapsed after the war terminated (Scofield, 1959). Interest in kelp for animal feed additives and chemicals led to renewed harvesting activity in the late 1920's. Demand for alginate products caused steady increases in harvests in the latter 1930's, the 1940's, and has sustained the industry ever since. High water temperatures, unusual storms and reduced availability of nutrients associated with major El Nino oceanographic events, were responsible for reduced harvests in certain years (1957, 1959, 1983).

Table 1. Estimated southern California kelp areas in hectares (modified from Neushul, 1981a) and annual Macrocystis harvest from California waters in wet metric tons (Pinkas, 1977 through 1976; subsequent figures courtesy of K. Wilson and E. Smith, California fish and Game). The area of kelp in hectares is underscored at the head of the respective list of paired years and tonnages.

Total area		Total area		Total area	
Year	Tonnage	Year	Tonnage	Year	Tonnage
13,171		1949	75,610	4,753	
1911		1950	91,265	1967	119,290
1916	122,050	1951	104,109	1968	122,337
1917	358,314	1952	99,935	1969	119,058
1918	358,425	1953	114,894	1970	115,248
1919	15,125	1954	96,358		
1920	23,101			5,971	
1931	236	7,110		1971	141,121
1932	9,358	1955	112,548	1972	147,428
1933	19,614	1956	106,881	1973	138,872
1934	14,406	1957	84,961	1974	154,386
1935	27,762	1958	103,475	1975	155,671
1936	44,740			1976	143,672
1937	39,874	6,510			
1938	43,270	1959	81,283	6,202	
1939	51,470	1960	109,	1977	143,918
1940	53,528	1961	117,259	1978	186,270
1941	50,546	1962	127,217		
1942	56,153			4765	
1943	43,507	2,818		1979	188,464
1944	48,108	1963	109,798	1980	162,693
1945	53,688	1964	115,443	1981	83,822
1946	82,616	1965	122,587	1982	95,326
1947	67,347	1966	108,376	1983	5,334
1948	71,342			1984	47,320

5.2 Principal factors affecting productivity

5.2.1 Physical factors

As noted above, wave exposure is reckoned as the primary environmental factor causing losses of kelp tissues and entire plants on exposed coasts (Rosenthal et al., 1974; Gerard 1976). High water temperatures and lack of nutrients lead to losses of canopy tissues during warm summers (Jackson, 1977; North, 1983). A combination of record storms, warm water and low nutrients associated with an El Nino event in 1983, destroyed more than 90 percent of the kelp canopies in southern California, leading to the poorest annual harvest yield in recent times (see **Table 1).** Factors affecting recruitment of juvenile plants have a delayed influence on the adult population. Increased sedimentation from construction projects and discharged waste materials may have temporary or long-lasting effects.

Figure 2. Historical charts showing changes in canopy size for a large Macrocystis pyrifera bed off Point Loma California. Kelp is shown as black. Kelp restoration activities (primarily sea urchin control) began near the south end of Point Loma in 1963.

Figure 3. Historical charts showing changes in canopy size for beds of Macrocystis angustifolia (before 1974) and M. pyrifera (after 1974) off the Palos Verdes coastline in southern California. Kelp is shown as black. Kelp disappeared completely from the area in 1968 but was restored by urchin control and kelp transplantation efforts.

5.2.2 Biological factors

Grazing by sea urchins has led to declines and, in some cases, complete disappearances of major kelp areas in California and Baja California during the period 1940 to 1965 (Leighton et al., 1965). Probably declines in major urchin predators such as sea otters, lobster, and certain fishes eliminated some of the natural factors controlling size of urchin populations (Tegner and Levin, 1983; Leighton et al. 1.c.). Programs of artificial control of urchins were associated with reappearances of Macrocystis beds at Pt. Loma and Palos Verdes, California, in the 1960's and 1970's respectively **(Figures 2 and 3)**.

Grazing by herbivorous fishes does not usually reach destructive proportions in large established Macrocystis beds. Fish grazing may cause significant difficulties, as noted above, when attempts are made to introduce transplants of adult or juvenile kelp into areas where no Macrocystis exists. Presence of the plants probably attracts herbivorous fishes to the transplant sites and a large amount of grazing is focused on their rather small biomass.

Competitive algae can be a serious impediment to either natural recruitment of juvenile Macrocystis or to reestablishment of this species in an area by transplanting or "seeding" with microscopic stages. Removal of competitors from 1 to 3 m of bottom provides an opportunity for a small transplant to grow to a size where it can overcome competitive effects.

Several kelp diseases have been described (North, 1979b; Scotten, 1971). Most are associated with summertime deterioration of canopies during periods of elevated water temperature and low nutrients. Some localized rotting of stipes near plant bases on Macrocystis holdfasts has been observed in areas of organic enrichment by sewage (North, 1979b).

5.2.3 Possibilities of control measures

Several techniques have been utilized in southern California for controlling overgrazing by sea urchins. Urchins have been destroyed by quicklime, crushed with hammers, and sucked up by dredging machinery (Wilson & McPeak, 1983; Wilson & North, 1983; Leighton et al., 1965). Attempts to control herbivorous fishes by gill-netting, spearing and dispersals of poisons were only partially successful.

As noted above, removal by cutting or plucking of competitive algae from the immediate vicinity of a young Macrocystis (either transplanted or naturally attached) will assist survival until the young plant attains a height of 2 to 3m and begins to eliminate surrounding competitors by shading them. There are no known methods for controlling diseases of Macrocystis plants. Since most of the diseases occur during summer when surface waters are warm and depleted of nutrients, fertilizing might be expected to improve plant healthiness. Research is needed, however, because excessive fertilizing might benefit the disease organisms.

5.3 Genetic studies and breeding studies

Neushul and coworkers have undertaken breeding studies involving crosses between the three species of Macrocystis, between Macrocystis and closely related kelps such as Pelagophycus and development of clones derived from highly productive adult Macrocystis raised on their test farm at Ellwood, California (Sanbonsuga and Neushul, 1978a, 1978b; Neushul, 1981b; Neushul and Harger, 1985). Work is still in progress and it is not yet established whether enhanced productivity will be possible. Stock cultures of gametophytes of the various species and strains are maintained by this research group. One possibility for enhancing Macrocystis productivity would involve development of a strain which would have tolerance for elevated water temperatures and could be cultivated at low latitudes where wintertime reduction in available sunlight is not as pronounced as in California. Clendenning (1971) reported that Macrocystis from Turtle Bay, Baja California (near the southern limit of the Macrocystis range in North America) exhibited a photosynthetic capacity per unit area that was about 50% higher than the capacity found for plants from California. The temperature optimum for photosynthesis from Turtle Bay kelp was between 25°C and 30°C, about 5°C higher than for kelp from southern California.

Another interesting possibility for improving harvest yield might be utilization of a Macrocystis strain occurring only in Paterson/inlet, New Zealand (Gerard and Kirkman, 1984). This plant can generate several apical meristems on a single frond through production of side branchings along the frond length. Use of this characteristic in a harvested crop might substantially reduce the period required for canopy regeneration after cutting.

5.4 Relative contributions from vegetative & sexual reproduction to the harvest

Both sexual and vegetative reproduction are important to maintaining the Macrocystis crops available for harvest. Effects of sexual reproduction, however, are indirect and serve only to replace adult plants lost to storm or other adversities. Vegetative growth by young fronds with intact apical blades is entirely responsible for regenerating kelp canopies following harvesting.

5.5 Environmental enhancement

Macrocystis populations in southern California are sometimes adversely affected by nutrient starvation. As noted above, depletion of nutrients in surface waters above the thermocline is probably a major factor causing canopy deterioration during summer. Nutrient depletion probably also occurs in association with major El Nino events (a complex sequence of oceanographic events beginning near the equator, spreading to higher latitudes, sometimes lasting from a few months to 2-3 years; Dayton and Tegner, 1984; Gerard, 1984a). Fertilizing Macrocystis canopies prior to deterioration might serve to preserve for harvesting much organic material that might otherwise be lost. Neushul and Harger (1983) observed greater yield during summer from fertilized than from unfertilized plots on their test farm. Fertilizing a kelp bed by crop dusting techniques using helicopters was described by North et al., (1982).

Fertilizing might also be helpful if a Macrocystis crop growing under low-nutrient conditions were to be utilized in preparation of animal feeds. Contents of N and C can be raised substantially in a few days by addition of nitrogen as nitrate or as ammonium to the medium (North, 1978). P-contents of kelp tissues also rise as external concentration of inorganic phosphate is raised (Manley et al., 1982b).

Sizes of Macrocystis beds can be increased by provision of artificial substrate for transplanting **(Figure 4).** All that is required is an anchoring mechanism. The adult plant does not need to be attached to the bottom (Wilson and North, 1983). Small plants can, however, easily be affixed to solid substrates if so desired (McPeak et al., 1973).

6. METHOD OF HARVESTING AND HARVESTING CYCLE

6.1 Annual operations
6.2 Manpower productivity
6.3 Alternate employment

6.1 Annual operations

Given appropriate environmental conditions favoring Macrocystis growth, canopies can be available throughout the year. Kelp beds occur in a variety of environments in southern California, so at least some canopy is available somewhere for harvesting at all times of the year. Winter storms and warm waters during summer can create seasonal scarcities of plant material available for harvesting.

6.2 Manpower productivity

Operational and economic statistics from the California kelp harvesting industry are closely guarded and not available to the public. It is believed, however, that manpower requirement for operation of even large harvesting vessels is modest, amounting to four to six individuals. Manpower for unloading and pro cessing the cut kelp is unknown and undoubtedly depends to some extent on intended uses of the kelp and the degree of automation available in the processing factory.

Figure 4. Technique for (A) threading a rope in a Macrocystis holdfast preparatory to transplanting, (B) moving several kelp transplants to a new location. (Threating the Holdfast)

Figure 4. Technique for (B) moving several kelp transplants to a new location. (Transplanting Operation)

Two economic analyses of kelp harvesting operations and costs were prepared for marine biomass studies undertaken by the U.S. Naval Ocean Systems Center (NOSC) and the Gas Research Institute (GRI). The NOSC study envisioned a Macrocystis farm of about 40,000 ha with an annual productivity of 946 wet metric tons per ha (Integrated Sciences, Inc., 1976). The personnel estimate specified 220 individuals required for harvesting the kelp and 403 shore-based personnel for processing the raw material into the ultimate product (methane gas). These figures indicate that 172,000 t/yr would be produced per individual involved in the harvesting. If we assume that the annual California kelp harvest of about 180,000 t **(Table 1)** can be obtained by three vessels or 15 individuals, a figure of 12,000 t/man-yr is calculated, considerably below the productivity estimate from NOSC. The discrepancy arises partially from the circumstance that productivity of the wild crop in California at about 35 t/ha/yr, is much lower than that assumed in the NOSC study. The comparison is much closer if it is drawn on the basis of areas harvested, 182 ha/yr/individual for the NOSC study and 333 ha/yr/individual for the California kelp industry.

The GRI-sponsored study envisioned a Macrocystis farm of 16/300 ha yielding an estimated 674 wet t/ha/yr (R.M. Parsons Co., 1983). Their scheme depicted two individuals working 12 hr. shifts in operating the harvesting vessel. This is equivalent to six individuals per day working 8 hr. shifts, giving 1,830,000 t/man-yr. or 2,700 ha/man-yr. These higher figures assume a much greater degree of automation in the harvesting machinery than actually exists in the California kelp harvesting industry.

6.3 Alternate employment

There is no need for alternate employment in the California kelp harvesting industry, as far as is known.

7. EQUIPMENT USED FOR HARVESTING

7.1 Wild resources
7.2 Macrocystis culturing
7.3 Sources of credit and insurance

7.1 Wild resources

As stated above, detailed operating characteristics and economics of harvesting are not available to the public from the California kelp harvesting industry. The harvesting barges carry the cutting apparatus at the sterns of the vessels and proceed in reverse when operating in a kelp canopy. Cutting is accomplished by reciprocating blades attached to a horizontal bar that is lowered to a fixed depth of 1.2 m below the waterline. Cut ends of the kelp fronds are carried against a conveyor belt just behind the cutting bar. The cut kelp is carried up on the belt over the gunwale, and deposited in an open hold that extends for most of the barge's length. A mechanically driven steel claw or grapnel is used to distribute the cut kelp evenly throughout the hold. The bridge crew's quarters and other necessary spaces are on the bow, forward of the hold. Typical harvesting vessels may load several hundred wet tons of kelp per trip. Cameron (1915) described a harvesting vessel of his day in considerable detail **(Figures 5 to 7).** The essential features of a kelp harvester, as described above, were fully developed even then.

Harger (1979) studied harvesting activity in Goleta Bay for four years, seeking correlations between amount of kelp obtained and ten environmental variables which he monitored. The most important were surface irradiance, water temperature, swell height, and nitrate concentrations (surface & bottom). He developed a model wherein environmental conditions accounted for 46% of the variability in harvest. Harger found that the harvest rate could vary from about 13 to 110 wet t/hr/with a majority of values lying between 40 and 80 wet t/hr.

Gerard and North (1984) calculated that their simulated harvesting operations removed about 50% of the plant biomass. Macrocystis beds are generally harvested only when dense canopies justify such activity, otherwise a bed is left unharvested until an adequate canopy develops. A bed may thus be left uncut for several years. Productive beds, however, will usually support three harvests per year (C. Martin, personal communication). Brandt (1923) reported that some beds were harvested continuously for five or more months per year, but yields fell significantly following such intense usage.

Capital and maintenance costs of harvesting vessels, docking and unloading facilities, etc., for the California industry are not public information. The NOSC economic analysis budgeted $133,800,000 for start-up harvesting costs with annual operating expenses of $17,400,000 (Integrated Sciences, Inc., 1976). Ralph M. Parsons Co. (1983) listed the cost of a 12x27 m harvesting vessel as $1,677,000 plus $805,000 for a 12x45 m barge to receive the cut kelp. Their operating expenses were $4,830,200 which included all activities, not just harvesting. Thus the NOSC estimates seem extremely high, but the number of harvesting vessels involved was not specified. Also, they planned to operate a kelp farm 160 km offshore, which would increase operating costs considerably since the processing plant was onshore.

The manpower requirement, as stated above appears to be in the range of 200 to 300 ha of kelp bed that can be harvested per man-year using mechanical harvesters as they presently exist. Automation might be able to increase these values.

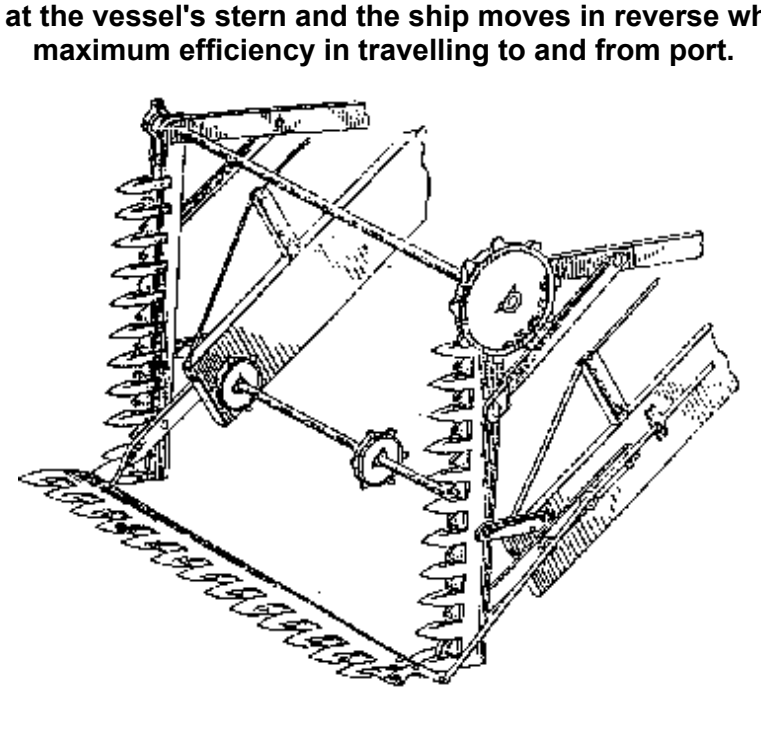
7.2 Macrocystis culturing

Presently no commercial-scale culturing of Macrocystis is conducted in California. North (1976, 1972) described experimental facilities for mass-culturing Macrocystis gametophytes and embryonic sporophytes for dispersal in kelp areas to enhance the recruitment processes. Wilson and North (1983) reviewed techniques for transplanting young and adult Macrocystis plants to initiate new populations in depleted areas. McPeak (1975) described a four-year transplantation effort that involved installation of about 28,000 young Macrocystis at the north end of the La Jolla kelp bed.

Figure 5. Elevation view, showing bow section of a Macrocystis harvesting vessel as used in the Palos Verdes area of southern California during World War I (from Cameron, 1915). Kelp cutting apparatus and conveyor belt arrangement are similar in principle to equipment in present-day usage.

Figure 6. Plan view of Macrocystis harvesting vessel as shown in Figure 4 (from Cameron, 1915). The cut kelp was loaded onto a barge on the starboard side, while propulsion through the water was supplied from a separate launch. Modern harvesters are larger vessels, loading the kelp onboard in a bin aft from the front conveyor, and are self-propelled.

Figure 7. Perspective view showing details of the cutting apparatus located at the bow of the harvesting vessel of Figure 4 (from Cameron, 1915). Modern harvesters have the cutting and loading equipment at the vessel's stern and the ship moves in reverse while cutting kelp. The prow is V-shaped/providing for maximum efficiency in travelling to and from port.



7.3 Sources of credit and insurance

Industrial loans from commercial banking sources presumably have been available and used by kelp harvesting concerns in California. The major remaining such organization at the present time is Kelco Company of San Diego, a division of Merck & Co., Inc. During periods of crop shortages in California waters, Kelco imports raw material from foreign sources. Dependence on imports, rather than insurance, appears to be the preferred method for sustaining operations in case of natural disasters.

8. PROTECTION AND MANAGEMENT OF THE RESOURCE

8.1 Management of Macrocystis resources
8.2 Regulation

8.1 Management of Macrocystis resources

Commercial harvesting of Macrocystis in the USA does not occur north of Monterey Bay in central California. Macrocystis is also harvested in northern Baja California, Mexico, and transported to the processing plant of Kelco.

The kelp harvesting concerns in California have all operated as private entrepreneurs, independent of linkages to governmental agencies. Interest in kelp resources led to formation of several kelp harvesting enterprises in the early 1900's (Scofield, 1959; P. Neushul in Neushul and Harger, 1985). Some of the organizations utilized harvesting techniques that may have damaged the resource and contributed unnecessarily to beach litter. Since all the kelp beds lie within three miles of the shoreline, their ownership resides in the State of California. The responsible State agency for management of living marine resources is the Department of Fish and Game with policy direction from the Fish and Game Commission. Concern about welfare of the kelp resource around 1916 led to a joint effort by the Commission, conserva-tionists, and the larger kelp harvesting concerns, to control harvesting methods and practices. Results were the first set of regulations covering kelp harvesting activities, enacted July 26, 1917. The regulations have been expanded and amended since then on several occasions.

Regulations now divide the California kelp beds into two categories: open beds (available for harvest by anyone) and closed beds (restricted for harvesting by a lessee only). A third of the beds are required to be held in the open category. Harvesters must purchase a license and pay a privilege fee of 10 cents for each wet ton harvested and a second assessment of $100 for each square mile of kelp bed harvested. Since 1950, leases are granted by negotiation (before, leases were awarded on the basis of sealed bids). Leases are granted for periods of fifteen years or less. Lease rights confer only harvesting privileges and have no control over fishing or navigational activities.

8.2 Regulation

In 1956, the Fish and Game Commission decreed that depth of kelp cutting should be no greater than four feet (1.22 m) below the surface and all material cut must be fully utilized (i.e. no escapement of cut fronds is allowed. This latter is to prevent increasing beach litter as a result of harvesting). Violations may result in fines or suspensions of the license to harvest. Enforcement is accomplished by wardens operating from patrol vessels.

9. UTILIZATION

9.1 Chemical and nutritional content
9.2 Human Food
9.3 Animal fodder and feed additives
9.4 Manure and fertilizer
9.5 Industrial products and processes

9.1 Chemical and nutritional content

Paine and Vadas (1969) reported the caloric content of M. pyrifera as 2.85 kcal/g dry wt, or 4.3 kcal/g dry minus ash. Similar values were obtained for a closely related kelp, Nereocystis leutkeana. Because of the high ash content, the above caloric values were among the lowest of seventeen seaweed species assayed by these workers. With ash corrections most species were very similar. Effects of various light intensities and nitrate concentrations on caloric value of cultured juvenile Macrocystis sporophytes were determined by Shivji (1985).

Extensive analyses of organic and salt composition of the Pacific coast kelps, including Macrocystis, were reported by Balch and by Turrentine from work in the early 1900's (cf. Cameron, 1912, 1915). The most recent general studies were conducted in connection with the Marine Biomass Program **(Tables 2 and 3).** As a result of these studies, it became known that concentrations of some of the organic and inorganic constituents vary substantially according to environmental conditions and the recent history of the tissue under analysis. Thus the ranges of mannitol contents of M. pyrifera fronds increased from 5 to 15% dry wt to 14 to 33% dry wt in a plant transferred for three weeks into a low-nutrient environment (Gerardy 1982b). Tissue contents of nitrogen and phosphorus in young M. pyrifera sporophytes reflected concentrations of the inorganic salts of these elements in the culturing media (P.A. Wheeler and North, 1980; Manley et al., 1982). Seasonal variations in dry weight, ash, N, P, S, Cu, Zn, Fe, ether solubles, algin, mannitol, laminarin, and fucoidin were studied for 2 years in M. integrifolia by Wort (1955).

Table 2. Gross composition of Macrocystis, combining data from Point Loma and San Clemente Island (Lindner et al. 1977) and from Monterey Bay, Santa Cruz, and Soquel Point (Hart et al., 1976). Standard deviations are shown for ash, solids, and alginic acid for all samples combined.

Substance and % Wet or Dry Wt.	Percent Composition		
	All Samples	So. Calif.	Cen. Calif.
% WET WT			
Water	88.2		
Solids	11.8 ± 1.0^a	12.2	11.3

% DRY (550°C)			
Ash	38.96 ± 6.24[b]	37.29	40.49
KCl	29		
NaCl	7		
Na_2SO_4	4		
Other	4		
Volatiles	66-53		
Mannitol	6-22		
Laminarin		1-2	
Fucoidan		0.5-2	
Alginic Acid	15.71 ± 2.56[c]	18.6	11.4
Cellulosics	3-8		
Protein	5-14		
Fat	0.5-2		

[a] 42 samples
[b] 44 samples
[c] 35 samples

Table 3. Concentrations of selected elements in wet Macrocystis tissues (modified from North, 1980) and in seawater according to Brewer (1975). The ratio of these two sets of numbers was taken as the concentration factor for each element. The tissue and seawater values are in micromoles per given unit.

Element	Concentration		
	Tissue per gm wet wt.	Seawater per liter	Concentration Factor
Phosphorus	11.6	0.2	58,000
Beryllium	0.025	0.00063	40,000
Nitrogen	10.5	0.5	21,000
Antimony	0.0125	0.002	6,000
Iron	0.175	0.05	5,000
Cobalt	0.00375	0.0008	4,700
Arsenic	0.175	0.05	3,500
Manganese	0.0125	0.0036	3,500
Aluminum	0.120	0.074	1,600
Copper	0.01	0.008	1,300
Iodine	0.588	0.5	1,200
Zinc	0.0688	0.076	900
Vanadium	0.0375	0.05	750
Nickel	0.00625	0.028	220
Molybdenm	0.00125	0.01	130
Boron	3.13	410	8
Lithium	0.19	26	7
Strontium	0.475	91	5
Silicon	0.35	71	5
Potassium	15	10,200	1.5
Uncertain			
Selenium	0.00125	0.0025	500
Chromium	0.00125	0.0057	220

Bromine, Rubidium, and Fluorine are not concentrated.

9.2 Human Food

Usage of Macrocystis tissues as human food is minor in North America. Macrocystis and Nereocystis slices are occasionally prepared as pickles by individuals, but there is no known commercial product of this kind. Dried powdered kelp (probably M. pyrifera) was formerly marketed by Philip R. Park, Inc. A fraction of the product entered specialty items in health food stores (P. Neushul in Neushul and Harger, 1985).

9.3 Animal fodder and feed additives

Dried kelp (probably Macrocystis pyrifera) was formerly produced by Philip R. Park Inc. and Kelp Organic Products Co. of Los Angeles. Most of the material was incorporated into animal feeds. Neither of these concerns exist at this time (P. Neushul, 1.c.). The value of this Macrocystis as fodder might be enhanced by fertilizing shortly before harvesting to increase nitrogen and phosphorus contents of the tissues via (cf. Mateus et al., 1976) its amino acid composition.

9.4 Manure and fertilizer

No present usage of Macrocystis as a manure exists in California. A large and successful effort was mounted during the first World War to secure kelp as a source of potash for manufacture of fertilizer and explosives (Cameron, 1915; Scofield, 1959; P. Neushul, 1.c.). Presently, all Macrocystis harvested in California and Baja California is processed for alginate production and the resource is fully utilized. An economic study of the feasibility of using Macrocystis for methane production proposed dispersal of sludge remaining from digestion of the kelp, into their kelp farm as a fertilizer (Ralph M. Parsons, 1983).

9.5 Industrial products and processes

As noted above, alginates are the only products currently manufactured from harvested Macrocystis in California. Various compounds of the complex polysaccharides, alginic acid, serve as stabilizers, thickeners, emulsifiers, water-holders, and film-forming or suspending agents. Most of the usages are in foods, pharmaceuticals, beverages, dairy products, and in the manufacture of latex, textiles, as well as paper and cardboard, plus other applications (Kelco, 1961; P. Neushul, 1.c.). Two methods for alginate manufacture are the Le Gloahec-Herter and Green's cold processes, both described with flow charts by Chapman (1970). Salts are first leached from cut or slurried kelp in weak acid. The alginate is then solubilized or induced to form a gel by soaking the kelp in a solution of sodium carbonate or other weak alkali. Reduction of pH by dilution with water or addition of acid causes precipitation and the recovered material can be sold as crude alginate or refined further by repeated solubilization and precipitation (Tseng, 1945).

In the past, a number of other industrial products have been derived from Macrocystis in California, particularly during the period of intense utilization during World War I. These included potash and acetone for explosives manufacturing (potash was also employed in manufacture of matches), iodine, and char (P. Neushul, 1.c.). The early kelp industry was unable to compete with German sources of potash which once more became available to American industry after termination of the war in 1919. The California kelp industry collapsed for about a decade until interests in alginate production and the uses of kelp in animal feeds revived harvesting activities in 1927-28.

A possible future usage of Macrocystis is as alternative sources of energy in the form of gaseous or liquid fuels. The feasibility of liquid fuel production has already been demonstrated on a commercial scale by production of acetone in World War I by Hercules Powder Company (P. Neushul, 1.c.). Extensive investigations of the potential for methane production from kelp were recently completed (Tompkins and Bryce, 1984). This study, the Marine Biomass Program, also yielded considerable information relating to Macrocystis biology, and many of the resulting publications were cited above. We also referred to two of the economic analyses that were performed (Integrated Sciences, Inc., 1976; Ralph M. Parsons, 1983). Macrocystis tissue proved to be an excellent substrate for methane production by bacterial digestion processes. Yields of 4.5 SCF/1bVS (0.28 liters of combustible gas per gram of volatile solids) were reported by Chenoweth et al. (1978). Maximal methane yields were recovered from those kelp samples highest in mannitol.

In closing, we should mention that the Macrocystis forests in nature provide an extensive habitat for fishes and shellfish utilized by humans (North and Hubbs, 1968; Leighton, 1971). As such, Macrocystis and other large kelps are an important sustaining element in recreational and commercial fisheries, both of which are well-established activities in California.

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