ASPECTS OF GROWTH AND PRODUCTION OF LAMINARIA PALLIDA (Grev.) J. Ag. OFF THE CAPE PENINSULA

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To Claudia and my parents
for their encouragement

FRONTISPIECE : Young Laminaria pallida sporophyte growing at 8 m depth on a granite boulder. In the background, a forest of large sporophytes.

ABSTRACT

Growth rates, chemical composition and annual production by sporophytes of Laminaria pallida at different localities and depths have been investigated.

Growth of L. pallida fronds measured as rates of frond elongation was seasonal and showed similar trends at Robben Island and Oudekraal and at different depths. Frond elongation rates of up to 1,3 cm day^{-1} were recorded in spring and early summer, whilst slow rates of 0,2 cm day^{-1} were measured in late autumn and winter at all stations.

The seasonal cycle of frond elongation rates appeared to be regulated by more than one abiotic factor, with light probably being the most important one.

Differences in stipe elongation rates of sporophytes growing 50 m apart, but at different depths, confirmed that light was an important factor in determining growth rates; at 8 m depth stipes attained a length of approximately 240 cm within five years, whereas stipes growing at 14 m depth only grew to a length of approximately 200 cm in nine years.

It appears that the reproductive phase of L. pallida sporophytes plays a major role in determining the observed seasonal growth pattern of the plants. In certain instances, grazing by isopods and colonization by epi-phytes and -zooids also affected sporophyte elongation rates.

Seasonal variation in percentage dry mass of L. pallida in this investigation was not as marked as in laminarians elsewhere. Carbon content and calorific values of L. pallida sporophytes showed almost no variation with season, while nitrogen content varied only slightly. This confirms indications that L. pallida is not subjected to heavy

environmental stresses. It does not appear to have to accumulate reserves of carbon and/or nitrogen to survive periods of extreme low light intensities and nutrient deficiencies.

L. pallida growing at 8 m and 14 m depth turned over its frond biomass 4,7 times and 3,5 times per year respectively. Since frond biomass comprises almost half the total plant biomass, it means that the total standing stock of L. pallida turned over its biomass approximately twice. Standing stock of L. pallida at 8 m was 13,56 kg wet mass m^{-2}. Of this, the fronds contributed 5,87 kg. In one year the fronds produced 27,59 kg wet mass m^{-2} or 869 g carbon m^{-2} with a calorific content of $3,77 \times 10^4$ kJm^{-2}.

These high production rates indicate the significance and importance of L. pallida as a primary producer in coastal waters of the Cape.

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CHAPTER 1

GENERAL INTRODUCTION

1.1 Importance of Kelp

Ecological studies of the kelp species growing off the South African coast have until recently been severely neglected. Although the three species, Ecklonia maxima, Laminaria schinzii and L. pallida, have in the past been exploited by collecting beach cast as a raw material for the alginic acid industry, harvesting of natural stocks has, under the Sea Fisheries Act of 1973, been prohibited due to a lack of information on the biology of these species.

Of greater importance than that of commerce is the biological contribution by seaweeds, in particular the kelps, to the marine coastal ecosystems. Chapman (1974) in a review of ecology of macroscopic marine algae states: "Seaweeds may have an indirect commercial importance far exceeding their immediate industrial application. The fate of much of the enormous production of coastal beds is unknown. It is conceivable that it enters the food chains of commercial fish. This is known with some certainty for lobsters which preferentially consume sea urchins that in turn graze on kelp."

During the last decade in particular it was postulated that attached plants form the basis of most food chains in inshore waters (Field et al., 1977). The importance of kelps as primary producers in coastal waters has also been claimed by others (Mann, 1972, 1973; Chapman, 1974; Mann and Chapman, 1975).

Kelp forests, similar to terrestrial forests, harbour a large population of fauna and flora benefiting directly from the mechanical protection afforded by the kelps which act as natural breakwaters. The sheltered environment within kelp holdfasts attracts a number of juvenile kelp bed organisms and functions as a nursery for isopods, amphipods, polychaetes and tunicates (Velimirov et al., 1978).

The order Laminariales is perhaps the most well represented in studies of growth and production of seaweeds, the majority of which were carried out in the Northern Hemisphere (Parke, 1948; Sundene, 1962, 1964; Kain, 1963, 1967, 1971a, 1971b, 1975a, 1975b, 1977; Lüning, 1968, 1969; North, 1971; Mann, 1971, 1972, 1973; Jackson, 1977, 1978).

1.2 Description and Distribution of L. pallida

This study deals with a member of the Laminariales, Laminaria pallida, a major constituent of kelp beds off the West coast of Southern Africa. L. pallida is a brown alga which demonstrates the complexity and anatomical specialization characteristic of the order Laminariales. The mature sporophyte has a large digitate blade or frond that appears to survive through the entire life of the plant. Its stipe, which may reach a maximum length of almost three metres, is massive proximally where it is attached by very well-developed branched haptera spreading laterally for a distance approximately twice the maximum stipe diameter; it tapers gradually upwards to a somewhat compressed apex, about 2,5 cm wide, before expanding into a palmate, digitate blade (frond) sometimes exceeding 100 cm across. The angle of emergence of the blade varies, but it is often as much as a right angle. The blade (frond) of a mature plant has an undivided portion, the meristematic zone, occupying the basal 20-30 cm and carrying distal digits all of about equal width primarily - usually between 7 and 10 cm - and equal length which may be as much as two metres. All blade margins are entire and square although terminally there are usually irregularities resulting from erosion. (Fig. 1.1 a).

Juvenile sporophytes, in their first few months of development, have an entire, truncated lanceolate blade (Fig. 1.1 b).

Reproductive tissue forms into extensive sori of irregular shape and size and occurs on both surfaces of digits of the mature blades.

L. pallida has a heteromorphic alternation of generations in which the dioecious gametophytes are microscopic and have only been observed in the laboratory (Branch, 1974; Papenfuss, 1942).

L. pallida occurs essentially off the West coast, extending from Namibia to Cape Point. Off the Southern Cape coast it probably occurs as far East as Cape Agulhas and has been observed at Betty's Bay at depths between 20 and 30 m (pers. obs.).

Sporophytes of L. pallida are entirely subtidal and are seldom exposed at low tides. Together with Ecklonia maxima and in some cases Macrocystis angustifolia, they form extensive kelp beds that characterize rocky shores. At depths beyond which E. maxima does not occur, 'forests' consisting entirely of L. pallida may be found to depths of up to 30 m, probably depending on availability of light and a suitable rocky substratum. Geographic distribution of L. pallida is probably determined mainly by water temperature. This is demonstrated by its confinement to areas off the South African coast that are affected largely by cold upwelled water.

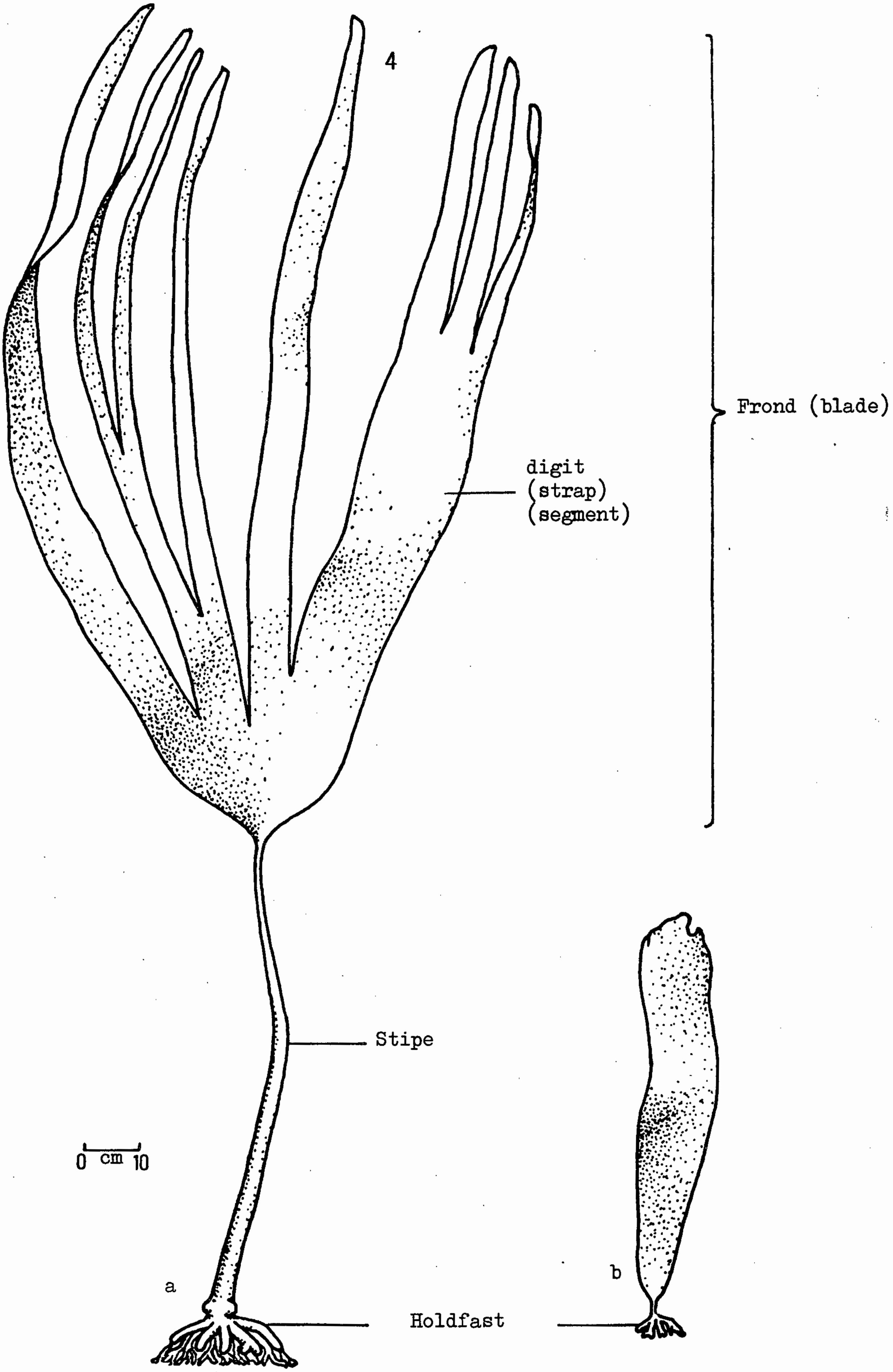

Fig. 1.1 : Laminaria pallida, mature sporophyte (a) and juvenile sporophyte (b).

1.3 Objectives of This Study

The ultimate objective of this study is to determine the productivity of L. pallida. This demands a knowledge of its growth rate and chemical composition. The study will be reported in three sections: Chapter 2 deals with the growth of sporophytes, Chapter 3 with dry mass, calorific content and C : N ratios, while Chapter 4 deals with biomass and production. Each chapter will include an introduction, a statement of methods used to yield reported results and a discussion and conclusions on the information gathered.

1.4 General Observations on Methodology

All field work was done in situ using SCUBA. Methods employed may appear to be simple. However, it must be appreciated that prevailing swell and weather conditions are often extremely hostile off the Cape coast. A major difficulty was relocating of stations and tagged plants.

The study was initiated in 1974 and many months were spent mastering underwater techniques, such as labelling and measuring plants. Relocation of underwater sites was made difficult, indeed sometimes impossible, by the removal of buoys and markers through natural and human causes.

Despite many problems, it was possible to obtain records of growth for L. pallida at different localities for a continuous period of almost three years.

1.5 Study Areas and Their Hydrology

The western coast of South Africa is characterized by a temperate climate. During spring and summer strong south-easterly winds are frequent, causing localised upwelling. Together with high light intensities, these conditions are optimal for plankton growth (Andrews, 1974; Andrews *et al.*, in press). During the winter months, northerly winds, often accompanied by large swells and rain, are frequent. Most of the southern Cape coast is directly exposed to the pounding of these large westerly swells.

1.5.1 Robben Island

Robben Island lies 7 km from Cape Town, opposite Table Bay ($33^{\circ}48'$S, $18^{\circ}22'$E; Fig. 1.2). This island was chosen as a study site mainly because it is a restricted area and free from interference by divers and fishermen. Because of apparently typical kelp beds off the island, it was initially considered to be typical of the Cape coast with regard to kelp growth.

Station A (Fig. 1.2) was established on the East side of the island within a kelp bed consisting of *Ecklonia maxima*, *Macrocystis angustifolia* and *Laminaria pallida*, 50 m from the shore at a depth of three metres. The substratum there is of Malmesbury shale forming rugged outcrops dissected by sandy gullies. This station is directly exposed to strong south-easterly winds, blowing offshore from the mainland, but is protected from the direct onslaught of the large westerly swells. Exceptionally strong swells are refracted around the northern and southern points of the island, breaking over the station on occasion. This situation, together with other anomalies which will

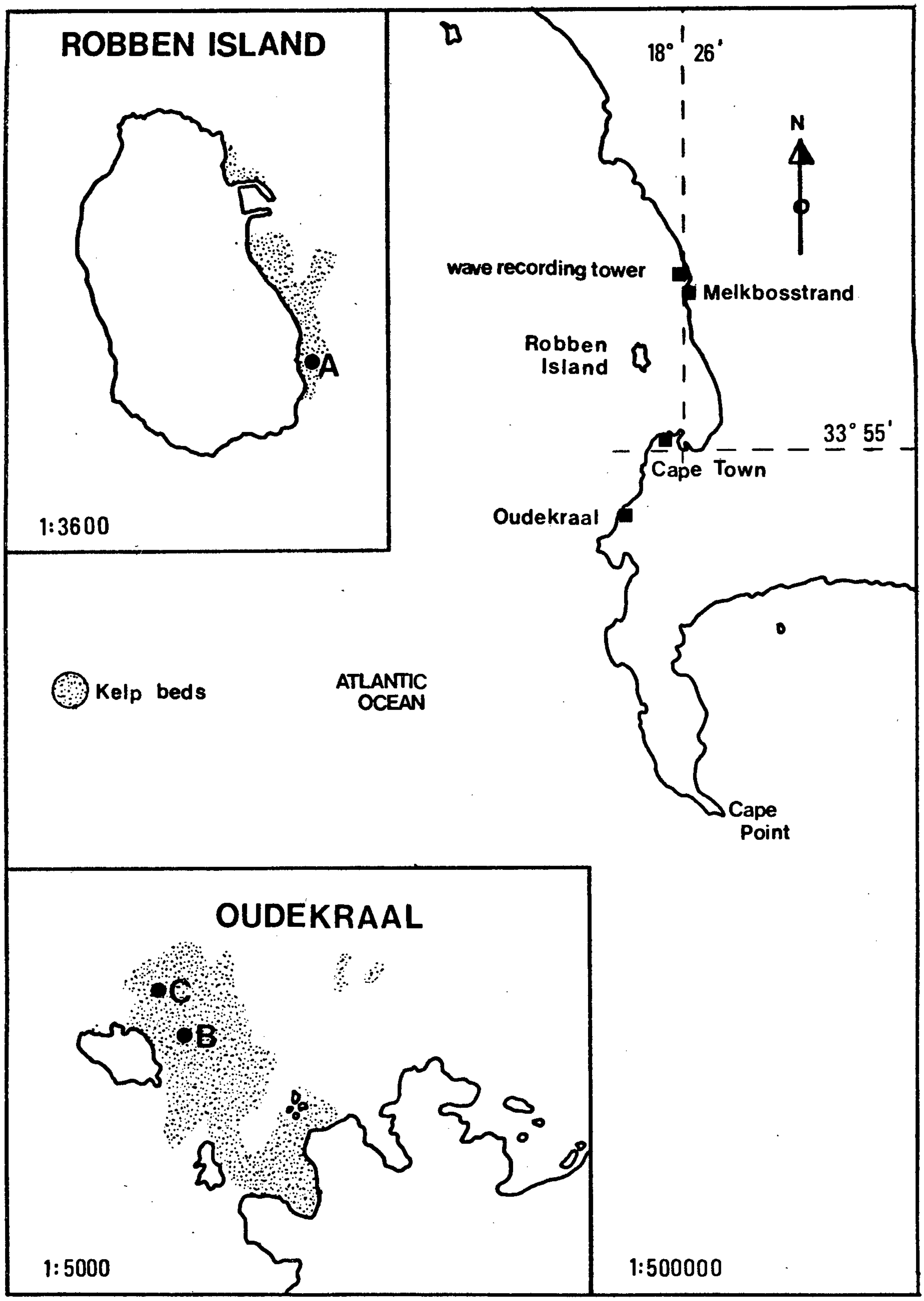

Fig. 1.2 : Study sites showing location of Stations A, B, and C in the kelp beds.

be discussed later in this study, has led to the conclusion that kelp growth at Station A, Robben Island, was not typical of the West coast of South Africa and, more specifically, of the Cape Peninsula.

1.5.2 Oudekraal

The site at Oudekraal was selected for a kelp bed ecosystem study by an interdisciplinary group of scientists (Field *et al*., 1977).

Since *L. pallida* is a major component of the benthic community at this site, it was appropriate to establish two stations; one at 8 m depth (Station B) and one at 14 m depth (Station C) (Fig. 1.2). *L. pallida* is the only kelp growing at these stations, on a substratum of submerged granite boulders. South-easterly winds are 'funnelled' down the slopes of the mountain ridge parallel to the coast at Oudekraal. Such winds, especially when they are of high velocity, are probably responsible for localised upwelling and related hydrological conditions observed at the site. The stations are pounded by large westerly swells up to 7 m high, especially during the winter months.

CHAPTER 2

GROWTH OF LAMINARIA PALLIDA SPOROPHYTES

2.1 Introduction

Sporophyte growth and development in the Laminariales has been investigated by several workers, among whom are: Sauvageau, 1918; Parke, 1948; Sundene, 1962, 1964; Kain, 1963, 1967, 1971b, 1975, 1977; Pérez, 1968; Lüning, 1968, 1969, 1970, 1971; Mann, 1971, 1972, 1973; North, 1971; Chapman, 1974; Drew, 1974; Jupp and Drew, 1974; and Grützmacher, 1976.

Sauvageau (1918) was the first to establish that Saccorhiza polyschides had a life cycle of alternating generations, with a macroscopic sporophyte generation developing from a microscopic gametophyte generation, an important foundation for future investigations of the Laminariales. Almost all subsequent investigations of the biology of Laminariales were done in the Northern Hemisphere. One of the most significant contributions was made by Parke (1948) who studied the growth of Laminaria saccharina (L) Lamour. growing off the British coast. She discovered that L. saccharina is a perennial whose seasonal growth pattern is influenced by a combination of environmental factors; growth of the stipe was incremental, whereas the fronds behaved differently, growing at the base whilst eroding at the tips.

Using the work of Parke (1948) as a basis, Mann (1972) found that L. longicruris and L. digitata, growing off Nova Scotia, behaved similarly to L. saccharina off Britain. He described the fronds as moving belts of tissue with growth at the base being balanced by erosion at the tips. Kain (1971b) prepared a synopsis of biological data on

L. hyperborea based on 10 years of research by herself and other workers. She compared the biology of L. hyperborea with other well-studied members of that genus and suggested that the behaviour of the Laminariales in the Northern Hemisphere is probably governed by prevailing seasonal climatic conditions.

Various authors, however, found that the familiar seasonal cycle of rapid growth in summer and quiescence in winter was not displayed by the Laminariales they were studying (Mann and Chapman, 1975). Mann (1972) found that L. longicruris elongates most rapidly during winter, that is, when days are short and light intensities and water temperatures are low. Lüning (1971) found that L. hyperborea growing in temperate waters is capable of seasonal adaptations of rates of photosynthesis and respiration, with the result that an assimilatory surplus may be built up in summer. This surplus is used to initiate growth during winter when light levels are low. Chapman and Craigie (1977) reported that the onset of seasonal growth in L. longicruris in shallow water stations in St. Margaret's Bay, Nova Scotia, coincided with improved dissolved nitrate conditions in the sea and suggested that nitrate availability is the determining factor of the seasonal growth pattern they observed. Drew (1974), working on L. ochroleuca in the Mediterranean, observed that this plant grew best at depths in excess of 50 m, where light was thought to be severely limiting, but where other conditions (low temperatures and strong currents) might enhance growth, which is in fact controlled endogenously.

It appears that in certain cases single measurable parameters determine patterns of seasonal growth observed for several species of Laminaria. However, a combination of factors is more likely to define the limits of distribution and behaviour of most of the large laminarians. Jackson (1977) states: "The interactions of factors, nutrients, light, temperature and plant history, make the study of any one in ignorance of the others a touchy thing!" Soeder and Stengel (1974) note that it is important to appreciate at the outset that the effects of external factors show complex interactions and that an optimum level of one factor under certain conditions may be sub-optimal under other conditions. This was well illustrated by the fact that the optimum temperature for growth under experimental conditions depended on light intensity employed.

An aim of this study was to establish if L. pallida has a seasonal growth pattern or whether its rate of growth is determined by non-cyclic factors. Methods chosen and used to measure sporophyte growth for this study were principally those applied by other workers so that results might be compared.

Physical parameters such as water temperature and surface global radiation were measured, as were nutrient levels; the relationship between observed growth pattern and these factors as well as biotic factors is discussed.

2.2 Methods

2.2.1 Measurement of Physical and Chemical Parameters

2.2.1.1 Temperature

Water temperature at Station A, Robben Island and Station B, Oudekraal, was recorded continuously by thermoscript (Fricke and Thum, 1975). The thermoscripts were placed in stainless steel housings which were secured to concrete blocks 80 x 40 x 15 cm with bolts. Blocks were placed centrally in the experimental sites (Fig. 1.2).

Thermoscripts were serviced at monthly intervals. Records of temperature at Robben Island were obtained from April 1974 to May 1976 and at Oudekraal from September 1974 to the present. Discontinuities in the records were caused by occasional equipment failure. Water temperatures for Melkbosstrand were supplied by the Atomic Energy Board (Bain and Harris, 1974-1978); continuous temperatures were recorded with a temperature probe situated at eight metres depth on a wave recording tower, one kilometre offshore (Fig. 1.2).

2.2.1.2 Nutrients

Monthly water samples were taken at Station A, Robben Island and Station B, Oudekraal. Samples were obtained from the surface and the bottom at both stations in 250 ml plastic bottles which were placed in a deep freeze on the research vessel. Analyses for nitrates and phosphates were done by autoanalyzer according to the methods of Strickland and Parsons (1968) and Grasshoff (1969) by the Sea Fisheries Branch.

2.2.1.3 Light

In situ recordings of light were done at Station B, Oudekraal on two occasions in 1976 (Chapman and Dieckmann, in prep.).

Other light data (global radiation for D.F. Malan Airport) were obtained from the South African Weather Bureau. D.F. Malan Airport is situated some 25 km South East of Robben Island.

2.2.2 Measurement of Growth

2.2.2.1 At Robben Island

Station A (Fig. 1.2) was chosen for two projects which ran concurrently. One included only newly settled plants and the second included only mature plants.

2.2.2.1.1 Growth of Sporophytes from Settlement

The concrete block used to attach the thermoscript (Section 2.2.1.1) was placed on a sandy patch on 25.3.74. Subsequently, the block became colonized by fauna and flora including *Laminaria pallida* sporophytes. Growth of the sporophytes was monitored.

The first sporophytes of *L. pallida* were observed in June 1974, approximately three months after the block had been placed in the sea. At that time the frond lengths as well as stipe lengths of several plants were measured. Punching of holes in their fronds was started on 8.11.74 when the sporophytes were robust enough to withstand handling during punching. The methods of Parke (1948), Sundene (1964), and Mann (1972) were used. Sporophyte stipes were tagged with "Dymo Tape" labels, attached by thin, plastic-covered copper wire. This method did not appear to damage the sporophytes in any way. At that time the sporophytes were treated as follows :

Holes of 4 mm diameter were punched in the fronds using a leather punch. In juvenile fronds (undivided), a single hole was punched 10 cm from the stipe apex (Fig. 2.1a); older fronds (divided) had three holes punched as shown in Fig. 2.1b; a hole was punched in a central segment and another in each marginal segment (strap). This mutilation is considered no more harmful to the plant than damage resulting naturally through the actions of surf and grazers. Care was taken to punch holes above the meristematic zone (in practice, 10 cm above the apex of the stipe); the line in which the primary holes were

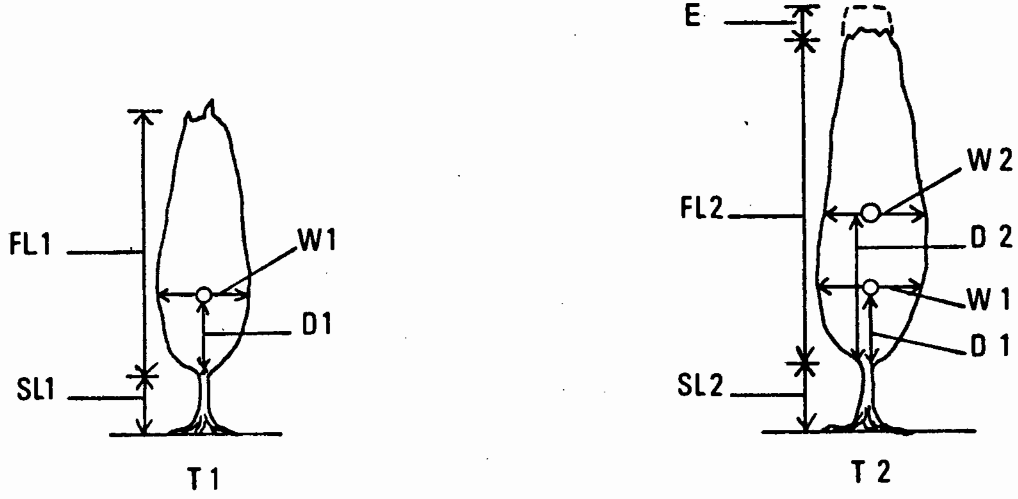

Fig. 2.1a : Method used to measure frond and stipe elongation rates of juvenile <u>L. pallida</u>. D1, distance from junction of stipe to hole punched at time T1; D2, distance at T2. E, erosion (FL1 + (D2 - D1) - FL2) where FL1 and FL2 are frond lengths at time T1 and T2 respectively. SL1 and SL2 are stipe lengths at T1 and T2; W1 and W2 are frond widths measured across the punched holes at T1 and T2. T2 becomes T1 at following visit.

T1 to T2 was approximately one month.

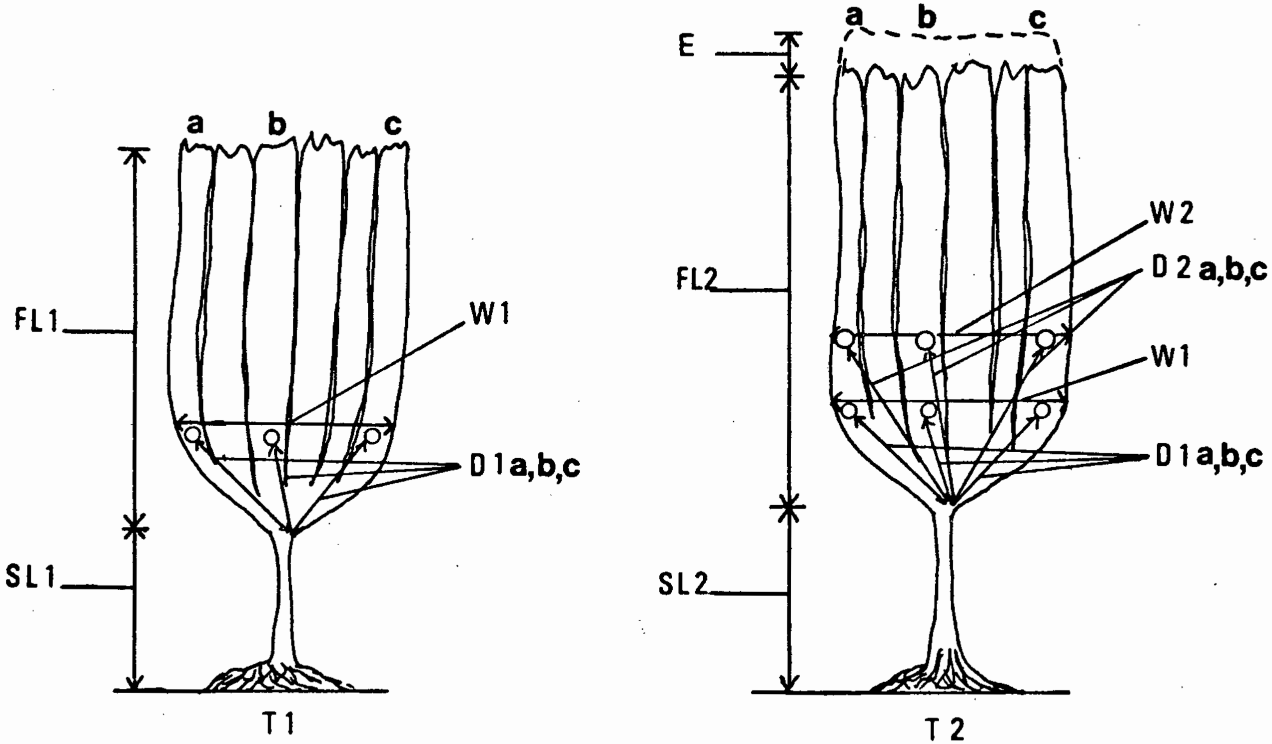

Fig. 2.1b : Method used to measure frond and stipe elongation rates of mature <u>L. pallida</u> sporophytes. Procedure is the same as that for juveniles except that distances D1 a, b, and c and D2 a, b, and c at T1 and T2 are measured in three digits (segments).

punched will be referred to as the base line. Thereafter, monitoring of performance by tagged plants occurred periodically at intervals of approximately one month. On the first and subsequent occasions, holes were punched in the base line, and the following measurements were taken: At T1 when visited for the first time, distance D1 or D1 a, b, and c from junction of stipe with frond, to punched hole or holes; W1, the frond width across punched hole or holes; total stipe length from substratum (SL1) and frond length FL1 or FL1 a, b, and c, depending on the form of plant (Figs. 2.1a and 2.1b). At T2 plants were re-punched and measurements as at T1 taken. In addition, the following was recorded: D2 and D2 a, b, and c, distance to previously punched hole or holes; SL2 and FL2 or FL2 a, b, and c, new stipe and frond lengths respectively; W2, the frond width across previously punched hole or holes. Erosion, E, was determined by adding the difference between D2 and D1 to FL1 and subtracting FL2 from the sum. At T3, procedure at T2 was repeated, except that the distances D1, D2 and distance to the third hole were recorded.

Increases in thickness of frond as well as in stipe diameter were not measured, but estimates of frond area were obtained from frond width and length measurements. In this way, growth of the sporophytes was followed until 30.10.75 (i.e., a period of almost one year), when most of the sporophytes had become overgrown by epiphytes and/or grazed by isopods (Paridotea reticulata)

2.2.2.1.2 Mature Plants

Treatment of these plants was different to that described in the preceding section, in that on successive visits to the station, new plants were tagged and punched, while as many as possible of those previously tagged and punched were harvested. In practice this ideal did not materialize because tagged plants were not always found, and many had in fact been lost. Anomalies in the results are therefore inevitable.

The plants were punched and measured as described in Fig. 2.1b at time T1. In all cases the base line was 20 cm above stipe apex. After removal, the position of the holes on the blades was recorded; frond and stipe lengths were also recorded.

Plants to receive treatment were selected at random (15 on each occasion). Tags consisting of handles of plastic spoons inscribed with numbers were loosely attached to the plants with plastic-coated 22 gauge galvanized wire tied around the base of the stipes.

2.2.2.2 At Oudekraal

Plants intended for study at both Stations B and C (Fig. 1.2) were selected at random and included a range of sizes. Approximately 20 plants at each station received treatment similar to that described for mature plants (Section 2.2.2.1.2) above, with important differences which will become apparent; in these cases the only hole punched was in the central segment (punching three holes was too time-consuming and did not alter results significantly). The base line was 20 cm above stipe apex.

Monitoring these stations continued for 34 months, but only two individual sporophytes were identifiable for as long as two years. Lost plants were made good by selecting new plants at random. An area of 2 x 1 m, immediately adjacent to Station B, was scraped clean of all macroscopic life, except encrusting algae, on 7.3.75. Growth of the stipes of all L. pallida sporophytes developing there was followed.

2.2.3 Data Processing

2.2.3.1 Interpretation of Growth

The terms 'growth' and 'growth rates' in this context refer to expansion or elongation rates of the fronds or stipes. Because of the varying time intervals between measurements of frond elongation at all three stations, results were standardized to enable comparisons. From Fig. 2.1a, D2-D1 (frond elongation) divided by the number of days of interval (T2-T1) gives frond elongation in cm day^{-1}. When more than one hole was punched in a frond (Fig. 2.1b), the mean distance to the holes was taken. Because growth was measured between holes along the whole length of the frond and not between junction of stipe and first hole only, the method of Sundene (1964) could not be applied.

2.2.3.2 Growth of the Stipe

Increments in length of the stipes was difficult to measure, especially in larger plants. Reliable results were obtained for juvenile plants and for plants which were monitored for a year or more. In most cases, except for plants growing on the concrete block at Robben Island or the cleared station at Oudekraal, the age of plants was not known. Ageing of stipes according to the methods employed by Parke (1948) and Kain (1963, 1967, 1971b), could not be applied to L. pallida as transverse sections through the stipes showed no seasonal growth rings. Size frequency distributions of stipes did not reveal polymodal curves which could be used to age plants. Velimirov and

Griffiths (1978) have discussed possible causes of irregular size frequency distributions of L. pallida at Oudekraal.

A method is used to estimate the age of stipes from a theoretical curve, fitted to data on plants of known age as well as plants for which stipe length increments were measured for a year or more. The method is similar to those used by fisheries biologists to estimate the age of fishes (Jones, 1976) and other marine organisms (Velimirov, 1975).

Growth of organisms may be exponential, or take the form of an S-shaped or sigmoid curve which in turn may be symmetrical or asymmetrical. In this study three growth curves of types described above were tested on L. pallida stipe data. Goodness of fit was obtained by least squares regression analysis using the BMDP 3R computer programme for non-linear regression (Dixon, 1975). Equations used are described below.

1. The von Bertalanffy growth equation :

$$L_t = L_\infty \left(1 - e^{-K(t - t_o)}\right) \quad \text{.........................} \quad (1)$$

where L_t is the length at time t, L_∞ is the asymptotic length when $t = \infty$ and K is the growth rate. t_o is the time when growth started (Jones, 1976).

2. The logistic equation after Bartlett (1960), and described in Velmirov (1975) :

$$N_t = \frac{N \max}{1 + e^{-a(t - t_o)}} \quad \text{..........................} \quad (2)$$

where N_t is length or size at time t, N max is the asymptotic length, t_o is equal to $\frac{N \max}{2}$, or age at half the asymptotic length and a is the growth rate.

3. The Gompertz equation (an asymmetrical sigmoid curve) from Riffenburgh (1959) and Newman (1969):

$$y = ab^{c^t} \quad \text{.....................................} \quad (3)$$

This equation also rises to an asymptotic length a when $t = \infty$. b and c are obtained by linear estimation. Estimates of c lie at $0 < c < 1$ and of b lie at $0 < b < 1$.

The asymptotic lengths for the stipes may be determined by the Ford-Walford method (Jones, 1976). For this study, however, the asymptotic length was taken to be the maximum length observed on stipes growing at Stations B and C respectively.

2.3 Results

2.3.1 Physical and Chemical Parameters

2.3.1.1 Temperature

Records of temperature for Robben Island, Oudekraal and Melkbos for 1975, 1976 and 1977 are shown in Fig. 2.2. Temperature records for the three stations are superimposed to show that, although the stations are far apart (Fig. 1.2), and two are of different depths, there is often a remarkable correlation between major trends in the records. Particularly good correlation may be seen between temperature records of Oudekraal and Melkbos in the summer of 1976/77. This indicates that temperature fluctuations are not always isolated.

Temperatures at Robben Island were usually higher than at the other stations. Probable causes may have been the shallowness of Station A as well as the protection from strong westerly swells.

From Fig. 2.2, it is clear that there is definite seasonal temperature variation. In all three years, the period September to

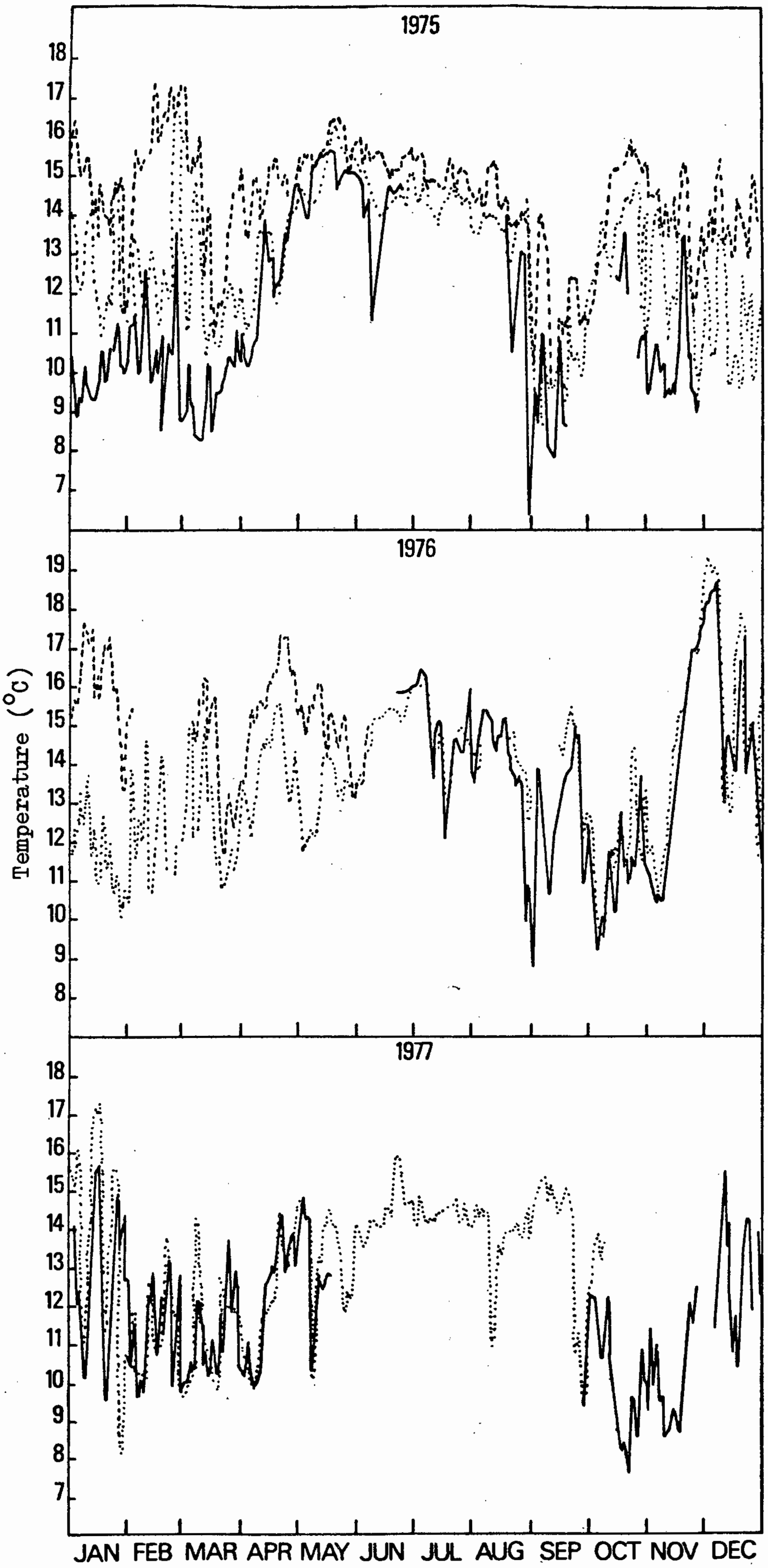

Fig. 2.2 : Continuous records of mean daily temperatures at Robben Island ---- (3 m depth), Oudekraal —— (8 m depth) and Melkbos •••• (8 m depth).

April is characterized by large fluctuations in temperature. Annual maxima and minima are both attained during this period. The annual minimum temperature appears to occur during the spring months, from late August to early October. The lowest temperature recorded in three years was 6,1°C in September 1975, while in subsequent years the temperature dropped to 7,7°C and 7,6°C respectively during September and October. Highest temperatures at Robben Island, Melkbos and Oudekraal were usually reached during the summer months, November to February. At Oudekraal, however, the highest annual temperatures for 1975 were measured during the beginning of winter. Towards the end of November and the beginning of December, 1976, apparently anomalous temperatures of up to 18,5°C were recorded at Oudekraal and Melkbos (Fig. 2.2).

The period May to August inclusive is usually characterized by stable temperatures, rarely dropping below 13°C or rising above 16°C.

2.3.1.2 Nutrients

The term 'nutrients' will, in this report, refer only to nitrates and phosphates. Nutrient values for Station B, bottom, at Oudekraal and Station A, bottom, at Robben Island are presented in Tables 2.1a and 2.1b respectively. Minimum water temperatures at time of sampling are also shown.

Correlation between temperature and nutrient concentrations was not tested, but it appears that high nitrate concentrations are associated with low water temperatures.

From data in Table 2.1a, it appears that the highest and lowest concentrations of nitrates occur during the upwelling season. During the winter months nitrate levels appear to be stable, but

TABLE 2.1a : Nitrate and phosphate concentrations sampled at different times of the year at Station B, Oudekraal. Minimum temperatures at time of sampling are shown. Temperature in brackets interpolated from Melkbos.

Date	7.2.75	6.3.75	7.4.75	1.5.75	5.6.75	2.9.75	22.9.75	16.10.75
Nitrates μg at. Nl^{-1}	18,55	18,47	/	4,47	4,28	18,11	2,48	2,37
Phosphates μg at. Pl^{-1}	0,24	1,02	1,76	1,30	0,81	1,45	0,50	0,82
Minimum Temperature °C	9,9	9,9	10,1	14,5	14,0	6,2	(11,0)	12,40

TABLE 2.1b : Nitrate and phosphate concentrations sampled at different times of the year at Station A, Robben Island. Minimum temperatures at time of sampling are shown.

Date	6.2.75	5.3.75	2.4.75	21.4.75	2.6.75	1.7.75	5.8.75	5.9.75	23.9.75	14.10.75
Nitrates μg at. Nl^{-1}	8,31	/	/	3,6	9,39	15,70	9,66	3,95	0,93	1,50
Phosphates μg at. Pl^{-1}	0,57	0,31	1,29	1,53	2,49	1,37	1,08	1,08	0,86	0,86
Minimum Temperature °C	15,0	14,4	14,7	14,7	15,8	15,3	14,5	12,5	11,7	14,6

relatively low. Phosphate concentrations appear to vary directly with nitrate concentrations.

At Robben Island (Table 2.1b), a different pattern to that of Oudekraal was observed. No obvious correlation between temperature and nutrients exists. The highest value of nitrate was recorded in winter. Lowest nutrient levels were also recorded during the spring upwelling season while more stable and on average higher values were recorded during winter.

2.3.1.3 Light

Mean daily global radiation in $cal.cm^{-2}\ day^{-1}$ recorded for every month over a period of three years at D.F. Malan Airport are shown in Fig. 2.3. Light energy reaching the earth's surface at D.F. Malan Airport is highest in mid-summer and lowest in mid-winter. Values of global radiation at D.F. Malan Airport for 11 years showed a mean of 218,2 $cal.cm^{-2}\ day^{-1}$ during June and 723,3 $cal.cm^{-2}\ day^{-1}$ in January. The summer irradiation is thus 3,32 times that in the winter.

Percentage of surface light reaching the bottom at Robben Island and Oudekraal station was not known. However, work done by Chapman and Dieckmann (in prep.) may give some indication of the percentage light reaching the bottom at Station B, Oudekraal. Using the technique of Drew (1972), the percentage of surface light (400-700 nm) penetrating to 8 m was recorded for the whole month of August and for the period October 7-18, 1976. From surface irradiance data for D.F. Malan Airport, the hourly means for the years 1971-1974 were averaged and multiplied by a factor of 0,47 to give total irradiance in the range 400-700 nm (Westlake, 1965). For the months July through

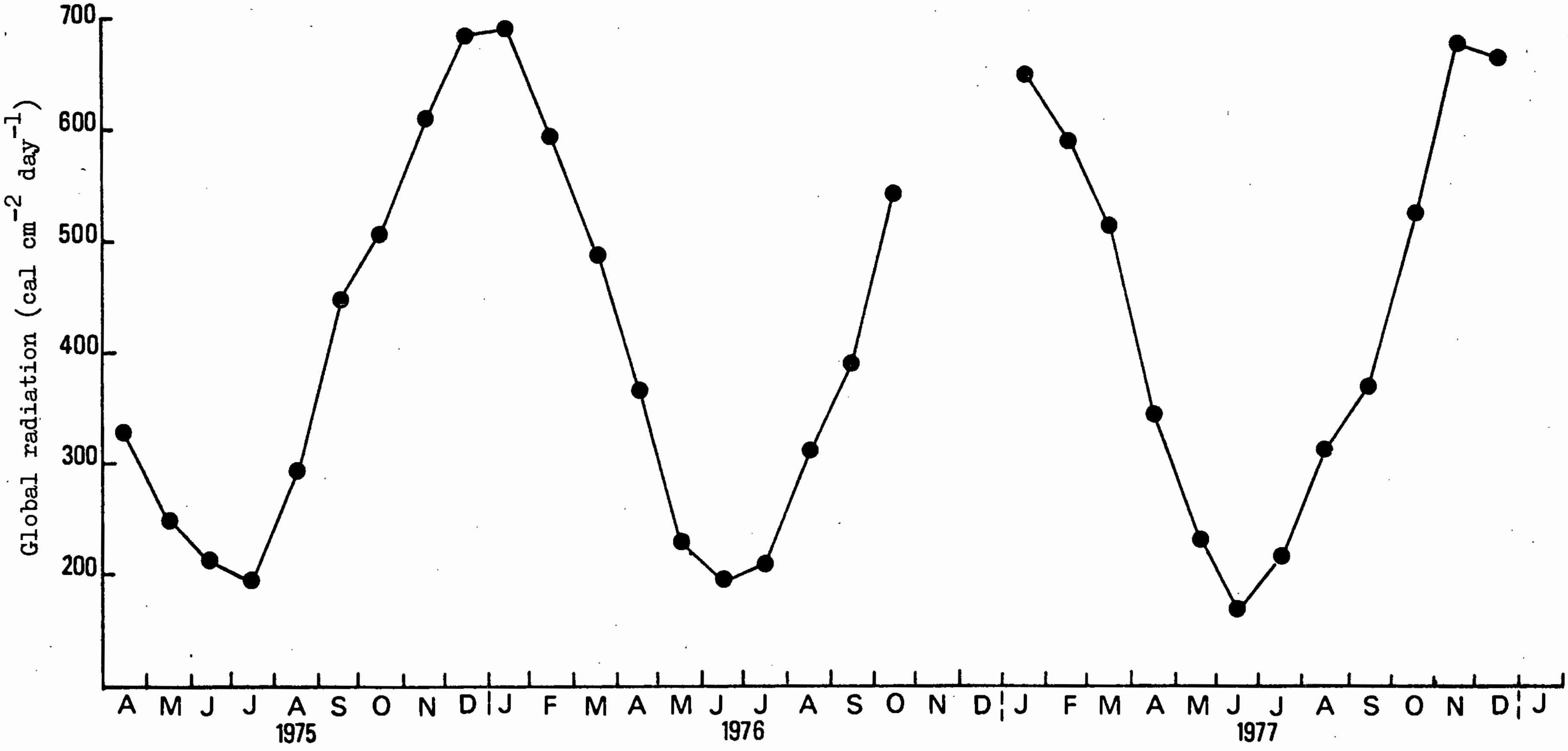

Fig. 2.3 : Mean daily global radiation per month for D.F. Malan Airport. (Data obtained from the Department of Transport.)

September the corrected hourly means were multiplied by a factor of 0,132, the proportion of surface light penetrating to 8 m during the month of August. For the period October through December, the hourly corrected means were multiplied by a factor of 0,178, the proportion of surface light penetrating to 8 m during the second week of October. The irradiance figures at 8 m recorded here are considered only as relative indicators of seasonal trends, showing that during spring and summer the proportion of light reaching the bottom is slightly higher than that reaching the bottom during winter.

2.3.2 Growth

2.3.2.1 At Robben Island

2.3.2.1.1 New Plants

Measurements for sporophytes growing on the concrete block during the period 5.6.74 - 24.7.74 are shown in Table 2.2.

TABLE 2.2 : Observations made on the growth of young L. pallida sporophytes from 5.6.74 - 24.7.74 on a concrete block at Station A, Robben Island.

Date Checked	No. of Sporophytes	Max. Frond Length (mm)	Max. Stipe Length (mm)	Remarks
5.6.74	None			
25.6.74	3	40	1	The largest was not the largest observed on 25.6.74.
24.7.74	16	130	10	

Sporophyte development and growth only became noticeable sometime in June, with the highest number appearing in July.

Results obtained on the growth of sporophyte fronds from punched plants between 8.11.74 and 5.9.75 are shown in Fig. 2.4. Also shown in the figure are the temperature at the station and global

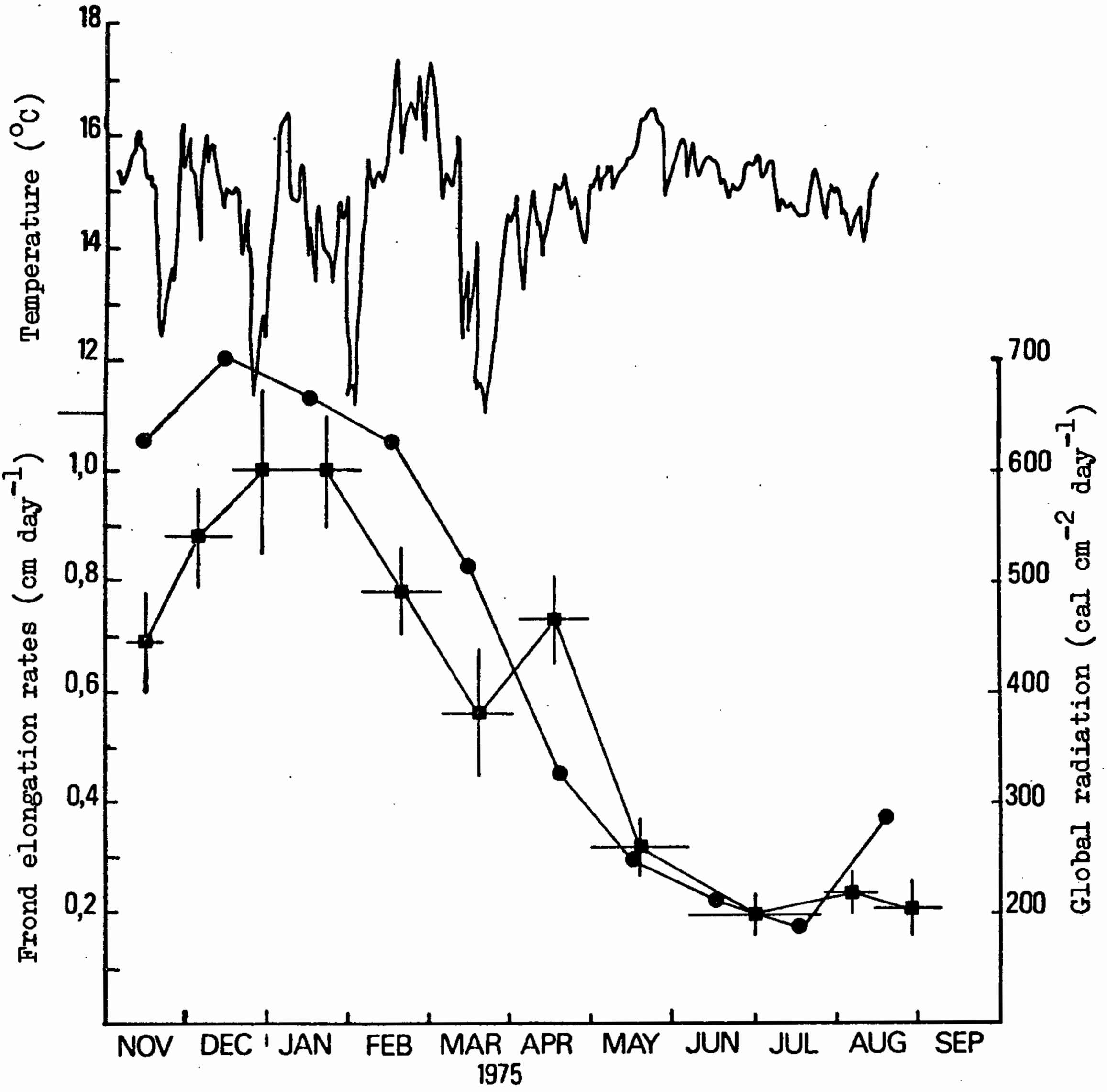

Fig. 2.4 : Composite graph showing frond elongation rates of young L. pallida sporophytes at Robben Island in relation to temperature and irradiance (●—●) at D.F. Malan Airport. Vertical bars are 95% confidence limits. Horizontal bars denote intervals between measurements.

radiation for D.F. Malan Airport. Rates of frond elongation increased through November to December. In January, the rate of 1,0 cm day^{-1}, measured during December, was maintained. From February to March growth rate began to slow down, but rose to 0,73 cm day^{-1} in April 1975, after which it again dropped to reach a minimum of 0,2 cm day^{-1} during June-July, 1975. At the beginning of August an increase in the growth rate was observed. The rate, however, again dropped in September.

The observed pattern of growth rate appears to be seasonal, with high rates observed during spring and summer and lowest rates during the winter months.

Measurements of frond erosion were very inaccurate because of irregular erosion at the tips and the difficulty in establishing the difference between grazing and erosion. This also resulted in incorrect estimates of increase in frond area so that the results are not presented.

Maximum stipe length recorded for the sporophytes was 18 cm at the end of one year's growth, while mean length attained after one year was 14,5 cm (Fig. 2.5). Variation in the growth rates was probably caused by slight differences in age, rather than by environmental factors. Underwater measurement errors may also have contributed to the variation. Stipes appeared to grow rapidly in length from November to May after which elongation rate slowed down until it almost ceased in June. This pattern of growth may, however, differ from the normal, owing to unusual temperature and nutrient conditions at Robben Island, which have been mentioned previously.

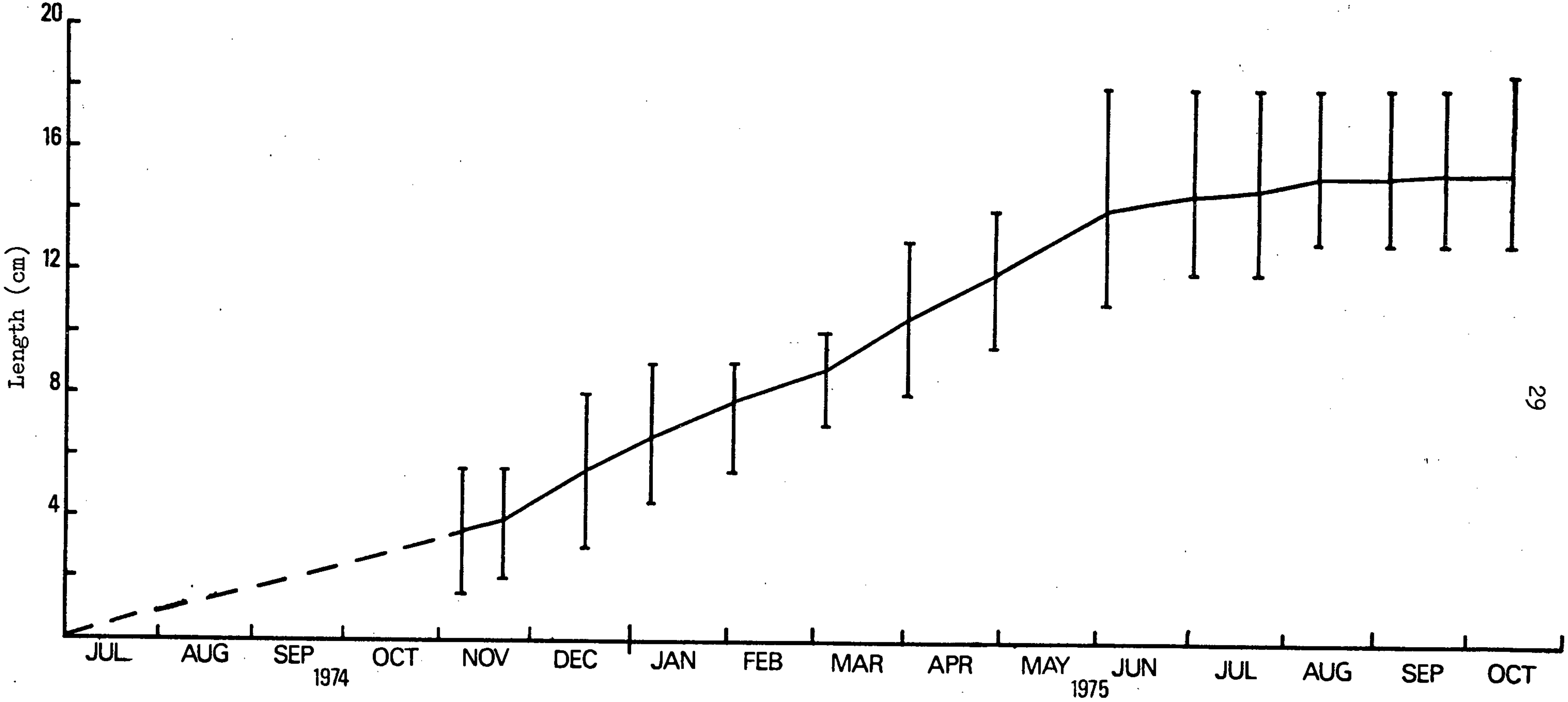

Fig. 2.5 : Mean elongation rates of ten juvenile L. pallida stipes at Robben Island. Vertical bars indicate range of lengths. Broken line is extrapolation of growth to month when sporophytes were first observed.

2.3.2.1.2 Mature Plants

Because of the difficulty in relocating and recovering labelled sporophytes, as many as possible were removed for measurement once they had been found. As a result, plants which had been punched and measured at different times were collected simultaneously so that periods between initial and final measurements varied.

Elongation rates of the fronds were calculated in cm day^{-1} for the period measured, but results were then grouped according to the months during which most of the growth had occurred (Fig. 2.6).

Elongation rates of the mature fronds appear to be different to those of juvenile fronds in their first year of growth. Maximum rates were reached either before or during September-October, 1974. A steady decrease in growth rate occurred after October, following a trend similar to that observed for juveniles, but without the secondary increase in April.

2.3.2.2 At Oudekraal

Elongation rates of fronds at Stations B and C are presented in Figs. 2.7 and 2.8 respectively.

It was found, particularly in the large plants, that elongation of fronds occurred above the base line as well as below. Growth of the fronds above the base line was determined for the plants at Oudekraal, but was seldom found to exceed 10% of the total growth. Elongation rate of fronds at both stations was seasonal, following a pattern similar to that observed for plants at Robben Island.

The period of rapid elongation of the fronds at Station B began during June-July every year. Maximum elongation rates were

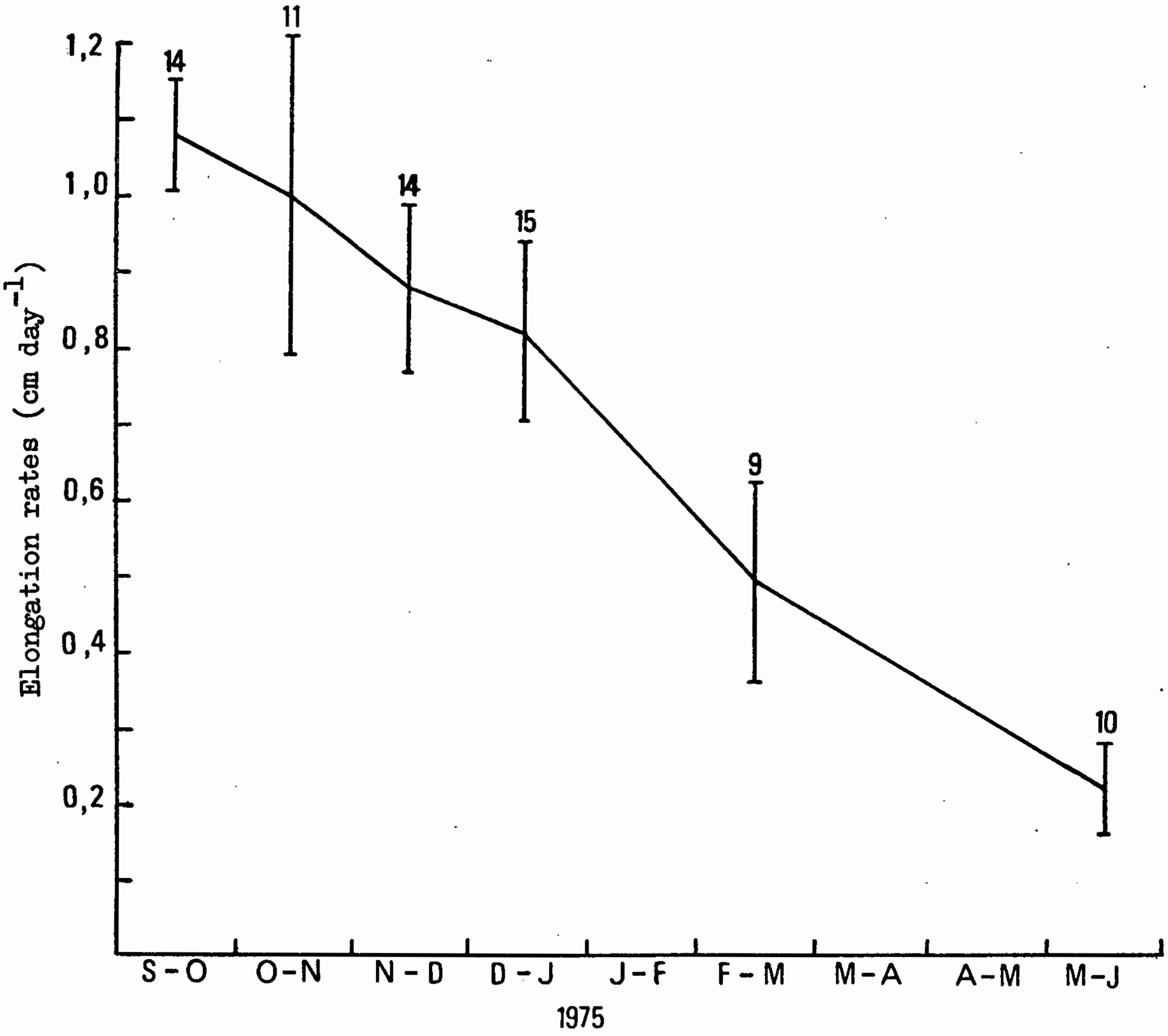

Fig. 2.6 : Frond elongation rates of mature L. pallida sporophytes at Robben Island. Vertical bars are 95% confidence limits. Numbers indicate sample size.

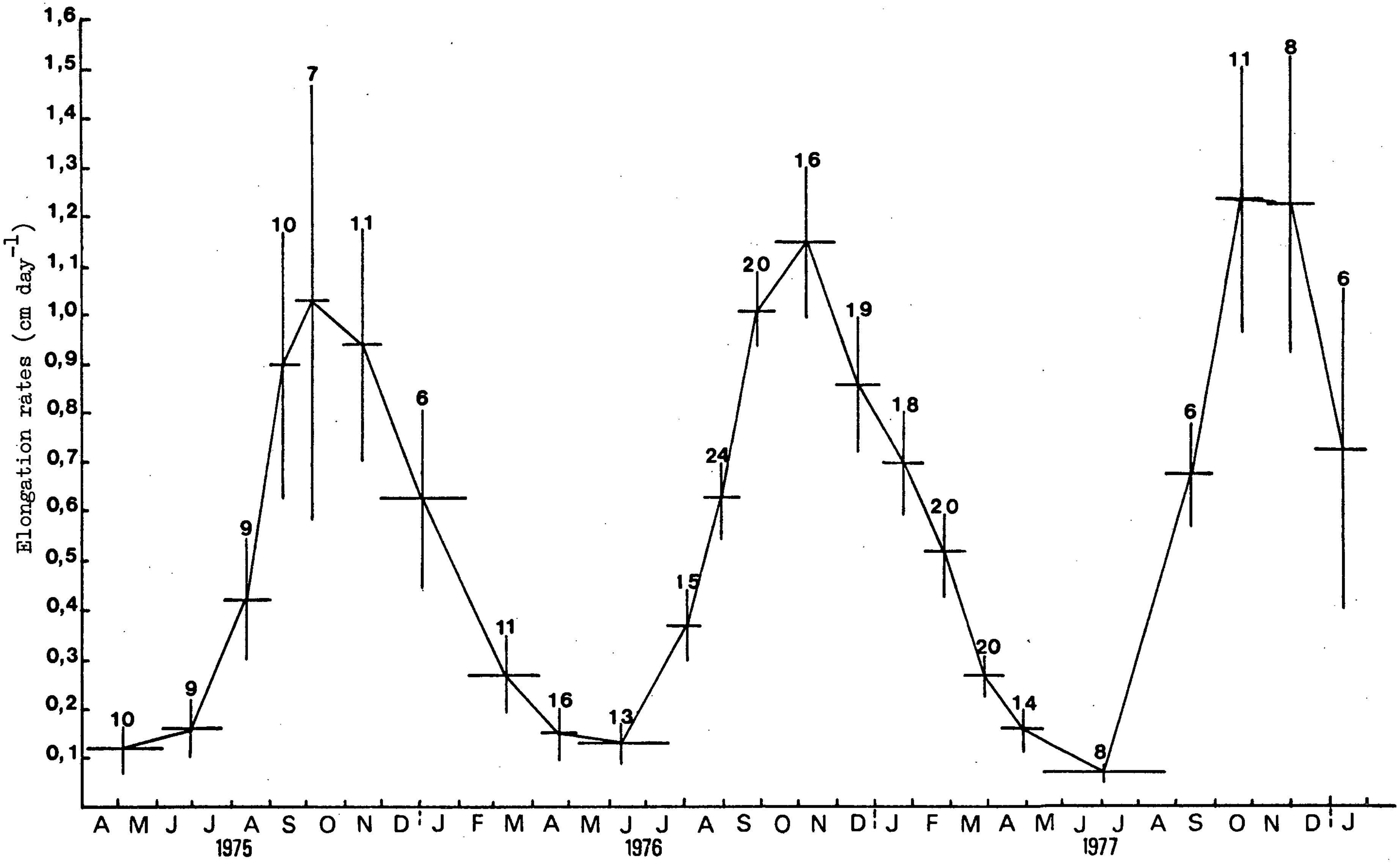

Fig. 2.7 : Frond elongation rates of L. pallida at 8 m depth (Station B, Oudekraal). Horizontal bars denote intervals between measurements. Vertical bars are 95% confidence limits. Numbers indicate sample size.

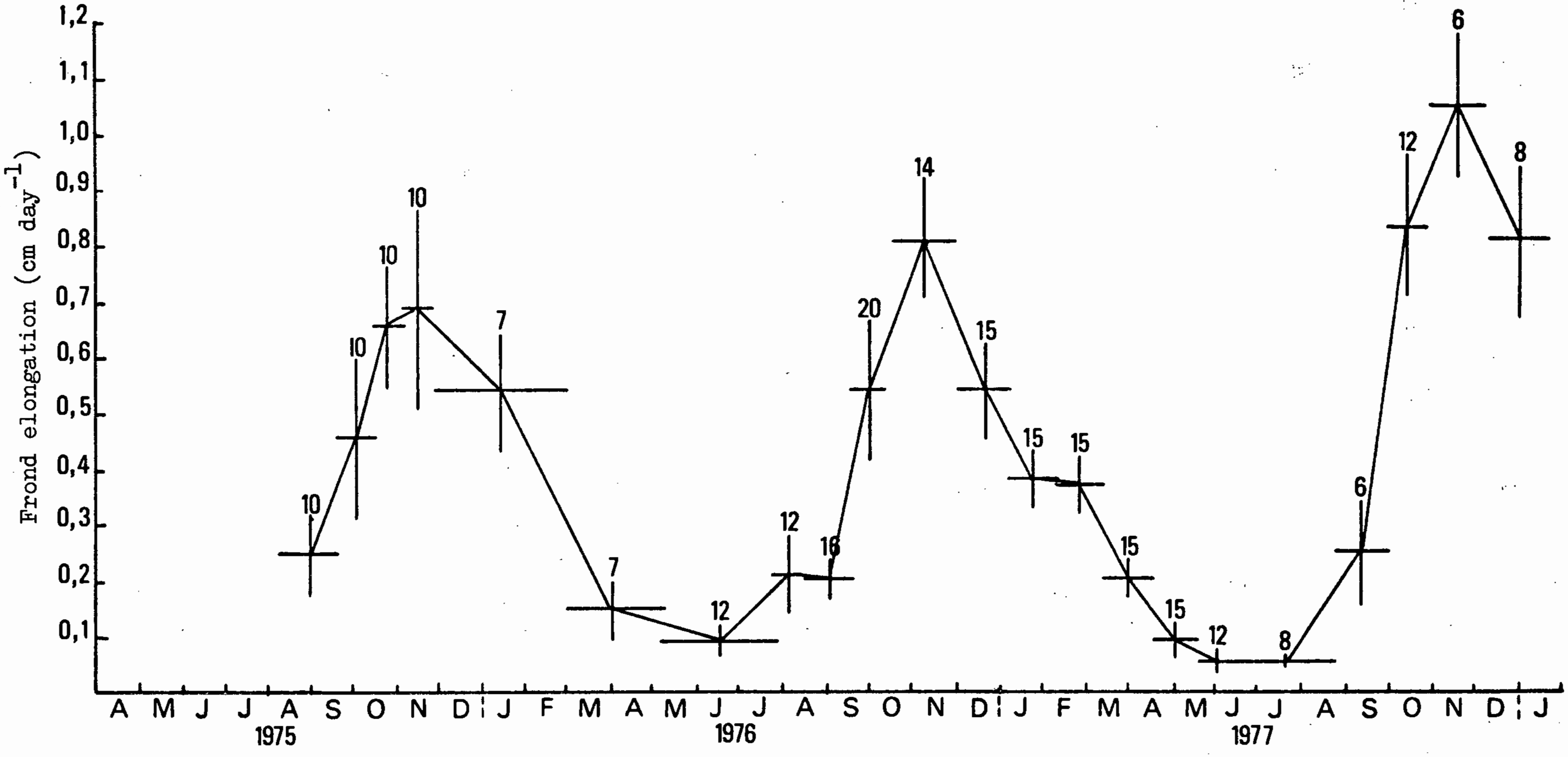

Fig. 2.8 : Frond elongation rates of L. pallida at 14 m depth (Station C, Oudekraal). Horizontal bars denote intervals between measurements. Vertical bars are 95% confidence limits. Numbers indicate sample size.

attained during the early summer months October to November when mean daily rates ranged from 1,0 to 1,3 cm day^{-1} for three years. Thus growth rate of the fronds increased almost 10 times during a period of approximately four months. The annual cycle repeated itself with differences in absolute elongation rates only.

Plants growing at Station C exhibited frond elongation rates which were generally lower, particularly in spring and summer (mean rates between 0,68 and 1,0 cm day^{-1}), and which had a slightly different pattern. Rapid elongation appeared to begin one month later while autumn and winter growth coincided with that of Station B plants. Maximum elongation rates were reached in November in all three years in which plants were observed. Though a difference between maximum elongation rates was observed at Stations B and C, the difference between the minimum rates was very small.

Growth of the frond at the deep station does not follow a curve as smooth as at the shallower station; during August-September 1976 the period of rapid elongation was interrupted by a slight decrease in the elongation rate, while at the beginning of 1977 rates remained constant at 0,38 cm day during January and February.

Results of stipe elongation in newly developed sporophytes were obtained from the cleared station adjacent to Station B, Oudekraal. The approximate time of development and growth of these sporophytes was known; no sporophytes were seen until three months after the station had been cleared. On 22.9.75 several sporophytes were visible, none larger than 1 cm total length. By 29.11.75 many sporophytes between 10-25 cm total length were recorded and by 30.3.76 the stipes of these sporophytes measured an average of 20 cm in length. One year after the sporophytes were first observed, three stipes measured 38, 46, and 50 cm. By 17.5.77 the one of 38 cm had grown to 99 cm. These data, together with the data on plants which were observed for a year or more at Station B, were used to construct the growth curve in Fig. 2.9. Increments in stipe length were plotted for months during which they were recorded, though the actual year of growth was not always known. The theoretical curve in Fig. 2.9 does not take into account the seasonal variation in growth of the stipe.

A best fitting curve, determined by least squares regression, was that of Gompertz and has the form: $y = ab^{c^t}$

where $a = 235.0$

$b = 0.008$

$c = 0.348$

The coefficient of determination r^2 was 0.956. The curve was plotted to fit the growth of stipes which had started growing between July and November approximately. Each year in the graph represents the period from August to July.

Stipes of L. pallida at Station B appear to attain a maximum length of 240 cm (personal observation). The asymptote was found to be 235 cm from the theoretical curve. Most stipes of upper canopy plants at the station range in length from 200-220 cm. From the curve the estimated age of these plants is between 3,5 to 4,5 years. Most elongation occurs between the ages of two and three years.

A curve for the growth of stipes at Station C was also constructed empirically. No plants of known age were used, however, and the age of the smallest plants was estimated. The theoretical curve is shown in Fig. 2.10. The curve is also a Gompertz curve of

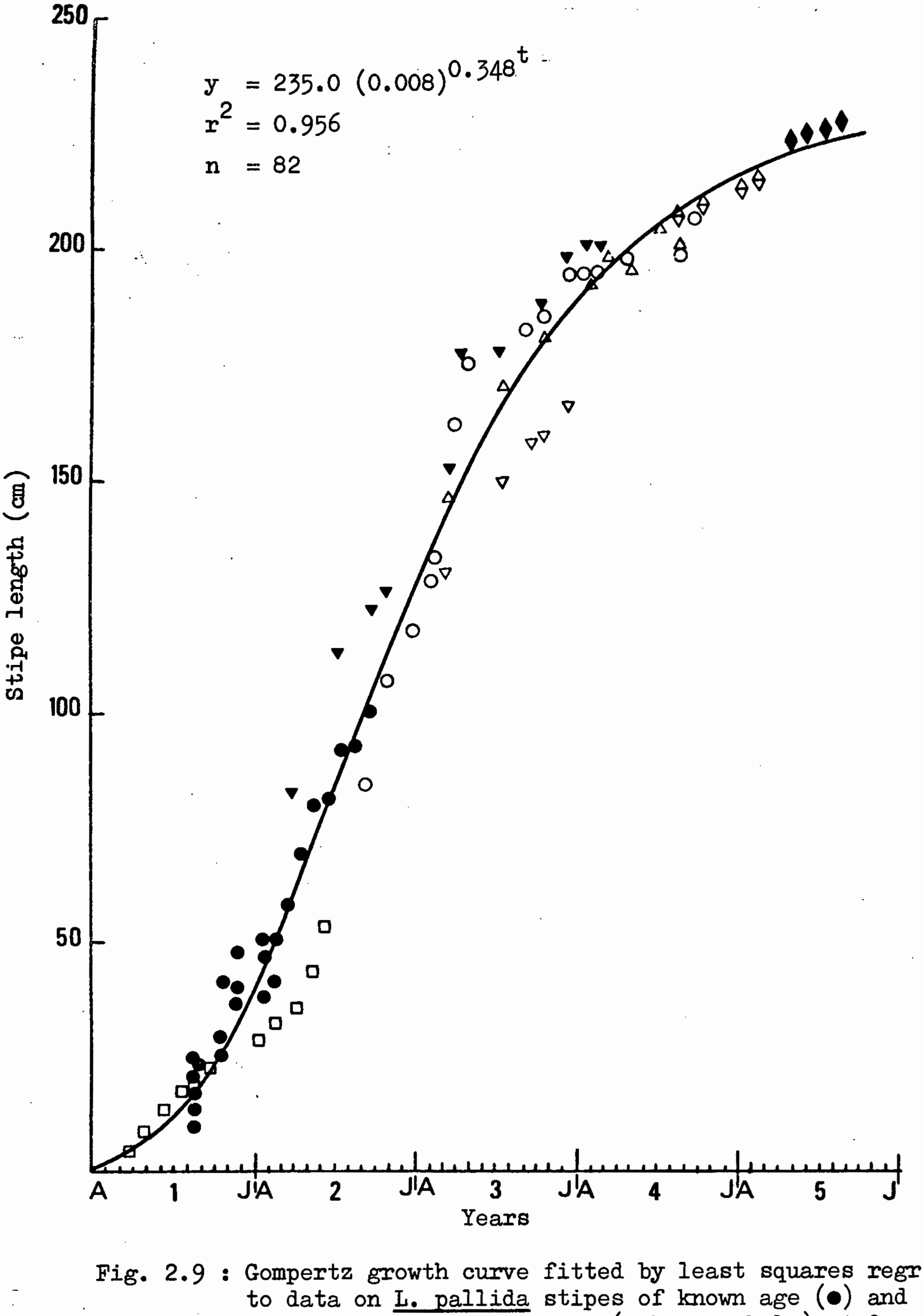

Fig. 2.9 : Gompertz growth curve fitted by least squares regression to data on L. pallida stipes of known age (●) and to data on stipes of estimated age (other symbols) at 8 m depth (Station B, Oudekraal). A = August J = July

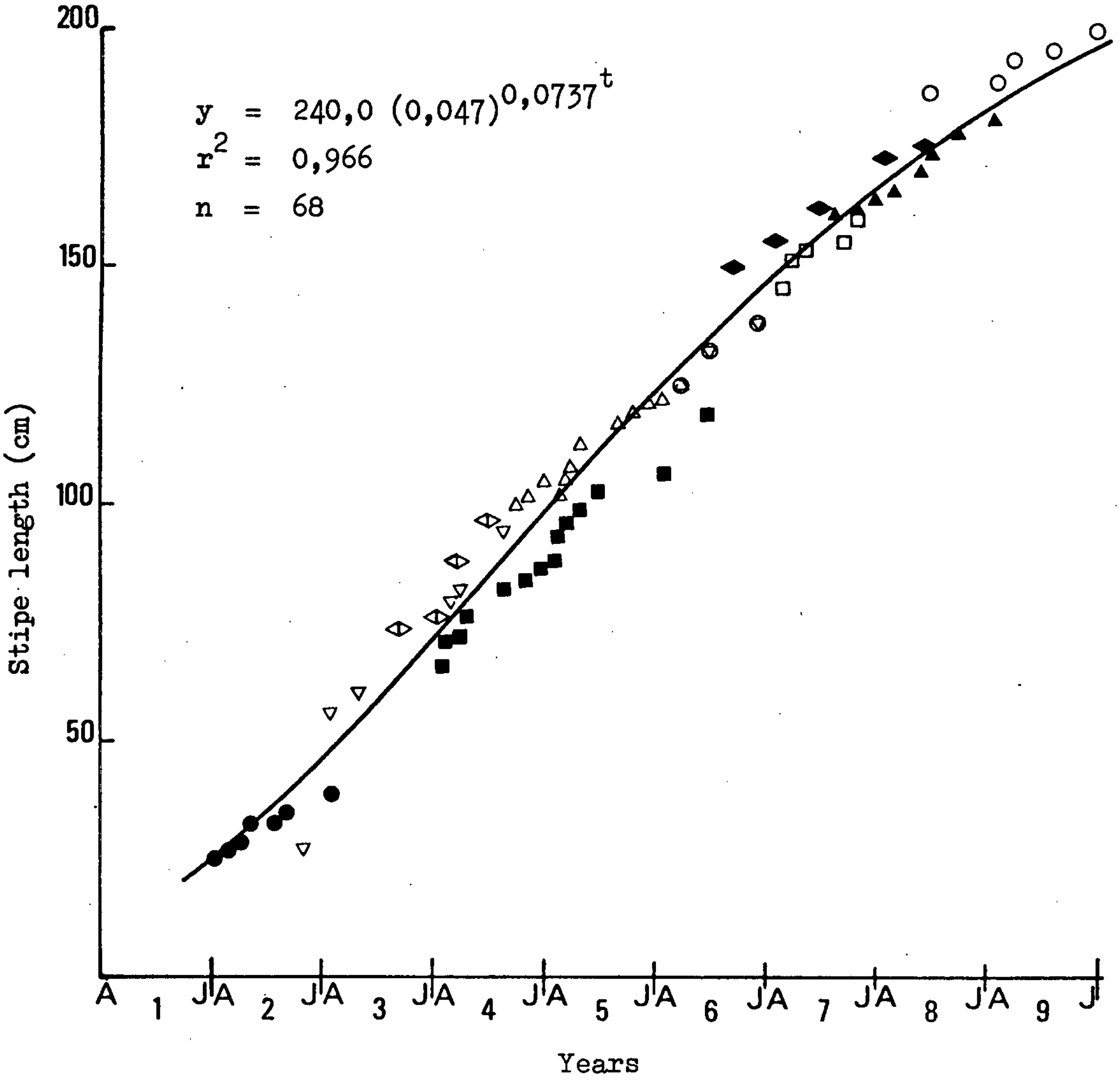

Fig. 2.10 : Gompertz growth curve fitted by least squares regression to data on L. pallida stipes of estimated age (different symbols) at 14 m depth (Station C, Oudekraal).

A = August; J = July

the form: $y = ab^{c^t}$

where $a = 240.0$
$b = 0.047$
$c = 0.0737$

The coefficient of determination r^2 was 0,966.

Lengths of stipes at Station C were seldom more than 200 cm. From the curve in Fig. 2.10 this length is attained after nine years. Canopy plants at Station C range in stipe length from 160-180 cm and are thus approximately 7-8 years old. Because no plants of known age were used to fit the curve, it is considered to be less reliable than that for Station B plants, but it is unlikely that plants are any older than estimated from the graph. The curve cannot be extrapolated to zero because no data on very small plants were available.

2.4 Discussion and Conclusions

2.4.1 Growth of L. pallida in Relation to Abiotic Factors

The temperature regime observed for three years at Robben Island and Oudekraal is similar to that observed by Andrews (1974) and Andrews *et al*. (in press) farther offshore. Thus during the summer months, temperatures below 10°C observed at all stations are probably indicative of recently upwelled water. Higher temperatures during the upwelling season are a result of mixing of upwelled water and oceanic water, but may also be caused by local heating of surface waters during stable conditions (Andrews, 1974). The station at Robben Island appears to be particularly prone to heating because of its shallow depth and sheltered position. An apparent anomalous situation which developed at Melkbos and Oudekraal during November-December 1976 resulted when stable conditions prevailed for an extended period due to a lack of south-easterly winds (Bain and Harris, 1976).

During the winter months, temperatures are indicative of mixed water (10°-18°C) but may be interrupted by weak upwelling. The first upwelling of the season is usually the most pronounced. Good correlation exists between temperature and nutrient concentrations (Andrews, 1974; Andrews et al., in press). They found that newly upwelled water with temperatures between 8-10°C was high in nutrients (20 ug at. Nl^{-1} and 1,5 ug at. Pl^{-1}), while nutrient depletion was caused between periods of upwelling when water temperatures rose and conditions became stable; depletion was probably caused by phytoplankton blooms. Jackson (1977) reports that the common pattern in temperate oceanic waters is for surface waters to be depleted of fixed nitrogen, phosphorus and silicon by phytoplankton growth in the summer, and to be enriched during the winter by mixing with high nutrient subsurface waters. A similar trend in nutrient regime is described by Norton and Burrows (1969) for Port Erin.

As the nutrient regime off the Cape and other coasts appears to be so closely related to temperature and upwelling conditions, the nutrient sampling schedule carried out for this study was inadequate. Short-term fluctuations in nutrient concentrations corresponding to similar fluctuations in temperature require almost continuous sampling. P. Brown (pers. comm.) recorded nutrient and temperature fluctuations over a period of nine days during November 1977, two kilometres off Oudekraal (Fig. 2.11). Nitrate concentration at 8 m depth dropped from over 20 ug at. Nl^{-1} to less than 1 ug at. Nl^{-1} in five days.

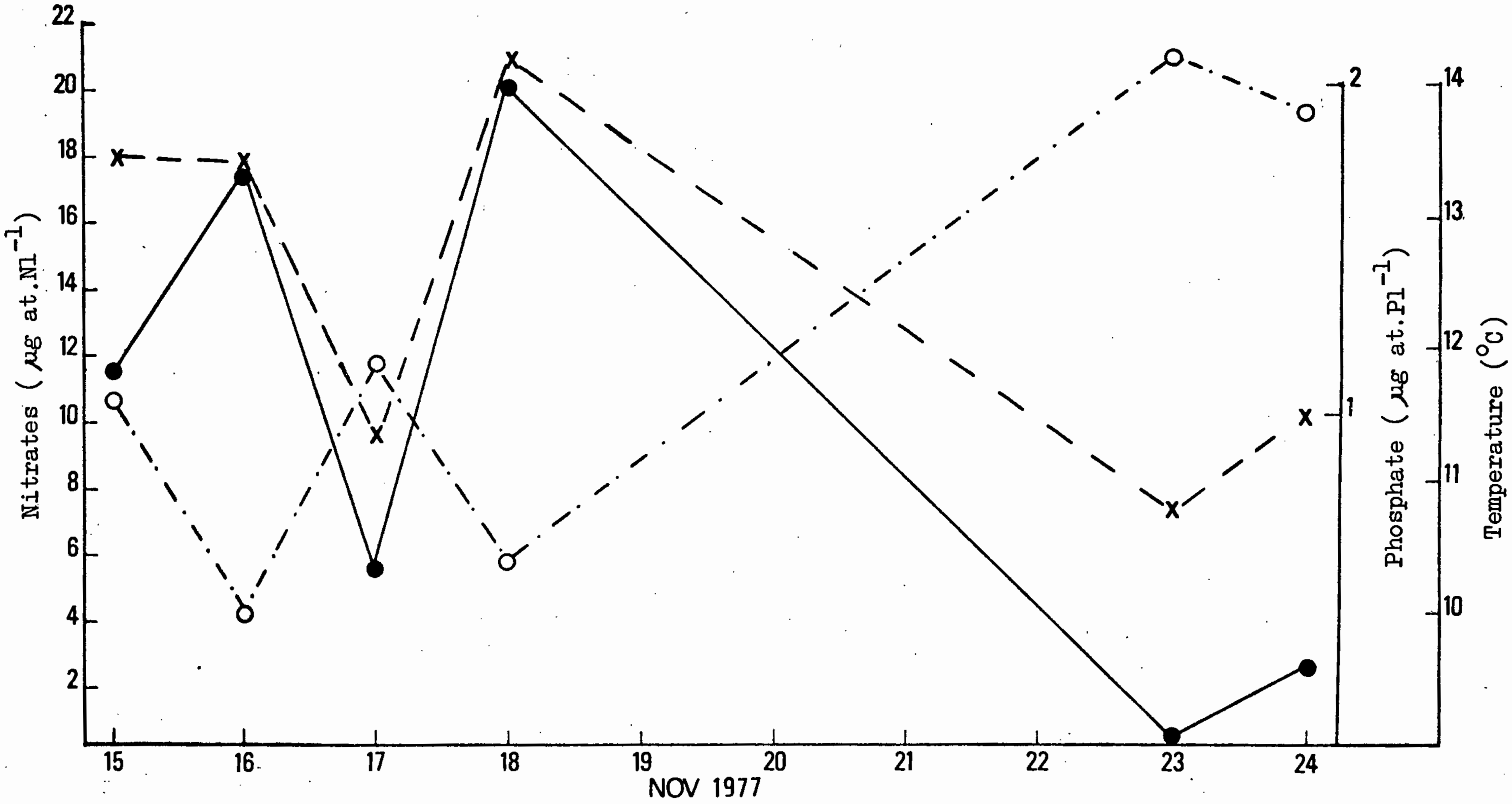

Fig. 2.11 : Nitrate (——) and phosphate (----) concentrations 2 km off Oudekraal at 8 m depth. Temperature at time of sampling is also shown (-·-·). (Data from P. Brown.)

Light intensity increases significantly during spring and reaches a maximum in summer. During this period the sun's angle is less oblique and light can therefore penetrate much deeper into the water. Added to this is the increased day length which also contributes to the plants receiving much more light. During winter the converse is true. Norton and Burrows (1969), at Port Erin, reported on similar findings.

What factors determine or influence the patterns of growth in Laminaria pallida?

2.4.1.1 Growth of the Fronds

Lüning (1968) found that light played an important role in the growth of laminarians, but that temperature and nutrients also influence growth. It appears that L. pallida is no exception and that it has a seasonal growth cycle which, according to Mann and Chapman (1975), is familiar enough with maximum growth occurring during spring and summer and minimum growth during the winter months.

Fig. 2.12 is a composite graph depicting linear expansion rates of L. pallida at Oudekraal in relation to temperature and light. At Oudekraal the period of rapid elongation of the fronds begins during winter, when temperatures range between 13° and 15°C and do not fluctuate much. Rapid acceleration of frond elongation occurs during August and September, coinciding with the first upwelling and a drop in temperature to below 10°C. This drop in temperature marks the beginning of the upwelling period with large temperature fluctuations. It is during this period that elongation rates reach their maximum and begin to decrease. No apparent abnormal temperature fluctuations,

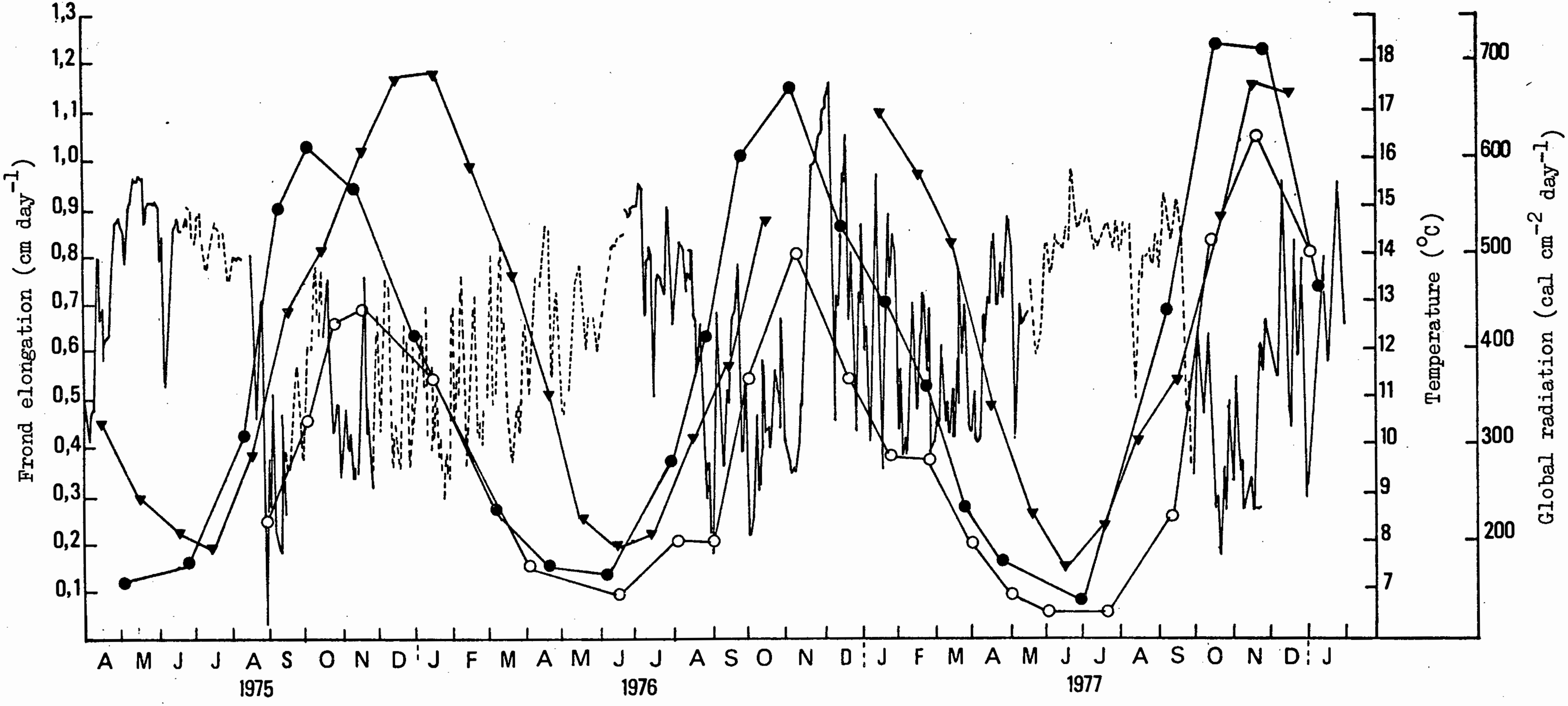

Fig. 2.12 : Composite graph showing L. pallida frond elongation rates at 8 m depth (●) (Station B) and 14 m depth (○) (Station C). Temperature at Station B, with interpolated data from Melkbos (----) and mean daily global radiation per month from D.F. Malan Airport(▼).

except during November and December 1976, occurred to initiate the decline in elongation rates (Fig. 2.12).

At Robben Island (Fig. 2.4), the role of temperature in determining changes in growth rate is perhaps more readily explained, but may be misleading. The period of rapid expansion of the frond occurred during the upwelling season and was maintained until the beginning of February when a decline in elongation rate coincided with a rise in temperature from 15°C to 17°C. By March the elongation rate had reached 0.56 cm day^{-1}. Towards the end of March, however, a dramatic drop in temperature was followed by an increase in the elongation rate during April. From May to July the elongation rate decreased steadily, while temperatures seldom dropped below 15°C, suggesting that low temperatures are conducive to growth, while warmer temperatures are not as favourable.

Horizontal distribution of <u>L. pallida</u> is almost certainly limited by high temperatures (Branch, 1974). Whether this is because of low temperature tolerance by the gametophyte is not known. Generally, however, gametophytes are more tolerant than sporophytes.

Jackson (1977) stated that whatever the exact mechanism of temperature interaction with growth rate, the general trend is clear. Increased temperature enhances growth until an optimum growth is reached; beyond this, further temperature increases decrease growth.

Sporophyte development occurred when temperatures appeared constant at 15°C. It is therefore not unlikely that 15°C is an optimum temperature for this stage of the sporophyte life cycle. Norton and Burrows (1969) find a close correlation between annual fluctuations in sea temperature at Port Erin and the seasonal behaviour of the Saccorhiza population. Immediately before the new generation of sporophytes appeared, the temperature was rising very rapidly; from the annual minimum of 5.5°C in mid-March, it reached 10.7°C by the end of May and it is possible that these temperature levels are critical for the development of the gametophyte and/or the sporophyte. However, the similarity in the timing of the developmental cycle in areas which have widely different temperature conditions indicates that within certain limits temperature may not be a critical factor.

Sundene (1964) found that L. digitata in Norway showed the slowest growth in late summer when temperatures were highest. When temperatures decreased in autumn, new growth started.

Temperature fluctuations alone most certainly do not determine the seasonal pattern observed for L. pallida. Branch (1974), in considering factors which play a limiting role in the distribution of the Laminariales of South Africa, suggested that nutrient availability is of prime importance. It is difficult to relate growth of L. pallida to nutrient availability because the nutrient sampling programme proved to be inadequate. Using the data available in conjunction with observations by other workers, it should, however, be possible to establish to a certain degree the importance of nutrients to L. pallida. During the beginning of the period of rapid growth in L. pallida fronds, nitrate levels are relatively low, but stable (Andrews, 1974; Andrews et al., in press). They do not, however, appear to be low enough to be limiting for growth (Chapman and Dieckmann, in prep). During the upwelling season when maximum acceleration of growth is observed, nutrient levels fluctuate between annual maximum and minimum values. It is during this period that nutrients may become limiting for plankton growth (Andrews, 1974). Renewal of nutrient stocks occurs frequently during the upwelling season; this is followed by plankton blooms which utilise the nutrients and possibly compete with L. pallida for nutrients. Decline in growth rate exhibited by L. pallida during the height of summer, however, does not appear to coincide with periods of reduced upwelling. Chapman and Craigie (1977) found that nitrogen availability plays an important role in the seasonal growth of Laminaria longicruris off Nova Scotia; the growth cycle in shallow water (6 and 9 m) was characterized by a rapid increase in the rate of elongation in January and February (winter), reaching a peak in early summer. The onset of rapid winter growth in shallow water correlated closely with improved levels of nitrate. They added that although available nitrogen had a significant regulatory role in the seasonal growth of L. longicruris, it is important to note that it acted in conjunction with other factors. Chapman and Dieckmann (in prep.) found that off Oudekraal, nitrate concentrations in the sea and in the plant tissues did not follow the seasonal trends in growth. In comparison with concentrations in St. Margaret's Bay, Nova Scotia, nutrient concentrations at Oudekraal were nearly always high. The changing concentrations of tissue nitrate followed seasonal changes in dissolved nitrate in the surrounding seawater. L. pallida, in contrast to L. longicruris, showed little ability to store nitrate ions. The differences may result from contrasting environments in which they occur. L. pallida seems to occur only under luxurious nutrient conditions whose long-term seasonal fluctuations do not relate to seasonal growth fluctuations of the kelp.

Light is perhaps the most important physical regulatory factor determining the seasonal patterns in frond elongation rates. At Station B, Oudekraal, the beginning of the period of rapid growth coincided with the increase in light levels in all three years studied. Subsequent elongation rates follow a pattern parallel to the increase in light until October-November, when elongation rates slowed down and began to decline, while irradiance increased to peak in December-January at which time elongation rates were about half of what they were in spring.

At Station C, rapid growth began up to one month later, but then followed a pattern similar to that at the shallower station.

As with temperature and nutrient concentrations, it appears that growth rate of the fronds slowed down when conditions were optimal.

Chapman and Dieckmann (in prep.) found that saturating levels of irradiance were not reached in the sea until October, after which saturating levels were recorded for 5 hr/day in October and 6 hr/day in November and December. On a daily basis, however, irradiance was suboptimal for growth at all times. Evidence that light should not be inhibiting is that the decline in growth rates of L. pallida fronds at different depths occurred almost simultaneously (Fig. 2.12) whilst irradiance was still increasing. During 1977, however, growth rates at both stations were maintained and the decline in growth rate coincided with a decline in irradiance.

At Robben Island, maximum frond elongation of juvenile sporophytes coincided with maximum irradiance while the decline in growth rate followed the decline in irradiance. Adult plants growing at Robben Island appeared to follow a pattern similar to that observed at Oudekraal.

2.4.1.2 Growth of the Stipes

The effects of abiotic factors on stipe growth are more difficult to assess. It was shown that stipes exhibit seasonal growth which is probably directly related to growth of the fronds (Fig. 2.5). As with growth of fronds at different depths, light probably played the most significant part in regulating growth of the stipes. This is shown by the tremendous difference in age of stipes of equivalent length growing only about 50 m apart, but at different depths. John (1968) also found that L. hyperborea stipes grew at a decreasing rate with increasing depth.

The present method of ageing of stipes of L. pallida has been viewed with scepticism, and has not been done elsewhere, apart from some similar work by Hayashida (1977). Kain (1977) emphasises that care must be taken in estimating stipe age because of the variation caused by different environmental conditions. She showed (by counting growth rings) that stipe growth in L. hyperborea is logarithmic at first, but changes after approximately five years to being roughly linear.

It appears that the physical and chemical factors complement each other (light playing the most significant part) in determining the seasonal growth cycle observed in L. pallida, but perhaps the final explanation does not rest with abiotic factors alone. Perhaps the cycle is endogenous and regulated by biotic factors.

2.4.2 Growth in Relation to Biotic Factors

Drew (1974), working on *L. ochroleuca* in the Mediterranean, found plants "much bigger than their counterparts elsewhere" at 50 m depth. He found it difficult to relate the growth of these plants to temperature and light conditions alone and suggests that growth is due to endogenous rather than environmental factors.

Reproduction is a major process in the life cycle of *L. pallida*. Production of spores in *L. pallida* is thought to occur throughout the year (Branch, 1974). This may indeed be true, but it appears that *L. pallida* has a peak sporing season. Counts of mature fronds showing reproductive activity (sori easily recognisable on blades), indicated that *L. pallida* had at least one peak fruiting period from December 1977 to June 1978. Of 100 plants checked in December 1977, only 5% had sporophylls. By February when plants in the same area were again checked, 50% had at least one or more sporophylls. In April, 80% of all sporophytes checked had sporophylls. At this time sori were easily visible and many sori appeared spent, showing signs of grazing. Plants which were in their first or second year of growth did not appear to be fruiting. Observations were not repeated, but indications are that the appearance of sori on mature plants occurred mainly after frond elongation rates had attained a maximum, during summer. Though only speculation at this stage, it is possible that photosynthetic assimilation continues to increase well into the summer, but that the products of assimilation are used for reproduction rather than for frond elongation. This theory may hold for mature sporophytes, but it does not explain why young sporophytes in their first or second year of growth and not reproducing follow a growth pattern similar to that of adult plants.

Because of rapid elongation rates and apparently slow erosion during summer, the fronds of L. pallida attain their greatest surface area during this period, thus providing a large area for the development of sori.

Chapman and Craigie (1977) found that the growth of L. longicruris reached a peak in early summer and was followed by a quiescent phase during which sporophyte reproduction occurred. L. hyperborea, growing at Port Erin, bears sori only between September and April (autumn and spring), while L. digitata is fertile only during the late summer and winter (August and December) and L. saccharina spores mainly between October and March (autumn to spring) (Kain, 1975a, 1975b). In Saccorhiza polyschides, fruiting began in October (autumn) and increased steadily throughout the autumn and winter until it reached a maximum in March. By May the proportion fruiting had dropped to only 2%.

From the study of settlement and growth of juveniles at Robben Island and at Oudekraal, it appears that although the concrete block and cleared rock surface were re-colonizable by sporophytes for some time, they were first colonized in June-July and between June and September respectively. This may indicate that spores produced in autumn settle and produce a gametophyte generation which survives and grows during autumn and winter to produce sporophytes when conditions become favourable. To Kain (1975b), it was apparent from clearance experiments that all winter-sporing species can arise on a cleared rock during summer, well outside their sporing season or outside their main time for spore release. Most of the winter-sporing algae did well in the spring and early summer, but the quantity arising in later two-month periods was much reduced in spite of irradiance still being high. She also found that from a point of view of competition, the most favourable time for a particular species to reproduce (other factors being equal) is when the surface area of other algae is minimal. From her results it is clear that this is in winter as expected. Thus those species with spores and young stages well adapted to winter conditions would be at an advantage through being fertile in winter. Members of the Laminariales are so adapted; the gametophytes of L. hyperborea, L. digitata, L. saccharina, and Saccorhiza polyschides can survive in the dark for at least 80 days and have very low light requirements for growth (Kain, 1971b). The reproductive cycle of L. pallida appears to follow this pattern as well.

Biotic factors not necessarily responsible for the seasonal growth cycle of L. pallida at Robben Island and Oudekraal, but coinciding with phases in the cycle, were also observed. L. pallida sporophytes were often colonized by epi-phytic and epi-zooic growth. At Robben Island, many sporophytes became heavily colonized by red epiphytes (Dieckmann, 1975a). The most common epiphyte was Carpoblepharis minima. An apparent effect of epiphytization is shown in Fig. 2.13. Sporophytes that had both fronds and stipes covered by epiphytes showed no recovery of growth the following spring. It appears that epiphytes are able to sustain and maintain growth during winter when L. pallida growth is at its slowest, thus increasing in size and probably preventing sufficient light from reaching the fronds in spring. It is also possible that Carpoblepharis minima is semi-parasitic on the host,

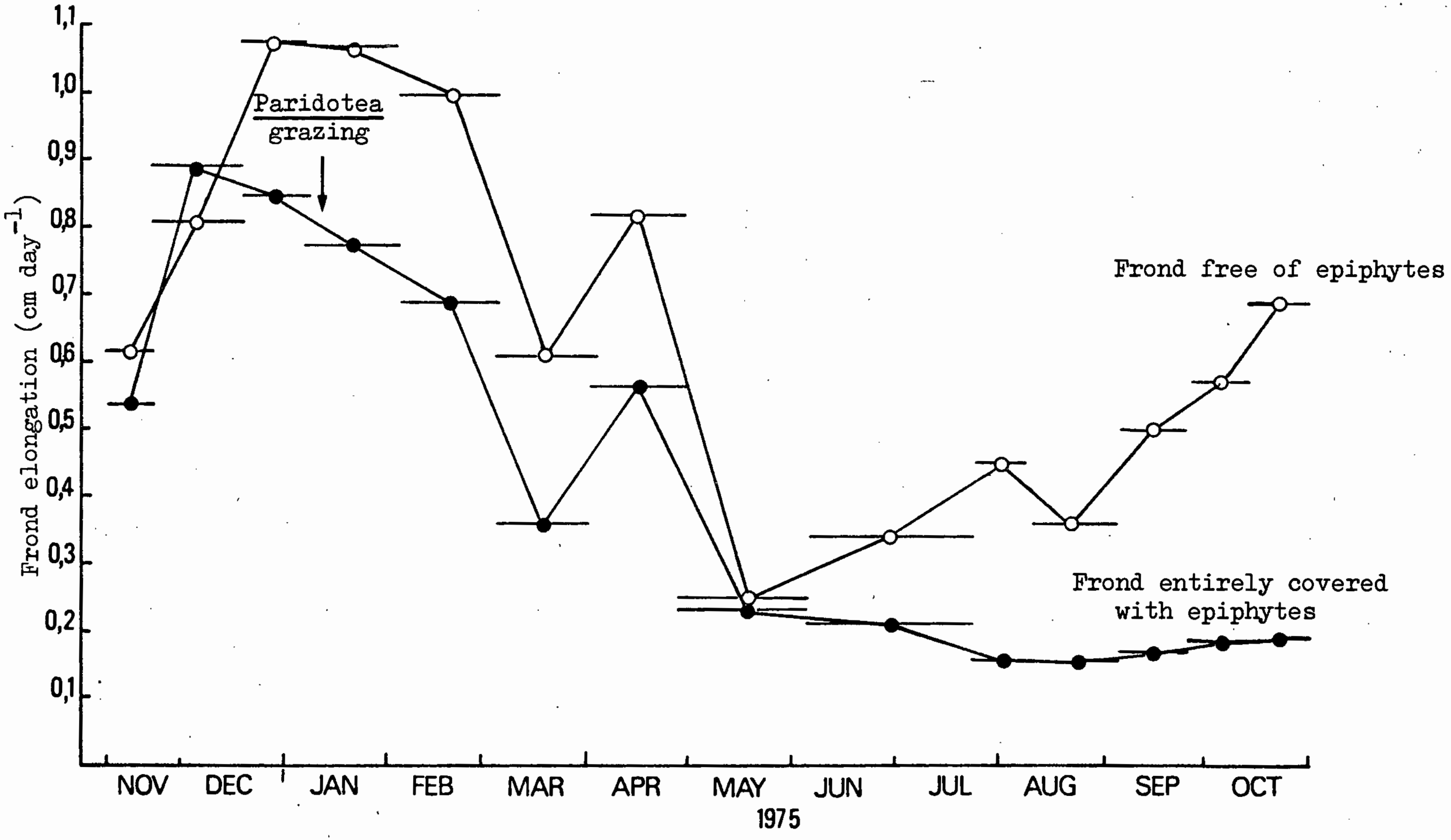

Fig. 2.13 : Frond elongation rates of two L. pallida sporophytes of equal age and size at Robben Island showing the effect of grazing by Paridotea reticulata and colonization by epiphytes (Carpoblepharis minima).

L. pallida (Dieckmann, 1975b).

As mentioned previously, the Oudekraal population of L. pallida, though exhibiting epiphytic growth, was not as severely affected as the Robben Island one.

Growth of L. pallida sporophytes at the deep station, Oudekraal, was in some instances affected by epi-zooic growth. Fronds were covered by bryozoan colonies which appeared visibly to affect them. As with epiphytic growth, it appears that colonization occurred during winter at which time growth of bryozoan colonies exceeded that of the plants, thus covering them (particularly fronds) and probably greatly reducing their photosynthetic capacity. Grützmacher (1976) found that epi-zooic growth on L. digitata occurred during periods of minimum frond expansion and was so severe as to almost completely inhibit growth. Lüning (1968) measured assimilation rates in fronds covered by bryozoans. He found that rates were one-third of the normal rate. Although bryozoans were noticed on fronds of L. pallida growing at the shallower station at Oudekraal, it was found that because of higher rates of frond elongation and shorter periods of slow elongation rates, bryozoan colonies could not establish themselves to the extent they did at the deep station.

Destruction of Laminaria pallida plants by grazers was observed at Robben Island and to some extent at the deep station at Oudekraal. Paridotea reticulata, a common isopod in kelp beds, destroyed entire plants at Robben Island. Fig. 2.13 shows the effect of P. reticulata grazing on a juvenile plant at Robben Island, compared with one which did not show signs of heavy grazing. It appears that grazers such as Paridotea reticulata and Turbo cidaris (a gastropod) are only effective in water of reduced turbulence. This fact became obvious at Oudekraal where both Turbo and Paridotea caused little visible damage to plants at Station B compared with Station C, where Turbo was seen to reduce frond area considerably.

CHAPTER 3

SEASONAL ANALYSIS OF DRY MATTER, CARBON AND NITROGEN CONTENT AND CALORIFIC VALUES OF LAMINARIA PALLIDA

3.1 Introduction

The chemical composition of marine algae was of major interest in the 1950's when the significance of seaweeds as raw material for the chemical industry was realised (Black, 1948; 1950; Black and Dewar, 1949; Haug and Jensen, 1954; Jensen and Haug, 1956, and Primo, 1956). In South Africa, Ligthelm *et al*. (1952) and von Holdt *et al*. (1955) reported on the growing interest in the production of algal chemicals from *L. pallida* and *E. maxima*, as well as other seaweeds.

Since then, the chemical composition of seaweeds has also received increasing attention in the field of ecological dynamics (Slobodkin and Richman, 1960; Crisp, 1971 and Mann, 1972).

In studies of productivity, production rates should be accompanied by factors for conversion into dry mass, organic mass, carbon or energy (Vollenweider, 1969). Such information is valuable for interpreting growth results in addition to its use for comparisons in studies of ecological energetics.

Growth (linear expansion) of *L. pallida* has been recorded (Chapter 2), and knowledge of its chemical composition and calorific value enables an assessment of its productivity to be made. This chapter deals with the comparison of two drying techniques as well as an assessment of the seasonal variation in percentage dry matter, carbon and nitrogen content and calorific values of *L. pallida*.

Drying of fresh plant material is a prerequisite for CHN and calorimetric analyses. The quality of a drying process, however, can only be considered satisfactory if after total water removal, the original chemical composition is retained. Organic content for instance is directly reflected in the energy value obtained by calorimetry; changes in chemical constitution may give invalid results.

Lovegrove (1962) determined the percentage loss of organic material during drying of marine organisms as 1-2%; Cummins and Wuycheck (1971) maintain that losses of over 5% are possible, depending on the methods of drying. Soeder and Talling (1969) found that freeze-drying or desiccation over agents like phosphopentoxide, are superior to oven-drying.

Most workers oven-dry their samples at 105°C (Soeder and Talling, 1969). The oven temperatures used may, however, range from 45°C to 173°C (Paine, 1964). Cummins and Wuycheck (1971) recommend drying of marine organisms at 105°C and subsequent storage in a desiccator, both for not longer than 24 hours, to reduce loss of organics below 5%. Pandian (1968) dried his material at 80°C for 24 hours and then raised the temperature to 105°C until constant weight was attained. In another communication, Pandian and Schuhmann (1967) dried at 80°C for four hours only. Comita and Schindler (1963) recommend drying of marine organisms at 60°C for 24 hours, while Wiegert (1968) dried plant material in an oven at 60°C, under vacuum. Slobodkin and Richman (1960), as well as Mann (1972), freeze-dried their animal and plant material. Schmidt (1976) carried out an intensive study of seaweed drying methods. He concluded that under all circumstances freeze-drying should be preferred to oven-drying; if oven-drying is used, under no circumstances should the material be dried at temperatures above 80°C.

From this short résumé, it is obvious that almost every worker has developed a method specifically suited to the material studied, or which by trial and error has proved to be the most successful method for his purpose.

Variations in dry mass, percentage ash, C:N ratios and calorific content, coincide with changes in growth and reproduction (Mann, 1972; Himmelman and Carefoot, 1975; Niell, 1976; and Johnston _et al_., 1977). Rapid growth is usually correlated with low dry matter content as well as high ash content and C:N ratios. Plants in a dormant or slow growth phase usually exhibit high dry matter content, low ash content and low C:N ratios (Mann, 1972 and Niell, 1976). Changes in calorific content are not necessarily related to changes in growth rates (Paine and Vadas, 1969; Mann, 1972; Schmidt, 1976).

Work by von Holdt _et al_. (1955) has shown that variations in chemical constituents of _L. pallida_ do not follow the same regular patterns observed for Laminarians elsewhere.

3.2 Materials and Methods

All plant material was collected at Oudekraal from Station B (Fig. 1.2). Plants were transported to the laboratory in seawater. There they were dried superficially with paper towelling and separated into fronds, stipes and holdfasts. Large portions were cut into smaller sections. Before weighing to obtain wet mass on a top-loading balance, epi-phytic and -zooic growth was removed. It was difficult to free holdfasts of foreign matter completely.

3.2.1 Comparison of Drying Techniques

The effect of oven-drying and freeze-drying on dry mass and chemical composition of L. pallida was investigated twice. For the first experiment, the fronds of five young sporophytes were used. These were halved along their longitudinal axes and again subdivided to yield two sets of 10 samples each. After drying, the sample pairs were used for further comparison of their ash, calorific, carbon and nitrogen content. Methods used are described below.

The second investigation was done on two sets of 23 samples, obtained from five mature sporophytes by punching out discs of equivalent area above the meristematic region of the frond. Differences between results of matched pairs were tested using the t test for related samples (Roscoe, 1969).

3.2.1.1 Freeze-Drying

Freshly weighed samples were frozen in a commercial freezer and subsequently dried in a 'New Brunswick' freeze-dryer for approximately 60 hours until manifold pressure remained constant. Dried samples were transferred to a desiccator and immediately weighed, after which they were returned to the desiccator and stored until further analysis.

3.2.1.2 Oven-Drying

Samples were dried to constant mass in a drying oven at 105°C (usually for approximately 24 hours) and allowed to cool in a desiccator before weighing.

3.2.1.3 Ashing

Percent ash was determined by burning dried samples in crucibles for four hours in a muffle furnace at 550°C.

3.2.1.4 CHN Analysis

Dried samples were milled in a hammer mill and placed in a desiccator to remove any moisture accumulated during storage or handling. Two subsamples of up to 1 mg dry mass were combusted at 1150°C in a Hewlett Packard 185B CHN analyser. A mean value for the two samples was obtained. When the difference between the two samples exceeded 10%, a third sample was combusted.

3.2.1.5 Calorimetry

Samples were treated as for CHN analysis, with the exception that 0,5 - 1 g subsamples were combusted in a Gallenkamp Ballistic Bomb Calorimeter.

3.2.2 Measurement of Dry Matter, Carbon and Nitrogen Content and Calorific Values

Fifteen sporophytes of different sizes were collected at random on four occasions during 1976 and 1977. Samples were treated as in section 3.2. All samples were oven-dried at 105°C since a freeze-dryer was not always available (results will reveal no apparent differences between drying techniques). Subsequent analysis of dried samples was done as described in sections 3.2.1.4. and 3.2.1.5.

Analysis of variance and multiple range tests according to Newman-Keul (Zar, 1974), were used to test the significance of differences between means.

3.3 Results

3.3.1 Comparison of Drying Techniques

Differences in percentage dry mass of oven- and freeze-dried fronds are shown in Tables 3.1 and 3.2. The difference between means in the first experiment was significant at the 0,05% level, using a t test for matched pairs. Freeze-drying yielded higher values than oven-drying. In the second experiment (Table 3.2), this was not the case.

Percentage ash, calorific, carbon and nitrogen content of freeze-dried samples were all slightly lower than in oven-dried samples.

The differences are, however, again not significant (t test for matched pairs, 0,05% level) (Table 3.3).

3.3.2 Seasonal Investigation of Dry Matter, Carbon, Nitrogen Content and Calorific Values

3.3.2.1 Dry Mass

Dry mass of sporophytes as percentages of fresh material collected on 6.4.76, 5.7.76, 14.10.76 and 11.2.77 are presented in Table 3.4. Though 15 sporophytes were collected on each occasion, these were not necessarily processed, resulting in different sample sizes.

Percentage dry mass of fronds and stipes varies significantly with season. (Analysis of variance using Newman-Keuls multiple range test at 0,05% level of significance). The high percentage dry mass in

TABLE 3.1 : Dry mass as percentage of wet mass of *L. pallida* fronds for oven- and freeze-dried samples. The means are different at the 0,05% significance level.

$\bar{X}$, means; $\bar{D}$, mean of the differences; S_D, standard deviation of the differences; t, the statistic; and df, degrees of freedom.

% Oven-dried	% Freeze-dried	Difference
15,07	15,88	+0,81
15,21	15,74	+0,53
15,58	17,74	+2,16
15,24	18,02	+2,78
14,19	15,55	+1,36
14,48	16,17	+1,69
17,72	18,95	+1,23
16,43	19,74	+3,31
12,89	13,54	+0,65
13,07	13,50	+0,43
$\bar{X}$ 14,99	16,48	$\bar{D}$ +1,50
		S_D 0,31
		t 4,79
		df 9

TABLE 3.2 : Dry mass as a percentage of wet mass of <u>L. pallida</u> fronds for oven- and freeze-dried samples.

$\bar{X}$, mean; $\bar{D}$, mean of the differences; S_D, the standard deviation of the differences; t, the statistic; and df, degrees of freedom.

There is no significant difference between the means at the 0,05% level.

% Oven-dried	% Freeze-dried	Difference
17,45	17,33	+0,12
17,12	18,16	-1,04
16,60	17,75	-1,15
16,79	18,06	-1,27
16,58	16,58	0
15,64	16,90	-1,26
14,79	16,09	-1,3
14,57	14,42	+0,15
13,94	15,09	-1,15
19,61	19,46	+0,15
18,27	17,75	+0,52
16,93	18,21	-1,28
18,10	18,22	-0,12
18,78	18,13	+0,65
13,71	15,04	-1,33
15,76	15,27	+0,49
16,32	17,09	-0,77
16,08	15,31	+0,77
15,68	17,59	-1,91
17,66	16,31	+1,35
14,86	16,85	-1,99
16,58	15,86	+0,72
17,04	16,44	+0,60
$\bar{X}$ 16,47	16,87	$\bar{D}$ -0,39 S_D 0,98 t -1,93 df 22

TABLE 3.3 : Calorific content in kJg^{-1} dry mass and carbon, nitrogen and ash content as percentages of oven-dried (O.D.) and freeze-dried (F.D.) L. pallida fronds. Differences between the means of paired samples are not significant at the 0,05% level.

$\bar{X}$, mean; $\bar{D}$, mean of differences, S_D, standard deviation of differences; t, the statistic; and df, degrees of freedom.

CALORIFIC CONTENT (kJg^{-1})			CARBON CONTENT (%)			NITROGEN CONTENT (%)			ASH CONTENT (%)		
O. D.	F. D.	Diff.	O. D.	F. D.	Diff.	O. D.	F. D.	Diff.	O. D.	F. D.	Diff.
12,92	12,88	+0,04	30,89	32,05	-1,16	2,02	1,94	+0,08	31,45	30,41	+1,04
13,55	13,38	+0,17	31,16	32,31	-1,15	2,02	1,75	+0,27	34,08	32,58	+1,5
13,94	14,36	-0,42	30,80	31,61	-0,81	1,84	1,73	+0,11	24,92	29,44	-4,52
13,97	13,80	+0,17	32,82	29,45	+3,37	1,83	1,58	+0,25	30,45	26,01	+4,44
13,06	12,81	+0,25	31,98	27,91	+4,07	1,92	1,59	+0,33	32,95	27,94	+5,01
13,03	13,07	-0,04	31,88	29,32	+2,56	1,88	1,84	-0,04	33,91	29,85	+4,06
15,12	14,42	+0,70	28,24	31,61	-3,37	1,71	1,87	-0,16	26,10	26,46	-0,36
14,61	13,98	+0,63	31,81	29,76	+2,05	1,90	1,76	+0,14	28,05	23,99	+4,06
12,25	12,25	0	31,72	29,79	+1,93	1,73	1,74	-0,01	36,68	31,00	+5,68
11,88	11,78	+0,10	26,13	26,50	-0,37	1,65	1,61	+0,04	28,76	34,26	-5,5
$\bar{x}$ 13,43	13,27	$\bar{D}$ 0,16	30,74	30,03	$\bar{D}$ 0,71	1,85	1,74	$\bar{D}$ 0,11	30,74	29,19	$\bar{D}$ 1,54
		S_D 0,32			S_D 2,41			S_D 0,15			S_D 3,95
		t 1,56			t 0,94			t 2,26			t 1,23
		df 9			df 9			df 9			df 9

TABLE 3.4 : Dry mass as percentage fresh mass of L. pallida at four different times of the year.

	WHOLE FROND				STIPE				HOLDFAST			
Date	6.4.76	5.7.76	14.10.76	11.2.77	6.4.76	5.7.76	14.10.76	11.2.77	6.4.76	5.7.76	14.10.76	11.2.77
	10,65	13,41	12,15	10,70	9,49	10,45	8,29	9,20	11,33	-	13,95	12,27
	10,66	12,98	12,86	10,88	10,00	11,22	8,30	9,60	12,07		15,14	14,00
	10,80	12,76	13,15	11,20	10,73	13,45	8,63	10,00	12,50		15,35	15,50
	11,36	13,57	13,49	11,60	10,81	13,86	9,90	10,20	13,67		16,57	16,00
	11,38	12,74	13,99	11,60	10,83	13,89	10,24	10,70	13,78		16,84	16,20
	11,43	12,88	14,00	11,90	10,85	13,95	10,35	11,10	14,39		17,93	16,40
	11,47	12,83	14,23	12,02	11,11	14,25	10,40	11,60	15,83		20,30	16,50
	11,80	12,89	14,40	12,71	11,18	15,19	10,42	12,50	16,04		22,51	
	12,00	13,09	14,49	12,00	12,50	15,63	10,90		18,02		25,29	
	12,08	13,19	15,79		13,70	17,92	12,70					
	12,08											
Mean $\bar{x}$	11,43	13,03	13,86	11,62	11,12	13,98	10,01	10,61	14,18	-	18,21	15,30
Standard Dev. Sx	0,54	0,28	1,01	0,63	1,20	2,11	1,35	1,09	2,14	-	3,76	1,46
Standard Error $S\bar{x}$	0,16	0,09	0,32	0,21	0,38	0,67	0,43	0,39	0,71	-	1,25	0,52
99% Confidence Limit	±0,51	±0,23	±1,04	±0,71	±1,24	±2,18	±1,40	±1,37	±2,39	-	±4,20	±1,82

the holdfast may be caused by contamination in the samples.

In fronds the highest percentage dry mass was recorded in spring and the lowest in autumn, whilst in the stipes the highest value was recorded in winter and the lowest in spring.

3.3.2.2 Carbon, Nitrogen and C:N Ratios of Dry Mass

Carbon content is presented as percentage dry mass in Table 3.5. Analysis of variance using the Newman-Keuls test showed that seasonal differences between the means for fronds, stipes and holdfasts are not significant at the 0,05% level. There was also no difference between carbon content of stipes and holdfasts, but both differed significantly from the fronds which had a content approximately 5% higher. The percentage nitrogen does vary with season (Table 3.6). Differences between means are statistically significant at the 0,05% level although there is considerable overlap between seasons as is indicated by 99% confidence limits. The highest percentage nitrogen was recorded in the fronds in winter and the lowest in summer. This was also found in the stipes which generally had a lower nitrogen content than the fronds. No significant seasonal variation occurred in the holdfasts which on average had the highest nitrogen content.

Changes in C:N ratios were caused by changes in the amounts of nitrogen relative to carbon (Table 3.7). In fronds, the mean C:N ratio was highest in summer and lowest in winter, while during spring and autumn, ratios were much the same. Because of very low nitrogen content in stipes during summer, the C:N ratio is very high compared to other times of the year and the grand mean. Low C:N ratios were also recorded in the winter. In the holdfasts, C:N ratios

TABLE 3.5 : Carbon as a percentage dry mass of *Laminaria pallida* fronds, stipes and holdfasts.

	WHOLE FROND				STIPE				HOLDFAST			
Date	6.4.76	5.7.76	14.10.76	11.2.77	6.4.76	5.7.76	14.10.76	11.2.77	6.4.76	5.7.76	14.10.76	11.2.77
	18.56	16,40	24,94	27,37	19,12	20,18	18,97	26,63	23,67	23,03	23,47	24,28
	21,69	26,16	25,68	23,37	21,58	27,37	16,24	22,32	18,25	29,81	28,10	21,81
	24,81	25,20	25,80	25,15	18,48	22,19	16,73	22,77	16,53	23,63	21,05	25,35
	24,59	25,82	27,79	27,05	25,35	18,46	19,51	22,11	21,54	23,10	23,34	24,75
	24,76	23,62	25,63	27,40	23,21	23,49	15,60	15,48	20,04	19,66	19,97	24,18
	26,27	25,92	25,62	26,76	23,22	21,15	15,72	20,49	21,44	26,18	18,33	
	20,65	32,46	27,53	30,09	18,89	28,89	24,82	22,38	25,87	21,55	21,36	
	29,73	27,40	19,88	27,25	18,36	22,84	21,49	20,23	26,48	18,61	28,17	
	28,31	23,73	27,02	23,22	23,84	24,84	22,12	21,52	19,37	16,25	19,13	
	26,34	19,45	22,01	20,20	18,27	24,72	21,80	19,57	19,44	16,87	15,08	
	26,05				21,93				16,32			
	26,48				18,96				23,52			
	26,50				20,68				21,92			
	25,73				18,78				18,71			
	28,86				23,96							
Mean $\bar{x}$	25,29	24,62	25,19	25,79	20,97	23,41	19,30	21,35	20,94	21,87	21,80	24,08
Standard Dev. Sx	3,02	4,36	2,47	2,84	2,78	3,19	3,20	2,83	3,15	4,21	4,13	1,35
Standard Error $S\bar{x}$	0,78	1,38	0,78	0,90	0,70	1,01	1,01	0,90	0,84	1,33	1,31	0,60
99% Confidence Limits	±2,32	±4,49	±2,54	±2,93	±2,07	±3,28	±3,28	±2,93	±2,53	±4,32	±4,26	±2,76

TABLE 3.6 : Total nitrogen as a percentage of dry mass in <u>Laminaria pallida</u> fronds, stipes, and holdfasts.

	WHOLE FROND				STIPE				HOLDFAST			
Date	6.4.76	5.7.76	14.10.76	11.2.77	6.4.76	5.7.76	14.10.76	11.2.77	6.4.76	5.7.76	14.10.76	11.2.77
	1,47	2,92	1,97	1,84	1,50	1,87	1,09	1,01	2,44	3,27	2,46	2,14
	2,39	1,34	1,62	1,50	1,39	1,15	0,79	1,08	2,10	2,04	3,37	1,05
	1,75	1,34	1,69	1,00	1,27	3,85	0,84	1,20	1,76	2,56	1,87	2,66
	1,59	1,43	1,81	1,53	1,54	1,93	0,86	0,77	1,85	1,57	1,90	1,92
	1,44	2,33	1,57	1,47	1,37	1,08	2,21	1,56	1,53	1,94	1,67	2,60
	1,39	2,13	1,64	2,03	2,57	1,45	1,49	1,05	2,32	2,96	1,79	
	1,65	2,40	2,02	1,68	1,05	1,77	2,11	0,90	1,92	1,29	1,70	
	1,64	2,35	1,34	1,85	0,95	1,50	1,13	1,26	1,89	1,69	2,41	
	1,93	1,81	1,62	1,89	2,27	3,51	1,30	1,32	2,17	1,47	2,07	
	1,73	2,98	1,70	1,64	1,26	1,26	1,45	1,49	1,76	1,38	1,10	
	1,62				1,49				1,73			
					1,19				1,90			
					0,97				1,36			
					0,88							
					0,93							
Mean $\bar{x}$	1,69	2,10	1,70	1,64	1,38	1,94	1,33	1,16	1,90	2,02	2,03	2,07
Standard Dev. Sx	0,28	0,61	0,20	0,29	0,48	0,97	0,50	0,25	0,30	0,69	0,61	0,65
Standard Error $S\bar{x}$	0,08	0,19	0,06	0,09	0,12	0,31	0,16	0,08	0,08	0,22	0,19	0,29
99% Confidence Limits	±0,25	±0,62	±0,20	±0,29	±0,36	±1,00	±0,52	±0,26	±0,24	±0,72	±0,62	±1,33

are lower than in fronds and stipes. Seasonal differences, however, do not appear to be significant.

TABLE 3.7 : Carbon : Nitrogen ratios for Laminaria pallida at different times of the year.

	6.4.76	5.7.76	14.10.76	11.2.77	Grand Mean
Fronds	14,96 : 1	11,72 : 1	14,82 : 1	15,73 : 1	14,30 : 1
Stipes	14,93 : 1	12,07 : 1	14,51 : 1	18,41 : 1	14,98 : 1
Holdfasts	11,02 : 1	10,83 : 1	10,74 : 1	11,63 : 1	11,06 : 1

Calorific content of dry and fresh mass was determined on three occasions only (Table 3.8). Fronds had the highest calorific content and only slight variation occurred with seasons, but this was not significant at the 0,05% level. Lowest calorific content was measured in the holdfasts, where seasonal differences are significant at the 0,05% level. The minimum was recorded in winter. In the stipes, the maximum calorific content was measured in autumn, but it does not differ significantly from other times.

3.4 Discussion and Conclusions

Differences in percentage dry weight of oven- and freeze-dried Laminaria pallida are probably due to incomplete water removal by freeze-drying and not because of loss of volatiles by oven-drying at 105°C. This is confirmed by results of analysis of dried sample pairs in the first experiment (Table 3.3), where in fact ash, carbon, nitrogen and calorific content were all slightly lower in freeze-dried samples than in oven-dried samples.

After drying and prior to further analysis, samples were stored in a desiccator, allowing supplementary or complete drying, hence the

TABLE 3.8 : Calorific content of <u>Laminaria pallida</u> fronds, stipes and holdfasts in kJg^{-1} dry mass.

	WHOLE FROND				STIPE				HOLDFAST			
Date	6.4.76	5.7.76	14.10.76	11.2.77	6.4.76	5.7.76	14.10.76	11.2.77	6.4.76	5.7.76	14.10.76	11.2.77
	12,10	9,57	11,07	-	7,13	7,22	7,74	-	8,70	9,22	8,92	-
	11,38	12,81	10,79	-	9,33	8,87	7,93	-	8,06	8,05	9,73	-
	13,82	11,77	9,80	-	8,40	9,06	6,47	-	10,39	9,36	5,96	-
	13,00	10,39	10,56	-	10,54	7,37	7,24	-	10,91	4,84	6,98	-
	11,25	10,70	10,06	-	8,79	7,18	8,30	-	10,26	8,14	7,84	-
	11,55	9,95	9,09	-	8,33	9,61	6,90	-	11,79	7,96	5,59	-
	13,62	11,02	10,70	-	11,55	9,79	8,71	-	9,77	3,88	7,92	-
	13,50	10,85	11,30	-	7,87	7,84	8,79	-	7,96	4,26	10,54	-
	12,24	10,25	11,04	-	11,64	8,48	9,50	-	7,21	4,15	7,03	-
	10,01	8,53	10,44	-	7,67	6,60	8,87	-	6,32		3,00	-
	9,80			-	9,70			-	8,93			-
	11,60			-	9,51			-	6,11			-
	12,09			-	11,58			-	11,19			-
	10,70			-	12,51			-				-
	9,72			-	9,53			-				-
Mean $\bar{x}$	11,76	10,58	10,49	-	9,60	8,20	8,05	-	9,05	6,65	7,35	-
Standard Dev. Sx	1,35	1,18	0,67	-	1,64	1,11	0,97	-	1,85	2,31	2,19	-
Standard Error $S\bar{x}$	0,35	0,37	0,21	-	0,42	0,32	0,31	-	0,51	0,77	0,69	-
99% Confidence Limits	±1,04	±1,20	±0,68		±1,25	±1,14	±1,01		±1,56	±2,59	±2,24	

insignificant (0,05% level) differences between carbon, nitrogen, calorific and ash content of oven- and freeze-dried samples. Crisp (1971) showed that 5% of water in tissue is difficult to remove by freeze-drying.

Repetition of the experiment, recorded in Table 3.2, did not yield different percentages of dry mass, indicating that freeze-drying had probably been more efficient than on the previous occasion (samples were also smaller than previously).

It appears that oven-drying at 105°C does not significantly alter the composition of L. pallida.

Paine (1971) compared freeze-drying with oven-drying (80°C) and found no significant differences in the final calorific content. In fact, he also recorded slightly lower calorific contents in freeze-dried samples. Schmidt (1976), on the other hand, found significant differences between calorific content of freeze- and oven-dried samples (100°C) of Fucus and Ulva; freeze-drying yielded 4% and 3.5% higher calorific content respectively.

Seasonal variation of the percentage dry mass in L. pallida is low. In the frond the highest mean value is 21% higher than the lowest, while in the stipes the difference is 39%. Mann (1972) found highest seasonal values in L. digitata and L. longicruris, 54% above the lowest values.

Percentage dry mass of L. pallida was determined only four times during a calendar year, and results may not give a true reflection of seasonal changes in dry mass. This is substantiated by von Holdt et al. (1955) who observed month-to-month variation of percentage ash and alginic acid content of L. pallida, much greater than actual seasonal variation (percentage ash is inversely proportional to percentage dry matter). Similarly, Mann's (1972) conclusions, based on data also collected at four different seasons, should be questioned.

Highest percentage dry mass in fronds was measured in spring when growth rates were at a maximum (see Chapter 2), while the lowest were recorded in autumn when growth was almost at a minimum. This was not so in the stipes where the highest value was recorded in winter and the lowest in spring. The increased dry mass in the fronds in spring may be explained by the accumulation of organic matter which accompanies rapid growth. This is substantiated by the high carbon content of fresh <u>L. pallida</u> fronds during this time. The pattern observed for stipes does not appear to be as straightforward. A possible explanation is that in spring, stipes increase their length by cell expansion, rather than cell multiplication. Increased water content of cells reduces the percentage dry matter. Paine and Vadas (1969) warn against assuming that the water content of seaweeds shows no major seasonal or environmental differences.

Carbon as percentage dry mass does not vary on the four occasions measured. Mann (1972) also found no significant seasonal variation in the carbon content of dry <u>L. longicruris</u> and <u>L. digitata</u>.

Low C:N ratios are characteristic of those phases in algal growth cycles when there is rapid increase in biomass, while higher values are obtained when there is low productivity (Mann, 1972; Niell, 1976). This statement does not apply to <u>L. pallida</u>. Since carbon content of dry matter in <u>L. pallida</u> appears to remain constant throughout the year, it is the variation in the nitrogen content which is responsible for the variation in C:N ratios observed. In both fronds and stipes, lowest C:N ratios were recorded in winter when growth rate is at its minimum or when the period of rapid growth is initiated. Highest C:N ratios were recorded in summer in all parts of the plant. At this time of the year, growth rates had reached a maximum or were already on the decline.

In Chapter 2 it was shown that the nutrient availability off the Cape coast is different to that off Nova Scotia. There, L. longicruris builds up nitrogen reserves during favourable nutrient conditions which it utilizes when nutrients have become depleted (Chapman and Craigie, 1977). This explains why Mann (1972) found very high C:N ratios in L. digitata and L. longicruris in December when nitrate levels in the sea and plant are at their lowest, as are growth rates.

In L. longicruris and L. digitata growth rates were most rapid after plants were able to accumulate nitrogen, thus reducing the C:N ratio. C:N ratios for L. longicruris and L. digitata vary with season from 19,4 :1 to 27,2 : 1 and 13,8 : 1 to 16,7 : 1 respectively (Mann, 1972), while in L. pallida they vary from 11,72 : 1 to 15,73 : 1 in fronds, 12,07 : 1 to 18,41 : 1 in stipes and 10,74 : 1 to 11,63 : 1 in the holdfasts, indicating that nitrogen is found in higher concentrations relative to carbon in L. pallida than in L. longicruris or L. digitata. (There is very little difference between percentage carbon of L. pallida and the other two species.)

The calorific content of L. pallida does not appear to change significantly with season. This is to be expected, since carbon content varies very little. Himmelman and Carefoot (1975) found a distinct annual cycle in calorific value of temperate seaweeds, related to seasonal periods of growth and reproduction. Mann (1972), as well as

Paine and Vadas (1969) found no significant changes in calorific content of laminarians with season.

Calorific content of L. pallida expressed as kJg^{-1} dry mass is lower on average than that of other laminarians (Table 3.9).

TABLE 3.9 : Calorific values of laminarians in kJg^{-1} dry mass.

Species	kJg^{-1} dry mass	Author
L. longicruris	12,85	Mann (1972)
L. digitata	12,65	" "
L. complanata	11,10	Paine and Vadas (1969)
L. saccharina	11,89	" " " "
L. setchellii	13,73	" " " "
L. pallida	10,94	

This difference is, however, probably due to differences in methods used to obtain dry mass by different workers.

CHAPTER 4

BIOMASS AND PRODUCTIVITY OF LAMINARIA PALLIDA

4.1 Introduction

Laminarians occupying coastal waters in temperate latitudes are probably the most important primary producers in these waters (Mann, 1972); yet their productivity has seldom been determined on an area basis.

Several authors have investigated the photosynthesis and respiration on individual plants or portions of plants, usually under laboratory conditions (Kanwisher, 1966; Brinkhuis and Jones, 1974; King and Schramm, 1976a; 1976b).

Quantitative ecological studies of sublittoral marine macrophytes, on a larger scale, have been carried out using surface operated spring grabs (Kain, 1971b). More accurate estimates of the biomass and productivity of sublittoral marine macrophytes have been made using SCUBA diving methods by Aleem (1956, 1973); North (1958); McFarland and Prescott (1959); Crosset, Drew and Larkum (1965); Kain (1963, 1967, 1971b); Larkum, Drew and Crosset (1967); Bellamy *et al*. (1968, 1973); John (1969, 1971); Lüning (1969); and Jupp and Drew (1974). Methods employed by the above authors usually involved a seasonal study of biomass, where peak annual biomass was considered to be equal to total annual production. It has only been in more recent years that well established methods to measure growth in laminarians (Parke, 1948; Sundene, 1968; and Lüning, 1968) were applied in the determination of their productivity (Mann, 1972). Mann was able to establish that the annual production of laminarians off Nova Scotia was 5 to 10 times their summer biomass. Although some tentative estimates of biomass and production of kelp growing off the South African coast were made (Dieckmann, 1975c; Field et al., 1977; and Velimirov et al., 1977), no long-term study with accurate information on the production by Laminaria pallida has yet been done. This present study, based on three years of biometric data collection, provides good estimates of the annual production by L. pallida at two different depths off Oudekraal, Cape Peninsula. Results are comparable to those obtained in similar studies elsewhere.

4.2 Materials and Methods

The experimental site, as well as methods used for monitoring physical parameters and growth of L. pallida, are described in Chapters 1 and 2. Methods used to determine biomass and to collect data for converting growth increments to production are reported in this chapter, while factors used for conversions to dry mass and energy units preceded in Chapter 3.

An estimate of kelp biomass was obtained by laying a transect line from the shore through Stations B and C (Fig. 1.2) (Field et al., 1977). Plants within 0,5 m of the line were cut and the crop derived from successive 2m steps along the line placed into labelled bags and taken ashore. There, individual plants were divided into fronds and stipes. Length measurements and wet mass were obtained. Holdfasts were not weighed, and holdfast biomass was estimated from a regression of holdfast mass against stipe length from 56 whole plants collected subsequently.

For converting frond and stipe length to biomass, data were obtained in the following way: One hundred sporophytes of all sizes were collected at random in the vicinity of Stations B and C (Fig. 1.2, Chapter 2). Treatment of collected plants was the same as for those from the transect, except that fronds were spread out on a large board to enable more accurate measurements of frond length.

4.3 Results

Annual mean percentage dry mass, carbon and calorific content of L. pallida were obtained from results in Chapter 3. They are summarized in Table 4.1.

TABLE 4.1 : Factors for converting biomass and productivity from fresh mass into percentage dry mass, percentage carbon and calorific content, expressed as annual mean values.

	FROND	STIPE	HOLDFAST	WHOLE PLANT
Dry mass as % fresh mass	12,49	11,43	15,9	13,27
Carbon as % dry mass	25,22	21,26	22,17	22,88
Calorific content kJg^{-1} dry mass	10,94	8,62	7,68	9,08

Density and biomass of L. pallida at Stations B and C are shown in Table 4.2; conversion of fresh biomass into dry biomass, percentage carbon and calorific content are also shown. Fig. 4.1 shows the regression power curve used to obtain holdfast mass from stipes of known length.

As was shown in Chapter 2, the sum of the growth increments as indicated by the movement of holes gives the amount of growth in terms of length. Because fronds are constantly eroding, this increment in

TABLE 4.2 : Biomass and density of L. pallida per m^2 of sea bottom at Station B (8m depth) and Station C (14m depth).

			FRESH MASS Kg m^{-2}				DRY MASS Kg m^{-2}				CARBON Kg m^{-2}				CALORIFIC CONTENT kJm^{-2}			
Station	Density	Depth (m)	Frond	Stipe	Holdfast	Total including juveniles	Frond	Stipe	Holdfast	Total including juveniles	Frond	Stipe	Holdfast	Total including juveniles	Frond	Stipe	Holdfast	Total including juveniles
B	12	8	5,87	3,94	3,69	13,56	0,73	0,45	0,57	1,76	0,19	0,10	0,13	0,42	8019	3888	4393	16388
C	5	14	1,77	1,29	1,02	4,14	0,22	0,15	0,16	0,54	0,06	0,03	0,04	0,13	2415	1271	1219	4905

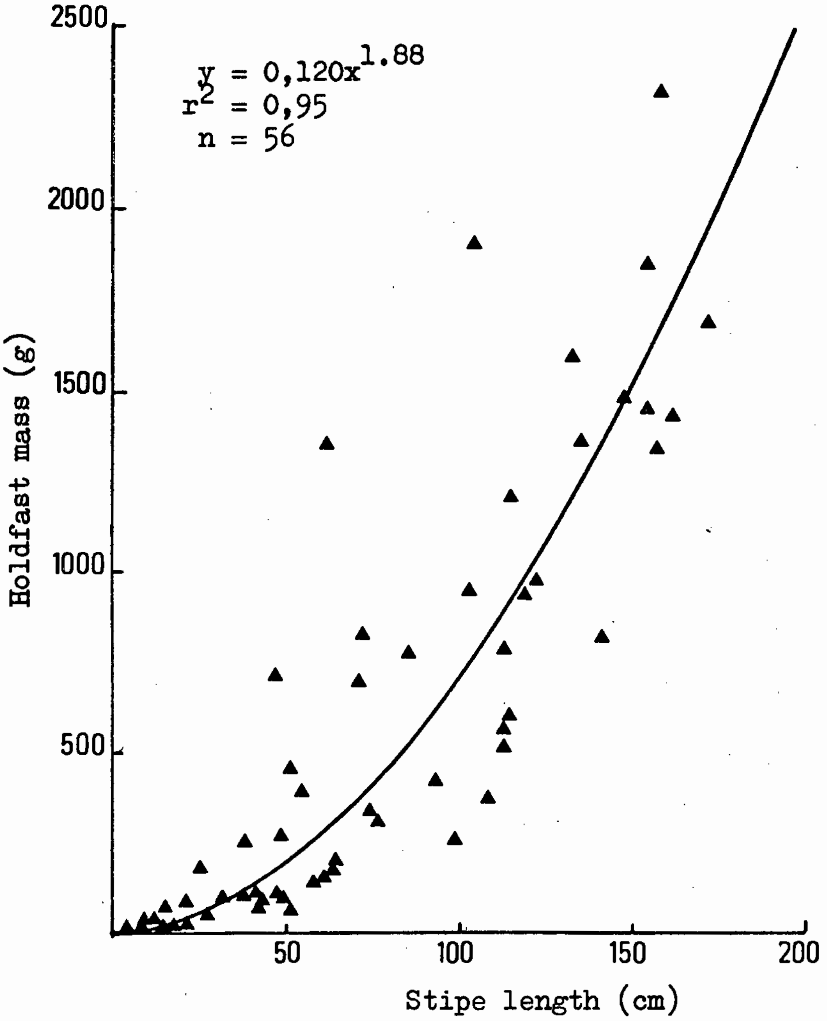

Fig. 4.1 : Stipe length to holdfast mass regression of L. pallida sporophytes. Power curve fitted by method of least squares.

length only represents the length the plants would have reached had no erosion occurred and not the actual length of the plant at the end of the period. In spite of erosion it was obvious that there was a correlation between frond length and stipe length (Fig. 4.2).

Increase in frond length, expressed as a percentage of initial length, appears to be greater in younger plants. If the sum of growth increments over the year is divided by initial length, a curve representing the annual turnover of tissue in terms of frond length is obtained. In Fig. 4.3 annual turnover has been plotted for plants which survived a whole year at both Stations B and C. It shows that in smaller plants fronds have higher turnover rates with a maximum increment of about three to four times their initial length, depending on the depth, and that large plants turn over their frond length about once a year.

As L. pallida increases in length, it becomes wider and thicker so that the length-to-weight relationship is not linear. Length/weight relationships are shown for stipes in Fig. 4.4 and for fronds in Fig. 4.5. In both cases the coefficients of determination are high. Using the equations derived for the curves by least squares it is possible to convert each observation on initial length and length increment to a corresponding biomass increment.

Since stipe increments are small and difficult to measure, no attempt was made to convert these into biomass units. An estimate of stipe mass at specific ages can be made by using growth curve data from Chapter 2 together with the regression in Fig. 4.4. Table 4.3 gives the estimated age and wet mass of stipes at Stations B and C.

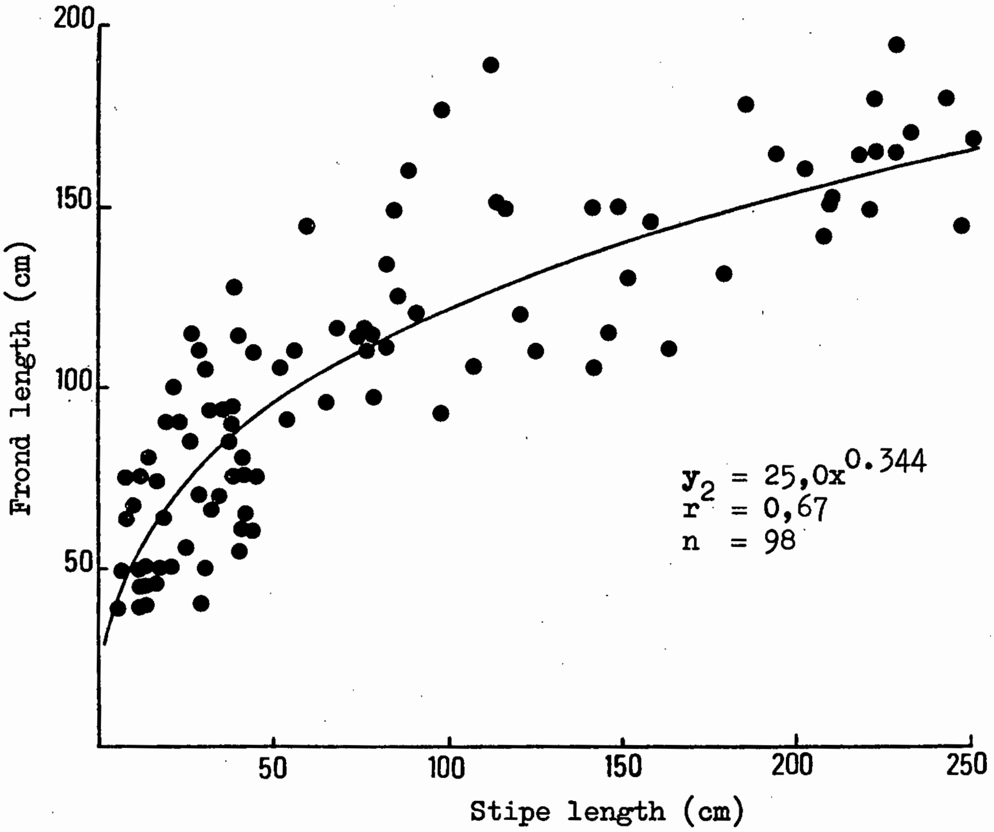

Fig. 4.2 : Stipe length to frond length regression of L. pallida sporophytes. Power curve fitted by method of least squares.

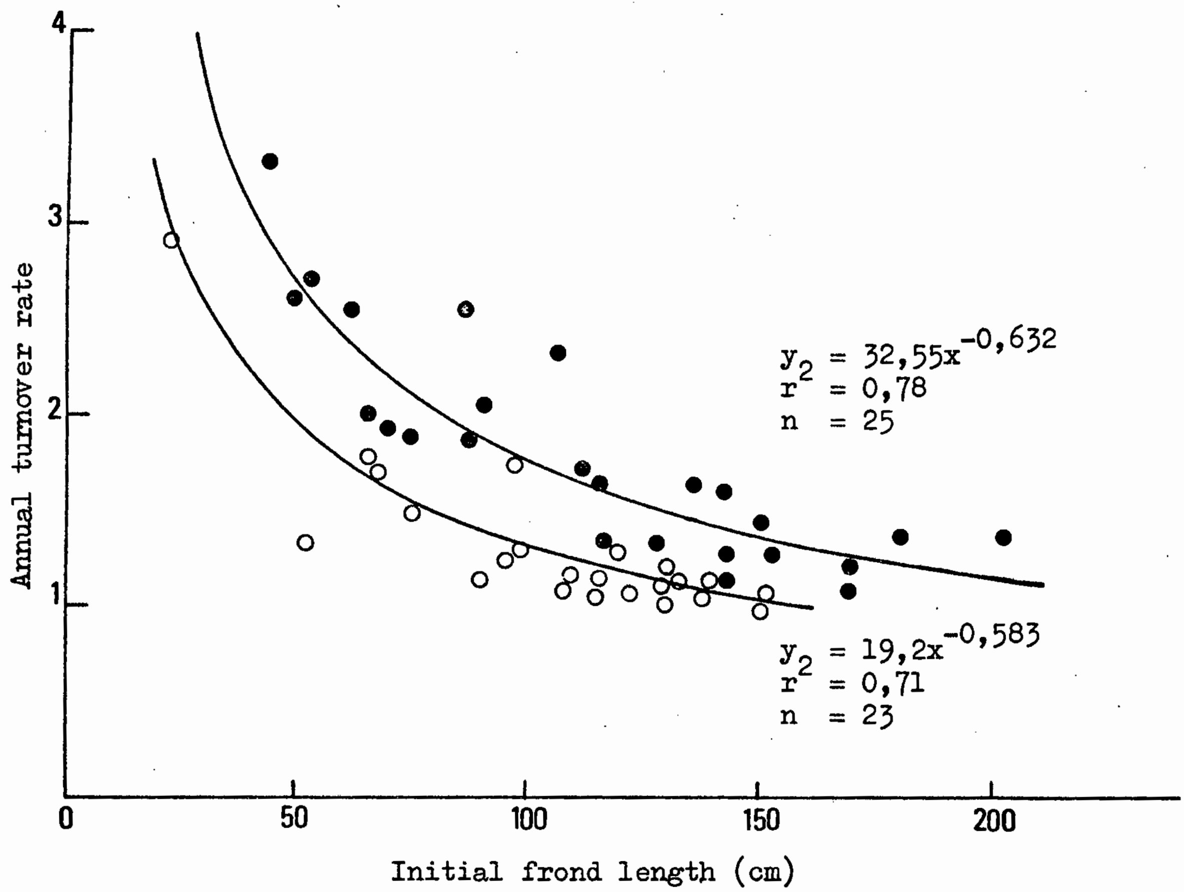

Fig. 4.3 : Annual turnover rates of L. pallida fronds plotted against initial frond lengths for those plants observed for a full year at 8 m depth, Station B (●) and 14 m depth, Station C (○), Oudekraal. Power curves were fitted by the method of least squares.

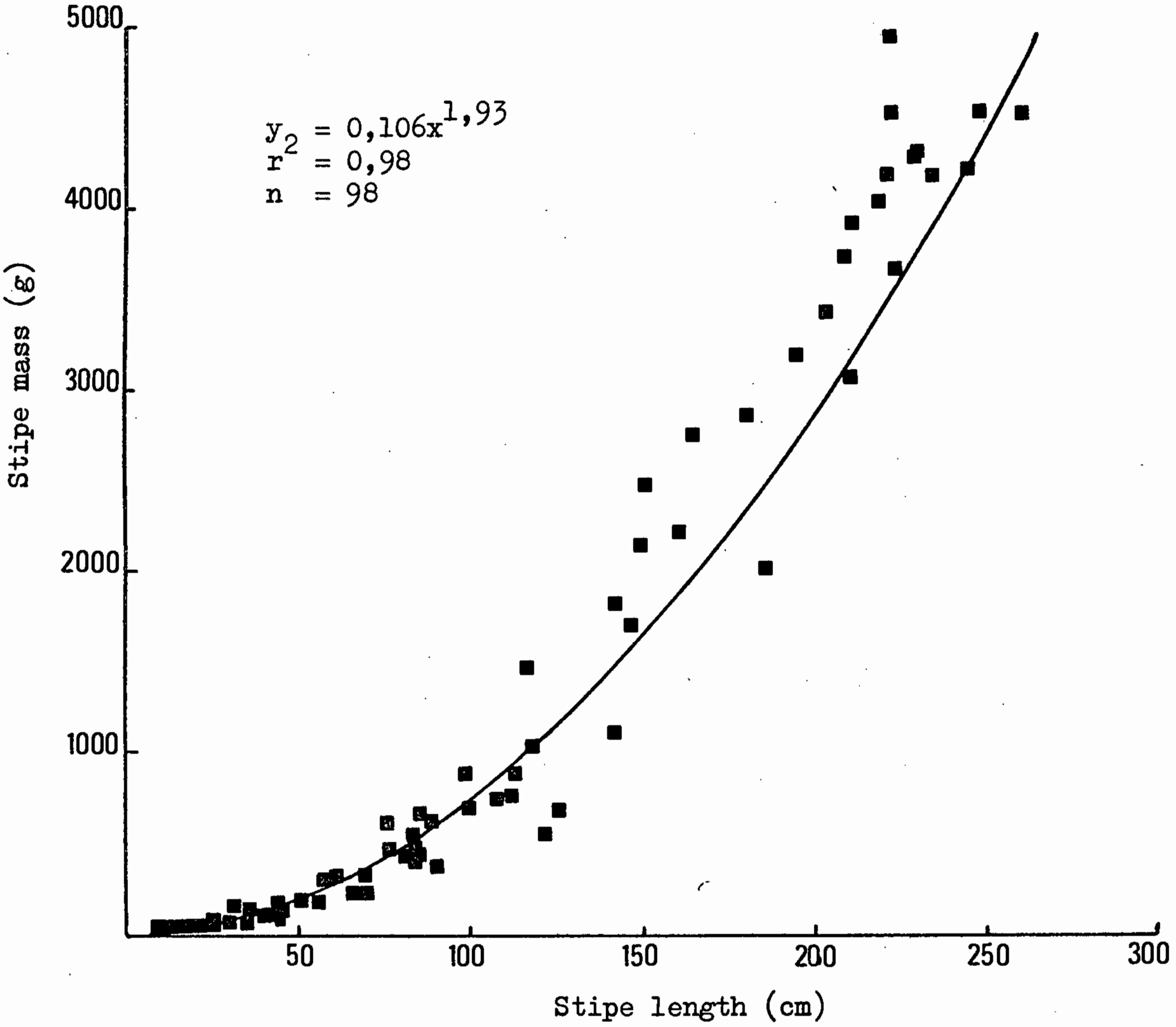

Fig. 4.4 : Stipe length to mass regression of L. pallida sporophytes. Power curve was fitted by the method of least squares.

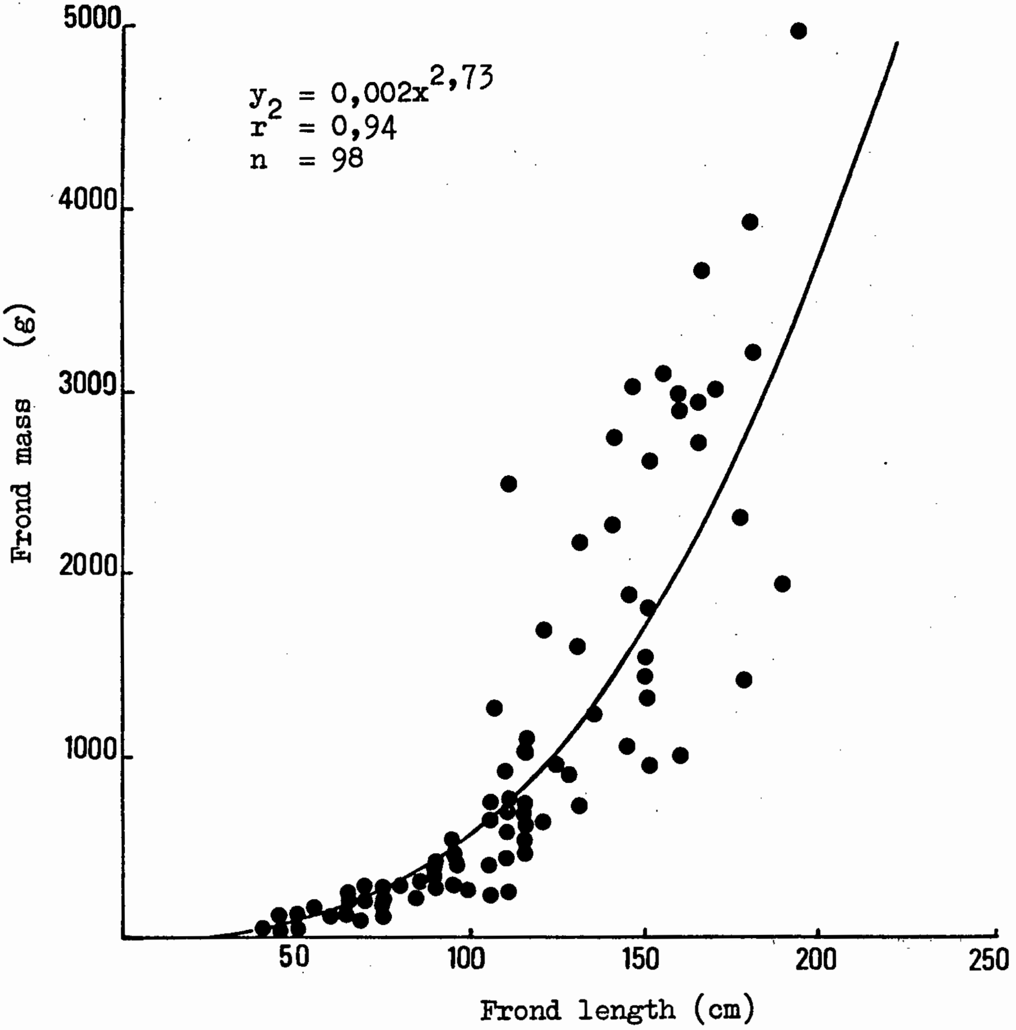

Fig. 4.5 : Frond length to mass regression of L. pallida sporophytes. Power curve was fitted by the method of least squares.

TABLE 4.3 : Age and estimated wet mass of stipes at Stations B and C, Oudekraal.

	Station B (8m depth)					Station C (14m depth)							
Age (yrs)	1	2	3	4	5	1	2	3	4	5	6	7	8
Wet Mass (g)	155	1277	2660	3433	3753	52	192	410	703	1068	1503	2006	2576

Increments of frond biomass were calculated for each period or interval between measurements; initial frond length at the beginning of each period was obtained from the frond length to stipe length regression in Fig. 4.2, using the stipe length at the beginning of each period. Length increments were converted to biomass increments using the length-to-mass relationship in Fig. 4.5.

Because plants varied in size and number during the sampling period, mean biomass increments for each period or interval were calculated per gram of initial frond mass (Tables 4.4 and 4.5). Annual biomass increments per gram of frond were obtained by adding increments obtained during 346-380 days, beginning at different times of the year and converting to total increment in 365 days. The figure thus obtained represents annual production by 1 g of frond.

Mean annual production by fronds at Station B was 4,70 g per gram of frond while at Station C it was 3,49 g (Tables 4.4 and 4.5).

Using frond standing stock from Table 4.2 and mean turnover rates from Tables 4.4 and 4.5, it is possible to convert biomass per square metre into annual production per square metre at both stations.

Production of wet mass into dry mass, carbon and calorific values were converted using values shown in Table 4.1. Table 4.6 gives the annual frond production by sporophytes at Stations B and C.

TABLE 4.4 : Biomass turnover measured over varying periods for <u>L. pallida</u> fronds at Station B (8 m depth), Oudekraal from 3.4.75 - 24.1.78.

Period	Number of days	Mean biomass increment g^{-1} initial mass in g	Sums of biomass increment (turnover rates) as g increment g^{-1} initial mass n^{-1} days (no. of days in parenthesis)	Turnover per annum g inc. g^{-1} init. 365^{-1} days
3.4.75 - 5.6.75	63	0,18		
5.6.75 - 24.7.75	49	0,20		
24.7.75 - 2.9.75	40	0,40		
2.9.75 - 22.9.75	20	0,43	4,04 (358)	4,12
22.9.75 - 17.10.75	25	0,63		
28.10.75 - 28.11.75	31	0,68	3,93 (346)	4,15
28.11.75 - 5.2.76	69	1,14		
5.2.76 - 6.4.76	61	0,38	3,73 (345)	3,95
6.4.76 - 6.5.76	30	0,09		
6.5.76 - 16.7.76	70	0,18	4,59 (367)	4,56
16.7.76 - 16.8.76	31	0,24		
16.8.76 - 13.9.76	28	0,39		
13.9.76 - 13.10.76	30	0,71	5,31 (373)	5,20
13.10.76 - 30.11.76	48	1,46		
30.11.76 - 5.1.77	36	0,93	5,11 (371)	5,03
5.1.77 - 9.2.77	35	0,67		
9.2.77 - 14.3.77	33	0,45	4,74 (350)	4,94
14.3.77 - 15.4.77	32	0,19		
15.4.77 - 17.5.77	32	0,13	5,95 (383)	5,67
17.5.77 - 20.8.77	97	0,18		
20.8.77 - 28.9.77	37	0,73		
28.9.77 - 7.11.77	36	1,46		
7.11.77 - 13.12.77	39	1,26		
13.12.77 - 24.1.78	42	0,88		
				Mean 4,70 S.D. 0,61

TABLE 4.5 : Biomass turnover measured over varying periods for L. pallida fronds at Station C (14 m depth), Oudekraal from 12.8.75 - 24.1.78.

Period	Number of days	Mean biomass increment g^{-1} initial mass in g	Sums of biomass increment (turnover rates) as g increment g^{-1} initial mass n^{-1} days (no. of days in parenthesis)	Turnover per annum g inc. g^{-1} init. 365^{-1} days
12.8.75 - 22.9.75	41	0,28		
22.9.75 - 17.10.75	25	0,31		
17.10.75 - 7.11.75	21	0,42		
7.11.75 - 28.11.75	21	0,39	3,79	3,74
28.11.75 - 3.3.76	96	1,89	(370)	
3.3.76 - 6.5.76	64	0,23	3,87	3,82
6.5.76 - 27.7.76	82	0,17	(370)	
27.7.76 - 16.8.76	20	0,10	3,94	3,91
16.8.76 - 20.9.76	35	0,18	(367)	
20.9.76 - 21.10.76	31	0,49		
21.10.76 - 29.11.76	39	0,88	3,16	3,07
29.11.76 - 7.1.77	39	0,54	(376)	
7.1.77 - 10.2.77	34	0,31	3,00	2,94
10.2.77 - 14.3.77	32	0,29	(372)	
14.3.77 - 15.4.77	32	0,14	3,26	3,17
15.4.77 - 17.5.77	32	0,06	(375)	
17.5.77 - 15.6.77	29	0,03	3,95	3,78
15.6.77 - 23.8.77	69	0,08	(381)	
23.8.77 - 28.9.77	36	0,20		
28.9.77 - 1.11.77	33	0,73		
1.11.77 - 13.12.77	42	1,20		
13.12.77 - 24.1.78	42	0,91		
				Mean 3,49
				S.D. 0,41

TABLE 4.6 : *L. pallida* frond biomass; conversion using mean turnover rates, into annual production per square metre of sea bottom at Stations B (8 m depth) and C (14 m depth) at Oudekraal.

	Wet mass $g\ m^{-2}$	Wet mass production $g\ m^{-2}$	Dry mass production $g\ m^{-2}$	Carbon production $g\ m^{-2}$	Energy production kJm^{-2}
Station B	5870	27589	3446	869	37699
Station C	1770	6177	772	195	8446

4.4 Discussion and Conclusion

Density and standing stock of *L. pallida* as presented in this study are only representative of the two depths at which they were measured. Both properties are considerably lower at 14 m than at 8 m depth. Frond biomass contributes almost half of the total standing stock on a basis of dry mass, carbon and calorific content.

An earlier study at Oudekraal (Field *et al.*, 1977) obtained a standing stock of 1678 g dry mass m^{-2} of *L. pallida* at a depth of eight metres. Velimirov *et al.* (1977) later estimated a standing stock of *L. pallida* at different depths on the same transect at Oudekraal, obtaining mean standing stock values of 10254 kJm^{-2} in a 4-8 m depth zone and 4631 kJm^{-2} in the 8-12 m depth zone. These figures compare well with those obtained in this study (Table 4.2). The differences observed are probably due mainly to the use of different conversion factors. *L. pallida* makes up 100% of the total kelp biomass at Stations B and C, while at shallower depths it constitutes approximately 50% of the total kelp biomass (Velimirov *et al.*, 1977). It is at eight metres that *L. pallida* appears to attain greatest density and biomass per m^2. One of the reasons may be that in this area it is not shaded by *Ecklonia maxima*.

A mean standing stock of 13,56 kg m^{-2} wet mass at this depth compares closely with optimal biomass figures obtained elsewhere. Lüning (1968) found a biomass of 14 kgm^{-2} for *L. digitata* in the sublittoral of Helgoland, while Mann (1972) found a biomass of 16 kg m^{-2} wet weight for *L. longicruris* in St. Margaret's Bay, Nova Scotia. Jupp and Drew (1974) determined the biomass of *L. hyperborea* on the

West coast of Scotland and found a mean biomass at three and nine metres of 20,4 kg m^{-2} and 7,7 kg m^{-2} respectively, also revealing a decrease of biomass with depth.

In Fig. 4.3 it is shown that the sum of annual length increment of fronds differs for plants at different depths. For instance, the 50 cm fronds at Station B (8 m depth) turned over their length approximately three times in one year while the 50 cm fronds at Station C (14 m depth) turned over their length only twice. The difference decreased as the fronds became larger; a frond of 150 cm will turn over its length about 1,5 times at 8 m depth and only once at 14 m depth.

Holdfast production, though not calculated, is of major significance and holdfasts growing under optimal conditions may attain a biomass of 2,5 kg wet mass on a four-year-old plant (Fig. 4.1). Similar production was found in the stipes growing at 8 m depth (Table 4.3).

Between the first and second year of growth stipes turn over their mass eight times, and two times in their third year of growth to attain a mass of approximately 3,5 kg within four years.

The mean frond biomass turnover rate was 4,7 and 3,49 per year for plants of all sizes at Stations B and C respectively and this accounts for most of the total production by sporophytes. Since the fronds behave like moving belts of tissue, with growth at the base almost balancing the erosion at the tips, most of this production is lost as detritus to consumers in the ecosystem; the plants usually retain a slight net increase in frond area. Thus almost all of the 869 g carbon m^{-2} or 37699 kJm^{-2} of energy produced annually by

L. pallida in the 8 m depth zone becomes available as a primary food source to suspension feeders which form almost the entire animal biomass in that area (Field et al., 1977; Velimirov et al., 1977).

In addition to the tissue eroded from the fronds, estimates of productivity must include whole plants which became dislodged, especially during storms, and therefore became potentially utilizable as food for consumers. It is difficult, however, to assess mortality rates of L. pallida because of the many causal factors involved. Field et al. (1977) estimated that annual production through plant mortality was in the region of 15% of the total kelp biomass. This figure is realistic and indicates that net productivity as calculated in this study is probably an under-estimate. Another important factor not considered in this estimate of productivity by L. pallida is the release of dissolved organic carbon by the plant. Some workers (Sieburth, 1969; Khailov and Burlakova, 1969 and Johnston et al., 1977) have found that up to 40% of the products of gross photosynthesis may be released in soluble form by some laminarians.

The production of L. pallida, as assessed in this study, is therefore an under-estimate of the ultimate annual production by these plants. Westlake (1963), in a review of plant productivity in all kinds of habitats, concluded that Laminaria growing in 'good sites' probably produced 2,6 to 3,1 kg m^{-2} yr^{-1} dry matter and that the best site produced 4,8 kg m^{-2} yr^{-1}. L. pallida fronds alone were capable of producing 3,446 kg m^{-2} yr^{-1} dry matter, growing under apparently optimal conditions.

Though the estimate of L. pallida production is probably a conservative one, it indicates the significance of this kelp as a primary producer in the coastal waters of the Cape. Furthermore, the information on seasonal growth rates, age, chemical composition and other aspects of the autecology of L. pallida reported in this thesis is fundamentally important in research of a potentially exploitable natural resource - the 'kelp forest'.

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