FAO Fisheries Synopsis No. 83 **FIRM/S83**
(Distribution restricted) **SAST - *bulbous Laminaria* - 7,77(02),012,01**

SYNOPSIS OF BIOLOGICAL DATA ON SACCORHIZA POLYSCHIDES

Prepared by

T. A. NORTON

FOOD AND AGRICULTURE ORGANIZATION OF THE UNITED NATIONS
ROME, 1970

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Special groups of synopses are identified by symbols followed by classification numbers based on indexed code of "Current Bibliography":

SAST	Data concerning certain species and fish stocks.
MAST	Information on methods and subjects.
OT	Oceanographic data.
IT	Limnological data.
	and
CART	Information concerning fisheries and resources of certain countries and regions (FID/S).

Des catégories spéciales de synopses sont identifiées à l'aide de symboles suivis des chiffres de classification basés sur le code d'indexation de la « Current Bibliography »:

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MAST	Renseignements sur des méthodes et des sujets.
OT	Données océanographiques.
IT	Données limnologiques.
	et
CART	Renseignements sur les pêcheries et les ressources de certains pays et régions (FID/S).

Grupos especiales de sinopsis se distinguen con las siglas siguientes, seguidas por números de clasificación que se basan en las claves de los índices de la « Current Bibliography ».

SAST	Datos relativos a ciertas especies y poblaciones.
MAST	Sinopsis sobre métodos y materias.
OT	Sinopsis sobre oceanografía.
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FAO Fisheries Technical Paper	**FIR /T (No.)**

Special groups of Technical Papers are identified by:

RE	Indexed lists of experts and institutions drawn from Registers maintained by the Fishery Resources Division.
CB	Lists of periodicals, special sections of "Current Bibliography for Aquatic Sciences and Fisheries," special bibliographies and papers concerning documentation problems.
MFS	Provisional editions of "FAO Manuals in Fisheries Science."

Des catégories spéciales de documents techniques sont identifiées à l'aide des symboles suivants:

RE	Listes indexées d'experts et institutions tirées des registres tenus à jour par la Division des ressources halieutiques.
CB	Listes de périodiques, des sections spéciales de la « Current Bibliography for Aquatic Sciences and Fisheries », des bibliographies particulières et des articles sur les problèmes de documentation.
MFS	Editions provisoires des « Manuels FAO de science halieutique ».

Grupos especiales de documentos técnicos se identifican por las siglas siguientes:

RE	Listas índices de expertos y de instituciones tomadas de los registros que se llevan en la Dirección de Recursos Pesqueros.
CB	Listas de periódicos, secciones especiales de la « Current Bibliography for Aquatic Sciences and Fisheries », bibliografías especiales y trabajos relativos a los problemas de documentación
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Some documents also have another identification, if, for example, they have been contributed to a meeting for which papers have been numbered according to another system.

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SYNOPSIS OF BIOLOGICAL DATA
ON *Saccorhiza polyschides*

Prepared by

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FOOD AND AGRICULTURE ORGANIZATION OF THE UNITED NATIONS
Rome, October 1970

PREPARATION OF THIS SYNOPSIS

This is the first in a series of species synopsis on biological data of large brown seaweeds which are known for their importance in the kelp industry and as a source of raw material for alginic acid and alginates.

The material presented in this synopsis is based on data collected by the author in the course of personal research work on the species and also, on information received from various sources, most of which are listed in the Bibliography.

Distribution

FAO Department of Fisheries
FAO Regional Fisheries Officers
Regional Fisheries Councils and Commissions
Selector SM
Author

"Current Bibliography" entry

Norton T.A. (1970) 17-6M350
FAO Fish.Synops., (83):pag.var.
Synopsis of biological data on *Saccorhiza polyschides*

ANE, ASE. Laminariaceae - biological synopsis. Taxonomy, morphology, geographical and ecological distribution. Chemical composition. Metabolism, nutrition, growth. Life cycle, reproduction, phenology. Population - structure, density, mortality, standing crop. Harvesting - techniques, seasons, yields. Protection and management. Utilization - food, fodder, industrial products. Selected bibliography.

CONTENTS

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* As no information was available to the author these items have been omitted from the text.

1 IDENTITY

1.1 *Nomenclature*

1.11 Valid scientific name

Saccorhiza polyschides (Lightf.) Batt. 1902. A catalogue of the British Marine Algae.

1.12 Nomenclatural synonyms

The first binomial applied to this species was *Fucus polyschides* Lightfoot 1777, Flora Scotica volume 2, p.936.

Other synonyms for this species are:

Fucus bulbosus Hudson 1778, p.579
Ulva bulbosa Beauvois May 1805, p.20, plate 13 (as *U. tuberosa*)
Ulva bulbosa (Huds.) Lamark et de Candolle Sept. 1805, p.16 nom. illeg.
Ulva tuberosa Beauvois May 1805, plate 13 pro synon. nom. illeg.
Polyschides bulbosa (Huds.) Stackhouse 1809, p.66
Laminaria bulbosa (Huds.) Lamouroux 1813, p.22
Laminaria belvisii C. Agardh 1820, p.115, nom. nov. = *Ulva bulbosa* Beauv. non. *U. bulbosa* (Huds.) Lamark & D.C.
Laminaria elliptica C. Agardh 1820, p.119
Laminaria punctata Bory 1826, p.190
Laminaria turneri Bory 1826, p.190
Saccorhiza bulbosa (Huds.) De La Pylaie 1829, p.23
Haligenia bulbosa (Huds.) Decaisne 1842, p.345
Phycocastanum bulbosum (Huds.) Kützing 1843, p.346
Saccorhiza elliptica (C. Ag.) Cruoan 1852, no.87

1.13 Vernacular names

The popular names given to this species include:

British Isles: bulbous Laminaria, bulbous-rooted tangle, furbelows, sea furbelows, great furlowed Laminaria, furbelowed hangers

Norway: sekktare

Portugal: carocha, caixeira, cintas, golfe or golfo, limo-correia, limo-corriola

1.2 *Taxonomy*

1.21 Affinities

Suprageneric

Saccorhiza polyschides (Lightf.) Batters (1902) belongs to the family Laminariaceae of the order Laminariales of the division Phaeophyta.

Generic

The genus *Saccorhiza* was established by de la Pylaie in 1829 (Flore de L'ile de Terre Neuve et les iles St. Pierre et Miclon p.23). The type species of the genus is *Saccorhiza bulbosa* (Huds.) de la Pyl. a synonym for *S. polyschides* (Lightf.) Batt.

The sporophytes of the genus are annual plants. They are characterised by a lamina which lacks a midrib, but possesses cryptostomata. The stipe is flattened and develops a distinct subsidiary holdfast above the original attachment organ. The unilocular sporangia of fertile sporophytes each contain 128 zoospores. The paraphyses which are also found in the reproductive sori are devoid of the hyaline tips found on those of *Laminaria*.

Specific

The type of the species is *Fucus polyschides* Lightfoot collected from the Island of Iona, West of Scotland. Lectotype material is located in the Herbarium of the British Museum, London.

The sporophyte of this species is readily distinguished from those of *Laminaria* by the cryptostomata on the lamina, the flattened and basally twisted stipe, the reproductive frills on the sides of the stipe and the large basal 'bulb' which is quite unlike the holdfast of *Laminaria*.

The only other species included in the genus is *S. dermatodea*, a species largely confined to the Arctic Ocean. The geographical distribution of the two species does not overlap. Recent culture studies of *S. dermatodea* have confirmed its affinities with *S. polyschides* (Norton, 1970).

Key to the species of *Saccorhiza*:

Lamina of sporophyte entire or divided into 30 or more digits, stipe long, up to 210 cm x 8 cm, twisted at base and in adult plant bearing undulating lateral extensions; secondary holdfast a hollow bulbous expansion up to 30 cm in diameter, bearing numerous whorls of unbranched haptera.....*S. polyschides*.

Lamina entire or divided into only 4 to 5 digits, stipe short up to 60 x 2 cm, lacking basal twist and lateral undulations; secondary holdfast a small umbrella-shaped expansion up to 5 cm in diameter, bearing only two whorls of haptera which may be branched......*S. dermatodea*.

1.22 Subspecies

No subspecies are recognised by the present author.

1.23 Genetic data

Some aspects of the cytology of *S. polyschides* have been examined by Evans (1965) using modified acetocarmine squash methods and Feulgen squashes. He found that the nuclei of *S. poly-*

schides were larger than those of the other laminarians he examined. The nuclei of the female gametophytes were 8–14µm in diameter, with a nucleolus of 3–4µm whilst the nuclei of the male gametophytes were 2.5–4.2µm in diameter. There was an increase in nucleus size prior to oogonial formation and oogonial nuclei of 18µm in diameter were not uncommon.

The number of chromosomes in S. polyschides is reported to be 62 in the diploid state and 31 in the haploid state (Evans 1965). Although the chromosomes varied in size, in the female gametophyte the majority were between 0.8µm and 1.0µm long, but there was always a very large chromosome 4µm–6µm long. This was designated the X-chromosome by Evans (1965). It stained well with Schiff's reagent and was present in the cells of female gametophytes and of young sporophytes, but was not found in male gametophytes. Evans (1965) postulated that there is probably an X/Y sex-determining mechanism in S. polyschides and that sex segregation takes place at the first meiotic division during spore formation. It is therefore probable that the zoospores from a single sporangium produce equal numbers of male and female gametophytes.

1.3 Morphology and anatomy

1.31 External morphology

The thallus is pale dark brown in colour and is clearly differentiated into lamina stipe and holdfast (Fig. 1). The lamina bears characteristic cryptostomata and may reach 150 cm or more in length. The stipe is flattened and twisted towards its base. It may measure up to 210 cm long and 8 cm wide. The stipe of the adult plant usually bears undulating lateral extensions, the reproductive frills. Obscuring the original Laminaria-like holdfast is the 'bulb', a hollow bulbous expansion up to 30 cm in diameter. It is covered with short protruberances above and attached by unbranched haptera below.

The appearance of the sporophyte varies greatly. At the Isle of Man and in South-West Ireland Norton (1969) observed striking differences in the morphology and the anatomy of sporophytes growing in different, although sometimes adjacent habitats. The variations were found to be associated with the different environmental conditions in the various habitats, and especially with the degree and type of water movements to which the plants were subjected. In areas of weak current the plants produced broad, curved blades, distinctly cordate at the base, devoid of digits and so flimsy that they tore under their own weight when removed from the water. In contrast, plants growing in strong currents developed very long, flat, tough blades, cuneate at the base and divided into 30 or more digits. In habitats without current but exposed to wave action, the sporophytes possessed short, flat extremely tough blades with few, usually only 3–10, digits.

It was found that the greater toughness of the blades in plants from areas of current, and more particularly turbulence, was the result of a larger number of cortical cells increasing the thickness of the thallus. Experiments in culture and transplants of labelled sporophytes in the sea indicated that these variations in morphology and anatomy were phenotypically based rather than genotypically selected. Spores taken from plants growing in three localities were cultured together under identical conditions for over six months. By this time, the largest of the resultant sporophytes were 32 cm long and, in contrast to the distinctions which would have arisen after a similar period of growth in their natural habitats, the plants were indistinguishable. In addition, young sporophytes were transplanted from one locality to another in the sea. Within 12 weeks of transplanting, the sporophytes had completely changed their morphology and had become indistinguishable from the control plants native to that habitat (Norton 1969).

1.32 Anatomy

The primary growth of the sporophyte results from cell divisions in the intercalary meristem which is situated at the junction of stipe and lamina. The meristem gives rise to new lamina tissue above and new stipe tissue below. Both stipe and lamina are essentially similar in transverse section. They are composed of a central medulla, a surrounding cortex and a peripheral meristoderm (Fig. 2). The superficial meristoderm is composed of small, cubical cells full of chromatophores and with a thicker outer wall. The cortical cells become larger towards the centre of the section, but their size and the number of cell rows depends upon the stage of development of the plant and upon the region of the plant from which the section is taken. In transverse section (Fig. 2) the cortical cells are usually square or rectangular in shape but in longitudinal section they are progressively more elongated towards the medulla. The distinction between cortex and medulla is not clear-cut, for the cortical cells adjacent to the medulla are distorted and merge with the medullary tissue. The medullary elements are often septate and branched and are invariably much elongated and predominantly longitudinal in arrangement. They also possess thick mucilaginous walls. None of the sieve-tube like elements which have been described in Laminaria saccharina (Sykes 1908) are found in S. polyschides, nor are there any mucilage ducts in the cortex, such as those found in Laminaria hyperborea and in the blade of L. saccharina. Although transverse sections through both stipe and blade show essentially similar structures, one taken across a hapteron is fundamentally different (Barber 1889).

The meristem of the transition zone appears to be the primary source of new cells, but the peripheral meristoderm also retains its meriste-

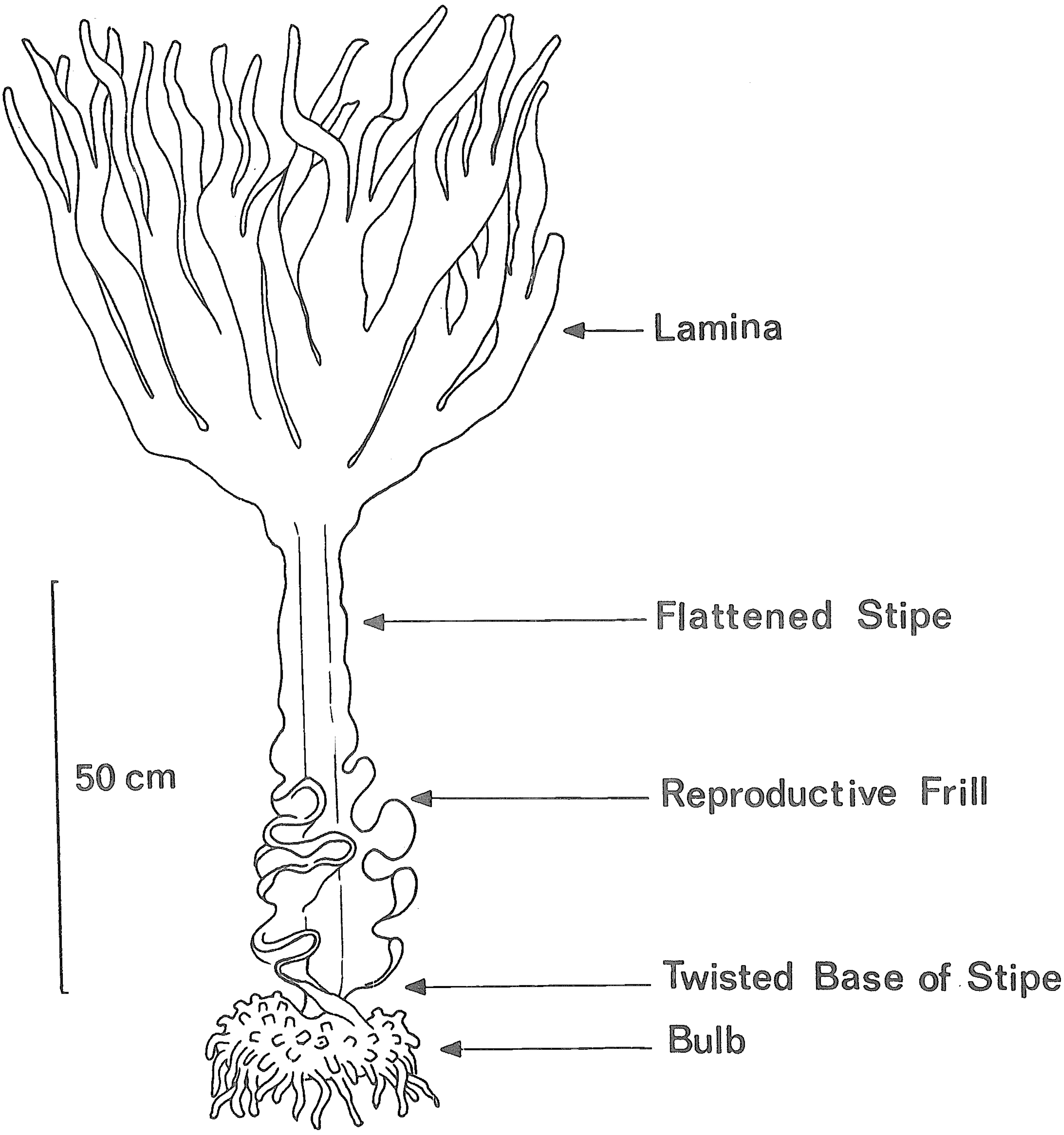

Fig. 1 A drawing of the adult sporophyte of S. polyschides showing the distinctive morphological features of the species

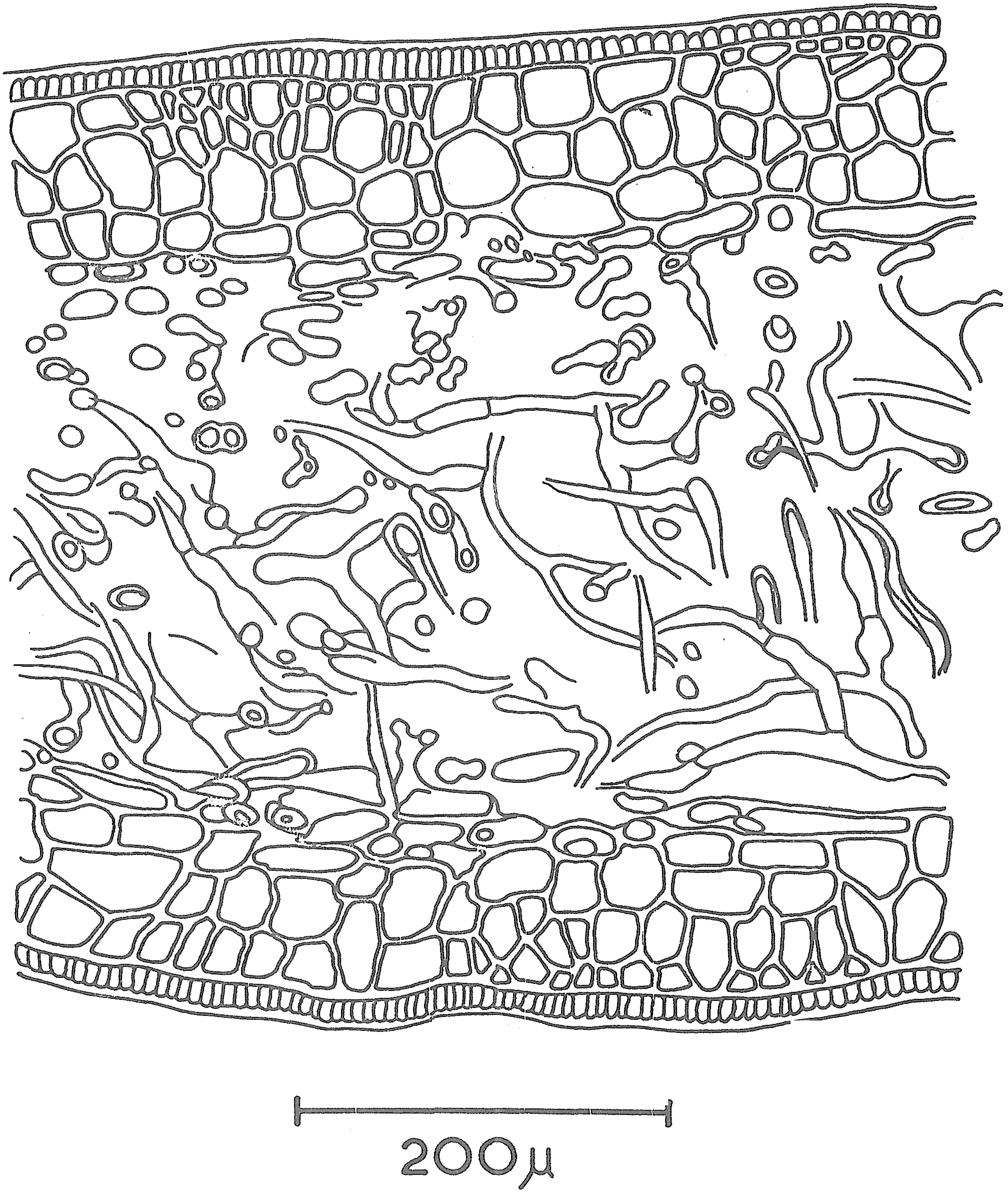

Fig. 2 A transverse section taken across the base of the lamina of a 22-week old sporophyte grown in culture

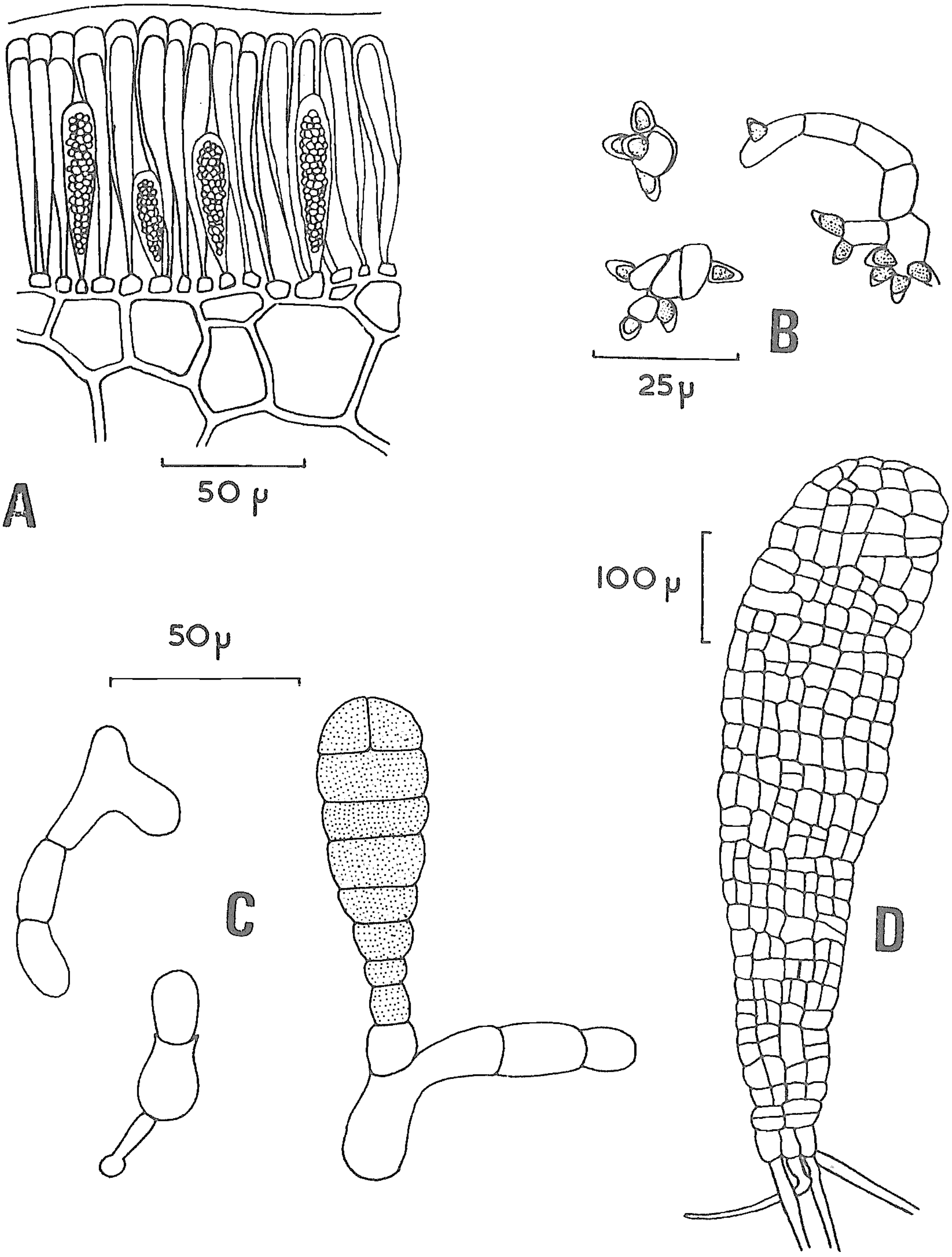

Fig. 3 The microscopic stages in the life history of S. polyschides

A A vertical section through a sorus on the lamina; the darker bodies are the spores in the sporangia which are surrounded by sterile paraphyses

B Male gametophytes bearing antheridia

C Female gametophytes; the stippled area represents the tissue of the developing sporophyte

D A 28-day old sporophyte with several rhizoids matic activity and adds to the length of the thallus by means of transverse divisions and to its girth by cutting off new cortical cells tangentially. The cortical cells seem to be unable to divide but are capable of considerable extension in a longitudinal plane. Thus, as the frond increases in length the meristoderm cells tend to retain their size and shape by repeated divisions. The cortical cells on the other hand become gradually more elongated until they eventually become distorted, swollen with mucilage, and lose their cellular appearance, thereby contributing more elements to the medulla.

The medullary elements also appear to have little meristematic activity and, as the surrounding tissues expand, they too are passively stretched. The chief distinction between the attenuated medullary elements and the innermost layers of the cortex is the copious production of mucilage by the former.

Other elements are also found in the medulla of S. polyschides. Septate cross connections are apparent in transverse section (Fig. 2). According to Sauvageau (1915) they are derived from the fusion of protrusions from the longitudinal walls of the innermost cortical cells. Hyphae are also produced. They differ from the cross connections in that they do not fuse with each other. The hyphae extend in all directions between the other elements but they are predominantly radial and must contribute to the strength of the thallus without greatly limiting its flexibility.

In mature plants the reproductive sori develop on the surface of the thallus at the base of the lamina, on the frills and on the bulb. The sori are composed of unilocular sporangia interspersed with sterile paraphyses (Fig. 3A). Mature sporangia reaches 124µm long and 20µm wide. Each sporangium produces 128 zoospores.

2 DISTRIBUTION, ECOLOGY AND METABOLISM

2.1 Total Area

S. polyschides is found all around the British Isles and on the Atlantic coasts of Norway, France, Spain, Portugal and Morocco (Fig. 4).

The northern limit of the species was established by Grenager (1955) at approximately 65°30'N. on the Norwegian coast, 225 km north of Trondheim. The species has not been found in the Arctic Circle.

The southernmost limit of the species would appear to be on the west coast of Africa. The species is recorded from Morocco (Dangeard 1949, Gayral 1958) and is reputed to occur as far south as the Rio de Oro, Spanish Sahara (Feldman 1951) and Shama, Ghana (Beauvois 1805). Beauvois' record is substantiated by a specimen of S. polyschides (in the Horneman herbarium at Copenhagen) which was sent by Beauvois from the coast of Guinea.

In the Mediterranean, S. polyschides is not usually found further east than Malaga, Spain, lat. 36°50'N, long. 4°50'W. (Seoane 1966) and Melilla, Spanish Morocco, lat. 35°17'N, long. 2°57'W. (Bellon 1925). Bornet (1892) reported the species from Italy at Portofino and in the Stretto di Messina, and Funk (1927) reported a specimen from Naples. Sauvageau (1918) emphasised that records from the Mediterranean were only isolated occurrences, the species being unable to maintain itself in this region. However, Molinier and Picard (1953) reported that S. polyschides had established itself in the region of Messina. They regarded this population as a recent introduction resulting from the installation of artificial substrates and the increase in shipping in the area.

2.2 Local vertical and horizontal distribution

S. polyschides is usually epilithic, but in sheltered-water localities at both Port Erin, Isle of Man, and Lough Ine, Ireland, it also grows loose-lying, attached only to small stones or shells. The species is usually, but not invariably, found in turbulent-water habitats and is characteristically abundant in areas subject to current. It is confined to the sublittoral region; even the uppermost plants in the Saccorhiza zone are only exposed by the Extreme Low Water of Spring Tides (E.L.W.S.).

The deepest attached plants of S. polyschides found by the author were 15 m below E.L.W.S. at Carsaig in Argyll, on the west coast of Scotland (McAllister, Norton and Conway 1967). In the Isle of Man, Kain (1960) recorded attached plants of this species down to 19 m and during the present work loose-lying specimens were found to survive in a healthy state at a depth of 24 m in Bay Fine, near to Port Erin. Isolated individuals have been reported from depths of 30-35 m by John (1968) in Cornwall.

Lewis (1964) stated that S. polyschides was usually found growing at a level immediately below that of Alaria esculenta or Laminaria digitata, but above that of Laminaria hyperborea. However, at Port Erin and at several seaward stations on the coast adjacent to Lough Ine, Ireland, S. polyschides was invariably found below the L. hyperborea zone. On Port Erin breakwater, the L. hyperborea zone ended abruptly at approximately 6 m below E.L.W.S. Whatever factors controlled the lower limit of this species, they did not appear to affect S. polyschides which was most abundant immediately below the L. hyperborea zone and extended down to a depth of 8 m.

2.3 Effects of ecological determinants

The environmental factors most likely to be responsible for the geographical distribution of S. polyschides are sea temperature, light and salinity.

The northern limits of the geographical distribution of S. polyschides seem to be most probably controlled by the low winter water temperatures or the six months Arctic night. In culture sporophyte production was inhibited and the gametophytes progressively lost their ability to form sporophytes at a temperature only 2°C below that at which the plants survive at the northern limit of their distribution. On the other hand, although a low light intensity of 37 μg cal./cm^2 sec had no effect on the ability of the gametophytes to produce sporophytes, it subsequently inhibited the growth of sporophytes.

The southern limits of distribution and the sparsity of the species in the Mediterranean may be related to the high water temperatures during the summer. In culture the plants were adversely affected by a temperature of 21-26°C. Only a few abnormal sporophytes developed and they quickly succumbed to contamination.

S. polyschides is not found in areas of reduced salinity and is completely absent from the Baltic Sea. In culture, the species was found to develop at a progressively slower rate at lower salinities and development was irreversibly inhibited at salinities below 9°/oo (Norton and South 1969).

The environmental factors most likely to be responsible for the local distribution of the species are desiccation and grazing.

As S. polyschides is confined to the sublittoral zone it would seem that the plants are unable to survive at a level where they would be subjected to the extreme fluctuations in conditions associated with the intertidal region. At Lough Ine, Ireland, in August 1964, the author observed that when large numbers of sporophytes were exposed to air by E.L.W.S. during a hot summer's day, the majority of the plants dried out rapidly and were killed.

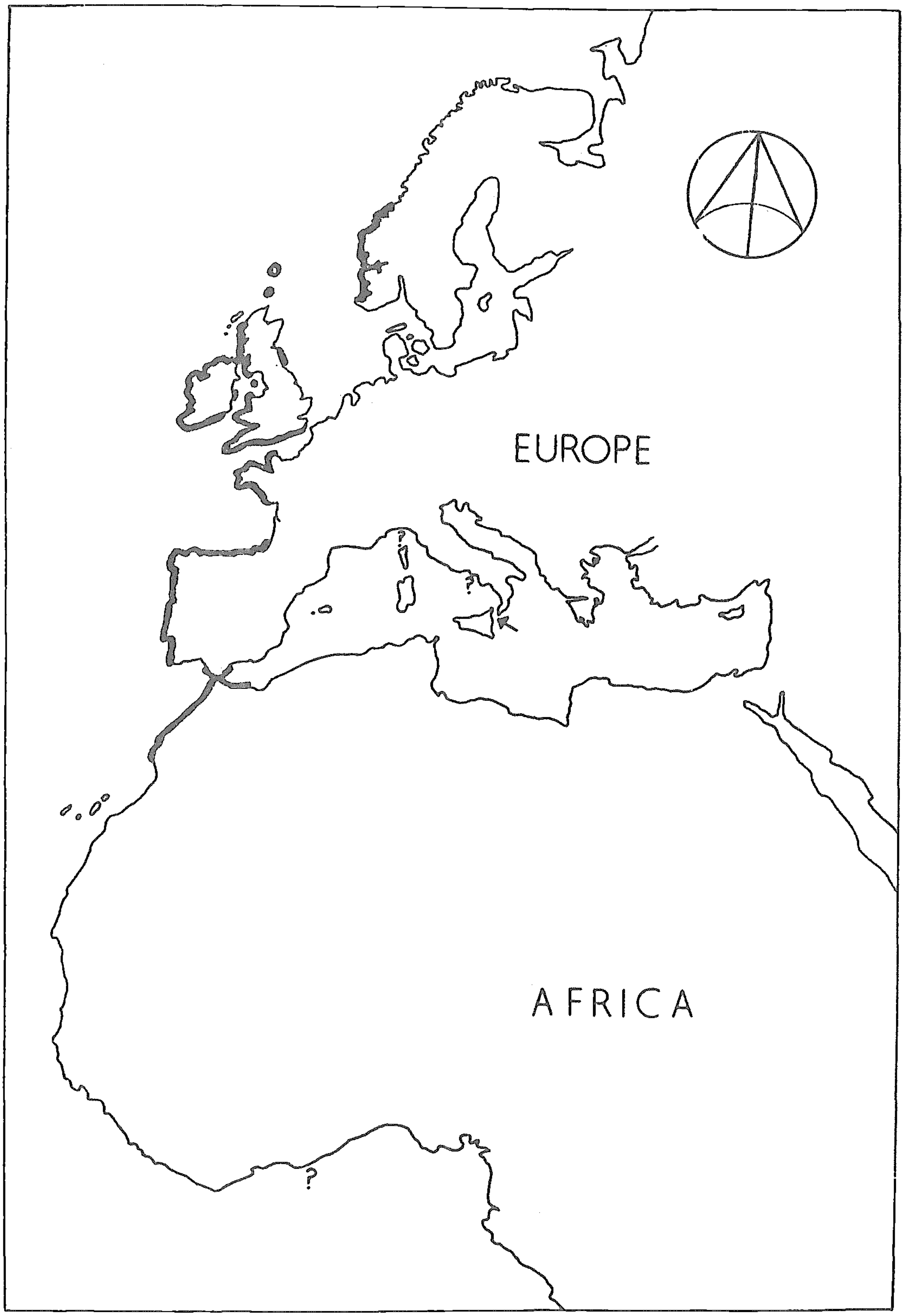

Fig. 4 The geographical distribution of S. polyschides

The major grazing animals influencing the distribution of *S. polyschides* are the echinoderms *Echinus esculentus* and *Paracentrotus lividus*. Kain and Jones (1966) have shown that on Port Erin breakwater, the lower limit of the *Saccorhiza* zone was at least partly controlled by the grazing pressure of the sea-urchin *Echinus esculentus* which feeds on both the gametophytes and sporophytes. The removal of the echinoderms enabled *S. polyschides* to colonise the lowermost available rocks, at a depth of 11 m below E.L.W.S., thus extending its depth range in this habitat by 3 m. Similarly Norton (unpublished) has found that grazing by *Paracentrotus lividus* is a major factor excluding *S. polyschides* from Lough Ine in Southern Ireland.

Herbivorous gastropods also feed on *S. polyschides*. *Patina pellucida* rasps out characteristic deep pockets in the host tissue. Such excavations undoubtedly weaken the plant and render it more likely to be damaged by wave action. The laminae of sporophytes at a locality near to Lough Ine were extremely tattered owing to the ravages of *P. pellucida* and *Lacuna vincta* which were very abundant on the fronds (Norton 1970a).

2.4 Nutrition and Growth

2.41 Assimilation and
2.42 Respiration

There has been little work on these aspects of the physiology of *S. polyschides*. However, Kain (1969) determined the minimum irradiance required for the growth of microscopic sporophytes. This is likely to be almost the same as the compensation point. At a temperature of 10°C the minimum irradiance required for growth in culture was between 1 and 3 μg cal./cm^2 sec(10-30 lux in daylight) (Kain 1969). There is, however, some evidence that the minimum irradiance for growth is higher for macroscopic sporophytes (Norton and Burrows 1969a).

2.43 Nutrition

Again, little information is available. Some indication of the plants' requirements may be gained from a consideration of the media in which they have been successfully cultured. Unfortunately they have never been cultivated in a defined medium. The present author found that they grew well in sea water to which were added soil-extract, solutions of sodium nitrate, sodium phosphate and the range of trace elements and vitamins listed in the ASP$_2$ medium of Provasoli, McLaughlin and Droop (1957).

2.44 Growth

The growth rates of microscopic sporophytes of *S. polyschides* have been investigated by Kain (1969). It would seem that below saturation irradiance (about 50 μg cal./cm.^{2} sec at 10°C) there is a straight-line relationship between cell divisions per day and irradiance. There is also a straight-line relationship between the logarithm of the sporophyte length and the logarithm of the number of cells per sporophyte, up to 1,000 cells when the sporophyte becomes polystromatic (Kain 1969).

The rate of thallus extension of macroscopic sporophytes has been determined by the present author in two ways: on the mean increase in plant size of a population and on the basis of measurements of marked individual sporophytes.

Table I gives the statistical analysis of the mean measurements of stipe length, stipe width and blade length of monthly samples of *S. polyschides* sporophytes taken from Port Erin breakwater. The annual cycle of the development and decay of the sporophyte is clearly seen. The maximum increase in mean blade length was 249 mm from June to July 1965 (Table I). This represents a mean rate of frond extension of 62 mm per week and the rate of increase of the fastest growing plants was probably far higher than this. A maximum increase in mean stipe length of 117 mm was recorded between June and August 1964 (Table I); a mean rate of stipe extension of only 13 mm per week.

Individual sporophytes of *S. polyschides* were marked and measured at monthly intervals (Norton and Burrows 1969). A total of 68 plants were labelled and remeasured at Port Erin, Isle of Man and 101 plants at Lough Ine, County Cork, Ireland. Although the rates of thallus extension they recorded were somewhat variable, certain generalisations emerged. Firstly, by far the greatest increase in blade length was found to occur in the proximal 25 mm immediately above the meristem. In the vast majority of sporophytes no measurable increase occurred further than 75 mm from the meristem. Secondly, there was an interrelationship between extension growth, fruiting, and the rotting of the thallus which followed maturity. The rate of blade extension was most rapid in juvenile sporophytes and rates of up to 145 mm/week were recorded. Many of the increases were, however, minimal readings, for as a result of distal decay some of the punched holes for measuring blade increase were lost. The rate at which new tissue was added decreased as the plant became larger, until eventually it stopped altogether. This point appeared to coincide with the beginning of the fruiting period. Not a single fertile sporophyte was found that was growing measurably. Moreover, although the distal decay of the thallus appeared to follow fruiting, it was in fact a more or less continuous process which only became apparent when growth ceased and the blade began to shorten.

TABLE I

Statistical data from the analysis of measurements of sporophytes in monthly samples taken from the *S. polyschides* population on Port Erin Breakwater

	Month	Mean in mm	Range in mm	Standard Deviation	Standard error of the mean
Stipe length					
1964	June	83.0	1.00 - 400	10.60	1.50
	August	200.0	1.00 - 560	15.64	2.21
	October	157.0	3.00 - 470	11.19	1.69
	November	117.0	0 - 470	11.39	1.61
	December	109.0	0 - 400	17.87	2.51
1965	March	74.8	0 - 330	9.76	1.38
	April	77.2	0 - 360	10.98	1.55
	June	10.0	5.00 - 20	-	-
	July	41.2	5.00 - 290	8.43	1.19
	October	229.0	35.00 - 510	12.18	1.72
Stipe width					
1964	June	6.1	1.00 - 20	0.51	0.07
	August	8.8	2.5 - 30	0.79	0.11
	October	13.5	2.5 - 30	0.69	0.10
	November	6.6	0 - 20	0.57	0.08
	December	1.2	0 - 2.5	-	-
1965	March	1.0	0 - 2.5	-	-
	April	0.6	0 - 2.5	-	-
	June	5.0	0	0	0
	July	10.0	0	0	0
	October	14.0	2.5 - 30	0.78	0.14
Blade length					
1964	June	180.0	10.0 - 560	12.30	1.74
	August	322.0	30.0 - 750	16.21	2.30
	October	315.0	0 - 730	14.55	2.06
	November	147.0	0 - 510	13.28	1.88
	December	142.0	0 - 430	13.11	1.86
1965	March	136.0	0 - 500	13.24	1.87
	April	122.0	0 - 500	15.27	2.16
	June	191.0	15.0 - 440	21.17	2.99
	July	440.0	70.0 -1010	30.45	4.30
	October	379.0	0 - 810	16.21	2.30

3 LIFE HISTORY

3.1 Life Cycle

3.11 Alternation of generations

S. polyschides exhibits a typical Laminarian life history in which a macroscopic sporophyte alternates with microscopic, dioecious gametophytes.

3.12 Nuclear phases

The sporophyte is diploid, the gametophytes are haploid. Evans (1965) has shown that meiosis occurs in the development of the sporangium. The zoospores are therefore haploid and the diploid state is restored at the fusion of gametes.

3.2 Reproduction

The reproduction of S. polyschides has been described from culture by Norton and Burrows (1969). They found that the development of the dioecious gametophytes from spores, the production of sporophytes and their subsequent development was a continuous sequence of events without a resting stage.

The pale, motile zoospores are pear-shaped, 5 µm in diameter and each is furnished with a single eye spot, a plate-like chromatophore and two unequal, laterally inserted flagella. The release of zoospores has been described by Norton and Burrows (1969). The sporangium was seen to burst at its apex and to exude a long mucilaginous envelope which rounded off immediately after extrusion. The active, biflagellate zoospores remained together only momentarily before swimming away, following spiral paths. Ripe sporangia dissected out from the sorus were not observed to burst and release their spores. This perhaps corroborates Schreiber's (1930) suggestion that the pressure of the surrounding sporangia may contribute to dehiscence.

In undisturbed medium the zoospores settle after only a few hours of motility. None remain planktonic after 24 hours. The swarmers are furnished with a pigmented eye spot and are photosensitive. When subjected to unilateral illumination in the laboratory, they invariably settle away from the light and they may therefore be considered to be photonegative.

After settlement, the zoospores germinate to produce gametophytes at water temperatures ranging from 2°C-26°C and at light intensities from 37 µg cal/cm^{2}sec-275µg cal/cm^{2}sec. Under conditions of full salinity, the percentage of spores that germinate is in the region of 76%, but at reduced salinities the percentage germination is drastically reduced. Less than 1% of spores germinate at a salinity of 11°/oo and there is no development whatsoever at salinities below 9°/oo (Norton and South 1969).

The microscopic gametophytes may be unicellular or filamentous and branched (Fig. 3). The male gametophytes are more branched than the female gametophytes and have more numerous, paler cells. The cells of the female gametophytes are usually 14-19µm in diameter and 1-2 times as long as broad, whereas the cells of the male gametophytes are only 9-11µm in diameter and are up to several times as long as broad. Often, in culture, the female gametophyte is confined to a single cell which acts as an oogonium and extrudes a single egg measuring 11 x 22µm. The male gametophyte produces clusters of tiny, conical antheridia each of which produces a single biflagellate antherozoid measuring approximately 5 µm in diameter. At a temperature of 10°C gametangia are usually produced within 10-12 days.

The antherozoid is released by the apical dehiscence of the antheridium. Similarly, the egg is extruded from the oogonium which bursts at its apex. The egg is not usually released, but remains perched on the empty oogonium during the early development of the sporophyte. Experimental work in culture suggests that the gametes can be produced and released over a similar range of temperatures, light intensities and salinities to those suitable for spore germination. The minimum irradiance for the maturity of gametes is 3 µg cal./cm^{2}sec (30 lux in daylight).

After fertilization the zygote swells and elongates. It divides repeatedly first transversely, then also longitudinally to produce the young sporophyte. The basal cells develop into colourless rhizoids to attach the developing sporophyte. Meristematic activity gradually becomes concentrated towards the base of the plant which becomes polystromatic as it increases in size.

The seasonal behaviour of S. polyschides at Port Erin, Isle of Man, has been described by Norton and Burrows (1969). The percentage of sporophytes at different stages of development and the percentage fruiting in monthly samples taken from Port Erin Breakwater is shown in Table II. Although juvenile plants were present all the year round, there was clearly an annual cycle with no overlap between the new generation of sporophytes and the decaying bulbs of the previous season. The new generation of sporophytes first became evident in late May. After a period of rapid growth during the summer, the onset of fruiting in October coincided with the cessation of growth. The percentage of the sporophytes that were fruiting steadily increased throughout the autumn and winter until it reached a maximum in March. By May, the proportion fruiting had dropped to only 2%.

Phillips (1896) was one of the first workers to suggest that S. polyschides was an annual species. Previous workers had considered it to be perennial as they had found adult sporophytes

TABLE II

The percentage of sporophytes at three stages in development and the percentage fruiting in monthly samples taken from the *S. polyschides* population on Port Erin breakwater

Months	Juveniles	Complete adults	Stipeless bulbs	Fruiting
1964				
J	32	54	14	22
F	40	28	32	42
M	43	9	48	53
A	-	-	-	-
M	40	60	0	2
J	60	40	0	2
J	90	10	0	2
A	72	28	0	10
S	-	-	-	-
O	52	46	2	24
N	52	12	36	34
D	30	18	52	48
1965				
J	-	-	-	-
F	30	16	54	56
M	24	16	60	64
A	28	14	58	60
M	30	70	0	2
J	98	2	0	0
J	94	6	0	0
A	-	-	-	-
S	64	36	0	15
O	42	55	3	22
N	40	30	30	38

at all times of year. Phillips (1896), however, clearly stated that although the majority of the plants in a population overwintered as stipeless bulbs, some healthy sporophytes also survived the winter. Spence (1918) in Orkney reported the persistence of large complete plants into the summer of their second year. This led him to describe S. polyschides as not so much an annual as a monocarpic plant. On Port Erin Breakwater too, in addition to the stipeless bulbs, some complete sporophytes overwintered. These plants did not fruit in the autumn with the majority of the population and the observation of labelled individuals showed that they did not become fertile until the following summer.

A study of the literature suggests that the seasonal cycle is essentially similar in various parts of the species' geographical range. Young sporophytes arose in May and lost their stipes by November in Norway (Printz 1926; Svendsen 1962) and Orkney (Spence 1918). In other localities such as Anglesey (Phillips 1896) and Northern France (Sauvageau 1918) the sequence was the same, but it began in mid-March. In all of these localities as well as in Morocco (Gayral 1958) the stipeless bulb overwinters.

The difference in the time at which the new population arises in different localities can be accounted for by seasonal rather than latitudinal differences, for in 1955, an exceptionally calm and sunny year, Burrows (1958) reported that S. polyschides plants first became evident in March at Port Erin. It should be noted that at Port Erin the climatic conditions, including water temperature, were very similar in both 1964 and 1965. This may account for the close similarity in the timing of the seasonal cycle in the two years.

S. polyschides seemed to be incapable of resuming growth after fruiting; no sooner had fruiting begun than decay became apparent on the blade and then on the stipe, both of which were subsequently lost. Fruiting bulbs, however, persisted throughout the winter until they too decayed and the majority became detached from the substrate by March. The overwintering, stipeless, bulbs were found to be capable of releasing viable zoospores throughout the winter months, even in March when parts of the bulbs were rotting. Whether, in fact zoospores were being released from the bulbs in nature is not known, but it seems likely that they were. If spores were being shed in the field throughout the winter, the bulbs must supply a vast reservoir of material from which the new population of the following spring may be derived.

Little information could be gained from the literature regarding possible differences in the fruiting period in different localities, for most authors failed to distinguish between the new generation of sporophytes and those which had arisen in the previous year and overwintered. The only clear accounts are those of Printz (1926) and Svendsen (1962), both working in Norway, where, as at Port Erin, the overwintering plants began to fruit in July and August. The majority of the plants, however, lost their stipes by November and overwintered as bulbs. In Morocco, Gayral (1958) reported that here too the plants decayed in the autumn and only the bulbs survived the winter "to bud" in the following spring. However, the exact meaning of the term bourgeoner (translated as "to bud") in this context is not clear. These references would seem to indicate that in two very different localities, at opposite ends of the geographical range of S. polyschides, the species exhibited a similar seasonal cycle to that described at Port Erin.

Norton and Burrows (1969a) have investigated the environmental factors which may initiate the development of macroscopic plants of S. polyschides in the spring. They concluded on the basis of experiments in culture that low light intensity is almost certainly an important factor preventing the development of new sporophytes during the winter, whereas low water temperature and short day-length are not.

3.3 Phenology

3.31 Seasonal variation in external appearance and morphology

Seasonal variations in the morphology of S. polyschides sporophytes have been studied by Norton and Burrows (1969) at Port Erin, Isle of Man.

When the new generation of sporphytes arose in the spring, the smallest plants that were recognisably S. polyschides possessed a round stipe, not yet twisted and the lamina was invariably entire. Above the prominent holdfast the stipe bore a small circular ridge from which the characteristic bulbous structure developed. The ridge produced from its margin 8 or so projections which became the first row of haptera. During the summer the ridge expanded both outward and downward and further whorls of haptera developed on its upper surface. It was usually possible to distinguish the separate whorls until 5 or more had been produced. By this time the basal structure had grown down around the holdfast obscuring it, much as a bell obscures its clapper. At this stage it greatly resembles the secondary holdfast of the adult sporophyte of S. dermatodea. The lowermost, first-formed rows of haptera elongated and attached themselves to the substrate thus supplementing the original holdfast. In the late summer and autumn the bell greatly expanded laterally and continued to produce small protruberances on its upper surface. This large, hollow, warty 'bulb' is characteristic of the adult plant. Bulb diameter was often restricted by the close proximity of adjacent bulbs. Meanwhile, the greatly expanded lamina almost invariably became divided into a number of digits. The stipe too legthened, became flattened and spirally twisted at the base, where it widened to merge into the top of the bulb.

The bulb continued to increase in size from October to December and produced numerous rows of haptera. Often adjacent bulbs coalesced extensively so that the individual plants were difficult to distinguish. This fact may have led to the erroneous statement of Barber (1889) that one bulb could have several stipes. Sometimes, quite a large plant had only a small, rudimentary bulb which was fused to a much larger bulb of another plant. Often, if the plant rubbed against rocks or other plants, the frill or stipe produced haptera-like proliferations from the region of contact.

Eventually the top of the bulb, where it joins the base of the stipe, became deeply concave. The stipe progressively widened from June to October especially distally so that it now tapered towards its base and not towards its tip as before. The blade also became larger but, whereas growth during the summer was much more pronounced in a longitudinal direction giving a long, narrow outline to the frond, in the autumn lateral expansion kept pace with longitudinal growth and the blade developed a much broader silhouette. The reproductive frills now developed on the lower regions of the stipe. They began as flat, lateral expansions of the stipe but subsequently, as a result of differential growth, they became undulated. Sometimes they became prominent structures several centimetres in width but often they remained in a rudimentary state.

No sooner had the plant become adult in appearance and begun to fruit, than decay became apparent at the tips of the blade. The rot spread down the thallus during the late autumn and winter until eventually both the blade and stipe were lost. The bulb persisted much longer and often overwintered in a fruiting condition, until it also decayed and became detached from the substrate by the following March or April.

Sporophytes which arose during the late summer and did not become fertile that year overwintered as intact sporophytes without decaying. At Port Erin these represented only a very small proportion of the population.

4 POPULATION

4.1 Structure

4.11 Age composition

As S. polyschides is an annual plant the population usually consists largely of plants which have arisen at more or less the same time of year, in the spring. If, however, space becomes available new sporophytes can develop during the whole of the summer and into the autumn. The observation of labelled sporophytes at Port Erin indicated that plants which arose late in the year did not fruit that winter (Norton and Burrows 1969). Such plants overwintered intact, without losing their stipes from decay as was usually the case, and they became fertile during the following summer. The proportion of these overwintering sporophytes in the population varied from one locality to another. On Port Erin breakwater in the summer of 1964 about 10% of the population had overwintered. In a loose lying community of S. polyschides plants which developed in the adjacent Port Erin bay, the entire population was cast up onto the shore by the first storms of winter and therefore no sporophytes overwintered. Differences in the proportion of the plants which had overwintered intact were also found in two localities at Lough Ine in Ireland. In August 1965 at Carrigathorna, a seaweed station, less than 1% of the population appeared to have overwintered and 90% of the plants were immature. However, in Lough Ine Rapids, almost 40% of the population appeared to have overwintered and 22% was fruiting as early as May, increasing to 76% by August.

4.2 Density

4.21 Average densities of defined areas

Few counts of number of plants of S. polyschides per unit area have been made. The present author denuded 24 m^2 of Lough Ine Rapids where the species was extremely abundant. The average density of S. polyschides sporophytes was 7.6/m^2.

4.3 Mortality, morbidity

Although sporophytes may be present in the sea throughout the year, individual plants do not usually survive for more than 10 or 11 months. Sporophytes which arise in the spring decay and become detached from the substrate by the following spring, whereas those which do not arise until later in the summer may survive until the following summer.

Sauvageau (1916) considered that the decay of the sporophytes of S. polyschides in the autumn was wholly the result of grazing by Patina (Helcion) pellucida, which lives on the fronds, but Norton and Burrows (1969) concluded that the action of Patina, serious as it may be, only aggravated and therefore accelerated an inherent pattern of decay.

It is significant that no matter where the Patina were aggregated, decay almost invariably began at the tips of the digits and progressed downwards until first the blade and then the stipe were gradually lost. For example, on Port Erin breakwater in October, 1964, 24% of the sample had rotting blades, but only 2% showed signs of decay on the stipe. A month later only 4% had rotting blades, but 35% had completely lost their blades and their stipes. Since Patina was rarely more abundant at the tips of the digits than elsewhere on the plant, it would seem unlikely that it could have been the fundamental cause of the decay. This conclusion was supported by observations of decaying plants which were hardly affected by Patina.

4.4 Total quantities (standing crop) of defined areas

The average standing crops of S. polyschides expressed in weight of plants per m^2 for various localities is shown in Table III. The figures are somewhat variable, but it is clear that the quantities recorded in Northern Spain were much greater than those found elsewhere. As can be seen from Table IV, in the Spanish material, the laminae of the plants constituted approximately half the total weight of the samples, the bulb and stipe combined constituting the remainder. The same is true of Scottish plants (Table VII).

There is no apparent correlation between the standing crop of S. polyschides and the type of substrate.

Table V shows the standing crop of S. polyschides at different depths in various localities. The species does not exhibit a clear-cut pattern of weight distribution with depth. This is due, no doubt, to the complicating effects of competition with other forest-forming laminarians and possibly different degrees of grazing at different depths.

4.5 Accompanying and competing species

Probably the most important competitor of S. polyschides in Britain is Laminaria hyperborea, but L. saccharina and L. ochroleuca are also undoubtedly important competitors in some areas.

Kain (1960) observed that at Port Erin the upper limit of the Saccorhiza zone was related to the lower limit of L. hyperborea, regardless of the depth at which this was. Only in the absence of L. hyperborea did S. polyschides reach up to low water mark. The possible existence of some form of competitive inhibition was investigated by Norton and Burrows (1969). They denuded an area in the L. hyperborea zone of all macroscopic sporophytes. The area was recolonised by S. polyschides although not a single sporophyte of S. polyschides developed

TABLE III

Mean standing crop of S. polyschides in various localities (recalculated from Grenager 1964; John 1968; Larkum and Norton, unpublished; Walker 1947, 1949, 1949a and 1949b, 1950 and 1955)

Localities	Depths sampled in metres	Weight in gm/m^2
Spain		Dry wt.
Playa de Lago	1 - 2	2677
Isla Onza	1 - 9	1934
Las Osas	1 - 8	1615
Punta de Alada	1 - 2	807
Punta Testada	1 - 8	765
		Fresh wt.
Norway		
Koløy	5.5 - 10.5	3000
Kuløsskjaerene	5 - 12.5	2320
Froøyene	0 - 24	1733
Sula	0 - 14	400
Dalskjaerene	2.5 - 3.5	280
Dagskjemmen	4 - 5.5	240
Nuvaerøy	2.5 - 3.5	40
Prestoy	5 - 6.5	40
Einholmene	4.5 - 6.5	40
Scotland		
Huip Holm, Orkney	3.5 - 13	973
North Switha, Orkney	2 - 13	700
Shapinsay, Orkney	2 - 13	447
Bay of Firth, Orkney	0 - 13	444
Risa, Orkney	2 - 13	436
Linga Holm, Orkney	2 - 13	425
Weddel Sound, Orkney	2 - 11	422
Sanday Sound, Orkney	2 - 13	365
Little Loch Broom, Ross and Cromarty	0 - 18	334
Papa Sound, Orkney	2 - 16	327
Kirk Hope Bay, Hoy, Orkney	2 - 13	312
Head of Work, Orkney	7 - 8	287
North Fara, Orkney	2 - 13	242
Rapness Sound, Orkney	2 - 13	147
Stywick Bay, Sanday, Orkney	2 - 13	138
Huip Ness, Orkney	2 - 18	134
East Flotta, Orkney	2 - 13	124
Deer Sound, Orkney	2 - 11	122
Car Ness, Orkney	2 - 11	118
East Fara, Orkney	2 - 13	105
South Flotta, Orkney	2 - 13	50
North Hoxa, Orkney	2 - 11	41
Ireland		
Lough Ine Rapids, Cork	1 - 2	8825
Whirlpool Point, Lough Ine, Cork	3 - 12	484

TABLE IV

The proportion of the dry weight/m^2 constituted by the bulb and stipe, and the lamina in various localities in Northern Spain (from John 1968)

Locality	Depth	Bulbs and Stipes	Laminae	Debris
Punta de Alada	1.8	366	409	32
Playa de Lago (inlet)	1.8	878	572	22
Playa de Lago (channels)	1.8	2047	1718	117
Punta Testada	1.8	466	486	46
	3.7	654	546	14
	7.3	29	53	0
Las Osas	1.8	593	479	16
	3.7	1114	707	0
	7.3	1069	851	14
Isla Onza	1.8	2159	1110	0
	5.0	910	921	211
	8.4	246	231	12
Total weights		10531	8083	484
Total percentages		55.2	42.3	2.5

beneath the adjacent forest of L. hyperborea. They concluded that the dim light beneath the canopy of the forest was insufficient to allow the growth of S. polyschides plants.

The faster growth rate of S. polyschides when compared with L. hyperborea as shown in culture, would enable the sporophytes to establish themselves more rapidly at the expense of slower-growing species. When De Valera and Booth (personal communications) independently cleared areas in the Laminaria digitata zone, both areas were recolonised by S. polyschides and not L. digitata. S. polyschides therefore may be considered to be an opportunist, forming casual populations and colonising any space that becomes available in the sublittoral region. It has, however, the disadvantage of being an annual species which must re-establish itself each year whereas its chief competitor, L. hyperborea, is perrenial and once established will, in all probability, remain for a number of years.

The dynamic equilibrium between populations of S. polyschides and L. hyperborea would help to explain the fluctuations in the abundance of S. polyschides which occur from year to year in some localities. For example in a lagoon at Rhosneigr in Anglesey, North Wales, only one plant was found in the autumn of 1963 and yet the species was abundant there at the same time of year in 1965. Grenager (1955), discussing a population in Norway, stated that the very rich community of 1952 had disappeared almost completely in 1953. Similarly, in Galway, Eire, large populations of S. polyschides appeared and disappeared in consecutive years (De Valera personal communication).

The species which accompany S. polyschides are the same as those normally found beneath the canopy of other laminarian algae. In addition, the sporophytes are often covered with epiphytic algae and animals. During the present work at Port Erin and Lough Ine 49 species of algae and 89 species of macroscopic animals were recorded on the thallus of S. polyschides. An ecological account of the epifauna of S. polyschides has been published (Norton 1970a).

Most of the epiphytic species were casuals rather than characteristic members of the epiflora and epifauna. Not a single species was confined to S. polyschides, but several were much more abundant on this host than on other algae or on

TABLE V

Standing crop of S. polyschides at different depths in various localities (recalculated from Grenager 1964; John 1968; Larkum and Norton, unpublished; Walker 1947, 1949 and 1949b, 1950 and 1955)

	Dry wt. gm/m^2			Fresh wt. gm/m^2											
	Spain			Norway				Scotland							Ireland
Depth in m-	Punta Testada	Las Osas	Isla Onza	Froøyene	Sula	Kulosskj-aerene	Dagsk-jemmen	Deer Sound, Orkney	Bay of Firth, Orkney	Car Ness, Orkney	Shapinsay, Orkney	Rapness, Orkney	Huip Holm, Orkney	Little Loch Broom, Ross & Cromarty	Whirlpool Cliff, Lough Ine, Cork
1.0	-	-	-	0	0	0	-	-	-	-	-	-	-	-	-
1.6	998	1088	3269	-	-	-	-	0	0	0	357	0	0	745	-
3.7	1214	1821	-	800	1600	-	-	0	0	0	516	96	0	482	1440
4.5	-	-	-	-	-	-	400	-	-	-	-	-	-	-	-
5.0	-	-	2042	-	-	-	400	-	-	-	-	-	-	-	-
5.5	-	-	-	-	-	-	1600	71	65	235	630	0		41	485
7.5	82	1934	-	8800	400	20000	-	110	392	53	396	128	810	70	-
8.4	-	-	489	-	-	0	-	-	648	-	-	-	-	-	0
9.0	-	-	-	-	-	2800	-	184	680	0	335	212	768	0	-
9.5	-	-	-	-	-	400	-	-	-	-	-	-	-	-	-
11.0	-	-	-	-	-	-	-	120	432	65	0	176	1340	0	-
11.5	-	-	-	800	0	-	-	-	-	-	-	-	-	-	10
12.8	-	-	-	-	-	0	-	0	0	0	0	120	0	0	-

the surrounding rock. These were the alga *Giffordia hincksiae* and the animals *Campanularia* sp., *Obelia geniculata*, *Halosydna gelatinosa*, *Nereis pelagica*, *Lineus longissimus*, *Gammarus locusta*, *Jassa falcata*, *Patina pellucida*, *Lacuna vincta*, *Gibbula cineraria*, *Asterias rubens*, *Psammechinus miliaris*, *Membranipora membranacea* and *Ascidiella aspersa*.

Most of the epiphytes used *S. polyschides* merely as a support and their attachment involved no penetration of the host. The epiphytic Polyzoa were in this category and of the algae, only *Ectocarpus siliculosus* and *Ptilota plumosa* were found to ramify into the host tissue. Even without directly damaging the tissue, however, epiphytes may be detrimental to the host. For example, a dense covering of epiphytic algae would undoubtedly prevent some of the available light from reaching the frond and might therefore impair the host's photosynthetic ability. To some extent the abundance of algal epiphytes was controlled by browsing animals such as *Gibbula cineraria* and *Patina pellucida*. Many animals, however, are harmful to the host plant and the grazing sea-urchins *Echinus esculentus* and *Paracentrotus lividus* are major factors controlling the distribution of *S. polyschides* in some areas.

5 HARVESTING

5.1 Methods of Harvesting

The problems of harvesting S. polyschides are the same as those which are encountered with other epilithic species inhabiting the sublittoral zone. However, it often forms extensive loose-lying populations on moveable substrates (Burrows 1958). Such plants could be easily and economically collected with a dredge or grapnel. Alternatively they could be collected from the drift for vast numbers of plants from loose-lying populations are usually cast up onto the shore by the first storms of winter.

S. polyschides is an annual plant. After fruiting, the sporophyte loses the entire stipe and lamina and they are usually cast up onto the shore in large quantities. They could be collected economically from the drift. The bulbs which persist longer are usually cast up during March and April.

5.2 Harvesting seasons

The sporophytes are the largest seaweeds found on the Atlantic coasts of Europe and are extremely fast growing. They achieve their maximum size in the late summer. If the plants were removed at this time a new generation of sporophytes would develop during the autumn. Thus one area would supply two harvests per year.

All parts of the sporophyte including the basal bulb produce reproductive sori. Therefore only the bulb need be left to overwinter to ensure a supply of spores from which next year's generation of sporophytes may be derived.

5.3 Harvesting areas and depths

Although its distribution is somewhat sporadic it can be extremely abundant locally, often to the exclusion of other laminarians. It is particularly abundant on the south-west coast of Ireland and on the north-east coast of Spain. Both countries already possess an industry harvesting and utilizing laminarian algae.

Although it can occupy a considerable depth range, in the absence of other laminarians it forms extensive populations in shallow water up to low water mark where it can be gathered easily by hand.

5.4 Regrowth on harvested areas

S. polyschides is an opportunist and if beds of Laminaria digitata or L. hyperborea are removed (by harvesting for example) they are often replaced by S. polyschides. It would therefore be more economical to utilise the S. polyschides which initially replaces the laminarians than to wait for the species of Laminaria to re-establish themselves.

Areas denuded in the spring, summer or autumn will probably be recolonised immediately, but if stripped during the winter an area will remain bare until the beginning of the growing season of S. polyschides in the following spring.

6 PROTECTION AND MANAGEMENT

6.4 Control of biological features

6.41 Control of predation and competition

In rocky areas colonisation by S. polyschides might be induced by the removal of competing species during the sporing season of S. polyschides. The colonisation of such areas would be encouraged by the removal of grazing echinoderms. Sea-urchins can be destroyed underwater by divers, providing animals are mostly more than 20 mm in diameter and their abundance does not exceed $4/m^2$. A relatively cheap alternative method for the routine eradication of sea-urchins is the periodic application of CaO (commercial quicklime). This induces tissue loss on contact and sea-urchins were found to be the organisms most sensitive to its effects both in culture and in the sea (Leighton *et al.*, 1966). A concentration of $0.5\ kg/m^2$ resulted in a marked reduction in the sea-urchin population with little effect on other animals and a great increase in the amount of laminarian algae. The easiest method of applying quicklime is to allow it to fall gradually into the wake of a moving boat as it passes back and forth over the area to be treated.

6.5 Artificial culture

It should be possible to introduce the species into areas where it is not at present found. It can grow well in sheltered areas on unstable bottoms if provided with small pebbles, shell fragments or possibly submerged ropes for attachment. Such substrates are unsuitable for the attachment of S. polyschides' main competitors Laminaria hyperborea and L. ochroleuca.

Sporophytes of S. polyschides are easily transplanted from one locality to another (Norton 1969). Sporing could be induced in fertile transplants by allowing the thallus to dry out slightly, without overheating, before submergence at the area to be colonised.

7 CHEMICAL COMPOSITION

7.1 Water content

The water content of sporophytes of *S. polyschides* from the coasts of Portugal is given in Table VI. It constitutes on average 15% of the plants weight.

7.2 Inorganic constituents

The chemical composition of *S. polyschides* has been studied on the coasts of Portugal (Machado *et al.*, 1966, Frazao 1966) and Scotland (Black 1948). Their data are summarised in Tables VI and VII respectively and show that:

a) The total ash content was much higher than in other laminarians although the content of water insoluble ash was similar to that of other *Laminariales*. It is interesting to note that high ash content of 54.5% has been recorded for *Nereocystis leutkeana*, also an annual plant.

b) The iodine content was considerably lower than in the other laminarians and was of the order found in *Ascophyllum nodosum*.

c) The potassium levels were high.

TABLE VI

The chemical composition of *S. polyschides* from the coast of Portugal (recalculated from Machado *et al.*, 1966 and Frazao 1966)

Composition	Maximum	Mean	Minimum
Water content (g%)	37.7	15.1	6.7
gm/100 gm dry wt.			
Total nitrogen	2.8	1.8	1.0
Ash	58.8	44.6	27.2
Iodine	0.11	0.09	0.01
Crude proteins	17.2	11.4	6.4
Fat	0.9	0.3	Trace
Cellulose	20.3	8.7	4.9
Mannitol	15.1	8.0	0.9
Laminarin	5.3	1.1	Trace
Alginic acid	29.7	21.9	14.6
Chlorides in NaCl	37.9	28.1	10.4
Sulphates in $CaSO_4$	5.7	3.8	2.5
mg/100 gm dry wt.			
Ca	2207	1340	897
Mg	1288	642	240
P_2O_5	1265	517	254
Fe	303	55.5	3343
Na	6991	5196	3343
K	18800	12218	6576
Na/K	0.7	0.44	0.3

TABLE VII

The seasonal variation in the composition of *S. polyschides* from Cullipool, West Scotland November 1945 - October 1946 (from Black 1948)

Composition % weight	November		June	July		August		September		October	
	frond	stipe	whole plant	frond	stipe	frond	stipe	frond	stipe	frond	stipe
Dry weight	9.94	9.76	10.0	9.82	7.39	11.03	9.68	10.27	8.89	-	-
Total ash	47.1	51.0	48.8	41.7	55.0	32.1	42.3	38.9	31.5	37.6	35.1
Iodine	0.12	0.12	0.07	0.06	0.09	0.10	0.1	0.05	0.13	0.16	0.11
Crude proteins	7.5	5.6	5.0	5.9	3.5	5.9	4.8	4.9	5.4	6.2	5.6
Mannitol	4.5	5.8	15.0	22.0	11.9	28.2	23.1	21.7	21.5	16.0	19.5
Alginic acid	14.8	15.8	13.1	11.8	14.5	12.9	13.1	14.0	14.0	15.7	15.6
Laminarin	<1.0	<1.0	<1.0	<1.0	<1.0	<1.0	<1.0	<1.0	<1.0	<1.0	<1.0

TABLE VIII

The seasonal variation in the composition of *S. polyschides* from the coasts of Portugal. March - November 1963 (from Machado *et al.*, 1966)

Composition % dry wt.	March-April	May	June	July-August	September-November
Total nitrogen	2.3	2.0	1.8	1.6	1.7
Ash	42.5	47.4	48.1	44.8	40.5
Crude proteins	13.9	12.3	11.4	9.7	10.5
Fat	0.2	0.4	0.3	0.3	0.3
Cellulose	8.0	7.6	6.7	8.6	12.4
Mannitol	7.6	6.2	8.0	11.5	7.2
Laminarin	1.2	1.0	0.6	0.8	1.9
Alginic acid	23.6	19.3	21.4	22.1	24.0

7.3 Organic constituents

The organic constituents of S. polyschides are also given in Table VI.

Seasonal variations in the organic constituents of S. polyschides have been studied on the coasts of Scotland (Black 1948) and Portugal (Machado *et al.*, 1966). Their data are summarised in Tables VII and VIII respectively.

7.31 Carbohydrates

The values of carbohydrates obtained by Black (1948) and Machado *et al.* (1966) for S. polyschides were compared with those obtained from other laminarians from the same localities and several points emerged:

a) Laminarin was present in only very small amounts.

b) The mannitol content was high, reaching a maximum value in August and decreasing to a minimum in November. It is interesting to note that an annual plant should build up such a large reserve of mannitol. No doubt a considerable amount of mannitol would be required to sustain the rapid growth of the sporophyte in the spring. Before November, however, the mannitol had practically disappeared, and it may be that mannitol and higher synthetic products were used up in sporing and maintaining life when photosynthesis had ceased.

c) The alginic acid content was somewhat lower than that found in Laminaria digitata, but was comparable with the levels recorded for other laminarians.

7.35 Other organic constituents

The biological activity of chemical extracts of S. polyschides has been tested by Vieitez, Areses and Loureiro (1968) using the elongation of Avena coleoptiles test. The acid fraction was found to have an Rf of 0.3 to 0.5 and the neutral fraction an Rf of 0.4 to 0.8. The phenolic fraction exhibited varying degrees of strong inhibition on growth.

8 UTILIZATION

8.2 Animal fodder

The species is little used today for commercial purposes although quantities cast up onto the shore are sometimes collected, together with other laminarians, and made into seaweed meal.

8.3 Manure

Saccorhiza polyschides has furnished an excellent manure for the land (Greville 1830).

8.4 Industrial products

Formerly, S. polyschides was one of the most widely used algae in the manufacture of kelp, although its use was largely confined to areas where large quantities were regularly thrown up onto the shore, e.g. in Western Ireland, in Scotland (Chapman 1950) and in the Isles of Scilly (Greville 1830). It was widely used for the extraction of iodine and in the manufacture of glass and soap (Landsborough 1851).

As it is relatively rich in mannitol, potassium, and to a lesser extent alginic acid, it may represent an important potential source of these substances.

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SYNOPSIS OF FISHERIES BIOLOGICAL DATA

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