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### ABSTRACT

## ON THE TAXONOMY, DISTRIBUTION, AND ECOLOGY OF THE BROWN ALGAL GENUS LAMINARIA IN THE NORTHEAST PACIFIC

This study of the brown algal genus Laminaria Lamour. consisted of (1) a critical review of the taxonomy and distribution of taxa of Laminaria occurring in the northeast Pacific, (2) a description of the life histories and growth patterns of long and short stipe forms of L. groenlandica and L. saccharina, (3) an evaluation of the roles of temperature, salinity, and water motion as possible determinants of local distributions of long and short stipe forms of L. groenlandica and L. saccharina, and (4) an evaluation of the roles of temperature, salinity, exposure, and submarine illumination in determining the vertical distribution of L. saccharina. These studies were made from 1961 to 1965.

Ten species of Laminaria are recognized for the northeast Pacific: <u>L. groenlandica</u> Rosenv.; <u>L</u>. <u>farlowii</u> Setchell; <u>L. saccharina</u> (L.) Lamour.; <u>L</u>. setchellii Silva; L. dentigera Kjellman; L. Longipes Bory; L. sinclairii (Harvey ex Hooker f. et Harvey) Farlow, Anderson et Eaton; L. ephemera Setchell; L. yezoensis Miyabe; and L. complanata (Setchell et Cardner) Setchell. Laminaria cordata Dawson is considered conspecific with L. saccharina, L. personata Setchell and Gardner is regarded conspecific with L. yezoensis, and L. platymeris De la Pyl. (sensu Setchell and Gardner) is considered conspecific with L. groenlandica. Four forms of L. groenlandica are recognized for the northeast Pacific. These forms are not considered as legitimate taxonomic entities but are distinguished merely to provide a means of facilitating discussion. The known habitat requirements for all ten species were broadened and the known distributions of all species, excepting L. groenlandica, were extended.

Laminaria saccharina and L. groenlandica produced sori in the late spring and winter. New sporophytes of L. groenlandica appeared throughout the year, whereas those of L. saccharina appeared in late winter and early fall. Depending upon culture conditions, two morphologically distinct forms of gametophytes were produced by both species: large gametophytes were produced in conditions of high temperature and low salinity; and small gametophytes in conditions of low temperature and high salinity. Abnormal sporophytes were observed under conditions conducive to formation of large gametophytes.

Patterns of growth for the blades of the two species were essentially the same. The growth rate decreased with increase in distance from the blade base, and the position of greatest longitudinal growth coincided with the position of greatest lateral growth.

The distributions of L. saccharina and the two forms of L. groenlandica about Vancouver Island were correlated with temperature, salinity, and water The two forms of L. groenlandica were absent motion, from areas of high temperature and low salinity; L. saccharina was absent from areas subjected to surf. These field conclusions were subjected to laboratory and field tests involving gametophytes and sporophytes of both species. The distributions of the two forms of L. groenlandica can be explained on the basis of temperature and salinity distributions. Both forms require low temperature and high salinity for survival. Laminaria saccharina has a wide range of tolerance to temperature and salinity. Surf appears to be the agent controlling the distribution of this species.

The upper limits of L. saccharina, as observed in Burrard Inlet, are thought to be directly related to air temperature and insolation and indirectly related to tidal characteristics. The lower limits appear to reflect the compensation depth of this species.

### GRADUATE STUDIES

Advanced Phycology Marine Phytoplankton Synoptic Oceanography Dynamic Oceanography Chemical Oceanography R. F. Scagel R. F. Scagel G. L. Pickard R. W. Burling P. W. Williams

# ON THE TAXONOMY, DISTRIBUTION, AND ECOLOGY

OF THE BROWN ALGAL GENUS LAMINARIA

IN THE NORTHEAST PACIFIC

by

## LOUIS D. DRUEHL

B.S. Washington State University, Pullman, Washington, 1959 M.S. University of Washington, Seattle, Washington, 1961

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We accept this thesis as conforming to the required standard

THE UNIVERSITY OF BRITISH COLUMBIA

August, 1965

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Department of Biology & Botany

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Date September 30, 1965

### ABSTRACT

This study of the brown algal genus <u>Laminaria</u> Lamour. consisted of (1) a critical review of the taxonomy and distribution of taxa of <u>Laminaria</u> occurring in the northeast Pacific, (2) a description of the life histories and growth patterns of long and short stipe forms of <u>L</u>. <u>groenlandica</u> and <u>L</u>. <u>saccharina</u>, (3) an evaluation of the roles of temperature, salinity, and water motion as possible determinants of local distributions of long and short stipe forms of <u>L</u>. <u>groenlandica</u> and <u>L</u>. <u>saccharina</u>, and (4) an evaluation of the roles of temperature, salinity, exposure, and submarine illumination in determining the vertical distribution of <u>L</u>. <u>saccharina</u>. These studies were made from 1961 to 1965.

Ten species of <u>Laminaria</u> are recognized for the northeast Pacific: <u>L. groenlandica</u> Rosenv.; <u>L. farlowii</u> Setchell; <u>L. saccharina</u> (L.) Lamour.; <u>L. setchellii</u> Silva; <u>L. dentigera</u> Kjellman; <u>L. longipes</u> Bory; <u>L. sinclairii</u> (Harvey <u>ex</u> Hooker f. <u>et</u> Harvey) Farlow, Anderson <u>et</u> Eaton; <u>L. ephemera</u> Setchell; <u>L. yezoensis</u> Miyabe; and <u>L. complanata</u> (Setchell <u>et</u> Gardner) Setchell. <u>Laminaria cordata</u> Dawson is considered conspecific with <u>L. saccharina</u>, <u>L. personata</u> Setchell and Gardner is regarded conspecific with <u>L. yezoensis</u>, and <u>L. platymeris</u> De la Pyl. (<u>sensu</u> Setchell and Gardner) is considered conspecific with <u>L. groenlandica</u>. Four forms of <u>L. groenlandica</u> are recognized for the northeast Pacific. These forms are not considered as legitimate taxonomic entities but are distinguished merely to provide a means of facilitating discussion. The known habitat requirements for all ten species were broadened and the known distributions of all species, excepting <u>L. groenlandica</u>, were extended.

Laminaria saccharina and L. groenlandica produced sori in the late spring and winter. New sporophytes of L. groenlandica appeared throughout the year, whereas those of L. saccharina appeared in late winter and early fall. Depending upon culture conditions, two morphologically distinct forms of gametophytes were produced by both species: large gametophytes were produced in conditions of high temperature and low salinity; and small gametophytes in conditions of low temperature and high salinity. Abnormal sporophytes were observed under conditions conducive to formation of large gametophytes.

Patterns of growth for the blades of the two species were essentially the same. The growth rate decreased with increase in distance from the blade base, and the position of greatest longitudinal growth coincided with the position of greatest lateral growth.

The distributions of <u>L</u>. <u>saccharina</u> and the two forms of <u>L</u>. <u>groenlandica</u> about Vancouver Island were correlated with temperature, salinity, and water motion. The two forms of <u>L</u>. <u>groenlandica</u> were absent from areas of high temperature and low salinity; <u>L</u>. <u>saccharina</u> was absent from areas subjected to surf. These field conclusions were subjected to laboratory and field tests involving gametophytes

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"Not everyone has peered into clear rock pools at the hour of dawn, when the tide is at its lowest ebb and recognized in the dusky shadowy forms of the young kelp, living creatures belonging to the far distant past. Only the fortunate can know the true meaning of the Greek work <u>phaios</u> and fully appreciate its beauty."

Josephine Tilden, 1935

## INTRODUCTION

The brown algal genus, <u>Laminaria</u> Lamouroux, is the most frequently encountered member of the Laminariales in northern temperate coastal waters. Along much of the northeast Pacific coast, particularly north of  $48^{\circ}$ N latitude, it is the dominant lower intertidal plant. Setchelland Gardner (1925) recognized 11 species and 7 forms of <u>Laminaria</u> in the northeast Pacific, and their treatise is the most recent comprehensive taxonomic treatment of this genus in this area. Since then Silva (1957) and Widdowson (1959) have contributed to an understanding of the taxonomy of individual species recognized by Setchell and Gardner; Dawson (1950) has recognized a new species, <u>L. cordata</u> Dawson. Biological studies on <u>Laminaria</u> in the northeast Pacific have been chiefly morphological (Setchell, 1905; Griggs, 1906; Fallis, 1916; and Myers, 1925).

The present investigation consists of two parts. The first, a critical evaluation of the taxonomy and species distribution of <u>Laminaria</u> in the northeast Pacific, was based on extensive collections available for the coasts of British Columbia and Alaska (Scagel, <u>in herb</u>., UBC). These were supplemented by collections of the author from northern Washington to the southern extreme of Alaska. For the remainder of the northeast Pacific, the study was based on herbarium material provided by the University of Washington (WTU), University of California, Berkeley (UC), and the Allan Hancock Foundation (AHFA). The second part is an evaluation of the effects of (1) temperature, salinity, and water motion in determining the horizontal distributions of <u>Laminaria saccharina</u> (L.) Lamour. and two forms of <u>L. groenlandica Rosenv. about Vancouver Island, British</u> Columbia; and (2) temperature, salinity, exposure, and submarine illumination in determining the vertical distribution of <u>L. saccharina</u> in Burrard Inlet, near Vancouver, British Columbia.

To accomplish the second part, the patterns of growth, growth rates, and life histories of <u>L</u>. <u>saccharina</u> and <u>L</u>. <u>groenlandica</u> were determined. An understanding of these biological aspects of the plants was necessary to evaluate plant response to various environmental conditions. The distributions of these two species were subsequently correlated with the above mentioned environmental parameters. Where possible the established correlations were subjected to laboratory and field tests.

Several features make species of <u>Laminaria</u> ideal for an ecological study of the type described above. The vertical distributions of the species extend from the subtidal to the lower intertidal regions. This vertical positioning minimizes the influence of environmental factors operative during periods of emergence, and supports the hypothesis presented here that horizontal distribution of <u>Laminaria</u> is controlled primarily by oceanographic factors rather than meteorological conditions. Since the species studied are perennial, their absence from any locality reflects the

unfavorableness of the environmental conditions in that area for the establishment and maintenance of a population. <u>Laminaria saccharina</u> and the two forms of <u>L</u>. <u>groenlandica</u> studied are easily recognized in the field. The ease with which the sporophytes and gametophytes of these two species can be cultured makes them ideal for in vitro experimentation.

The taxonomy and distribution of <u>Laminaria</u> was studied throughout its known northeast Pacific range--California to Alaska. The distributions of <u>Laminaria saccharina</u> and the two forms of <u>L. groenlandica</u> were correlated with oceanographic factors at several stations about Vancouver Island. <u>In situ</u> studies on <u>L. saccharina</u> were made in Burrard Inlet (49°18'9"N 123°7'30"W) near Stanley Park, Vancouver, British Columbia; on <u>L. groenlandica</u> long stipe form at Glacier Point (48°23'40"N 123°59'10"W), Vancouver Island, British Columbia; and on <u>L. groenlandica</u> short stipe form at the Ogden Breakwater (48°24'50"N 123°23'30"W), Victoria, Vancouver Island, British Columbia.

### GENERAL METHODS AND MATERIALS

The methods and materials described below apply generally to all aspects of this study. Specific information describing experimental conditions is discussed along with the results of the individual experiments.

### Field Methods

To facilitate relocating plants employed in field studies two types of plant markers were used. When it was necessary to relocate a specific plant, the plant was tagged with a coded plastic label secured to the stipe with a nylon line. When it was not necessary to identify individuals specifically, the plants were tagged with red or blue nylon tape tied to the stipe.

Transport of living material was accomplished by wrapping the plants in newspaper saturated in seawater and storing in an iced chest. The period from collection to establishment in a new environment never exceeded 24 hours. Plants transported in this manner showed no signs of injury.

When placed in the new environment, the transplanted plants were attached to rocks by rubber bands overlapping the haptera.

The vertical limits of distribution for <u>L</u>. <u>saccharina</u> were determined by measuring the vertical distance from the plants to the water surface and from the water surface to a bench mark. The lower limits were measured with a metered line, oriented by a SCUBA diver, and the upper limits

with a meter rule. The position of the bench mark in relation to various tidal heights was found by measuring the vertical distance between the bench mark and the water surface and then relating this measurement to the tidal height predicted for the time of measurement (Anon., 1962).

# Culture Facilities and Methods

Four different facilities were employed in culturing Laminaria.

(1) Plastic (lucite) aquaria. Five plastic aquaria were employed as culture chambers for large plants and as incubators for small sporophyte and gametophyte cultures. These aquaria measured 45 cm long x 25 cm wide x 60 cm high. When culturing large plants directly in these aquaria, 40 to 50 l of seawater were used. When incubating culture dishes the water level was maintained immediately below the lip of the dishes. The culture dishes used for small sporophytes were l litre glass covered dishes. Those used for the gametophytes were 250 ml glass covered dishes.

The aquaria were kept in a 7°C constant temperature room. Temperatures higher than 7°C were maintained by small aquarium heaters equipped with thermostats.

(2) Constant temperature water bath table. This table consisted of a 20 cm deep galvanized iron tray measuring l.l m x 2.2 m. Temperature was controlled by means of a refrigeration coil flush with the bottom of the tray but external to the water bath. This table was used as an incubator for BOD (Biological Oxygen Demand) bottles employed

in physiological studies.

(3) Culture tank. A large tank (3.8 m long x 0.8 m wide x 1.0 m high) was provided by the Vancouver Public Aquarium at Stanley Park. This culture tank was connected to a circulating seawater system which was augmented with fresh seawater every day. The replacement time of seawater in the culture tank was approximately 7 hours. Temperature was controlled by passing the incoming water through a refrigerated coil.

(4) Constant temperature rooms. Constant temperature rooms of 5, 10, 15, and 20<sup>°</sup>C were employed. These are maintained by the Department of Botany, University of British Columbia.

All experiments employing culture facilities (1), (2), and (3) were illuminated with two green fluorescent tubes (Westinghouse F40HE 37) to each blue fluorescent tube (Westinghouse F40 Blue). The spectrum of light resulting from the above combination is shown in Figure 1. The light transmission curve as observed in inshore waters (after Jerlov, 1951) is shown in Figure 3b.

Experiments conducted in the constant temperature rooms were illuminated with Sylvania fluorescent tubes (FT12/CW) filtered through stained glass (Fig. 2, 3a).

All light measurements were made with a Photovolt Electronic Photometer (Photovolt Corporation, New York 16, N.Y., Model 501-M). The relative sensitivity of this light meter at various wave lengths is illustrated in Figure 4. б

The seawater employed in culture studies was usually obtained from the same area from which the plants were collected. One exception was a study on the response of plants to waters collected from different regions. No nutrients were added to the seawater in any of the culture experiments.

Filtration of the seawater was effected by passing the water through a column of packed glass wool 2 to 3 times for sporophyte culture, and 6 to 7 times for gametophyte culture. The filtering of seawater for gametophyte culture usually resulted in unialgal cultures. Contaminated cultures were discarded.

Salinity adjustment was achieved by heating seawater at 30 to 35<sup>°</sup>C until a concentration of 35 to 50% was reached. Subsequently, concentrated seawater was added to a larger volume of raw seawater and the salinity was determined using an inductively coupled salinometer (Model 601, MK III, Auto-Lab Industries, Sydney, Australia). Lower salinities were obtained by diluting this seawater mixture with distilled water.

# Evaluation of Plant Response

(1) Responses of entire sporophytes to conditions of light, temperature, and salinity were determined by measuring the surface area of plants at the beginning, during, and at the end of the experiment. The surface area was determined by measuring the outline of the blade with a compensating polar planimeter (Keuffel & Esser Co., Germany, Model 4236). The blade outline was obtained by either a paper tracing or

a photograph of the blade against a metered grid.

(2) Responses of discs of sporophyte blades to conditions of temperature, light, salinity, and different water origins were determined by measuring apparent photosynthesis and respiration, and by calculating the net photosynthesis and the ratio of net photosynthesis to respiration in the following manner.

(a) Net photosynthesis was determined by the equation: Net Photosynthesis<sub>02</sub> = Apparent Photosynthesis<sub>02</sub> + Respiration<sub>02</sub> where Apparent Photosynthesis<sub>02</sub> is determined by subtracting the initial 0<sub>2</sub> content of the culture medium from the 0<sub>2</sub> content present after a period of exposure to light. Respiration<sub>02</sub> is the difference between the initial 0<sub>2</sub> content and the 0<sub>2</sub> content after a period of darkness. The units employed were  $\mu$ l 0<sub>2</sub> evolved or utilized/cm<sup>2</sup>/hr.

(b) The Net Photosynthesis to Respiration ratio was determined by dividing the rate of Net Photosynthesis by the respiration rate.

The above measurements were made on discs having an area of 33 square cm. These were cut distally to the basal 15 cm of the blade in areas of uniform color and free from apparent injury. After cutting, the discs employed in temperature and salinity studies were preconditioned for five days in the situation to be tested. In studies on light the discs were not preconditioned but kept in darkness for 24 hours prior to testing. At the time of measurement, one disc was placed in each 300 ml BOD bottle. Five discs were tested in each temperature and salinity situation, and six discs

were employed in each light intensity tested. The BOD bottles were then filled with filtered seawater of a known oxygen concentration and of the desired temperature and salinity. These bottles were then placed in light for 2 hours. At the end of the period 150 ml aliquots of the seawater were siphoned from the 300 ml BOD bottles to 150 ml BOD bottles and the oxygen content was determined by the Winkler Method as described by Strickland and Parsons (1960). The seawater remaining with the plant discs in the 300 ml BOD bottles was then replaced with new seawater of known oxygen content and the bottles were placed in darkness for 4 hours. At the end of the dark period the oxygen content was determined. Control BOD bottles were employed in each experiment to detect changes in oxygen concentration due to microbial activity. The control bottles differed from the experimental bottles only in that they did not contain plant discs.

(3) Responses of gametophytes to various temperature, salinity, and light situations were determined by the ability of the plants to produce sporophytes.

(4) Responses of gametophytes to samples of seawater from different areas were determined by measuring the length of the resulting sporophytes after a period of growth. Measurements were made with a calibrated ocular micrometer.

### Oceanographic and Meteorologic Data

With the exception of oceanographic data from Burrard Inlet all data employed in this study were available in published form. Where pertinent references to these data

are provided in the text. Monthly determinations of the temperature and salinity structure of the water column in Burrard Inlet were made from June, 1963 to May, 1964. An inductive salinometer (Model RS52, Industrial Instruments Inc., New Jersey) was used.

Approximate submarine light intensities for three depths in Burrard Inlet were determined using the following expression (after Strickland, 1957):

$$I_z = antilog (log_{10} I_o - Kz),$$

where  $I_0$  is the light of the visible range (3800-7200 Å) entering the water, K the extinction coefficient of the water and z the depth investigated.

The manner in which the values for these three terms was determined is as follows:

 $(I_0)$   $I_0 = 0.96 (I_1 \cdot 0.5),$ 

where  $I_1$  is the monthly mean incident light as recorded from 12:00 noon to 1:00 PM by an Eppley Pyrheliometer at the University of British Columbia for the wave band 3000-50,000 Å (Anon., 1964). The value 0.5 is a conversion factor for determination of the percentage of  $I_1$  in the visible range. This value assumes clear sky and unobscured sun, with sky light contributing one third of the total radiation (Strickland, 1957). The value 0.96 corrects for 4% reflection of the incident light from the water surface (Holmes, 1957). (K) The extinction coefficient (K) is derived from the equation:

$$K_{.} = \frac{0.8}{D}$$
,

where D is the secchi disc depth expressed in meters (Strickland, 1957). The mean secchi disc depth for Burrard Inlet as determined from monthly readings (June, 1963 to May, 1964) taken at high tide was 3.2 m. This value was used in the last equation. (z) To relate the distance that light must pass from the water surface to the three depths investigated, it was necessary to compensate for tidal fluctuations. This compensation was achieved by employing the monthly mean tidal height as observed at 12:30 PM.

The resultant values for submarine illumination are approximations and are employed here to illustrate the seasonal trend (Fig. 83).

# TAXONOMY AND DISTRIBUTION OF NORTHEAST PACIFIC SPECIES OF LAMINARIA

The following taxonomic and distributional treatment of taxa of <u>Laminaria</u> occurring in the northeast Pacific constitutes the first critical review of this large and important genus since Setchel and Gardner's study in 1925. Extensive intertidal collections and a few subtidal collections in British Columbia and Alaska have altered previously reported distribution patterns.

All distributional records north of  $48^{\circ}$ N latitude have been taken from collections available in the Phycological Herbarium, University of British Columbia, and the Friday Harbor Laboratory Herbarium, University of Washington. Distributional data for collections made north of  $48^{\circ}$ N latitude are presented in Figures 50 to 53. Further distributional data are provided in Appendix I.

The limits of <u>Laminaria</u>, south of 48<sup>0</sup>N latitude, are taken from floristic studies of Smith (1944), Doty (1947), and Dawson (1961).

A listing of some of the plants studied for their particular taxonomic significance is given in Appendix II.

The descriptions and phenological data of taxa of northeast Pacific Laminaria were derived from plants collected in northern Washington, British Columbia, and Alaska. Where possible, species are distinguished on the basis of qualitative characters. The use of size measurements has been minimized because of the considerable variation encountered.

Classification

Division:	Phaeophyta	
Class:	Phaeophyceae	
Order:	Laminariales	
Family:	Laminariaceae	
Genus:	Laminaria Lamouroux,	1813

### Generic Diagnosis

Holdfast of branched haptera or a continuous disc. Stipe simple, solid or hollow, complanate or terete, with or without mucilage ducts. Transition region between stipe and blade undivided. Blade entire or longitudinally dissected, with or without bullae, with or without mucilage ducts. Sori occurring on blade as continuous or isolated patches.

Key to the Species of Laminaria of the Northeast Pacific

- 1. Holdfast discoid ..... 2
- 1. Holdfast of distinct, branched haptera ..... 3
  - 2. Mucilage ducts absent from blade.. L. ephemera, p. 16.
  - 2. Mucilage ducts present in blade... L. yezoensis, p. 17.
- 3. Numerous stipes, each terminated by a single blade arising from an extensive holdfast.... 4

Mucilage ducts absent from stipe ...... 6 5. 5. 6. Stipe complanate, usually longer than 30 cm ..... L. complanata, p. 25. Stipe terete, usually shorter than 20 cm. 7 6. 7. Bullae, when present, in two rows oriented parallel to the margin of the blade. L. saccharina, p. 22. 7. Bullae covering entire blade..... L. farlowii, p. 24. 8. Stipe terete throughout; blade deeply dissected into many narrow, uniform segments ..... 9 8. Stipe often slightly to extensively complanate; blade, when dissected, of few segments varying in width and length ..... L. groenlandica, p. 18. Mucilage ducts positioned near surface of 9. stipe ..... L. dentigera, p. 27. Mucilage ducts positioned in the mid-cortical 9. region of the stipe ..... L. setchellii, p. 26.

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# Description of Species

# Laminaria longipes Bory

Setchell and Gardner, 1925, p. 597.

Dawson, 1961, p. 396.

<u>Description</u>. Fig. 5, 25, 37. Holdfast an extensive system of branched haptera, the haptera giving rise to many stipes, each terminated by a single blade. Stipe usually less than 20 cm long, mucilage ducts absent. Blade linear, cuneate, usually less than 5 cm wide, of variable length, mucilage ducts present. No plants observed with sori. Northeast Pacific Distribution. Fig. 50; App. I, Sect. A. Attu Island to Kenai Peninsula, Alaska. Known earlier only from the Bering Sea.

<u>Habitat</u>. Growing on rocks in the lower intertidal region, often in muddy or sandy areas.

Comments. Only herbarium specimens observed.

Laminaria sinclairii (Harvey ex Hooker f. et Harvey),

Farlow, Anderson et Eaton

Setchell, 1905, p. 139.

Setchell and Gardner, 1925, p. 598.

Smith, 1944, p. 135.

Scagel, 1957, p. 98.

Silva, 1957, p. 43.

Dawson, 1961, p. 396.

<u>Description</u>. Fig. 6, 7, 26, 38. Sporophyte perennial from the stipe, of variable length and width. Holdfast composed of extensive, branched haptera, the haptera giving rise to many stipes, each terminated by a single blade. Stipe usually not exceeding 20 cm in length, mucilage ducts present. Blade of intertidal plants of variable length, usually less than 5 cm wide, mucilage ducts present. Blade of subtidal plants of variable length, up to 20 cm wide, with mucilage ducts. Plants with sori in February.

Northeast Pacific Distribution. Fig. 51; App. I, Sect. B. Hope Island, British Columbia to Ventura County, California. Earlier known from southern British Columbia to Ventura County, California.

Habitat. Growing on rocks in the lower intertidal region in areas of surf. Known only from the subtidal region in sheltered areas.

Laminaria ephemera Setchell

Setchell, 1901, p. 121.

Griggs, 1906, p. 247 (as Renfrewia parvula).

Setchell and Gardner, 1925, p. 603.

Smith, 1944, p. 136.

Doty, 1947, p. 40.

Scagel, 1957, p. 95.

Dawson, 1961, p. 396.

<u>Description</u>. Fig. 8, 27, 39. Sporophytes annual, mucilage ducts wanting. Holdfast a small disc. Stipe terete,  $15^+$  cm long in exposed intertidal regions, much shorter for subtidal plants. Blade linear,  $6^+$  cm wide, of variable length, infrequently dissected. Plants with sori in May and June.

Northeast Pacific Distribution. Fig. 51; App. I, Sect. C. Amphitrite Point, Vancouver Island, British Columbia to Monterey Peninsula, California. Earlier known from Port Renfrew, British Columbia to Monterey Peninsula, California.

<u>Habitat</u>. On rocks in the lower intertidal and upper subtidal regions in areas subjected to surf; restricted to the subtidal region in sheltered areas.

## Laminaria yezoensis Miyabe

Saunders, 1901, p. 429 (as <u>L</u>. <u>solidungula</u>), see comments on page 18.

Miyabe, 1902 (English edition, 1957, p. 23).

Setchell and Gardner, 1924, p. 10 (as <u>L. personata</u>). Setchell and Gardner, 1925, p. 599 (as <u>L. personata</u>). Dawson, 1961, p. 396 (as <u>L. personata</u>).

<u>Description</u>. Fig. 9, 10, 28, 40. Sporophytes up to l m long. Holdfast a scutate disc, often very expansive and united with other discs. Stipe terete, up to 40 cm long, mucilage ducts absent. Blade of variable length, entire or longitudinally dissected, mucilage ducts present. One plant with sorus collected from Queen Charlotte Islands in July.

Northeast Pacific Distribution. Fig. 52; App. I, Sect. D. Adak Island, Alaska to Hope Island, British Columbia. Heretofore not known from the northeast Pacific.

Habitat. Growing on rocks in exposed areas in the lower intertidal region. No subtidal data available.

<u>Comments</u>. The plants observed displayed much variability but were in complete accord with Miyabe's description (1902).

Setchell and Gardner, in their original description of <u>L. personata</u> S. & G. (1924) and in a later discussion (1925) of this species, make no mention of <u>L. yezoensis</u>. However, it must be assumed that Setchell was aware of this species since he discussed it in an earlier paper (1908). From comparison of Setchell and Gardner's description (1924) of L. personata and Miyabe's description (1902) of
<u>L</u>. <u>yezoensis</u> it is apparent that the two authors are describing the same species. The type specimen of <u>L</u>. <u>personata</u> (N.L. Gardner #3951, UC#266491) appears to be a juvenile form of <u>L</u>. <u>yezoensis</u> and has all the diagnostic characteristics of that species. The species <u>L</u>. <u>personata</u> S. & G. is here reduced to synonomy under the older name L. yezoensis Miyabe.

Saunders (1901) described <u>L</u>. <u>solidungula</u> J. Ag. from Yakutat Bay, Kukak Bay, and Popof Island, Alaska. <u>Laminaria</u> <u>solidungula</u>, common to the northwest Atlantic, is distinguished from <u>L</u>. <u>yezoensis</u> by the presence of mucilage ducts in its stipe. Subsequent collections (Scagel, <u>in herb</u>.) made in the Yakutat region specifically and Alaska generally have failed to rediscover <u>L</u>. <u>solidungula</u>. Possibly the entity referred to <u>L</u>. <u>solidungula</u> by Saunders was <u>Cymathere triplicata</u> (Post. and Rupr.) J. Ag.. <u>Cymathere triplicata</u> is found throughout the range collected by Saunders and is similar to <u>L</u>. <u>solidungula</u> in that it has mucilage ducts in the stipe and a well developed discoid holdfast.

#### Laminaria groenlandica Rosenvinge

Setchell and Gardner, 1925, p. 600 (as <u>L</u>. <u>cuneifolia</u>) and p. 605 (as <u>L</u>. <u>platymeris</u>).

Doty, 1947, p. 39 (as <u>L. cuneifolia</u>).

Scagel, 1957, p. 93 (as L. cuneifolia) and p. 95 (as

L. platymeris).

Widdowson, 1959, p. 56 (as <u>L. cuneifolia</u>).

Wilce, 1959, p. 158 (as L. cuneifolia).

Wilce, 1960, p. 203.

Dawson, 1961, p. 396 (as L. cuneifolia and L. platymeris).
<u>Description</u>. Fig. 11, 12, 13, 14, 15, 16, 29, 30, 31,
41, 42, 43, 44. Sporophyte perennial from the stipe.
Holdfast of many branched haptera. Stipe varying in length
from 1 to 60 cm, terete to complanate, mucilage ducts present. All plants producing sori in winter; plants older than
one year often producing sori in early summer.

<u>Northeast Pacific Distribution</u>. Fig. 53; App. I, Sect. E, F, G. Attu Island, Alaska to Cape Blanco, Oregon.

Habitat. Growing on rocks in the lower intertidal region and upper subtidal region in areas exposed to considerable water motion. Restricted to the subtidal region in sheltered, estuarine waters.

<u>Comments.</u> Wilce (1959) did not retain in <u>L. cuneifolia</u> (= <u>L. groenlandica</u>) those plants from the northeast Pacific referred to this species by Setchell and Gardner (1925). Wilce's decision to remove the northeast Pacific plants from <u>L. cuneifolia</u> was based on a comparative study of the color and texture of the plants, and of the size, shape, and arrangements of the surface cells and their protoplasts. However, Wilce.did agree that the general shape of the northeast Pacific plants and the distribution of their mucilage ducts conforms with the Atlantic L. groenlandica.

I cannot agree with Wilce's choice of characteristics for distinguishing the northeast Pacific plants from <u>L. groenlandica</u>. The surface cells, because of the meristematic nature, are prone to be variable. Inherent and environmental factors affecting the rate and mode of growth would influence the character of the meristematic cells. Burrows (1964) in a study of <u>L. saccharina</u> related variability of cell size, blade thickness, and other blade characteristics to temperature. In my study, those plants conforming to Setchell and Gardner's (1925) <u>L. cuneifolia</u> are considered to be L. groenlandica.

Setchell and Gardner (1925) distinguished <u>L</u>. <u>platymeris</u> De la Pyl. from <u>L</u>. <u>cuneifolia</u> on the basis of the abullate blade and long, often complanate stipe of the former in contrast to the bullate blade and short, often terete stipe of the latter.

Widdowson (1959) suggested that Setchell and Gardner misinterpreted De la Pylaie's description of <u>L</u>. <u>platymeris</u>. Setchell and Gardner characterize <u>L</u>. <u>platymeris</u> as having a stipe up to 1 m long and compressed from just above the holdfast. De la Pylaie (1829, p. 52) states: "<u>L</u>. stipete brevi, tereti, minuto...." and below he says "Le stipe est cylindrique et égal dans toute sa longeur...seulement long de 9 à 12 centimetres...."

Results from a series of <u>in situ</u> studies on <u>L. groenlandica</u> at Glacier Point indicate that the form referred to as <u>L. platymeris</u> by Setchell and Gardner is a form of <u>L. groenlandica</u> at least one year old. These studies are discussed in detail on page 30.

The above-mentioned field studies combined with Setchell and Gardner's apparent misunderstanding of De la Pylaie's description of <u>L</u>. <u>platymeris</u> lead me to place plants fitting

this species description (<u>sensu</u> Setchell and Gardner, 1925) in <u>L. groenlandica</u>.

During the course of my study four forms of <u>L. groenlandica</u> were recognized for the northeast Pacific. These forms are not considered by me at present as legitimate taxonomic entities but are distinguished merely to provide a means of facilitating discussion until such time as a critical monographic study for the entire genus is made.

Laminaria groenlandica flat stipe form. Fig. 16, 31, 44, 53; App. I, Sect. E. This form is typified by having an abullate blade and complanate stipe usually exceeding 40 cm in length. Plants fitting this description have been collected only from exposed areas in the lower intertidal region about north Graham Island, Queen Charlotte Islands, British Columbia.

Laminaria groenlandica short stipe form. Fig. 13, 15, 53; App. I, Sect. F. Blade with or without bullae. Stipe usually less than 10 cm long, terete to slightly complanate. Two patterns of bullation have been observed for this form. The first pattern consists of two longitudinal rows of bullae running the length of the blade. This form closely fits Setchell and Gardner's (1925) <u>L. cuneifolia f. subsimplex</u>. The second pattern is characterized by having the entire blade irregularly bullate. This form fits Setchell and Gardner's (1925) <u>L. cuneifolia</u> f. <u>amplissima</u>. The short stipe form occurs intertidally and subtidally in regions of little surf action from northern Washington to Attu Island, Alaska.

Laminaria groenlandica long stipe form. Fig. 14, 30, 43, 53; App. I, Sect. G. Blade with or without bullae. Stipe slightly flattened or terete, usually 10 to 30 cm long. This form is similar to Setchell and Gardner's (1925) <u>L. cuneifolia</u> f. <u>cuneifolia</u> and encompasses at least in part their <u>L. platymeris</u>. The long stipe form is common in regions of heavy surf from southern Vancouver Island, British Columbia

to Attu Island, Alaska.

To understand better the relationship between the long and short stipe forms, a series of transplantations were performed involving these two forms. Complete detail of these studies is presented on page 34.

Laminaria groenlandica shade form. Fig. 11, 12, 29, 41. This form is the same as Setchell and Gardner's (1925) L. cuneifolia f. angusta. This is a shade form of the long and short stipe forms. The habitat and distribution of the shade form is thought to coincide with that of the long and short stipe forms. The plants are small, usually less than 30 cm long and 5 cm wide. The stipe is usually terete and less than 5 cm long. For a complete discussion of the shade form and its relationship to the long and short stipe forms see page 29.

Laminaria saccharina (L.) Lamouroux

Setchell and Gardner, 1925, p. 595. Doty, 1947, p. 39. Scagel, 1957, p. 96. Dawson, 1950, p. 153 (as <u>L. cordata</u>). Dawson, 1961, p. 396 (as L. cordata and L. saccharina).

<u>Description</u>. Fig. 17, 18, 32, 45. Sporophyte perennial from the stipe. Holdfast of many branched haptera. Stipe of varying length, terete to slightly complanate, mucilage ducts absent. Blade usually entire, cuneate to cordate, of varying length and width, with or without bullae, mucilage ducts present. All plants producing sori in winter; plants older than 9 months often producing sori in late spring.

Northeast Pacific Distribution. Fig. 53; App. I, Sect. H. From Kenai Peninsula, Alaska to Coos Bay, Oregon, with an isolated population on Santa Catalina Island, California. Earlier known from the Alaskan Peninsula to Coos Bay, Oregon.

Habitat. Growing on shell, wood, and rock in sheltered waters from the lower intertidal region to the upper subtidal region. Known only in the subtidal region in areas exposed to surf.

<u>Comments</u>. Setchell and Gardner (1925) recognized three forms of <u>L</u>. <u>saccharina</u> in the northeast Pacific. The form <u>saccharina</u> is most often encountered. This form fits the description given above. Form <u>linearis</u> differs from form <u>saccharina</u> in that in the former the haptera extend up the stipe whereas in the latter the haptera are restricted to the lower end of the stipe. Setchell and Gardner (1925) describe the distribution of form <u>linearis</u> as extending from Unga, Alaska to northern Washington, growing on rocks in the upper subtidal region. In this study form <u>linearis</u> has been observed only as drift. Form membranacea is the

third form recognized by Setchell and Gardner. This plant is characterized by having an ample and membranous blade. Plants fitting the description of form <u>membranacea</u> have been collected in the lower intertidal region at Sechelt Inlet, Strait of Georgia, and Bull Harbour, Hope Island, British Columbia. Setchell and Gardner describe its distribution as extending from Alaska to Coos Bay, Oregon.

Dawson (1950) justified describing <u>L</u>. <u>cordata</u> Dawson as a new species from Santa Catalina Island, California on the grounds that "...this species is unlike any previously described from the north Pacific by manner of its shortstipitate, non-bullate, entire but terminally eroded, broadcordate blade, and holdfast of branched haptera." This species described by Dawson has the same mucilage duct distribution as does <u>L</u>. <u>saccharina</u>. Further, the characteristics employed in setting <u>L</u>. <u>cordata</u> apart from other north Pacific <u>Laminaria</u> are all shared by the variable species <u>L</u>. <u>saccharina</u>. Examination of the type specimen (Dawson #5600, AHFH #36922) revealed that this plant is similar in all regards except the slightly coarser haptera to the <u>Laminaria</u> <u>saccharina</u> observed by me in the northeast Pacific.

These observations lead me to reduce <u>L</u>. <u>cordata</u> Dawson to synonomy with the older species, <u>L</u>. <u>saccharina</u> (L.) Lamour. f. <u>saccharina</u>.

Laminaria farlowii Setchell.

Setchell, 1891, p. 220. Setchell, 1905, p. 139.

Setchell and Gardner, 1925, p. 599.

Smith, 1944, p. 136.

Dawson, 1961, p. 396.

<u>Description</u>. Fig. 19, 33, 46. Sporophyte 40<sup>+</sup> cm long. Holdfast of many, branched haptera. Stipe 4 cm long, terete, without mucilage ducts. Blade entire, cuneate, entire surface irregularly bullate, mucilage ducts present.

Northeast Pacific Distribution. Fig. 51; App. I, Sect. I. Central to southern California and one isolated collection at Comox, British Columbia. Earlier known from Santa Cruz, California to Bahía del Rosario, Baja California.

Habitat. The Comox specimens were collected in sheltered waters.

<u>Comments</u>. The above description is based on two plants (V 001484) collected by John Macoun, 1915, at Comox, British Columbia.

Laminaria complanata (Setchell and Gardner) Setchell

Setchell and Gardner, 1903, p. 262. (as L. saccharina

f. <u>complanata</u>).

Setchell, 1912, p. 149.

Setchell and Gardner, 1925, p. 596.

Scagel, 1957, p. 93.

Dawson, 1961, p. 396.

<u>Description</u>. Fig. 20, 34, 47. Holdfast of stout, branched haptera. Stipe less than 50 cm long, of variable width, being terete below and complanate near the blade base, mucilage ducts absent. Blade of variable size, truncate to cordate, mucilage ducts present. No plants with

sori observed.

Northeast Pacific Distribution. Fig. 51; App. I, Sect. J. Known only from northern Washington, James Bank, British Columbia, and Graham Island, Queen Charlotte Islands, British Columbia. Earlier known only from Friday Harbor, Washington.

<u>Habitat</u>. Growing on rocks in the subtidal region in sheltered areas. The Queen Charlotte collection was made from an exposed area in the intertidal region.

<u>Comments</u>. The species referred to here as <u>L. complanata</u> S. closely fits Kjellman's (1877) <u>L. digitata</u> f. <u>complanata</u> and may well be an isolated population of that form.

#### Laminaria setchellii Silva

Setchell, 1905, p. 139 (as L. andersonii).

Setchell and Gardner, 1925, p. 605 (as <u>L</u>. <u>andersonii</u>). Smith, 1944, p. 137 (as <u>L</u>. <u>andersonii</u>).

Scagel, 1957, p. 97.

Silva, 1957, p. 42.

Dawson, 1961, p. 396.

<u>Description</u>. Fig. 21, 22, 23, 35, 48. Sporophyte perennial from the stipe, up to 1.5 m long. Holdfast of many stout, branched haptera. Stipe terete, rigid, up to 50 cm long, usually greater than 2 cm thick at the base, mucilage ducts present in the mid-cortical region. Blade of variable length, cuneate, deeply dissected into many segments, mucilage ducts conspicuous. Plants producing sori in late winter and early summer.

Northeast Pacific Distribution. Fig. 52; App. I, Sect. K. From Yakutat, Alaska to southern California. Earlier known from northern British Columbia to southern California.

Habitat. Growing on rocks in the lower intertidal region and upper subtidal region in areas of heavy surf. Restricted to the subtidal region in sheltered areas.

<u>Comments</u>. <u>Laminaria setchellii</u> displays considerable morphological variation characterized by the blade becoming broader and the degree of dissection decreasing with a transition from exposed to sheltered water (Fig. 21, 22).

Plants with newly rejuvenated blades are easily recognized as belonging to <u>L. setchellii</u> by their heart shaped blades (Fig. 23).

A strong affinity between <u>L</u>. <u>setchellii</u> and <u>L</u>. <u>sinclairii</u> is suggested on the basis of the blade and stipe anatomy. Both species have distinct medullary regions in the blade and deep seated mucilage ducts which are positioned in the mid-cortical region in both the blade and stipe.

#### Laminaria dentigera Kjellman

Setchell and Gardner, 1925, p. 604.

Dawson, 1961, p. 396.

<u>Description</u>. Fig. 24, 36, 49. Holdfast of stout, branched haptera. Stipe terete, usually more than 2 cm thick, usually less than 40 cm long, mucilage ducts present. Blade dissected into many narrow segments of variable width and length, mucilage ducts present but sparse. Northeast Pacific Distribution. Fig. 51; App. I, Sect. L. From Attu Island, Alaska to Yakutat, Alaska. Earlier reported (Setchell and Gardner, 1925) as extending from the Aleutian Islands to the Bering Strait.

Habitat. Growing on rocks in the lower intertidal region in exposed areas.

Comments. Only herbarium specimens studied.

This species is easily distinguished from <u>L</u>. <u>setchellii</u> on the basis of the mucilage duct positioning. In <u>L</u>. <u>setchellii</u> the ducts are deep seated while in <u>L</u>. <u>dentigera</u> they are positioned near the periphery of the blade and stipe. In the field these two species are difficult to distinguish. One characteristic which is of assistance in distinguishing these species is the depth to which the blades are dissected. In <u>L</u>. <u>setchellii</u> the blades are dissected almost to the blade base, whereas in <u>L</u>. <u>dentigera</u> the dissection ceases some distance above the base.

Yakutat, Alaska appears to be the northern extent of L. setchellii and the southern extent of L. dentigera.

LIFE HISTORIES AND GROWTH PATTERNS OF <u>LAMINARIA</u> <u>GROENLANDICA</u> LONG AND SHORT STIPE FORMS AND <u>LAMINARIA</u> <u>SACCHARINA</u>

Studies on the life histories and growth patterns were made to increase our understanding of the plants, to apply this to subsequent studies on distribution, and to develop a basis for evaluation of plant response to environmental factors. Further, it was intended that the following studies on the two forms of <u>L</u>. groenlandica might lead to a better understanding of the taxonomic limits of this species.

## Life Histories of Laminaria groenlandica Long and Short Stipe Forms

Studies on the life histories of intertidally occurring <u>L. groenlandica</u> long and short stipe forms were made during the years 1962-1964, at Glacier Point and Ogden Breakwater. These studies consisted of observations on populations and tagged individuals. The life histories of both forms are essentially the same.

With both forms, the sporophytic generation first became conspicuous in February (Fig. 54). By April two types of plants were apparent: large plants typical of both forms, and small plants typical of the shade form (= <u>L</u>. <u>cuneifolia</u> f. <u>angusta</u> Setchell and Gardner, 1925). From observational studies, the small form is thought to result from shading in areas heavily populated by larger seaweeds. In June, 1962 and 1964, many of the larger plants became fertile, whereas in June, 1963, the larger plants remained in the vegetative state. Failure of the June, 1963 plants to produce sori may have resulted from the severe sunburn received by them during the spring tides of that period. In June, 1962 and 1964, there was no evidence of severe sunburn. The small plants (shade form) were not observed with sori in June. The large plants generally disappeared after releasing their meiospores.

Natural removal of some of the larger plants in June and July exposed many of the small plants. These newly exposed plants grew rapidly, whereas those still shaded remained essentially the same size.

During the November to January period there was no measurable vegetative growth and all observed <u>L. groenlandica</u> produced sori. Following release of meiospores, most of the blade was lost. In February regeneration of a new blade was initiated, and by June it was not possible to distinguish between the shade form and the long and short stipe forms. In June most of the two-year plants became fertile except those severely sunburnt.

Laminaria groenlandica long stipe form, persisting into the second year, closely fits the description of <u>L. platymeris (sensu Setchell and Gardner, 1925)</u>. The stipe length of the former exceeded the greatest length attributed by Setchell and Gardner (1925) to <u>L. cuneifolia</u>  $(= \underline{L}, \underline{\text{groenlandica}})$ . The stipe was usually flattened and the blades, as observed in June, were free of bullations and

#### irregularly dissected.

A large population of new sporophytes became conspicuous in February and was augmented throughout the year. The February plants apparently had their origin from gametophytes arising from meiospores released in the November to January period. Sporophytes arising at times other than February may have their origin from meiospores released from intertidal plants in June or from subtidal plants. However, the phenology of the subtidal plants is unknown.

### Gametophyte and Microscopic Sporophyte Phases of Laminaria groenlandica Long Stipe Form

One of two forms of gametophyte was produced under culture conditions. Under unfavorable conditions of salinity and temperature (p. 47) the unicellular female gametophytes produced larger oogonia (Fig. 55b) than were produced under favorable conditions (Fig. 55c). The male gametophytes grown under favorable conditions were small, consisting of a few cells most of which became antheridia (Fig. 55d). When cultured under unfavorable conditions, the male gametophytes were quite large, consisting of many cells few of which became antheridia (Fig. 55a).

Sporophytes grown under favorable culture conditions were at first uniseriate filaments which later became broader by a series of periclinal divisions (Fig. 55e, 55f). When grown under adverse conditions, structures which are thought to be abnormal sporophytes developed; these were irregular, consisting of a globular mass of large cells

### Growth Patterns of Laminaria groenlandica Long and Short Stipe Forms

To define the growth patterns in the blades of these two forms, the growth of the plants was followed in both culture and <u>in situ</u>. This was accomplished by punching a series of holes at close intervals along the longitudinal axis of the blade. Both the distances between holes and the blade width at each hole were recorded at the beginning of the experiment and again after 30 days.

In situ growth studies were made on three plants of each form ranging from 40-60 cm in length from July 20 to August 19, 1962. Similar studies were made under culture conditions from September 23 to October 23, on five plants of each form ranging in length from 20-30 cm. These plants were cultured in plastic aquaria at 10°C, 28-31% salinity, and 450 ft-c illumination, with a regime of 12 hours light and 12 hours dark.

Distribution of meristematic activity in the blades of the long and short stipe forms was similar. In all cultured plants 90% of the measurable longitudinal growth was in the basal 7 cm of the blade (Fig. 56, 57). No longitudinal growth was recorded more than 11 cm distal to the blade base. In all of the <u>in situ</u> plants, 90% of the longitudinal growth was observed in the basal 17 cm of the blade (Fig. 58). Longitudinal growth was restricted to the basal 22 cm of the blade. Measurable lateral growth in the cultured plants was limited to the basal 12 cm of the blade (Fig. 59, 60), but in plants studied <u>in situ</u>, lateral growth extended 20 cm distal to the blade base (Fig. 61). The greatest per cent increase in width for the cultured plants was 80% and for the <u>in situ</u> plants, 450%.

The gross morphology of <u>L</u>. <u>groenlandica</u> long and short stipe forms is illustrated in Figures 13, 14, and 15. Large plants of the short stipe form are characterized by a broad blade with a truncate-cordate base and a short stipe. The long stipe form has a linear blade usually with a cuneate base and a long stipe. Young plants of both forms, when subjected to shading, produce a growth form typical of Setchell and Gardner's (1925) <u>L</u>. <u>cuneifolia</u> f. <u>angusta</u>. This growth form is distinguishable by its small size.

### In Situ Growth Rates of Laminaria groenlandica Long and Short Stipe Forms

The longitudinal growth rates for small groups of long and short stipe forms of <u>L</u>. <u>groenlandica</u> were determined at different periods of the year (Table I). This was accomplished by punching holes at short intervals along the length of the blade and observing the distributions of holes after a period of time. The greatest growth rates were observed prior to July; the slowest rates were recorded in the fall, prior to sorus development.

### Transplant Studies on Laminaria groenlandica Long and Short Stipe Forms

As was mentioned above, two of the characteristics distinguishing long and short stipe forms are blade width and stipe length. To quantify these characteristics the stipe length to blade width (St/W) ratio of several populations was determined at different times of the year (Table II). Measurements were made on tagged populations several times and on untagged populations once.

The grand mean St/W ratio for all measurements of long stipe populations was 0.52 and the means of the various populations measured varied from 0.29-0.85. The grand mean St/W ratio for all short stipe populations measured was 0.16 while the means of the individual populations varied from 0.12-0.22. The general trend was for the young plants of both forms to have a St/W ratio of 0.20-0.40. As these plants increased in size, the long stipe St/W ratio increased and the short stipe St/W ratio decreased.

Between February 22 and April 28, 1963, twenty-five long stipe plants from Glacier Point and 20 short stipe plants from the Ogden Breakwater were transplanted to a sheltered area in Burrard Inlet near Stanley Park, Vancouver. The plants selected for transplantation were the smallest that could be handled conveniently. None of these plants exceeded 45 cm in length.

The St/W ratio was determined at the time of transplantation and fortnightly as long as the plants remained in Burrard Inlet. It was possible to follow change in the

St/W ratio for only 12 long stipe and 14 short stipe plants. Of the 19 plants lost early in the study most were thoughtlessly destroyed by picnickers. Remaining transplants were last observed on June 10, 1963. Subsequent loss of these plants was thought to be the result of unfavorable oceanographic conditions. The final mean St/W ratio was determined by averaging the last individual measurements regardless of when they were made.

The initial mean St/W ratio for the long stipe plants was 0.27; the final mean ratio was 0.40. The St/W ratio for the short stipe plants changed from an initial mean of 0.20 to a final mean of 0.17 (Table III).

Five short stipe plants were transplanted from Ogden Breakwater to Glacier Point on May 22, 1963. The St/W ratio of these plants changed from an initial mean of 0.23 to a final mean of 0.34 as observed October 6, 1963 (Table III).

Results of the transplantations of long and short stipe plants to Burrard Inlet indicate that the differences in stipe length and blade width between these forms is genetically controlled and is not the result of environmentally induced phenotypic plasticity. However, response of short stipe plants placed in the long stipe plants' environment contradicts this hypothesis. The results of both transplant experiments are considered inconclusive because of the small number of plants tested and the possibility of preconditioning of the plants prior to transplantation.

#### Life History of Laminaria Saccharina

The life history of <u>L</u>. <u>saccharina</u> was followed in Burrard Inlet near Stanley Park, Vancouver from 1962 to 1965. This study consisted of general observations of the entire population and specific observations of tagged plants.

The sporophytes first became evident in the February-March period. Measurable growth of these plants continued until mid-November, by which time all plants had produced sori (Fig. 62). After release of the meiospores a large portion of the blade was lost. Those plants surviving the remainder of the winter initiated blade regeneration in February. All plants of this second year group became fertile in June, after which the intertidal plants were lost.

Young sporophytes, presumably resulting from meiospores released in June, became apparent in September. These plants, through a rapid growth phase, became fertile in October-November. Unlike <u>L. groenlandica</u>, new <u>L. saccharina</u> sporophytes became apparent only in two brief periods, February-March and September, and the population was not augmented throughout the year.

### Gametophyte and Microscopic Sporophyte Phases of Laminaria saccharina

The gametophytes took on one of two forms, depending upon culture conditions. In adverse conditions (p. 47) the male and female gametophytes were large, filamentous, and consisted of many cells (Fig. 63a, 63b). Under favorable conditions the female gametophytes were unicellular,

the single cell arising at the end of a germination tube through which the protoplasm passed from the meiospore (Fig. 63c). This cell functioned as the oogonium. Under favorable conditions the male gametophyte was greatly reduced in size, consisting of many cells most of which became antheridia (Fig. 63d).

Young sporophytes arising from the fusion of egg and sperm typically underwent a series of anticlinal divisions resulting in a uniseriate filament. Later, the sporophyte thallus became wider as a result of periclinal divisions (Fig. 63e, 63f). Under unfavorable conditions plants thought to be abnormal sporophytes were produced; these were irregular, globular masses of cells (Fig. 63g). The origin of these structures is questionable, as gametes were not observed in adverse culture conditions.

In October, 1963 and 1964, glass slides were inoculated with meiospores and placed in Burrard Inlet near Stanley Park. Inoculation was achieved by placing slides in dishes of meiospore-suspension for 24 hours. Then the slides with the attached meiospores were placed in shallow staining dishes and established in Burrard Inlet at the one foot tide level. A few slides were removed each fortnight for microscopic examination.

Sporophytes were produced by December of both years. In all cases only 6-12 sporophytes were produced on each slide. The sporophytes and remnants of the female gametophytes were of the type shown in Figures 63e, 63f. No male or unfertilized female gametophytes were observed.

#### Growth Pattern of Laminaria saccharina

The distribution of lateral and longitudinal growth was determined in 1962 for 6 plants in culture and 3 plants <u>in</u> <u>situ</u>. The cultured plants varied in length from 14-19 cm at the start, and their growth was followed from June 10-23. The <u>in situ</u> plants were 26-35 cm long at the beginning, and were studied from August 1-13. The method for culturing and for growth study of these plants was the same as described for L. groenlandica (p. 32).

All measurable longitudinal growth in the cultured plants was in the basal 5 cm of the blade, 90% of the growth being in the basal 4.5 cm (Fig. 64). Observed longitudinal growth <u>in situ</u> was in the basal 14 cm of the blade; 90% of the growth was restricted to the basal 8 cm (Fig. 65).

Measurable lateral growth in both cultured and <u>in situ</u> plants was restricted to the basal 15 cm of the blade. The <u>in situ</u> plants increased in width a maximum of 100%, and the cultured plants a maximum of 30% during the 13 day period of study.

#### Growth Rates of In Sity Laminaria saccharina

In May, 1962, twenty-five plants were punched in the manner described on page 33 for <u>L</u>. <u>groenlandica</u>. The longitudinal growth of these plants was followed until December, 1962. Figure 68 depicts the theoretical length of the population and the growth rate throughout the period of measurement. The theoretical length was determined by adding the increase in length by the intercalary meristem

to the initial length of the plants as observed in May. This measurement did not take into account loss of the blade through erosion at the distal end. The mean theoretical length of the population at the end of the growth period was 195 cm, whereas the mean actual length of the population was approximately 30 cm.

The longitudinal growth rate of this population shows a normal distribution from August to December (Fig. 68). Prior to August the growth rate was irregular. This can be accounted for in part by the severe sunburn these plants received during the spring tides in June. The greatest mean growth rate was approximately 1.4 cm per day for the August to September period.

#### LOCAL DISTRIBUTIONS OF LAMINARIA SACCHARINA AND OF LAMINARIA

GROENLANDICA LONG AND SHORT STIPE FORMS AS RELATED

TO TEMPERATURE, SALINITY, AND WATER MOTION

This study was confined to the coastal region from north Vancouver Island to the southern extent of the San Juan Archipelago because of the abundance of oceanographic and distributional data available for this region.

The distributions of <u>L</u>. <u>saccharina</u> and the two forms of <u>L</u>. <u>groenlandica</u> about Vancouver Island and adjacent waters are illustrated in Figure 53.

The intertidal distribution of <u>L</u>. <u>saccharina</u> on the west coast of Vancouver Island is restricted to sheltered bays and inlets, and on the east coast it is abundant from Hope Island  $(50^{\circ}58'N 127^{\circ}55'W)$ , at the north, to the San Juan Archipelago in the south. <u>Laminaria saccharina</u> is known, in the subtidal region only, at Amphritrite Point ( $48^{\circ}56'N 125^{\circ}33'W$ ), on the west coast of Vancouver Island, and at Salmon Bank ( $48^{\circ}26'N$  $123^{\circ}01'W$ ), in the San Juan Archipelago.

Laminaria groenlandica long stipe form is found predominantly in exposed regions along the north and west coast of Vancouver Island, the southern extent of its continuous west coast distribution being Sooke (48°21'N 123°43'W), with a population occurring on the southwest coast of San Juan Island.

The distribution of <u>L</u>. groenlandica short stipe form is intermediate between that of <u>L</u>. groenlandica long stipe form and that of <u>L</u>. saccharina, often overlapping the distribution

of the latter. The short stipe form is encountered intertidally at the mouths of inlets along the west coast of Vancouver Island. This form is abundant from Sooke to Jan Juan Island and along the east coast of Vancouver Island from the south side of Hope Island to the southern end of Johnstone Strait ( $50^{\circ}20'N$ ) and is infrequently encountered from this point to the southern end of Texada Island ( $49^{\circ}30'N$ ). One subtidal collection of the short stipe form has been made, near Keats Island, Howe Sound ( $49^{\circ}24'N$  123<sup>o</sup>28'W).

The relationships between the horizontal distributions of <u>L</u>. <u>saccharina</u> and the two forms of <u>L</u>. <u>groenlandica</u> and temperature and salinity were established by comparing the species' distributions in selected areas with the seasonal variation of surface temperature and salinity. This seasonal variation was characterized by plotting mean monthly temperatures against mean monthly salinities in a T-S diagram.

The relationship of seasonal variation for surface temperature and salinity as related to the variation in subsurface waters is illustrated in Figures 69 and 70. Variation of temperature and salinity in the upper 6 m is negligible at Sheringham Point, a region inhabited by <u>L. groenlandica</u> long stipe form, and at Gordon Head, a region inhabited by both <u>L. saccharina</u> and <u>L. groenlandica</u> short stipe form (Fig. 69). In Burrard Inlet, a region occupied by <u>L. saccharina</u>, considerable variation of temperature and salinity is encountered in the upper 5 m (Fig. 70).

Laminaria groenlandica long stipe form occurs in areas with cold, high salinity water having little seasonal

variation and exposed to heavy surf (Fig. 71, 72). Pine Island and Kains Island typify this habitat (Fig. 71). This form is absent from areas with considerable temperature and salinity variations and from areas where surf action is negligible, e.g., Friday Harbor (Fig. 71).

Laminaria groenlandica short stipe form is absent from areas having extreme seasonal variation of temperature and salinity, e.g., Deep Cove and Departure Bay, and from areas subjected to heavy surf (Fig. 71, 72).

Laminaria saccharina inhabits temperature and salinity situations typical of those encountered by the two forms of <u>L. groenlandica</u> (Fig. 71, 72) as well as situations of extreme temperature and salinity variation. <u>Laminaria</u> <u>saccharina</u> is absent from intertidal areas subjected to surf.

Available subtidal distributional data suggest that <u>L. groenlandica</u> short stipe form and <u>L. saccharina</u> may succeed in geographical areas where surface water conditions are prohibitive, providing they grow at a depth below the influence of these conditions. This hypothesis is supported by subtidal collections of <u>L. saccharina</u> from Salmon Bank and Amphritrite Point, places where it is not known interdially. Both of these areas are subjected to heavy surf. <u>Laminaria groenlandica</u> short stipe form is known subtidally only from one collection, that in 35 to 40 feet of water near Keats Island, Howe Sound. Here, surface temperature and salinity conditions (Table IV) appear unfavorable for this form on the basis of the data presented in Figures 71 and 72. However, temperature and salinity conditions near Keats

Island, at the depth inhabited by the short stipe form, are much less variable (Table IV).

From the above analysis of field data the following correlations have been made:

Laminaria saccharina distribution is independent of local temperature and salinity conditions and dependent upon the presence of calm water.

Laminaria groenlandica short stipe form distribution is restricted by temperature and/or salinity only when any mean monthly value of temperature exceeds  $18^{\circ}C$  and/or when salinity is lower than 23% (Fig. 72). Further, this form is excluded from areas of heavy surf.

Laminaria groenlandica long stipe form distribution is restricted to areas of heavy surf. These areas are characterized by low temperature and high salinity.

# EXPERIMENTAL EVALUATION OF THE EFFECTS OF VARIOUS OCEANOGRAPHIC FACTORS ON LAMINARIA SACCHARINA AND TWO FORMS OF LAMINARIA GROENLANDICA

The following experiments were designed to test the responses of vegetative and reproductive phases of the two species to various temperature, salinity, and water motion regimes. Culture studies were restricted to <u>L. saccharina and L. groenlandica long stipe form; transplant</u> studies were conducted on two forms of <u>L. groenlandica</u>. Also, a preliminary study was conducted to evaluate the possible effects on the plants of seawater from different origins.

### Whole Plant Response of Laminaria saccharina Sporophytes to Various Temperature and Salinity Situations

Two plants were placed in each of a variety of temperature-salinity situations on May 16, 1963. These situations consisted of 10, 20, 30, 40, and 50% salinities, at 5, 10, 15, and 20°C. The plants were cultured in 1 litre dishes in constant temperature rooms, under 330-345 ft-c light intensity, 12 hours light alternating with 12 hours dark. The culture medium was changed weekly.

The increase in surface area of the plants' blades was determined every 7 days for 4 weeks after which time the experiment was terminated. Injury to or death of the plants was recorded. Injured plants were characterized by a greenwhite color and were considered dead upon disintegration of the thallus. All plants maintained at 10 and 50% salinities died, death being earlier at the higher temperatures (Table V). All plants cultured at  $20^{\circ}$ C died by the end of the third week. Plants maintained at 5 to  $15^{\circ}$ C, in 20 to 40% salinity, survived the full four weeks. Optimal conditions for growth were 10 to  $15^{\circ}$ C, in 20 to 30% salinity.

# <u>Whole Plant Response of Laminaria saccharina Sporophytes</u> to Various Temperatures at Constant Salinity and to Various Salinities at Constant Temperature

In the spring of 1964 five plants were subjected to each of 5 salinities ranging from 16 to 31%, at a constant temperature of  $10^{\circ}$ C, and to 4 temperatures ranging from 7 to  $16^{\circ}$ C, at a constant salinity of 28‰. These plants were cultured in 1 litre dishes using plastic aquaria as incubators. The culture medium was changed every 5 days. Light conditions were 425 ft-c, 12 hours on and 12 hours off.

The mean increase in blade surface area per day was determined after 13 days for the plants subjected to various salinities and after 15 days for the plants subjected to various temperatures.

The optimal temperature tested was  $10^{\circ}$ C (Fig. 73). However, with the exception of one plant at  $10^{\circ}$ C, plants grown at 7.5 and  $12.5^{\circ}$ C responded similarly. Plants grew most rapidly at the higher salinities (Fig. 74).

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Photosynthetic and Respiratory Responses of Laminaria saccharina and Laminaria groenlandica Long Stipe Form Sporophytes to Various Temperature and Salinity Situations

This study employed discs cut from the blades of <u>L. saccharina</u> collected May 10, 1964 and <u>L. groenlandica</u> collected June 5, 1964. One disc from each of five plants was placed in a 1 litre culture dish for each of the following temperature-salinity conditions: salinities of 20, 24, 26, 28, 30, and 32‰, at 7, 10, 13, 15, and 18°C. The discs were preconditioned to these temperature-salinity situations for 5 days. Light conditions were 425 ft-c, 12 hours light alternating with 12 hours dark. The seawater was changed on the second and fourth days of preconditioning. On the morning of the sixth day the photosynthesis and respiration rates were determined. The light period during which photosynthesis was measured lasted 2 hours at an intensity of 650 ft-c and the dark period for respiration, 4 hours.

In general, net photosynthesis and respiration in <u>L. saccharina</u> discs increased with increase in temperature but were relatively uniform at all salinities (Table VI). The resultant net photosynthesis/respiration ratio remained fairly constant at all temperatures and salinities.

For <u>L</u>. <u>groenlandica</u> long stipe form discs, the rate of net photosynthesis and the net photosynthesis/respiration ratio decreased with increasing temperature but increased with increasing salinity (Table VI). There was no measurable

net photosynthesis at salinities lower than 28%, for temperatures greater than  $10^{\circ}$ C, or in any salinity at  $18^{\circ}$ C. The rate of respiration increased with increasing temperature to  $15^{\circ}$ C, above which the rate decreased. The respiration rate was nearly constant at all salinities. Measurable respiration occurred in all temperature-salinity situations tested.

Responses of Laminaria saccharina and Laminaria groenlandica. Long Stipe Form Gametophytes to Various Temperature and Salinity Situations

Meiospores of these two species, attached to glass slides were placed in 250 ml dishes, incubated in plastic aquaria. Duplicate cultures were established for salinities of 17, 20, 23, 26, 29, and 32%, at 7, 10, 13, and 16°C. Light intensity was approximately 100 ft-c; the regime was 12 hours on and 12 hours off. The culture medium was changed weekly. <u>Laminaria saccharina</u> gametophytes were maintained under the above conditions from October 23 to December 15, 1964, and <u>L. groenlandica</u> long stipe form gametophytes, from December 20, 1964 to January 25, 1965.

Suitability of the gametophytes' environment was determined by the plants' ability to produce normal sporophytes (Table VII).

Laminaria saccharina gametophytes produced normal sporophytes under most of the tested temperature-salinity conditions (Fig. 63e, 63f). Plants thought to be abnormal sporophytes, consisting of irregular, globular masses of

cells (Fig. 63g) were produced at 17, 20, and 23‰ salinity and 16°C.

Gametophytes of <u>L</u>. <u>saccharina</u> produced in high temperature, low salinity situations were large and filamentous (Fig. 63a, 63b). Similar gametophytes were produced in crowded cultures. Gametophytes produced under uncrowded conditions, at low temperatures and high salinities, were very small, the majority of their cells functioning as gametangia (Fig. 63c, 63d).

Gametophytes of <u>L</u>. groenlandica long stipe form produced normal sporophytes (Fig. 55e, 55f) in all salinities, at 7 and  $10^{\circ}$ C, and only in 29 and 32% salinities, at  $13^{\circ}$ C (Table VII). Plants thought to be abnormal sporophytes (Fig. 55g) were observed in 17% salinity, at  $10^{\circ}$ C, and in 20-32% salinities, at  $13^{\circ}$ C. Structures resembling sporophytes were not observed in 17% salinity, at  $13^{\circ}$ C, or in any salinity, at  $16^{\circ}$ C.

Gametophytes of <u>L</u>. groenlandica long stipe form, grown under conditions conducive to normal sporophyte production, were smaller than those grown under conditions giving rise to abnormal sporophytes. Development of what were thought to be gametophytes, in all tested salinities, at  $16^{\circ}$ C, was restricted to a few cellular divisions resulting in coccoid thalli. It was not possible to distinguish male from female gametophytes.

Photosynthetic and Respiratory Responses of Laminaria saccharina and of Laminaria groenlandica Long Stipe Form Sporophytes to Seawater of Different Origins

The experimental procedure employed here was identical to that described on page 46. Discs from five plants of each species were placed in three water types: Glacier Point seawater, Burrard Inlet seawater, and Glacier Point seawater diluted with Capilano River water. (This river enters the north side of Burrard Inlet.) Salinity of the three types of water was adjusted to 28‰ and the cultures were maintained at 7°C. After 5 days preconditioning, respiration and net photosynthesis of the discs were determined.

No significant differences in response of the two species to the three water types was observed.

## <u>Responses of Laminaria saccharina and Laminaria groenlandica</u> Long Stipe Form Gametophytes and Microscopic Sporophytes to Seawater of Different Origins

Responses of <u>L</u>. <u>saccharina</u> and <u>L</u>. <u>groenlandica</u> long stipe form to seawater of different origins were observed in November-December, 1963, and, for <u>L</u>. <u>saccharina</u>, again in June-July, 1964. The method of culture was as described on page 47. In the November-December tests water from Burrard Inlet, Glacier Point, and the Ogden Breakwater was adjusted to 28‰ salinity and maintained at  $7^{\circ}$ C. In the June-July tests water from Burrard Inlet and Glacier Point was adjusted to 28, 30, and 32‰ salinities and maintained at  $7^{\circ}$ C.

Both the November-December and June-July cultures were maintained for 35 days after inoculation with meiospores. At the end of this time 25 sporophytes, randomly selected, were measured with an ocular micrometer.

In both experiments the longest <u>L</u>. <u>saccharina</u> sporophytes developed in the Burrard Inlet water (Fig. 75, 76). The longest <u>L</u>. <u>groenlandica</u> sporophytes were produced in Glacier Point and the Ogden Breakwater seawater.

#### Transplantation Studies

A series of transplantations was made to test the effect of oceanographic conditions encountered in Burrard Inlet and Departure Bay on two forms of <u>Laminaria groenlandica</u>. These areas are inhabited by <u>L</u>. <u>saccharina</u> but not by <u>L</u>. <u>groenlandica</u>. Further, they are characterized by having considerable temperature and salinity variations and are not exposed to any surf (Fig. 70, 86).

Twenty young sporophytes of <u>L</u>. <u>groenlandica</u> long stipe form and 25 of <u>L</u>. <u>groenlandica</u> short stipe form were transplanted to Burrard Inlet between February 22 and April 28, 1963. Plants of both forms survived until June 10, 1963.

On August 5, 1963, twenty plants of both forms were transplanted to Departure Bay. Only remnants of these plants were observed at the next low tide series, 14 days later.

Ten plants of both forms were transplanted to Burrard Inlet on January 13, 1964. All of these plants had initiated soral production by the time of transplantation. The majority of these plants survived in Burrard Inlet until May 28, 1964.

On December 20, 1964, ten plants of the long stipe form were transplanted to Burrard Inlet. Microscopic examination of representative plants disclosed that apparent soral production had not yet been initiated. All plants had produced sori by mid-January. Fragments of these sori, when placed under culture conditions, released meiospores.

One set of gametophytes of <u>L</u>. <u>groenlandica</u> long stipe form were placed in Burrard Inlet on glass slides January 20, 1965. Subsequent observations of the glass slides revealed no laminarialean gametophytes, and the slides were overgrown with diatoms.

### STUDIES ON THE VERTICAL DISTRIBUTION OF

#### LAMINARIA SACCHARINA

### The Vertical Distribution of Laminaria saccharina as Related to Possible Determining Factors

The upper limits of <u>L</u>. <u>saccharina</u> distribution were observed at intervals from November, 1962 to December, 1963 (Fig. 77). Three positions for the upper limits were observed, the first near Point Atkinson in Burrard Inlet  $(49^{\circ}20'N 123^{\circ}16'W)$ , an area with tide pools, the remaining two in Burrard Inlet, near Stanley Park.

Position 1. Plants occupied tide pools situated above the mean low water (MLW) throughout the year.

Position 2. Plants were found above MLW in areas free of tide pools only when the spring low tides occurred at night (September-April).

Position 3. The upper-most extent of <u>L</u>. <u>saccharina</u> was below MLW when the spring low tides occurred during the day (April-September).

The lower limits of <u>L</u>. <u>saccharina</u> were found on two occasions in June, 1963 to be approximately 6.5 m below MLW.

The occurrence of <u>L</u>. <u>saccharina</u> throughout the year in tide pools situated above MLW suggests that factors operative during emergence are responsible for determining the upper limits of this species. First, only those plants which are constantly submerged may remain above MLW throughout the year. Second, water temperature encountered in the tide pools would approximate or exceed extreme values encountered in the inlet.

The upper vertical limits of <u>L</u>. <u>saccharina</u> are lowered from 20 cm above MLW to 40 cm below MLW with a shift from night to day of the spring low tides (Fig. 77). From September to April the plants above MLW are subjected to greater frequency and accumulative duration of emergence and longer individual emergences than are plants situated below MLW from April to September (Fig. 78). This suggests that the factors determining the upper limits are more severe during the day than during the night.

Air temperature and insolation are thought to be agents responsible in determining the upper limits of <u>L</u>. <u>saccharina</u> (Fig. 79-82). Plants exposed by low spring tides occurring during the day are subjected to more insolation and higher air temperatures than are plants exposed by low spring tides occurring during the night. The lower insolation values encountered by the first group result from lower incident radiation and a greater mean water depth through which the light must pass.

The lower limits of <u>L</u>. <u>saccharina</u> are thought to reflect the compensation depth of this species. The compensation depth is mainly a function of submarine illumination and temperature (Fig. 70, 83).

Experimental Evaluation of Some Factors as Possible Determinants of Distribution of Laminaria saccharina

Temperature and Salinity. The in vitro response of
L. <u>saccharina</u> sporophytes illustrates the ability of this species to thrive in conditions of temperature and salinity exceeding extremes encountered in Burrard Inlet (Fig. 70; Tables V, VI).

Cultured gametophytes of <u>L</u>. <u>saccharina</u> grew under temperature and salinity conditions representative of extreme values for Burrard Inlet (Table VII). However, production of normal sporophytes was restricted to temperatures below and salinities above the extremes encountered during summer months in the Inlet. These summer extremes were  $18^{\circ}$ C and 15% salinity. Gametophytes grown under conditions prohibitive to formation of normal sporophytes may produce normal sporophytes when subsequently introduced to favorable conditions. If this is the case, then extreme temperatures and salinities encountered in Burrard Inlet would not determine the upper limits of <u>L</u>. <u>saccharina</u> but would only delay normal sporophyte production.

<u>Submarine Illumination</u>. Several young plants were cultured under 6 different light intensities at the Vancouver Public Aquarium in the spring of 1964. The water temperature was 10°C and the light regime was 12 hours light, 12 hours dark. The increase in blade surface area was determined after 22 days (March 21-April 13). The greatest growth occurred at 700 ft-c (Fig. 85). Blades of plants cultured under 850 ft-c were a yellow-white color.

The apparent photosynthesis of blade discs was determined at 10 light intensities ranging from 20 to 900 ft-c

at 10°C. The discs were cut at the time of collection (June 1, 1964) from injury free blades and placed in darkness for 24 hours at 10°C. Then, the apparent photosynthesis of each disc was determined in the manner described on page 46. The light compensation point was found to be between 20 to 40 ft-c (Fig. 84). The rate of apparent photosynthesis increased with increasing light intensity to 500 ft-c, above which it was constant.

The ability of <u>L</u>. <u>saccharina</u> gametophytes to produce sporophytes under various light intensities was tested in June, 1964. Meiospores attached to glass slides were placed in eight light intensities ranging from 25 to 710 ft-c. They were maintained in open dishes submerged in the culture tank at the Vancouver Public Aquarium. The water temperature was 10<sup>°</sup>C, light regime 12 hours light and 12 hours dark. Gametophytes produced normal sporophytes within four weeks under all light intensities tested.

#### DISCUSSION AND CONCLUSIONS

## Taxonomy and Distribution

Ten morphologically distinct species of <u>Laminaria</u> are recognized by me for the northeast Pacific. In many instances these species form morphologically similar pairs. The members of a pair are usually distinguishable by one characteristic and often occupy similar ecological niches separated geographically. These species pairs are described below.

Laminaria yezoensis--Laminaria solidungula. These two species can be distinguished on the basis of the distribution of mucilage ducts. Laminaria solidungula has mucilage ducts in the stipe, <u>L</u>. <u>yezoensis</u> does not. <u>Laminaria</u> <u>yezoensis</u> is found in the northern Pacific (Miyabe, 1902) and <u>L</u>. <u>solidungula</u> in both the northern Atlantic (Taylor, 1957) and Arctic Oceans (Kjellman, 1883).

Laminaria saccharina--Laminaria farlowii. Laminaria farlowii can be distinguished from <u>L</u>. saccharina by having the entire blade bullate; in <u>L</u>. saccharina the bullae, when present, are restricted to two rows parallel to the blade margin. <u>Laminaria saccharina</u> is known in the north Atlantic (Taylor, 1957), the Arctic (Kjellman, 1883), the northwest Pacific (Tokida, 1945), and the northeast Pacific south to Oregon, with an isolated population at Santa Catalina Island, California. <u>Laminaria farlowii</u> is known from several locations in California and one in British Columbia.

Laminaria saccharina-Laminaria agardhii. The members of this pair can be separated from each other on the basis of the distribution of mucilage ducts; <u>L. saccharina</u> has ducts in the blade, <u>L. agardhii</u> does not. <u>Laminaria agardhii</u> is known from the north Atlantic (Taylor, 1957) and the Arctic (Kjellman, 1883). The distribution of <u>L. saccharina</u> is given above.

Laminaria longipes--Laminaria sinclairii. Laminaria sinclairii can be distinguished from <u>L. longipes</u> by the presence of mucilage ducts in its stipe. <u>Laminaria sinclairii</u> is known from California to central British Columbia, L. longipes, from central Alaska to Japan (Tokida, 1954).

Laminaria setchellii--Laminaria dentigera. These two species can be separated from each other by the positioning of the mucilage ducts. In <u>L. setchellii</u> the ducts are deep seated; in <u>L. dentigera</u> they are situated near the periphery. Laminaria setchellii is known from California to southern Alaska and <u>L. dentigera</u> from central Alaska to Japan (Tokida, 1954).

Recent field and culture studies have demonstrated considerable morphological plasticity of many characteristics used for specific distinction in Laminaria. Burrows (1964, 1964a) studied the effect of temperature on the blade morphology and anatomy of <u>L. saccharina</u> and <u>L. agardhii</u>. Results from this study indicate that temperature can modify such characteristics as bullation, mucilage duct production, thickness of blade, and cell size. Sundene (1962, 1964, 1964a) observed considerable morphological plasticity in two

forms of <u>L</u>. <u>digitata</u> subjected to transplantation. He noted that plants from exposed regions when grown in sheltered areas developed a broader blade and became more bullate, thus resembling the form native to the sheltered areas.

Evidence of morphological plasticity presented by Burrows and Sundene suggests a closer relationship between the members of the above listed pairs than accorded them at present. Clarification of the taxonomy of <u>Laminaria</u> depends upon (1) definition of phenotypic plasticity for those characteristics employed in delineating species and (2) an understanding of the genetic relationships between species. The first can be accomplished by culture and transplant studies similar to those of Sundene (1962, 1962a, 1964) and Burrows (1964, 1964a). The second may be accomplished by interfertility studies comparable to those of Sundene (1958) and Tokida and Yabu (1962), and by cytological studies similar to those of Kemp and Cole (1961), Evans (1964), and others.

The geographical ranges of all the species studied, with the exception of <u>L</u>. <u>groenlandica</u>, have been extended in this study. Further, the habitats to which some species were previously thought to be restricted have been enlarged. <u>Laminaria saccharina and L. complanata</u> were thought to be limited to sheltered waters; both have been revealed in exposed regions, <u>L. saccharina</u> subtidally and <u>L. complanata</u> intertidally. <u>Laminaria setchellii</u>, <u>L. ephemera</u>, and <u>L. sinclairii</u> were previously thought to be restricted to exposed areas. They have recently been disclosed subtidally in sheltered areas.

These results emphasize the importance of an integrated submarine and intertidal exploration program for studying distributions of benthic organisms which occur both intertidally and subtidally. This approach has not been extensively employed in the past.

## Life History and Morphology

Both intertidally occurring <u>L</u>. <u>groenlandica</u> long and short stipe forms and <u>L</u>. <u>saccharina</u> produced sori in October-January, and again in June. Parke (1948) observed sori of <u>L</u>. <u>saccharina</u> in Great Britain throughout the year. She noted the greatest numbers of fertile plants between October and March. Her investigation encompassed intertidal and subtidal plants. Failure of intertidal <u>L</u>. <u>saccharina</u> in British Columbia to produce sori throughout the year may result from damage to potentially reproductive tissues during low daytime spring tides. The reproductive cycle of subtidal plants in British Columbia is unknown.

Parke (1948) noted that sporophytic tissue must be at least 6 months old for soral initiation in <u>L</u>. <u>saccharina</u>, whereas Kireeva and Schapova (1938) stated that this species does not reach maturity until the third year of growth. In this study, all observed <u>L</u>. <u>saccharina</u> produced sori in the October-November period, including plants which first became conspicuous in February and September of the same year. Plants which produced sori in June were at least 9 months old. It would appear from my study that soral production by British Columbia plants in the winter is independent of

the age of sporophytic tissue, but in June may be dependent in part upon the age of this tissue.

Much morphological variability of gametophytes under culture conditions was observed for <u>L</u>. <u>saccharina</u> and to a much lesser degree for <u>L</u>. <u>groenlandica</u> (Fig. 55, 63). <u>Laminaria saccharina</u> meiospores produced filamentous gametophytes under crowded culture conditions and in situations of high temperature and low salinity. Under conditions of low temperature and high salinity and in uncrowded culture conditions the meiospores produced female gametophytes of a single cell, which functioned as the oogonium, and male plants of several cells, most of which functioned as antheridia. <u>In situ</u> observations of <u>L</u>. <u>saccharina</u> gametophytes in the winter revealed unicellular female plants but no male plants.

Filamentous gametophytes have been observed by Kemp and Cole (1961) for <u>Nereocystis luetkeana</u> under conditions of high temperature; by Sundene (1962) for <u>L</u>. <u>digitata</u> under conditions of feeble day light, low temperature, and unchanged media; and by Kain (1964) for <u>L</u>. <u>hyperborea</u> under conditions of high temperature, low illumination, and unchanged media.

In many species of Laminariales vegetative growth of gametophytes can occur at temperatures above those conducive to gamete production (Myers, 1928; Schreiber, 1930; Hollenberg, 1939; Saito, 1956, 1956a; Kemp and Cole, 1961; Sundene, 1963).

From the above studies it would appear that <u>Laminaria</u> can produce one of two forms of gametophytes depending upon environmental conditions: a small gametophyte consisting of few cells most of which function as gametangia, and a large filamentous gametophyte which may or may not produce gametangia while subjected to the environmental conditions under which the gametophyte developed. The small form appears adapted for immediate sporophyte production. However, fertilization limits the reproductive potential of the female plant. The large form may remain in the vegetative state until conditions become favorable for sporophyte production.

Consideration of results obtained from culture studies, here and elsewhere, and of the life history of <u>L</u>. <u>saccharina</u> as observed in British Columbia have led me to the following opinion. Gametophytes developing from meiospores released in June are of the large and vegetative type. These plants remain in the vegetative condition through most of the summer while conditions of high temperature and low salinity persist. In the late summer when the temperature is lower and salinity higher, gametes are produced and fertilization occurs. The resultant sporophytes are first conspicuous in early fall. Gametophytes resulting from the fall and winter crops of meiospores develop into small gametophytes and are almost immediately fertile. The resultant sporophytes first become conspicuous in February.

Plants thought to be abnormal sporophytes are produced by <u>L. saccharina and L. groenlandica</u> long stipe form under culture conditions of high temperature and low salinity

(Fig. 55, 63). Similar plants have been described from culture by Schreiber (1930), Segi and Kida (1958), Kemp and Cole (1961), and Tokida and Yabu (1962). These plants have been referred to as parthenogenetic sporophytes. Only Kemp and Cole (1961) were able to demonstrate that these plants had the haploid number of chromosomes.

Intercalary growth observed in both <u>L</u>. <u>groenlandica</u> long and short stipe forms and <u>L</u>. <u>saccharina</u> is greatest in the lower-most portion of the blade, and decreases distally. The region of greatest longitudinal growth coincides with the region of greatest lateral growth (Fig. 58-61, 64-67). Similar distributions of intercalary growth have been observed by Fallis (1916) for <u>L</u>. <u>saccharina</u> in Washington, by Parke (1948) for <u>L</u>. <u>saccharina</u> in Great Britain, and by Hasegawa (1962) for <u>L</u>. <u>angustata</u> in Japan. Sundene (1964) noted considerable variation in the distribution of intercalary growth in <u>L</u>. <u>digitata</u>. During June he observed some plants in which the greatest increments of growth occurred distal to the basal 5 cm of the blade base.

There is a seasonal variation in the growth rates of both <u>L. saccharina</u> and <u>L. groenlandica</u> long and short stipe forms as observed in this study (Fig. 68; Table I). In both forms of <u>L. groenlandica</u> vigorous growth commences in February when blade regeneration is initiated. Rapid growth continues until May-June. The growth rate then diminishes until November when sorus development is initiated. Growth is negligible from November until February. In <u>L. saccharina</u> the growth rate increases throughout the spring and summer

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until September after which time it decreases. No measurable growth was observed in December and January.

Seasonal variation of growth for <u>L</u>. <u>groenlandica</u> is in close accord with that reported by others in that the most active growth occurs in late winter and in spring (Printz, 1926, for <u>L</u>. <u>hyperborea</u>; Parke, 1948, for <u>L</u>. <u>saccharina</u>; Tseng, Wu, and Sun, 1957, for <u>L</u>. <u>japonica</u>; Hasegawa, 1962, for <u>L</u>. <u>angustata</u>; Sundene, 1964, for <u>L</u>. <u>digitata</u>). The period of active growth in <u>L</u>. <u>saccharina</u> as observed in British Columbia differs from the above species in that it extends from late winter until September.

## Local Distribution in Relation to Oceanographic Factors

The approach used in this study is an extension of a discipline initiated on the west coast of North America by the late William Albert Setchell at the turn of the century. Setchell (1893, 1917, 1935) attempted to explain marine algal distributions on the basis of temperature distribution at a time when the marine environment was poorly defined. Following his studies little was done in this field until the recent studies of Scagel (1961, 1961a, 1962, 1963, 1963a). Scagel related the distributions of marine algae in the northeast Pacific to various oceanographic and meteorologic conditions. He has pointed out that one can suggest the role of particular environmental factors in governing algal distributions by relating environmental conditions to algal distributions, and that the ultimate determination of the effect of any factor on algal distributions may be established by both experimental field and laboratory studies (Scagel, 1962).

In the present study the distributions of <u>L</u>. <u>saccharina</u> and <u>L</u>. <u>groenlandica</u> are related to factors that are conspicuously different between the habitats of these species: viz., water motion, temperature, and salinity. Conditions of light and substratum were considered insignificant because the species are known to have approximately the same vertical and latitudinal distributions and substratum requirements. The significance of biological and chemical factors other than those related to salinity were only investigated in a superficial fashion, and should be followed up in future studies.

Distributional studies on the two forms of <u>L. groenlandica</u> and on <u>L. saccharina</u> indicate that the former are excluded from areas having high temperature and low salinity, and the latter is excluded from areas of surf action (Fig. 71). Further, <u>L. groenlandica</u> long stipe form is found only in areas subjected to considerable surf, and is replaced by the short stipe form in quieter waters.

Evaluation of responses of <u>L</u>. groenlandica long stipe form and <u>L</u>. saccharina sporophytes and gametophytes to several temperature and salinity situations demonstrates that the range of tolerance to these factors is narrow in the former plants but wide in the latter (Fig. 73, 74; Tables V, VI, VII).

Transplant studies on <u>L</u>. <u>groenlandica</u> long and short stipe forms illustrate that these plants are restricted to narrow ranges of both temperature and salinity. They are

able to grow well in Burrard Inlet, an area where they do not occur naturally, only from December to June, the period when temperature is low and salinity high (Fig. 86). In the long stipe form vegetative growth and soral production proceed in the sheltered transplant area, and are not dependent upon surf action.

Responses of gametophytes of <u>L</u>. <u>groenlandica</u> long stipe form and <u>L</u>. <u>saccharina</u> to water of different origins indicate that conditions most favorable for growth are encountered in water from the plant's natural habitat (Fig. 75, 76). The differential responses may result from differences in ionic ratios of the seawater constituents, or from the presence and/or absence of organic substances. Physiological response of sporophytes of both species was similar to all water types tested.

From the above culture and transplant studies the following conclusions are drawn:

(1) The local distribution of <u>L</u>. groenlandica is independent of surf conditions. This, indirectly, suggests that the two forms are ecological adaptations of one geno-type.

(2) Temperature and salinity acting upon the sporophyte of the two forms of <u>L</u>. groenlandica determine their distributions about Vancouver Island. Considering the temperature and salinity conditions, the gametophytes of these forms could produce normal sporophytes during the winter and early spring in all local environments inhabited by L. saccharina. In the summer sporophyte production

would be prohibited.

No attempt has been made to separate the effects of temperature and salinity on the physiology and growth of <u>L. groenlandica</u>. The culture experiments indicate that the best situation for growth is low temperature in combination with high salinity. The detrimental effects of high temperature may be offset by high salinity, and the harmful effects of low salinity, by low temperature.

Earlier culture studies have illustrated the importance of temperature in limiting growth and reproduction in <u>Laminaria</u> (Burrows, 1961, in <u>L. saccharina;</u> Tokida and Yabu, 1962, in <u>L. religiosa</u>; Kain, 1964, in <u>L. hyperborea</u>; Sundene, 1964, in <u>L. saccharina, L. hyperborea</u>, <u>L. digitata</u>).

Transplant studies on <u>L. japonica</u> (Tseng, Wu, and Sun, 1957) and on <u>Alaria esculenta</u> and <u>L. digitata</u> (Sundene, 1962, 1962a, 1964) have yielded results similar to those recorded here. These authors found that plants transplanted from a colder to a warmer region were able to grow successfully through the winter and spring months but were severely injured or killed by summer temperatures.

Sundene's (1964a) studies on <u>L</u>. <u>saccharina</u>, <u>L</u>. <u>hyperborea</u>, and <u>L</u>. <u>digitata</u> in Norway indicate that salinity is a minor factor in determining regional distributions.

(3) The local distribution of <u>L</u>. <u>saccharina</u> is independent of temperature and salinity with the possible exception of extreme estuarine conditions. Its distribution is restricted by surf action since (a) the plant was observed in

areas subjected to surf only when positioned below the direct influence of this factor and (b) the delicate nature of the plant, its thin blade and stipe, and fine holdfast do not equip it for survival in areas subjected to surf.

(4) Competition between <u>L</u>. <u>saccharina</u> and <u>L</u>. <u>groenlandica</u> may be an important factor influencing the distributions of these species in areas not subjected to surf. This is indicated by the responses of gametophytes to water of different origins.

## Vertical Distribution of Laminaria saccharina.

The upper limits of <u>L</u>. <u>saccharina</u> as observed in Burrard Inlet are thought to be determined by air temperature and insolation (Fig. 77). The tide is considered an indirect agent influencing the upper limits, as it determines the time and duration of exposure to air and direct insolation.

Culture studies show that prolonged exposure to light of an intensity above the saturation level (500 to 700 ft-c) results in a growth decrease and in tissue injury (Fig. 85). Brief exposures to these intensities do not appear to be detrimental (Fig. 84). These studies suggest that submarine light intensities may play a significant role in determining the upper limits. However, because of the greater intensity and spectral distribution of light striking emerged plants, direct insolation would be more harmful.

Other workers have recorded considerably lower saturation levels. Segi and Kida (1958) found the best growth of Undaria undariodes occurred between 1500 to 2000 lux

(ca. 140 to 180 ft-c); at 4800 lux (ca. 440 ft-c) growth was inhibited. Kain (1964, 1965) reports a saturation value of 1000 lux (ca. 93 ft-c) at  $10^{\circ}$ C for sporophytes and 350 lux (ca. 33 ft-c) for gametophytes of <u>L</u>. <u>hyperborea</u>. These workers employed light sources of different spectral qualities than those used in this study, thus a comparison of results is not meaningful.

The lower limits of <u>L</u>. <u>saccharina</u> as observed in Burrard Inlet are thought to reflect the compensation depth of this species. There was no evidence of competition with other algae and the substratum was uniform from above the upper limits to below the lower limits of vertical distribution.

The culture studies on sporophytes of <u>L</u>. <u>saccharina</u> have shown the light compensation point to be between 20 to 40 ft-c at  $10^{\circ}$ C (Fig. 84). Increase in blade surface was approximately 1% per day at 180 ft-c and  $10^{\circ}$ C (Fig. 85). Gametophytes cultured under 20 ft-c illumination at  $10^{\circ}$ C produced normal sporophytes. Lower intensities were not tested. Kain (1964, 1965) found 20 lux (ca. 1.9 ft-c) at  $10^{\circ}$ C to be the minimal light intensity for development of gametophytes and young sporophytes of L. hyperborea.

The lowest values of submarine illumination in Burrard Inlet are encountered during the winter months. <u>Laminaria</u> <u>saccharina</u> gametophytes resulting from the June crop of meiospores should be able to establish themselves at a greater depth than the winter population because of the greater light intensity in June. The resultant sporophyte

generation could be eliminated, as the light intensity may fall below the compensation point in the winter months (Fig. 83). During this period gametophytes would not succeed to the depth populated by the summer ones. Insufficient data on fluctuations of the lower limits and on the life history of the subtidal plants precludes precise definition of agents responsible for the lower limits.

#### SUMMARY

Ten species of Laminaria are recognized by me for the northeast Pacific: L. groenlandica Rosenv.; L. farlowii Setchell; L. saccharina (L.) Lamour.; L. complanata (Setchell et Gardner) Setchell; L. setchellii Silva; L. dentigera Kjellman; L. longipes Bory; L. sinclairii (Harvey ex Hooker f. et Harvey), Farlow, Anderson et Eaton; L. ephemera Setchell; and L. yezoensis Miyabe. Laminaria cordata Dawson is considered conspecific with L. saccharina, L. personata Setchell and Gardner is regarded as conspecific with L. yezoensis, and L. platymeris De la Pyl. (sensu Setchell and Gardner, 1925) is considered conspecific with L. groenlandica. Four forms of L. groenlandica are recognized for the northeast Pacific: long stipe form, short stipe form, flat stipe form and shade form. These forms are not considered by me at present as legitimate taxonomic entities but are distinguished merely to provide a means of facilitating discussion until such time as a critical monographic study for the entire genus is made.

The geographical ranges of all the species studied, with the exception of <u>L</u>. <u>groenlandica</u>, have been extended in this study. Further, the habitats to which all ten species were previously thought to be restricted have been enlarged. <u>Laminaria saccharina and L. complanata</u> were thought to be limited to sheltered waters: both have been revealed in exposed regions. <u>Laminaria setchellii</u>, <u>L</u>. <u>ephemera</u>, and <u>L</u>. <u>sinclairii</u> were previously thought to be restricted to exposed areas. They have recently been disclosed subtidally in sheltered areas.

Laminaria saccharina and L. groenlandica produced sori in the late spring and winter. Sorus production by L. saccharina in the winter is independent of the age of the sporophyte tissue but in spring may be dependent in part upon the age of this tissue. New sporophytes of L. groenlandica appeared throughout the year, whereas those of L. saccharina appeared in late winter and early fall. Depending upon culture conditions, two morphologically distinct forms of gametophytes were produced by both species: large gametophytes in conditions of high temperature and low salinity; and small gametophytes in conditions of low temperature and high salinity. Abnormal sporophytes were observed under conditions conducive to formation of large gametophytes. These may be parthenosporophytes.

Patterns of growth for the blades of the two species were essentially the same. The growth rate decreased with increase in distance from the blade base, and the position of greatest longitudinal growth coincided with the position of greatest lateral growth.

The distributions of <u>L</u>. <u>saccharina</u> and the two forms of <u>L</u>. <u>groenlandica</u> about Vancouver Island were correlated with temperature, salinity, and water motion. The two forms

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of <u>L</u>. <u>groenlandica</u> were absent from areas of high temperature and low salinity, <u>L</u>. <u>saccharina</u> was absent from areas subjected to surf. These field conclusions were subjected to laboratory and field tests involving gametophytes and sporophytes of both species. The distributions of the two forms of <u>L</u>. <u>groenlandica</u> can be explained on the basis of temperature and salinity distributions. Both forms require low temperature and high salinity for survival. <u>Laminaria</u> <u>saccharina</u> has a wide range of tolerance to temperature and salinity. Surf appears to be the agent controlling the distribution of this species.

The upper limits of <u>L</u>. <u>saccharina</u>, as observed in Burrard Inlet, are thought to be directly related to air temperature and insolation and indirectly related to tidal characteristics. The lower limits appear to reflect the compensation depth of this species.

The above studies illustrate the potential value of combined field and laboratory studies in solving problems of algal taxonomy, morphology, physiology, and ecology. In the laboratory it is possible to define and control environmental parameters and to monitor the organisms studied. However, culture conditions as used at present are poor approximations of the natural environment. In the

field one deals with a natural environment, however, in this case the environment is usually poorly defined and the specimens are not readily accessible for monitoring. Employment of modern oceanographic instrumentation and SCUBA gear assists in overcoming these difficulties.

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Appendix I. Voucher Specimens of Laminaria

(LD)

(RN)

(RFS)

(NLG)

#### Legend

Area. The northwest coast of North America north of  $48^{\circ}$ N Latitude has been divided into five areas. Voucher specimens of <u>Laminaria</u> have been catalogued alphabetically for each of these areas. The map on the facing page shows the distribution of these areas.

Louis Druehl;

R. F. Scagel;

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N. L. Gardner;

Collectors.

Herbaria.

- (TBW) T. B. Widdowson.
  (WTU) Friday Harbor Laboratory, San Juan Island, Washington. Operated by the University of Washington.
- (UBC) University of British Columbia, Canada.
- (V) Provincial Museum of British Columbia, Victoria, Canada. Held in the herbarium of U.B.C.
- (D) Indicates the occurrence of the species in the subtidal region only.

Appendix	I.	Section A.	Voucher	Specimens	of	Laminaria	longipes
<b>- -</b>				· •			

Area	Location	Approximate Latitude	Position Longitude	Coll. No.	Acc. No.
I I I I I	Cape Agagdak, Adak Cape Chiniak, Kodiak Cape Sarichef, Unimak Casco Bay, Attu Chichagof Point, Attu	51° 60' N 57° 37' N 54° 35' N 52° 48' N 52° 57' N	176° 37' W 152° 10' W 164° 56' W 173° 10' E 173° 15' E	4068 RFS 4359 RFS 4192 RFS 4052 RFS 4050 RFS	UBC 8363 UBC 8161 UBC 8217 UBC 8311 UBC 8381
I I I I I I	English Bay, Kenai Peninsula Murder Point, Attu North Island, Adak Pasagshak Point, Kodiak Trappers Cove, Adak Zeto Point, Adak	59°21'N 52°48'N 51°50'N 57°25'N 51°48'N 51°55'N	151° 56' W 173° 09' E 176° 48' W 152° 29' W 176° 50' W 176° 34' W	4261 RFS 4004 RFS 4115 RFS 4381 RFS 4099 RFS 4143 RFS	UBC 8235 UBC 8225 UBC 8398 UBC 8176 UBC 9632 UBC 8361
Appendix	I, Section B. Voucher	Specimens of <u>L</u>	aminaria sinclair	<u>ii</u>	
III III IV V V	Box Island Whiffin Spit Plover Island Partridge Bank Salmon Bank	49°04'N 48°21'N 50°56'N 48°16'N 48°26'N	125° 47' W 123° 43' W 127° 58' W 122° 51' W 123° 01' W	500 LD 611 LD 562 RFS 4942 RN 4791 RN	UBC 17012 UBC 20124 UBC 413 WTU 2079
Appendix	I, Section C. Voucher	Specimens of <u>L</u>	aminaria ephemera	•	
III(D)	Amphitrite Point	48° 54′ N	125° 33' W	568 LD	UBC 18056
III V(D) V(D) V(D)	Botany Beach (unoff.), Port Renfrew Glacier Point Hein Bank Salmon Bank Smith Island	48°33'N 48°23'N 48°21'N 48°33'N 48°19'N	124°26'W 123°59'W 123°02'W 123°10'W 122°51'W	536a LD 1176 RFS 4869 RN	UBC 4492 UBC 19290 WTU 322 UBC 2632 WTU 2077

Appendix I, Section D. Voucher Specimens of Laminaria yezoensis

Area	Location	Approximate Latitude	Position Longitude	Coll. No.	Acc. No.
I . T	Cape Sarichef, Unimak	54° 35' N	164° 56' w	4204 RFS	UBC 8232
, t I T	Kenai Peninsula Khantaak Island, Yakutat	59°21'N 59°35'N	151 <sup>°</sup> 56' W 139° 46' W	4279 RFS 4430 RFS	UBC 8352 UBC 8419
I I II II IV	Biorka Island Yakutat Roads, Yakutat Zeto Point, Adak Mazzaredo Islands Striae Point Hope Island	56° 51' N 59° 33' N 51° 55' N 54° 05' N 54° 05' N 50° 58' N	135° 32' W 139° 44' W 176° 34' W 132° 34' W 132° 15' W 127° 55' W	4530 RFS 4462 RFS 4143 RFS 892 RFS 802 RFS	UBC 9644 UBC 9800 UBC 8416 UBC 2046 UBC 1987 UBC 20123
Appendix	I, Section E. Voucher S	pecimens of <u>La</u>	aminaria groenlar	dica flat sti	pe form
II II II	Langara Island Marchand Reef Mazzaredo Islands	54° 12' N 54° 10' N 54° 05' N	133° 02' W 133° 00' W 132° 34' W	7249 RFS 7278 RFS 7306 RFS	UBC 16925 UBC 17029 UBC 16933
Appendix	I, Section F. Voucher S	pecimens of <u>La</u>	aminaria groenlar	dica short st	ipe form
I I I	Casco Bay, Attu Harbor Point, Sitka Khantaak Island, Yakutat Saddle Point, Cordova	52° 48' N 57° 06' N 59° 35' N 60° 32' N	173° 10' E 135° 15' W 139° 46' W 145° 46' W	4053 RFS 4511 RFS 4431 RFS 4405 RFS	UBC 12709 UBC 9714 UBC 8471 UBC 8337
L I I	Seldovia Point, Kenai Peninsula Symonds Bay, Biorka I. Western Channel, Sitka	59°28'N 56°51'N 56°51'N	151° 42' W 135° 32' W 135° 22' W	4247 RFS 4530 RFS 4606 RFS	UBC 8411 UBC 9714 UBC 8213

	Appendix J	Ε,	Section	F.	cont.	Voucher	Specimens	of	Laminaria	groenlandica	$\mathtt{short}$	stipe
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Area	Location	Approximate Latitude	Position Longitude	Coll. No.	Acc. No.
I III III	Yakutat Roads, Yakutat Island Catala Island Garden Island	59 <sup>°</sup> 33' N 49° 50' N 50° 01' N	139 <sup>°</sup> 44' W 127° 00' W 127° 21' W	4458 RFS 2333 RFS 3406 RFS	UBC 8299 UBC 4084 UBC 6862
III(D)	Lorenz Point, Nasparti Inlet	50° 09' N	127° 36 <b>'</b> W	8149 RFS	UBC 17790
IV IV IV IV IV IV IV IV IV IV IV IV IV I	Tofino Walters Cove Whiffin Spit Williams Head Balaklava Island Comox Deer Island False Head Keats Island Keogh River Klucksiwi River Maude Island Numas Islands Port Neville Trinity Island Victoria, Cadboro Point Victoria, Gonzales Point Victoria, Gordon Head Victoria, Harling Point	490 09 N 500 01 N 480 21 N 500 52 N 500 52 N 500 51 N 500 39 N 500 31 N 500 37 N 500 37 N 500 37 N 500 36 N 500 30 N 500 41 N 500 31 N 500 24 N 500 20 N 500	125° 54' W 127° 23' W 123° 43' W 123° 35' W 127° 35' W 125° 05' W 127° 22' W 127° 15' W 123° 28' W 127° 11' W 127° 11' W 127° 06' W 127° 06' W 127° 06' W 127° 05' W 127° 05' W 123° 16' W 123° 16' W 123° 18' W 123° 18' W 123° 19' W 123° 20' W	574 LD 3582 RFS 99 LD 594 LD 6633 RFS 3663 RFS 6204 RFS 6202 RFS 612 LD 6200 RFS 193 RFS 3641 RFS 6721 RFS 6136 RFS 6896 RFS 505 LD 504 LD 508 LD 407 LD	UBC 18143 UBC 7389 UBC 14376 UBC 19057 UBC 17015 UBC 7415 UBC 16980 UBC 17000 UBC 20017 UBC 17010 UBC 20017 UBC 17010 UBC 17010 UBC 16983 UBC 16983 UBC 16983 UBC 16987 UBC 16987 UBC 17004 UBC 17004
IV IV	Victoria, McMicking Pt. Victoria, Ross Bay	48° 23' N 48° 25' N	123° 18' W 123° 20' W	506a LD 510 LD	UBC 16997 UBC 17003
v	American Camp, San Juan I. Kanaka Bay	48° 27¦ N 48° 29' N	122° 59' W 123° 05' W	584 LD 590 LD	UBC 18836 UBC 18832

Area	Location	Approximat Latitude	e Position Longitude	Coll. No.	Acc. No.
A A	Minnesota Reef West Beach	48° 32' N 48° 14' N	122° 59' W 122° 46' W	587 LD 593 LD	UBC 18840 UBC 18831
Appendix	I, Section G. Voucher	Specimens of	Laminaria groenl	andica long st	ipe form
I I I I I I I I I I I I I I I I I I I	Casco Bay, Attu Cape Chiniak, Kodiak Harbor Point, Sitka Khantaak I., Yakutat Knight Island, Yakutat Mills Bay, Kodiak Symonds Bay, Biorka I. Zeto Point, Adak Antony Island Digby Island Frederick Island Hippa Island Marchand Reef Mazzaredo Islands Qlawdzeet-Bell Passage Striae Islands Amos Island Brooks Peninsula Bunsby Island Cuttle Island Experiment Bight Glacier Point Guise Bay Look Out Island Muir Point Noble Island	52°° 48' N 57°° 335' N 57°° 000 555° 555°	$173^{\circ} 10' W$ $152^{\circ} 10' W$ $135^{\circ} 15' W$ $139^{\circ} 38' W$ $139^{\circ} 38' W$ $152^{\circ} 21' W$ $135^{\circ} 32' W$ $135^{\circ} 32' W$ $137^{\circ} 32' W$ $137^{\circ} 28' W$ $130^{\circ} 28' W$ $132^{\circ} 57' W$ $132^{\circ} 57' W$ $132^{\circ} 50' W$ $132^{\circ} 50' W$ $127^{\circ} 32' W$ $127^{\circ} 36' W$ $128^{\circ} 25' W$ $128^{\circ} 25' W$ $128^{\circ} 25' W$ $128^{\circ} 25' W$ $128^{\circ} 25' W$ $127^{\circ} 35' W$	$\begin{array}{c} 4052 \ \mathrm{RFS} \\ 4358 \ \mathrm{RFS} \\ 4576 \ \mathrm{RFS} \\ 44576 \ \mathrm{RFS} \\ 4431 \ \mathrm{RFS} \\ 4472 \ \mathrm{RFS} \\ 4472 \ \mathrm{RFS} \\ 4532 \ \mathrm{RFS} \\ 4532 \ \mathrm{RFS} \\ 4532 \ \mathrm{RFS} \\ 7664 \ \mathrm{RFS} \\ 7064 \ \mathrm{RFS} \\ 7004 \ \mathrm{RFS} \\ 7004 \ \mathrm{RFS} \\ 7004 \ \mathrm{RFS} \\ 7290 \ \mathrm{RFS} \\ 7307 \ \mathrm{RFS} \\ 7608 \ \mathrm{RFS} \\ 7487 \ \mathrm{RFS} \\ 7837 \ \mathrm{RFS} \\ 8209 \ \mathrm{RFS} \\ 7837 \ \mathrm{RFS} \\ 8082 \ \mathrm{RFS} \\ 7927 \ \mathrm{RFS} \\ 8334 \ \mathrm{RFS} \\ 511 \ \mathrm{LD} \\ 8334 \ \mathrm{RFS} \\ 511 \ \mathrm{LD} \\ 8334 \ \mathrm{RFS} \\ 7728 \ \mathrm{RFS} \\ 758 \ \mathrm{RFS} \ \mathrm{RFS} \\ 758 \ \mathrm{RFS} \$	UBC 8281 UBC 9618 UBC 9618 UBC 8293 UBC 8234 UBC 9246 UBC 13032 UBC 9650 UBC 16922 UBC 16944 UBC 16945 UBC 16945 UBC 16945 UBC 16948 UBC 16948 UBC 16948 UBC 16948 UBC 17869 UBC 17863 UBC 17863 UBC 17871 UBC 17687 UBC 19338 UBC 16986 UBC 19334 UBC 17849 UBC 17849 UBC 16927

Appendix I, Section F. cont. Voucher Specimens of Laminaria groenlandica short stipe

Appendix I, Section G. cont. Voucher Specimens of Laminaria groenlandica long stipe form

Area	Location	Approximate Latitude	e Position Longitude	Coll. No.	Acc. No.
III III III IV IV	Tofino Triangle Island Walters Island Whiffin Spit Roller Bay, Hope Island Rosebush Island	49° 09' N 50° 55' N 50° 02' N 48° 21' N 50° 56' N 50° 14' N	125° 54' W 129° 05' W 127° 23' W 123° 43' W 127° 56' W 125° 09' W	578a LD 8539 RFS 7861 RFS 114 LD 8613 RFS 3624 RFS	UBC 18138 UBC 19342 UBC 17847 UBC 14383 UBC 19436 UBC 7381
v V	San Juan I. Neah Bay	48° 27' N 48° 22' N	122° 46¦ W 124° 37' W	583 LD 3843 NLG	UBC 18839 UBC 399
Appendi	x I, Section H. Voucher S	Specimens of <u>I</u>	aminaria saccha	rina	
I I I I I I I I I I I I I I I I I I I	Homer, Kenai Penin. Knight I., Yakutat Saddle Point, Cordova Yakutat Hazardous Cove Refuge Bay Welcome Point Catala Island Hisnit Islands Matlset Narrows McLean Island Nasparti Inlet Ououkinsh Inlet Sooke Harbour Tofino William Head Winter Harbour Ucleulet Blenkinson Bay	59° 39' N 59° 32' N 59° 33' N 59° 33' N 59° 05' N 54° 05' N 54° 05' N 59° 00' N 59° 00' N 50° 00	151°    34'    W      139°    38'    W      139°    46'    W      139°    44'    W      139°    44'    W      139°    22'    W      130°    22'    W      130°    22'    W      130°    22'    W      127°    29'    W      127°    38'    W      127°    38'    W      127°    38'    W      123°    55'    W      123°    34'    W      128°    02'    W      125°    33'    W      126°    06'    W	4217 RFS 4470 RFS 4405 RFS 4466 RFS 683 RFS 2085 RFS 3532 RFS 8151 RFS 8035 RFS 221 LD 579 LD 595 LD 2725 RFS 570 LD	UBC 8404 UBC 14202 UBC 8319 UBC 14140 UBC 1413 UBC 3293 UBC 6924 UBC 4086 UBC 19013 UBC 19013 UBC 17909 UBC 17908 UBC 17908 UBC 14749 UBC 18137 UBC 19059 UBC 18054 UBC 7431

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## Appendix I, Section H. cont. Voucher Specimens of Laminaria saccharina

Area	Location	Approximate Latitude	Position Longitude	Coll. No.	Acc. No.
IV IV IV IV IV IV IV IV IV IV IV IV IV I	Bull Harbour Burdwood Bay Comox Deep Cove Departure Bay Dodd Narrows Dorcas Point Egmont Point False Narrows Ganges Harbour Klucksiwi River Keats Island Point Atkinson Port Neville Qualicum Beach Rouche Point Sidney Stanley Park Tsawwassen Victoria, Cattle Point Victoria, Gonzales Point	50° 55' N 50° 09' N 49° 20' N 49° 20' N 49° 11' N 49° 13' N 49° 13' N 49° 18' N 49° 47' N 49° 37' N 49° 37' N 49° 37' N 49° 37' N 49° 30' N 49° 30' N 49° 19' N 50° 30' N 49° 19' N 50° 30' N 49° 19' N 50° 21' N 49° 18' N 49° 19' N 50° 21' N 49° 19' N 49° 20' N 49° 18' N 49° 20' N 49° 18' N 49° 19' N 48° 27' N 48° 29' N	127° 56' W 125° 66' W 124° 52' W 123° 58' W 123° 58' W 123° 49' W 123° 49' W 123° 57' W 123° 28' W 123° 28' W 123° 28' W 123° 28' W 123° 16' W 123° 16' W 123° 28' W 123° 16' W 123° 26' W 123° 66' W 123° 17' W 123° 17' W 123° 18' W	8629 RFS 526 LD 514 LD 3721 RFS 3711 RFS 532 LD 580 LD 531 LD 520 LD 3749 RFS 610 LD 549 LD 509 LD 504 LD 518 LD	UBC 19345 UBC 7206 V 001484 UBC 19239 UBC 16978 UBC 7382 UBC 7417 UBC 19233 UBC 3101 UBC 3101 UBC 3101 UBC 3101 UBC 2081 UBC 19234 UBC 19234 UBC 19234 UBC 19245 UBC 19245 UBC 19332 UBC 19332 UBC 19332 UBC 19226 UBC 16994 UBC 16955 UBC 17005
V V V(D)	Kanaka Bay Minnesota Reef Salmon Bank	48° 29' N 48° 26' N 48° 26' N	123° 05, W 122° 59, W 123° 01, W	588 LD	UBC 18833 UBC 7054
Appendix	I, Section I. Voucher Sp	pecimens of <u>La</u>	minaria <u>farlowwi</u>	i	
IV	Comox	49°39'N	124 <sup>0</sup> 52 <b>'</b> W		UBC 001484

Area	Location	Approximate Latitude	Position Longitude	Coll. No.	Acc. No.
II IV(D) V(D)	Marchand Reef James Bank Brown Island	58° 10' N 48° 36' N 48° 32' N	133° 00' W 123° 21' W 123° 00' W	7273 RFS 1104 RFS 274 TBW	UBC 16966 UBC 2455 UBC 3000
Appendix	I, Section K. Voucher	Specimens of <u>L</u>	aminaria <u>setche</u>	llii	
I I II II II II III	Biorka Island Ocean Cape, Yakutat Western Channel, Sitka Chanal Reef Frederick Island Langara Island Mazzaredo Islands Amphitrite Point	56° 51' N 59° 31' N 57° 03' N 54° 12' N 53° 55' N 54° 11' N 54° 05' N 48° 55' N	135° 32' W 139° 52' W 135° 24' W 133° 02' W 133° 10' W 133° 01' W 132° 34' W 125° 32' W	4518 RFS 4419 RFS 4613 RFS 926 RFS 7035 RFS 7370 RFS 670 LD	UBC 9610 UBC 8181 UBC 8218 UBC 2107 UBC 16936 UBC 2485 UBC 16940 UBC 18057
III III III III III III III III III II	Botany Beach (unoff.) Port Renfrew Box Island Brooks Peninsula Bunsby Island Cape Cook Cuttle Island Estevan Point Experiment Bight Garden Island Guise Bay Hisnit Islands Kains Island Look Out Island Nasparti Inlet Maquinna Point McLean Island Mills Peninsula	48° 31' N 49° 04' N 50° 05' N 50° 06' N 50° 08' N 50° 06' N 50° 00' N 50° 00	$124^{\circ} 26' W$ $125^{\circ} 47' W$ $127^{\circ} 46' W$ $127^{\circ} 32' W$ $127^{\circ} 55' W$ $127^{\circ} 36' W$ $127^{\circ} 36' W$ $128^{\circ} 25' W$ $128^{\circ} 25' W$ $128^{\circ} 25' W$ $127^{\circ} 29' W$ $128^{\circ} 02' W$ $127^{\circ} 37' W$ $127^{\circ} 37' W$ $127^{\circ} 26' W$ $127^{\circ} 11' W$	170 LD 500 LD 8173 RFS 8081 RFS 8264 RFS 7974 RFS 2839 RFS 8410 RFS 2419 RFS 8341 RFS 7922 RFS 8341 RFS 7922 RFS 2633 RFS 7760 RFS 2633 RFS 3450 RFS 3450 RFS 3085 RFS	UBC 14754 UBC 17006 UBC 17859 UBC 17846 UBC 17865 UBC 17870 UBC 7391 UBC 19339 UBC 4111 UBC 19336 UBC 17893 UBC 17863 UBC 17868 UBC 17861 UBC 17861 UBC 4106 UBC 7409 UBC 7380

# Appendix I, Section J. Voucher Specimens of Laminaria complanata

Appendix I, Section K, cont. Voucher Specimens of Laminaria setchellii

Area	Location	Approximate Latitude	Position Longitude	Coll. No.	Acc. No.
III III III III III III IV IV IV IV V(D)	Ogden Point Breakwater Otter Point Perez Rocks Sharp Point Sheringham Point Solander Island Spring Island Tofino Triangle Island Wouwer Island Cape Sutile Roller Bay, Hope Island Rosebush Island Neah Bay Salmon Bank	48° 24' N 49° 25' N 49° 225' N 49° 225' N 49° 222' N 50° 000' N 50° 00' N 500' N 50° 00'	123° 23' W 123° 49' W 126° 37' W 126° 16' W 123° 55' W 127° 56' W 127° 25' W 129° 25' W 129° 25' W 129° 25' W 129° 25' W 129° 25' W 129° 26' W 125° 09' W 125° 09' W 125° 09' W 124° 37' W	3851 RFS 2886 RFS 2986 RFS 191 TBW 8293 RFS 569 LD 8436 RFS 2028 RFS 6409 RFS 6323 RFS 3626 RFS 1125 RFS	UBC 12677 UBC 12173 UBC 7418 UBC 7379 UBC 3448 UBC 17851 UBC 18055 UBC 19340 UBC 16998 UBC 16998 UBC 16993 UBC 6947 UBC 399 UBC 2363
Appendix	I, Section L. Voucher S	pecimens of La	aminaria dentiger	ca	
I I I I I	Cape Agagdak, Adak Cape Sarichef, Unimak Chicagof Point, Attu Murder Point, Attu Ocean Cape, Yakutat Pasagshak Point, Kodiak	51° 60' N 54° 35' N 52° 27' N 52° 48' N 59° 31' N 57° 25' N	176° 37' W 164° 56' W 173° 15' E 173° 09' E 139° 52' W 152° 29' W	4070 RFS 4204 RFS 4049 RFS 4003 RFS 4419 RFS 4377 RFS	UBC 8277 UBC 8278 UBC 8248 UBC 8258 UBC 8315 UBC 8175

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Appendix II. Observed Specimens of Particular Taxonomic

Significance

(EYD)

### Legend.

Collectors.

(MF) M. Foslie

(NLG) N. L. Gardner

(WAS) W. A. Setchell

E. Y. Dawson

(S&G) W. A. Setchell & N. L. Gardner

(JT) J. Tokida

(JMW) J. M. Weeks

Herbaria.

(UC) University of California, Berkeley.

(AHFH) Allan Hancock Foundation Herbarium, University of Southern California.

Appendix II. Obser	ved Specimens	OI.	Particular	Taxonomic	Significance
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Specimen	Location	Collector No. Date	Herb No.
<u>L. bullata f. amplissima</u> (= L. groenlandica short stipe)	Esquimalt, B.C., Canada	S&G, 680a May, 1901	UC 96926
<u>L. bullata f. angusta</u> (= <u>L. groenlandica</u> shade form)	Whidbey Island, Wash., U.S.A.	S&G 109	UC 96932
<u>L. bullata f. subsimplex TYPE</u> (= <u>L. groenlandica</u> short stipe)	Whidbey Island, Wash., U.S.A.	S&G 157	UC 96920
L. cordata HOLOTYPE (= $L.$ saccharina)	Santa Catalina Island, California, U.S.A.	EYD 5600 Dec. 1, 1948	Анғн 36922
L. ephemera TYPE	Carmel Bay, California, U.S.A.	JMW April 29, 1898	UC 96965
$\frac{L}{(= L. yezoensis)}$	Sitka, Alaska, U.S.A.	NLG 3951 July, 1917	UC 266491
<u>L. platymeris</u> $(= L. groenlandica long stipe)$	Sooke Harbour, Vancouver Island, Canada	WAS June 30, 1930	UC 463996
$\underline{L}$ . platymeris (= $\underline{L}$ . groenlandica long stipe)	San Juan Island, Wash., U.S.A.	NLG	UC 396701
<u>L. solidungula</u>	Dievie Bay, Spitsbergen, Norway	MF	UC 97132
L. yezoensis	Nishiwada, Nemuro, Hokkaida, Japan	JT 350 Sept. 2, 1925	UC 54392

Table I. Longitudinal Growth Rates in Situ of Laminaria groenlandica

No.	Pl.	Ini	tial	Date	Mean Ir Lengt	n <b>itial</b> th	Fina	al Da	ate	Mean Ir Lengt	n <b>crease</b> ch/Day
Lam	inar	ia gro	penla	andica	short s	stipe fo	rm				
,5		July	20,	1962	12.4	cm	July	30,	1962	0.59	cm/day
4		July	30,	1962	18.8	cm	Aug.	14,	1962	0.36	cm/day
4		Aug.	14,	1962	31.8	cm	Sept.	12,	1962	0.38	cm/day
8	`	Apr.	26,	1963	90.3	cm	May	22,	1963	0.64	cm/day
4		May	22,	1963	106.4	cm	June	9,	1963	0.71	cm/day
			. •	÷ .							
Lam	Inar	La gro	penla	andica	long st	tipe for	m				
8		July	30,	1962	21.3	cm	Aug.	14,	1962	0.40	cm/day
3		Aug.	14,	1962	26.9	cm	Sept.	12,	1962	0.15	cm/day
3		Sept	.12,	1962	31.3	cm	Nov.	15,	1962	0.05	cm/day
5		Apr.	26,	1963	72.4	cm	May	22,	1963	1.68	cm/day
3		May	22,	1963	118.2	cm	June	· 9,	1963	0.26	cm/day
										•	

			•							
	. Da	ate		No. Pl.	No. Pl. Mean Stipe Length			Mean Blade Width		
Lami	naria	gro	enland	icalong st:	ipe for	'n				
1.	July	20,	1962	8	3.1	cm	4.2	cm	0.1	73
2.	Aug.	14,	1962	8	3.2	cm	6.9	cm	0.	46
3.	Apr.	26,	196 <b>3</b>	5	4.7	cm,	16.0	cm	.0.2	29
4.	May	22,	1963	5	7.0	cm	18.2	cm	0.3	38
5.	Apr.	26,	1963	10	4.9	cm	14.9	cm	0.3	32
6.	Aug.	4,	1963	8	10.3	cm	14.3	cm	0.	72
7.	Aug.	4,	1963	17	4.9	cm	5.7	cm	0.8	85
8.	Sept	.15,	1962	9	1.3	cm	3.1	cm	0.1	41
Lami	naria	gro	enland	ica short :	stipe f	orm				
9.	July	20,	196 <u>2</u>	. 5	,1.3	cm	5.8	cm	.0.2	22
10.	Aug.	14,	196 <b>2</b>	<sup>,</sup> 5	2.0	cm	14.8	cm	0.	13
11.	Apr.	<b>2</b> 6,	1963	8	2.4	cm	1 <b>2.</b> 6	cm	0.1	19
12.	Мау	22,	1963	8	3.0	cm	14.5	cm	0.2	20
13.	Apr.	<b>2</b> 6,	196 <b>3</b>	. 9	2.7	cm	.14.7	cm	0.1	18
14.	Aug.	4,	1963	8	3.9	cm	<b>25.</b> 7	cm :	0.3	15
15.	Aug.	4,	196 <b>3</b>	17	1.3	cm	7.8	cm	0.3	16
16.	Sept	.15,	196 <b>2</b>	10	0.7	cm	5.6	cm	0.2	12

Table II. Stipe Length/Blade Width as Determined in Situ

## for Laminaria groenlandica

# Table III. Stipe Length/Blade Width as Determined from Transplants of Laminaria groenlandica

		Date			No.	Pl.	Mean Len	Stipe gth	Mean Wid	B <b>lade</b> th	Mean St/W			
Lam	Laminaria groenlandica long stipe form													
la	Feb.	22-Apr.	28,	1963	12		2.1	cm	7.6	cm	0.27			
lb	Apr.	28 <b>-J</b> une	10,	1963	12		3.2	cm	8.0	cm	0.40			
Lam	Laminaria groenlandica short stipe form													
2 <b>a</b>	Feb.	22-Apr.	28,	1963	14		1.6	cm	8.0	cm	0.20			
<b>2</b> b	Apr.	28–June	.10,	1963	. 14		2.7	cm	15.3	cm	0.17			
3a	May	22, 1963	3		5		2.3	cm	9.9	cm	0.23			
Зр 	Oct.	6, 1963	3		5	:	3.0	cm	8.7	cm	0.34			

Laminaria groenlandica Long and Short Stipe Forms as Observed at the Beginning (a) and End (b) of Transplant Studies. Numbers 1 and 2 were transplanted to Burrard Inlet, number 3 to Glacier Point.

Table IV. Values of Temperature and Salinity at Three Depths in Howe Sound, near Keats Island (49°24'N 123°17'W)

			m	-9- 6	m	-0- 1	O m
Date		TC	S%0	Т°С	S%o	Ъс	S%o
				<u> </u>	<u> </u>		
June,	1957	16.9	9.3	11.4	22.1	9.2	27.1
July,	1957	18.3	15.0	12.6	25.9	11.2	26.9
Sept.,	1957	15.2	12.1	14.1	25.9	12.2	27.0
Nov.,	1957	7.8	27.4	9.0	28.0	9.1	28.4

Anon., 1958. Station 2.

Table V. Initial Tests on the Salinity and Temperature Tolerance of Laminaria saccharina (L.) Lamour. May 16 to June 11, 1963

Temperature	Salinity	May 21	May 28	June 4	June 11
	10%0	I I	I I	I I I	D D
2	20%0	7% 28%	23% 35%	32% 47%	34%
5°C	30%0	12% 21%	20% 51%	23% 62%	32% 69%
	40%0	-	20% -	33%	53% -
	50%	I I	I I	D D	
	10%0	I I	Ĭ	D D	
0	20%0	24% 16%	43% 28%	49% 37%	64% 40%
10°C	30%0	9% 17%	22% 34%	31%	37% 41
	40%0	13% 17%	19% <u>33</u> %	30% 45%	34% 5 <u>3%</u>
	50% <b>o</b>	I I	I I	D D	
	10%.	6% 15%	I I	D D	
0	20‰	15% 18%	27% 38%	42% 47%	46% 52%
15°C	30%	28% 	41% 52%	42% 67%	51% 74%
	40%	20% <u>15</u> %	34% 22%	- 31%	45% 36%
	50%0	I	D D		
	10%0	D D			
00 <sup>9</sup> 7	20%0	20% 7%	I I	D D	
20°C	30%	6% <u>7%</u>	1 	D D	
	40%0	1% 4%	<u>I</u>	D D	
	50%	ע D			

Two plants were placed in each temperature-salinity situation. (D) Death; (I) Injury; (%) increase in area of the blade from May 16, 1963.

Table VI. Net photosynthesis, respiration, and net photosynthesis/respiration ratios of Laminaria saccharina and Laminaria groenlandica long stipe form in various temperature-salinity situations. Units:  $\mu lo_2/cm^2/hour$ 

#### LAMINARIA SACCHARINA

PHOTOSYNTHESIS

20

6.1

8.T

7.8

10.0

18 10.8

m 8.6

RESPIRATION

0.5

1.0

0.7

0.7

0.6

0.7

8.1

18 18.0

而 12.7

PHOTOSYNTHESIS

7

10

13

15

7

10

13

15

18

m

SAL

24

8.3

8.0

8.5

11.0

11.9

9.5

0.5

0.5

0.7

1.0

0.8

0.7

16.6

16.0

12.1

11.0

14.9

14.1

14.3

15.0

14.9

13.8

11.7

11.5

11.9

12.9

14.8

11.8

16.0

13.3

12.3

13.3

13.4

13.3

12.7

12.8

14.9

;					PH	OTOSY	NTHESIS	5			
	Y %.						SA		Y %.		
26	28	30	32	កា		20	24	26	28	30	32
6.8	6.8	7.0	7.5	7.1	7	5.7	5.7	6.0	5.6	5.7	7.0
8.1	.7.9	8.0	8.3	8.1	10	2.4	3.7	2.5	4.2	5.9	5.0
8.6	8.2	8.9	8.6	8.4	13	0	0	0	0	2.7	2.7
10.5	9.2	10.6	9.3	10.1	15	0	0	0	2.9	1.4	0
10.4	8.3	12.8	12.1	11.1	18	0	0	0	0	0	0
8.9	8.1	9.5	9.2	-	ħ	1.6	1.9	1.7	2.5	3.1	2.9
				_	RE	SPIRA	TION				
0.6	0.7	0.5	0.7	0.6	ය 7	1.6	1.2	1.2	1.1	1.0	0.7
0.6	0.4	0.8	0.5	0.6	° 10	1.8	1.8	0.8	1.9	1.1	].2
0.6	0.7	0.6	0.7	0.7	닕 13	2.2	2.3	2.2	1.6	2.4	1.8
0.7	0.8	0.9	0.7	0.8	15	2.2	2.2	2.5	2.6	2.8	2.4
0.7	0.7	0.8	0.9	0.8	18	1.2	0.5	1.5	1.6	1.8	2.1
0.6	0.7	0.7	0.7	-	TA EWD	1.8	1.6	1.6	1.7	1.8	1.6
/ RE	SPIRAT	ION			PH	OTOSY	NTHESIS	5 / RES	SPIRAT	ION	
11.3	9.7	14.0	10.7	12.4	7	3.6	4.8	5.0	5.1	5.7	10.0
13.5	19.8	10.0	16.6	14.0	10	1.3	2.1	3.1	2.2	5.4	4.2

13

15

18

m

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1.0

LAMINARIA

GROENLANDICA

កា

6.0

4.0

0.9

0.7

0

1.1

1.4

2.1

2.5

1.5

5.7

3.1

0.4

0.3

1.1

0.5

-

2.5

1.1

1.7

1.6

1.4

1.5

\_

-

3.1

ပ 0 TEMPERATURE

7, 12.2 10

13 11.1 15 14.3

#### LAMINARIA SACCHARINA SALINITY %. 17 20 23 26 29 32 7 N N N Ν N N 10 N N N N N N 13 N N N N N N 16 A A A N N Ν ပ LAMINARIA GROENLANDICA TEMPERATURE SALINITY' %. 17 20 23 26 29 32 7 N N Ν N N N 10 NA N N N N N 13 A NA A NA A 16

Ο

## N = NORMAL SPOROPHYTE

### = ABNORMAL SPOROPHYTE A

Sporophyte production by gametophytes of <u>Laminaria</u> <u>saccharina</u> and <u>Laminaria</u> groenlandica long stipe form in various temperature-salinity situations. Table VII.



- Figure 2. Spectral curve of Sylvania Cool White (F48T 12-CW) fluorescent tubes.
- Figure 3. (a) Percent transparency of stained glass used in filtering light in constant temperature control rooms. (b) Percent transparency per meter for coastal

(b) Percent transparency per meter for coastal waters with sun at an altitude of 45° (After Jerlov, 1951, water type no. 7.)

Figure 4. Relative sensitivity of the Photovolt Electronic Photometer Model 501-M.



Figure 5. Habit of Laminaria longipes.

Figure 6. Habit of Laminaria sinclairii, exposed form.

- Figure 7. Habit of Laminaria sinclairii, sheltered form.
- Figure 8. Habit of Laminaria ephemera, exposed form.



Figure 9. Habit of Laminaria yezoensis.

Figure 10. Discoid holdfast of Laminaria yezoensis.

Figure 11. Habit of Laminaria groenlandica shade form.

Figure 12. Regeneration of Laminaria groenlandica shade form.



Figure 13. Habit of Laminaria groenlandica short stipe form, bullate.

Figure 14. Habit of Laminaria groenlandica long stipe form.

Figure 15. Habit of Laminaria groenlandica short stipe form, abullate blade.

Figure 16. Habit of Laminaria groenlandica flat stipe form.



Figure 17. Habit of <u>Laminaria saccharina</u>, bullate blade.
Figure 18. Habit of <u>Laminaria saccharina</u>, abullate blade.
Figure 19. Habit of <u>Laminaria farlowii</u>.
Figure 20. Habit of <u>Laminaria complanta</u>.



Figure 21. Habit of Laminaria setchellii, Glacier Point form.

Figure 22. Habit of Laminaria setchellii, Botany Beach form.

Figure 23. Regeneration of Laminaria setchellii.

Figure 24. Habit of Laminaria dentigera.



- Figure 25. Laminaria longipes, cross section of blade.
- Figure 26. Laminaria sinclairii, cross section of blade.
- Figure 27. Laminaria ephemera, cross section of blade.
- Figure 28. Laminaria yezoensis, cross section of blade.
- Figure 29. Laminaria groenlandica shade form, cross section of blade.
- Figure 30. Laminaria groenlandica long stipe form, cross section of blade.
- Figure 31. Laminaria groenlandica flat stipe form, cross section of blade.
- Figure 32. Laminaria saccharina, cross section of blade.
- Figure 33. Laminaria farlowii, cross section of blade.
- Figure 34. Laminaria complanata, cross section of blade.
- Figure 35. Laminaria setchellii, cross section of blade.
- Figure 36. Laminaria dentigera, cross section of blade.

<sup>( ---- )</sup> indicates the position of mucilage ducts.



- Figure 37. Laminaria longipes, cross section of stipe.
- Figure 38. Laminaria sinclairii, cross section of stipe.
- Figure 39. Laminaria ephemera, cross section of stipe.
- Figure 40. Laminaria yezoensis, cross section of stipe.
- Figure 41. Laminaria groenlandica shade form, cross section of stipe.
- Figure 42. Laminaria groenlandica short stipe form, cross section of stipe.
- Figure 43. Laminaria groenlandica long stipe form, cross section of stipe.

( ----- ) indicates the position of mucilage ducts. The line drawings indicate the relative shape and size (2X) of the stipes as observed in cross section. The area of these drawings darkened represents the position of the section represented in the accompanying photograph.



Figure 44. Laminaria groenlandica flat stipe form, cross section of stipe.

Figure 45. Laminaria saccharina, cross section of stipe.

- Figure 46. Laminaria farlowii, cross section of stipe.
- Figure 47. Laminaria complanata, cross section of stipe.
- Figure 48. Laminaria setchellii, cross section of stipe.
- Figure 49. Laminaria dentigera, cross section of stipe.

( \_\_\_\_\_\_) indicates the position of mucilage ducts. The line drawings indicate the relative shape and size (2X) of the stipes as observed in cross section. The area of these drawings darkened represents the position of the section in the accompanying photograph.





Figure 50. Northeast Pacific distribution of Laminaria longipes and Laminaria dentigera.



Figure 51. Northeast Pacific distribution, north of 48° N latitude, of <u>Laminaria sinclairii</u>, <u>Laminaria</u> <u>ephemera</u>, <u>Laminaria farlowii</u>, and <u>Laminaria</u> <u>complanata</u>.









Figure 54. Life histories of Laminaria groenlandica long stipe form, short stipe form, and shade form as observed at Glacier Point and Ogden Breakwater, Vancouver Island. Large arrows denote phenology of the sporophyte generation, small arrows, the gametophyte generation.



Figure 55.

Gametophyte and microscopic sporophyte phases of Laminaria groenlandica long and short stipe forms: (a) male gametophyte developed in adverse culture conditions, (b) female gametophyte developed in adverse culture conditions, (c) female gametophyte developed in favourable culture conditions, (d) male gametophyte developed in favourable culture conditions, (e, f) sporophytes developed in favourable culture conditions, (g) plants, thought to be sporophytes, developed in adverse culture conditions.

- Figure 56. Distribution of longitudinal growth, in culture, of the blade of Laminaria groenlandica short stipe form.
- Figure 57. Distribution of longitudinal growth, in culture, of the blade of <u>Laminaria groenlandica</u> long stipe form.
- Figure 58. Distribution of longitudinal growth, in situ, of the blades of Laminaria groenlandica long stipe form  $(\Delta)$  and short stipe form  $(\circ)$ .


- Figure 59. Distribution of lateral growth, in culture, of the blade of Laminaria groenlandica short stipe form.
- Figure 60. Distribution of lateral growth, in culture, of the blade of Laminaria groenlandica long stipe form.
- Figure 61. Distribution of lateral growth, in situ, of the blades of Laminaria groenlandica long stipe form  $(\Delta)$  and short stipe form (0)

I





gametophyte generation.

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Figure 63. Gametophyte and microscopic sporophyte phases of Laminaria saccharina: (a) Female gametophyte developed in adverse culture conditions, (b) male gametophyte developed in adverse culture conditions, (c) female gametophyte developed in favorable culture conditions, (d) male gametophyte developed in favorable culture conditions, (e. f) sporophytes developed in favorable conditions, (g) plants, thought to be sporophytes, developed in adverse culture conditions.



Figure 64. Distribution of longitudinal growth, in culture, of the blade of Laminaria saccharina.
Figure 65. Distribution of longitudinal growth, in situ, of the blade of Laminaria saccharina.



% INCREASE IN WIDTH AFTER 13 DAYS

Figure 66. Distribution of lateral growth, in culture, of the blade of Laminaria saccharina.

Figure 67. Distribution of lateral growth, <u>in situ</u>, of the blade of <u>Laminaria</u> saccharina.



Figure 68. Longitudinal growth rates ( $\bigtriangleup$ ) and theoretical lengths (o) of the blades of Laminaria saccharina, as observed in 1962, in Burrard Inlet. Numbers accompanying each growth rate value denote number of plants measured. The vertical bars represent extent of the extreme values.



Figure 69. Seasonal variation in temperature and salinity at three depths for Sheringham Point (48° 23' N 123° 59'W), on the right, and Gordon Head (48° 30'N 123° 17'W), on the left. Anon., 1955, stations 3a and 10a.

Figure 70.

Seasonal variation in temperature and salinity at three depths for Burrard Inlet near Stanley Park.

Figure 71.

Seasonal variation in surface temperature and salinity at localities inhabited by Laminaria groenlandica long stipe form (1), Laminaria saccharina (2), and Laminaria groenlandica short stipe form and Laminaria saccharina (3), as observed at Amphitrite Point, Kains Island, Race Rocks, Departure Bay, Cape Mudge, Pine Island, for 1948-57, (Anon., 1958); Beaver Point 1954-57, (Anon., 1958); Pulteney Point, 1955-57, (Anon., 1958); Nootka, 1942-51 (Anon., 1952); Ladysmith Harbour, 1950-56, (Anon., 1957); Texada Mines, 1954-56, (Anon., 1957); William Head, 1921-38, (Anon., 1948); Friday Harbor, 1935-52, (Anon., 1962a); Neah Bay, 1936-60, (Anon., 1962a); Deep Cove, 1963, (Anon., 1964).







Figure 73. Percent increase in blade surface per day for Laminaria saccharina after 15 days culture at 7.5, 10, 12.5, and 15.5°C, at 28 % salinity.

Figure 74. Percent increase in blade surface per day for Laminaria saccharina after 15 days culture at 16, 19.5, 23.5, 27, and 31% salinity, at 10°C.



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L. SACCHARINA

- Figure 75. Sporophyte growth of Laminaria saccharina and Laminaria groenlandica long stipe form in seawaters from different areas: Burrard Inlet (B.I.), Victoria (V.), Glacier Point (G.P.). The horizontal line represents the mean length; the rectangle, the 95% confidence limits; the vertical line, the extent of variation.
  - Figure 76. Sporophyte growth of Laminaria saccharina in seawater from Burrard Inlet and Glacier Point at three salinities.



Figure 77. Upper vertical limits of L. saccharina as observed in Burrard Inlet near Stanley Park. D, A, O, represent different year classes.

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Figure 78.

Some tidal features for Burrard Inlet (after Anon. 1962). The three vertical bars under each month represent three intertidal positions. Reading from right to left: 30 cm above MLT, MLT, and 30 cm below MLT.





Figure 79. Air temperature for Kitsilano, Vancouver, 1963 (Anon. 1964a). (c) the monthly mean temperature range mid-point, (^) monthly mean maximum and (=) monthly mean minimum.

Figure 80. Daylength as calculated for 49<sup>0</sup>N (Anon. 1961).

Figure 81. Hours bright sunshine observed for the Univ. British Columbia, Vancouver, 1963 (Anon. 1964a).

Figure 82. Approximate monthly mean daily insolation for light in the visible range (3800-7200 A) as observed for the Univ. British Columbia, 1963. (After Anon. 1964b).









Figure 86. Mean monthly seawater temperature and salinity at Departure Bay and Pine Island, 1931-1958 (Anon. 1959).