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ADAPTATION OF *LAMINARIA GROENLANDICA* ROSENVINGE TO *IN SITU* LIGHT CONDITIONS ON A BATHYMETRIC GRADIENT AND FOR TWO YEAR CLASSES

by

Serge Villeneuve

B.Sc. Université de Montréal 1979

THESIS SUBMITTED IN PARTIAL FULFILLMENT OF

THE REQUIREMENTS FOR THE DEGREE OF

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of

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APPROVAL

NAME: Serge Villeneuve

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ABSTRACT

Environmental parameters such as light, nutrients and temperature may vary greatly seasonally and with depth. Consequently, such variations may bring about morphological and physiological adjustments in plant growth. In this study, I investigated some plant responses for two year classes of *Laminaria groenlandica* Rosenvinge. The 1st year plants were obtained from laboratory cultures and the 2nd year plants from a nearby kelp bed. The plants were maintained on a rope structure at constant depths between 1 and 12m below the surface. The growing season, in terms of net length increase, of the 1st year plants extended from March to September whereas 2nd year plants showed a net increase in length from January to July. The 1st year plants exhibited their highest blade elongation rate in June. At 1-3m the blade elongation rate of the 2nd year plants attained maximum values in March-April; lower maxima were attained in May at the deeper levels. Blade margin thickness increased from March to December and decreased with depth in late spring and summer. In December, the plants had lost between 40 and 65% of their total blade tissue; all 1m plants had died in summer. When expressed on a wet weight or surface area basis, the total photosynthetic pigment (chl *a*, chl *c* and fucoxanthin) concentrations increased as the growing season advanced. Pigment concentrations remained constant or decreased slightly with depth. The chlorophyll *c* to chl *a* and the fucoxanthin to chl *a* ratios did not vary seasonally except in June for the 1st year

plants but not in a predictable pattern on a bathymetric gradient. The light saturated rate of photosynthesis (Pmax) varied inversely with the photosynthetic pigment concentration, being maximal in spring and minimal in fall for the 2nd year plants. Incomplete data for the 1st year plants indicate that Pmax increased from April to August and then decreased in November. The initial slope (α) of the photosynthesis-irradiance curve varied in a way similar to Pmax. The photosynthetic and growth related data can be interpreted in relation to some environmental parameters. Whereas light may be a limiting factor year around at depth, it may attain inhibiting levels in shallow waters in the summer. This situation, coupled with a near to zero concentration of nitrate in spring and summer in shallow waters, may be responsible for the differences in growth patterns observed along the depth gradient. The 1st year sporophytes of *L. groenlandica* seem unable to adjust to as broad a range of environmental parameters as the 2nd year plants of this species. The 1st year plants appeared to follow a light cycle and 2nd yeat plants a nutrient cycle. Aspects of their behavior can best be related to genetic variation.

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Many people deserve recognition for their assistance in this project. First, I would like to express my sincere gratitude to my supervisor Dr. Louis D. Druehl for his pertinent suggestions, moral and financial support and his never failing patience towards a graduate student who arrived in his laboratory with a limited knowledge in phycology and an even more restricted knowledge of the english language. Merci mille fois Louis. I am indebted to the other members of my committee, Drs. W. Vidaver and G. Lister for their valuable comments during the course of this study.

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TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

INTRODUCTION

Growth

The seasonal growth of *Laminaria* has been the focus of a large body of research in the last four decades, starting with the growth studies of Parke (1948) on *L. saccharina* (for a review, see Kain, 1979). Most studies demonstrated a fast growth period from January to June , followed by a slow growth period during the second half of the year.

Initially, temperature and light were regarded as the limiting factors regulating the seasonal growth of *Laminaria* (Parke, 1948; Tseng *et al*, 1957; Sundene, 1962, 1964). Black and Dewar (1949) were the first to relate the seasonal variation of some chemical constituents in *L. saccharina* and *L. cloustoni*, with the seasonal changes in ambient nutrient concentrations. By the end of the sixties and during the following decade, much controversy arose on the importance of nutrient levels in sustaining summer growth or on the role of reserve carbohydrates on the onset of growth in late winter-early spring (Lüning, 1969, 1979; Lüning *et al*, 1973; Chapman and Craigie, 1977, 1978; Hatcher *et al*, 1977; Johnston *et al*, 1977; Gerard and Mann, 1979; Chapman and Lindley, 1980; Gagné *et al*, 1982).

Some reports on the seasonal growth of *Laminaria* dealt with plants in their first year (Tseng *et al*, 1957; Sundene, 1962, 1964; Lüning, 1979) or with mature plants, i.e. plants in their second year or older (Kain, 1963, 1976; Mann, 1972; Calvin and Ellis, 1981; Abe *et al*, 1983). The growth of juvenile sporophytes up to their third or forth year was also investigated (Hasegawa, 1962; Pérez, 1969, 1970; Sasaki, 1969; Kawashima, 1972; Braud, 1974). None of these authors looked, during the same growth season,at the possibility of a different seasonal growth pattern between plants in their first year and older ones. Chapman (1974) suggested that the first year plants of perennial laminariacean species may behave like annual species of the same family.

Earlier studies on a bathymetric gradient were performed in natural *Laminaria* beds and did not reveal a pronounced decrease in growth rate with increasing water depth as would be expected from the decline in photosynthetic photon flux density (Kain, 1967, 1977; Jupp and Drew, 1974). This has been attributed to the reduction in plant density with depth, resulting in the shallower plants being more self-shaded than the deeper plants. John (1970) and Boden (1979) used buoyed artificial structures to evaluate the variation in *Laminaria* growth rate on a vertical gradient. The former study provided limited information due to the very long period between measurements (154 days) whereas the latter was limited to summer growth. The most extensive growth study related to depth is the work of Lüning (1979) on first

year sporophytes of *L. digitata*, *L. hyperborea* and *L. saccharina*. To my knowledge the only published report on the seasonal growth of *Laminaria* from the Pacific Northwest, is of a natural population of *L. groenlandica* on the coast of Alaska (Calvin and Ellis, 1981). Fallis (1916) studied the growth of *L. saccharina* and other Laminariaceae from Puget Sound (Wash., USA) but limited her observations to the months of July and August.

Photosynthetic studies

It has always been difficult to isolate the effects of light intensity (quantity) from those of spectral composition (quality) on the photosynthetic apparatus as both are altered with increasing water depth. Towards the end of the previous century, a concept arose to be later accepted as a dogma. The so-called 'theory of complementary chromatic adaptation' (Engelmann, 1883, 1884, quoted by Larkum and Barrett, 1983) stipulated that the red algae were better suited than the brown or green algae to grow at the lower limit of the photic zone owing to their phycobilin pigments which complemented the light field (green) at those depths. This hypothesis was used to explain the vertical distribution of the different seaweed Divisions. The green algae with their photosynthetic pigments similar to higher plants would be limited to shallow waters while the brown algae would occupy an intermediary vertical position between the green and red algae. To this phylogenetic

hypothesis, Gaidukov (1903, 1906, quoted by Ramus, 1982) put forth an ontogenetic (also referred to as 'phenotypic') corollary based on his studies with blue-green algae. These plants would adjust to changes in the spectral quality of light by complementary pigment changes. Both hypotheses of complementary chromatic adaptation were widely accepted until recently despite early criticisms that light intensity was solely responsable for these pigment changes (Berthold, 1882, Oltmann, 1892, 1905, quoted by Larkum and Barrett, 1983). In the last decade, the universality of these hypotheses has been refuted. Ramus (1981, 1982) and Larkum and Barrett (1983) have reviewed the subject exhaustively . Green and brown algae have been found at great depths along with red algae (Crosset *et al*, 1965; Drew, 1969). True complementary chromatic adaptation has been reported for some but not all blue-green algae (Tandeau de Marsac, 1977; Bryant, 1981) and never in other algal Divisions (Bogorad, 1975; Larkum and Barrett, 1983).

Using a green mutant lacking phycoerythrin and a wild (red) population of the red alga *Gracilaria tickvahiae*, Ramus and van der Meer (1983) demonstrated that the green mutant showed similar growth and photosynthetic capacities in white and green light fields; thus invalidating the presumed advantages of phycoerythrin to fill the 'green window'. In a subsequent paper, Ramus (1983) presented similar results for species of brown, green and red algae. Using photosynthetic action spectra, Dring (1981) modelled the photosynthetic efficiency of selected

Chlorophyta, Phaeophyta and Rhodophyta in different optical water types (Jerlov, 1968). He concluded that the Rhodophyta were best adapted chromatically to photosynthesize in all water types but the clearest oceanic waters. However, field observations on the vertical distribution of benthic algae as well as physiological and morphological evidence led him to recognize that such a distribution was more a response to light intensity. This is not to say that algae do not show other forms of chromatic adaptation (for a review, see Larkum and Barrett, 1983). Green and red algae are known to undergo large variations in their ratio of accessory pigments to chlorophyll *a* (Calabrese, 1972; Waaland *et al*, 1974; Ramus *et al*, 1976a; Rhee and Briggs, 1977; Li and Titlyanov, 1978; Lapointe, 1981; Rosenberg and Ramus, 1982). Brown algae, however, display smaller variations in their photosynthetic pigment ratios (Duncan, 1973; Ramus *et al*, 1977; Wheeler, 1980; Perez Bermudez *et al*, 1981; Smith *et al*, 1983; Lewey and Gorham, 1984; Wheeler *et al*, 1984). The observed concomitance between the increase in pigment content with increasing water depth is now perceived as an adaptation to the quantity of incident light (PFD, photon flux density) Similar pigment responses have been obtained for macroalgae along a bathymetric gradient or inhabiting shallow water grottos where the PFD decrease is more pronounced relative to spectral changes (Crosset *et al*, 1965; Li and Titlyanov, 1978).

The seasonal photosynthetic performance and/or capacity of a variety of macroalgae is well documented (Lüning, 1971, 1979; Mathieson and Norall, 1973; Zavodnik, 1973; Littler and Murray, 1974; King and Schram, 1976; Brinkhuis, 1977a, 1977b; Drew, 1977; Hatcher *et al*, 1977; Johnston *et al*, 1977; Chock and Mathieson, 1979; Littler *et al*, 1979; Wheeler, 1980; Matsuyama, 1983; Smith *et al*, 1983; Wheeler *et al*, 1984). However few studies have dealt with the effect of depth on the light dependent or light saturated rate of photosynthesis in marine macroalgae (Drew *et al*, 1976; Ramus *et al*, 1976b, 1977; Lüning, 1979; Wheeler, 1980; Smith *et al*, 1983).

The light-saturated rate of photosynthesis (Pmax), on a per cell or surface area basis, has been found to vary inversely with depth while the slope of the light-limited rate of photosynthesis (α) showed a positive correlation with depth (Prézelin, 1981; Ramus, 1981; Larkum and Barrett, 1983; Richardson *et al*, 1983).

In this study, I investigated the seasonal adaptation of first (1st) and second (2nd) year plants of *L. groenlandica* on a bathymetric gradient according to their growth, photosynthetic pigment composition and photosynthetic performance.

MATERIAL and METHODS

Environmental data

Nitrate concentrations were monitored weekly at the surface and at depths of 1, 4, 7 and 10m. Soon after collection, the water samples were filtered, frozen and later analysed with a Tecknicon II autoanalyser, according to the methods described in Strickland and Parsons (1972). Temperature and salinity were determined at the depths mentioned above and at 2m. Photosynthetic photon flux density (PPFD) was measured at midday with a Li-Cor quantum meter (Lambda, model 185) above and just below the surface, from 1 to 5 m and at 7, 9 and 12m.

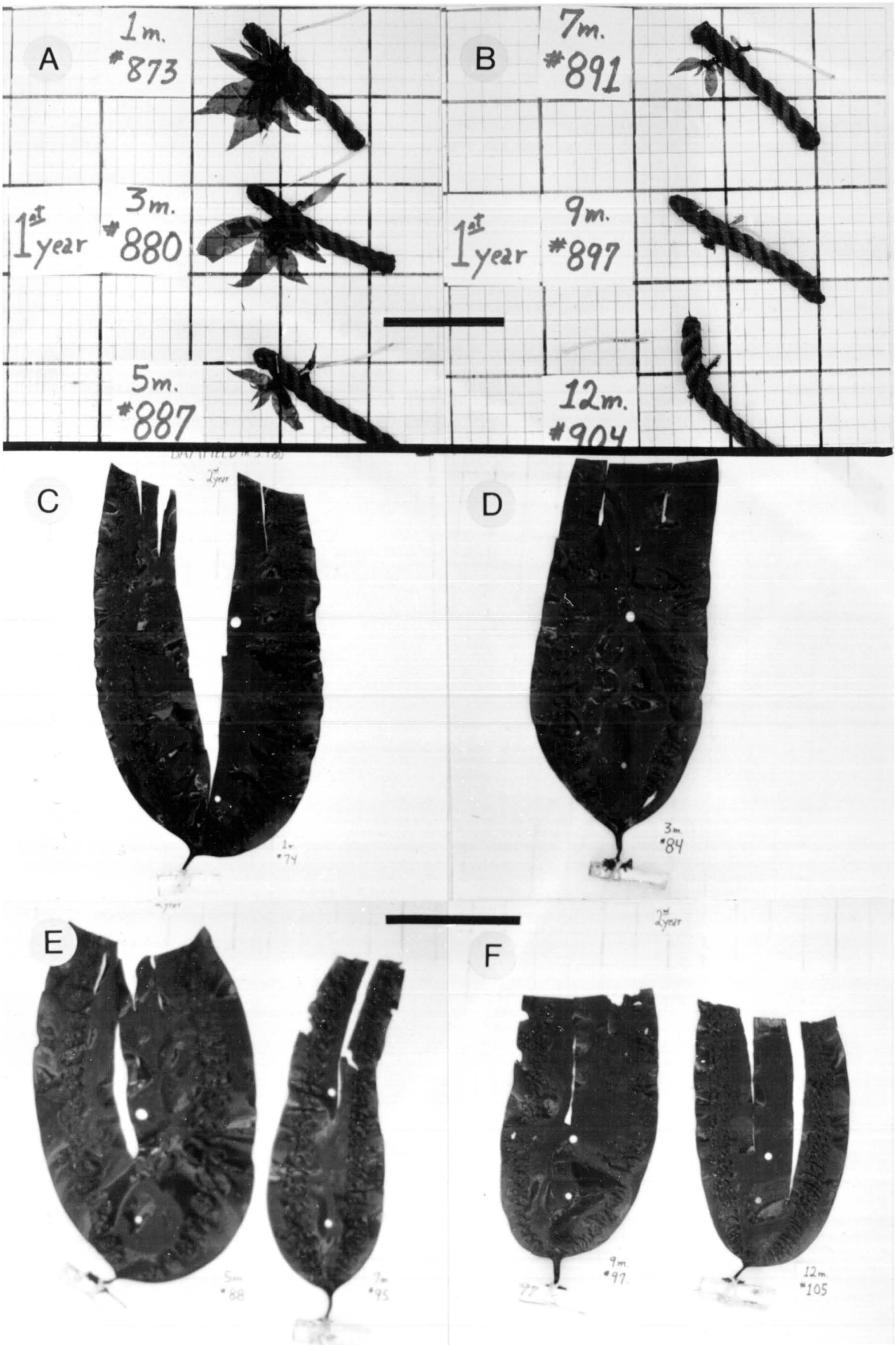
Collection of plants and farm description, 1980

The 1st year sporophytes of *L. groenlandica* were obtained from cultures according to the methods of Druehl (1980). A small piece of hydrophillic rope supporting small sporophytes (*ca* 4 mm long) was inserted in a 10 cm long, 1.2 cm diameter polypropylene rope (Fig 1,A and B) and secured on the farm. The second year sporophytes were collected by SCUBA on March 13 at Aguilar Point, at the mouth of Bamfield Inlet, Barkley Sound, B.C., Canada . These plants were attached by a rubber band to a

Figure 1. Photographs of 1st and 2nd year plants of *L. groenlandica* from the 1980 growth experiment.

The plants were photographed April 5, 1980.
(A-B, bar= 5 cm ; C-F, bar= 20 cm)

A. 1st year plants at 1, 3 and 5m.
B. " " " " 7, 9 and 12m.
C. 2nd " " " 1m.
D. " " " " 3m.
E. " " " " 5 and 7m.
F. " " " " 9 and 12m.


A
1m.
#873
3m.
#880
1st year
5m.
#887
B
7m.
#891
9m.
#897
1st year
12m.
#904
C
2nd year
1m
#74
D
3m
#84
E
5m
#88
7m
#95
F
2nd year
9m.
#97
12m.
#105

small piece of PVC pipe cut in half lengthwise (Fig 1,C-F) and then secured on the farm March 15.

The kelp farm consisted of 1inch PVC pipes 3 m long maintained at the constant depths of 1,3,5,7,9 and 12m by vertical 0.5in polypropylene ropes buoyed by floats (see figure 2 for general orientation). These ropes were anchored by 50 kg concrete blocks (see Druehl, 1980 for anchoring details). Six second year sporophytes and 6 clusters of first year sporophytes, later thinned to 1 or 2 sporophytes per clump, were attached at 30 cm intervals at each depth. The farm was established at the mouth of the Bamfield Inlet, a wave sheltered site.

Growth measurements

The growth parameters analysed were the blade length, blade margin thickness at 10 cm from the transition zone and the blade elongation rate, by following the distal movement of a hole (diameter=0.6cm) punched at 10 cm from the transition zone (Parke, 1948; Sundene, 1964). A new hole was punched at each measuring session. The term 'potential blade length' refers to the total length of blade tissue produced, assuming no distal erosion occurred; it was computed by adding the blade growth increment at each measuring session to the initial blade length. During the active growth period, from March to June, the plants were measured at three week intervals and subsequently at an

interval of four to five weeks. The plants were brought to the laboratory in the morning and kept in a holding tank with running seawater from the Bamfield Marine Station seawater system (intake depth= 25 m). They were returned to the farm later the same day or the following morning.

Collection of plants and farm description, 1981-1982

A 30m long farm (Fig 2) was established in January 1981 at the mouth of Bamfield Inlet. The purpose of this farm was to determine the late winter growth response of *L. groenlandica* and provide experimental plants for photosynthesis studies. The second year sporophytes were carefully chosen in order to be of a similar morphology and size (Fig 3). All second year plants bore sori distally on the tissue persisting from the previous growth season. Sixty clusters of 1st year sporophytes, later thinned to one or two plants, and sixty 2nd year sporophytes were attached at 25 cm intervals at 1,5,7 and 9m below the surface. The ropes holding the plants were brought to the surface and the plants were measured on site at 2-3 month intervals until June 1982.

In January 1982, 15 plants of both age classes were added to each depth of the 30m long farm. These plants were measured at the same periods as the 1981 set.

Figure 2. Diagram of the 30m kelp farm used for the 1981 and 1982 growth experiments.

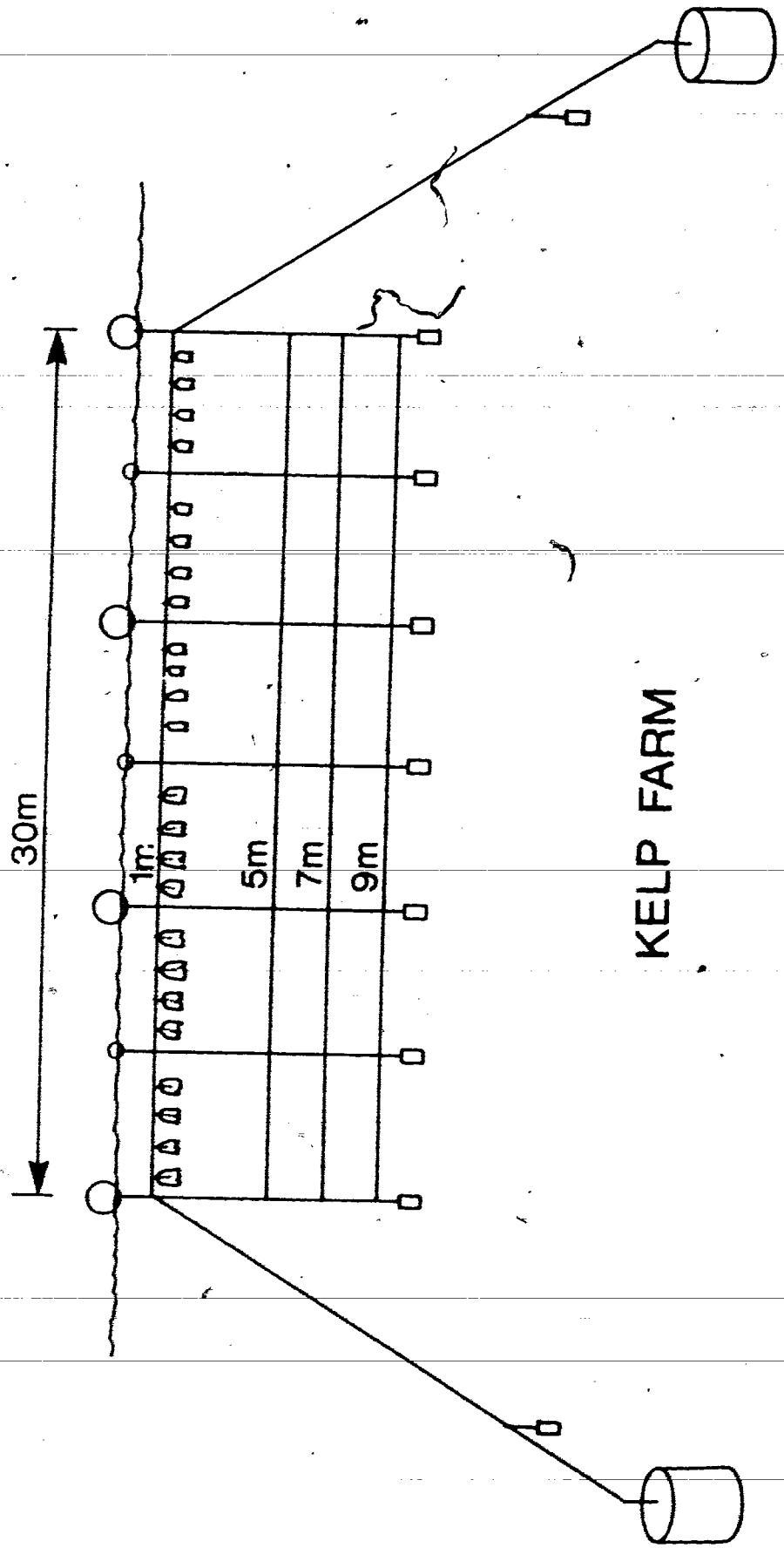
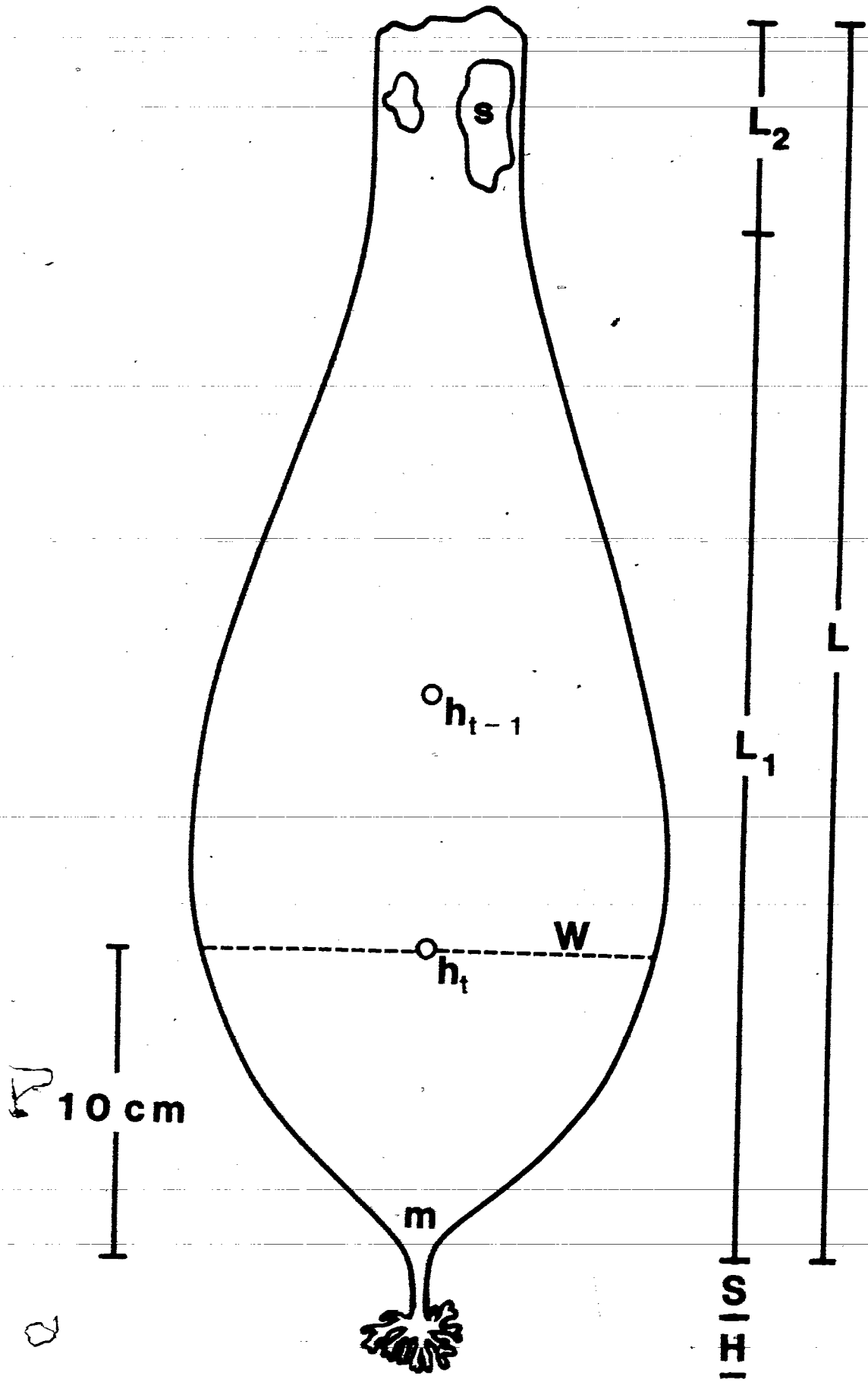

30m
1m
5m
7m
9m
KELP FARM

Figure 3. Diagram of a 2nd year plant of *L. groenlandica* used for the 1981 and 1982 growth experiments on the 30m kelp farm.

H= Holdfast
S= Stipe
L= Lamina, L_1= New tissue
L_2= Old tissue
s= sorus
m= region of intercalary meristem
h t= hole punched at this measuring session
h t-1= hole punched at the previous measuring session


s
L_2
L_1
L
h_{t-1}
h_t
W
10 cm
m
S
H

Pigment extraction

Chlorophyll *a* (chl *a*), chlorophyll *c* (chl *c*) and fucoxanthin (fx) were analysed according to the DMSO method of Seely *et al* (1972) with the modifications proposed by Wheeler (1980). One disc per plant, 3.1cm in diameter, was punched 10-15cm from the transition zone or the entire blade was used when the plant was a few cm long. All analyses were initiated within 15 min of collection. Extractions were performed plus or minus 2 hours from zenith time. Optical densities were read with a Perkin-Elmer spectrophotometer (model 139).

Oxygen exchange

Plants were collected from the farm the day prior to the experimental period. The plants were trimmed distally and laterally (if necessary) in order to fit the holding frame as shown in figure 4 and cleaned of all visible epiphytes. They were then maintained overnight at the depths at which they occupied on the farm. Generally two plants were used per experiment; however 3-5 plants per chamber were used at times for small plants (1st year plants). Three size chambers of 32.2, 9 and 4.5 l were used (Fig 4), although most experiments were performed in the large chambers. For the 2 h experiments, the biomass to volume ratio ranged from 0.40 to 2.17 g dw.l^{-1} in the large chamber, from 0.26 to 0.65 g dw.l^{-1} in the medium chamber

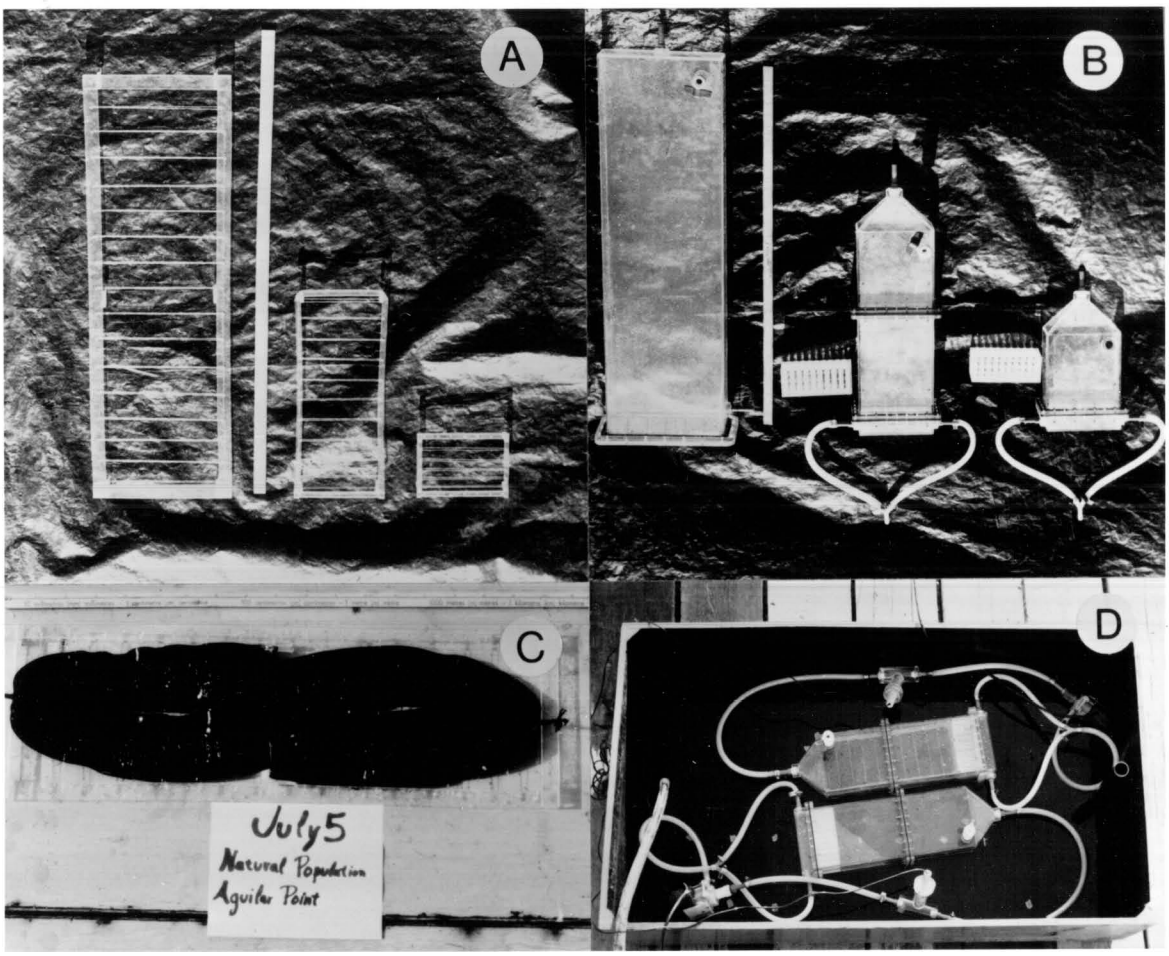
Figure 4. Photographs of the experimental set-up for the photosynthesis experiments.

A. Frames used to hold the plants in the chambers (the 1 m ruler gives the scale).

B. The 32, 9 and 4.5 l chambers used for the photosynthesis experiments (the 1 m ruler gives the scale).

C. Two plants (trimmed distally) per experiment were used in the 32 l chamber.

D. The 9 l chambers with their oxygen electrode and submersible pump mounted in series in the cooling tank.


A
B
C
July 5
Natural Population
Aguilar Point
D

and from 0.15 to 0.42 g $dw.l^{-1}$ in the small chamber. These ratio fall within the limits recommended by Johnston (1969): 0.1-0.3 g $dw.l^{-1}$ for 24h experiments. Submersible pumps (March epoxy-clad pump, model LC-2C-MC) circulated the water within the chambers at the rate of 14.8 $l.min^{-1}$. One experiment was carried out at a time along with a control. The experimental chambers, the submersible pumps and the oxygen electrodes, with their holding chambers installed in series, were maintained in a cooling tank as illustrated in figure 4. A Jacuzzi pump insured a constant flow of seawater in the cooling tank and provided water for the experimental chambers. The Jacuzzi intake could be lowered to the appropriate depth in such a way as to supply the experimental chambers with water typical to the depth the plants under investigation had been grown. Once the experimental chambers were sealed, the plants were acclimatized for 10 min to low light and subsequently exposed for 20 min to a series of increasing PPFD: 15, 36, 67, 85, 130 and 265 $\mu E.m^{-2}.sec^{-1}$. The light panel, consisting of 16 'daylight' fluorescent tubes (General Electric, model F40D), could be moved vertically in order to provide the appropriate PPFD. Following the light treatment, the plants were maintained in darkness for 30-60 min in order to assess dark respiration. Oxygen exchange in this closed system was monitored with an oxygen electrode (YSI, model 5739) and an oxygen meter (YSI, model 57). The oxygen electrode was air calibrated at ambient seawater temperature and was checked for calibration drift at the end of each experiment. All

photosynthetic experiments were conducted within 3h of zenith time.

Plant substantiality and C-N analysis

Soon after the photosynthetic measurements, the plant fresh weights were recorded. The plant surface area was calculated by tracing its outline on paper. The latter was then weighed and equated to a given surface area obtained from linear regression analysis between the weights and the known surface areas of paper samples. The plants were oven dried at 60°C for 48 hours and then weighed.

Kawashima (1972) defined the substantiality as the fresh weight per unit of surface area (mg $fw.cm^{-2}$). I used this index of tissue density for both fresh and dry weights. The plant substantiality data are derived from the above material.

The dry tissues were ground, subsampled and analysed for total nitrogen and carbon content with an elemental analyser (Carlo Erba, model 1106).

RESULTS

Environmental Parameters

The seasonal and bathymetric variations in temperature and nitrate concentration, over a two year period, are summarized in figure 5. At 1m, the temperature ranged from 8-10°C in January-February to 14-16°C in July-August. A similar pattern but with a smaller range of values was recorded for the greater depths. From October to April, no bathymetric difference in temperature was detected at the depths studied.

Nitrate values from October to March were similar at all depths and rarely fell below 6 µM (Fig 5). At 1 and 4m the early spring nitrate decline was more pronounced and lasted for a longer period than at 7 and 10m. The nitrate concentration at 1m never exceeded 2 µM from May to August. Following the early spring decline, the nitrate level at 7 and 10m increased from May to September, then declined until November to rise again in the following months to levels above 10 µM. Intermediate values were observed at 4m in spring and summer.

The annual variation in the incident photon flux density (PFD) above the water surface (Fig 6) may not always correspond to a similar seasonal pattern underwater. The extinction coefficient (K), computed from the instantaneous weekly light

Figure 5. Seasonal and bathymetric variations in seawater temperature and nitrate concentration.

1m=solid line.
4m=dotted line.
7m=chaindotted line.
10m=dashed line.

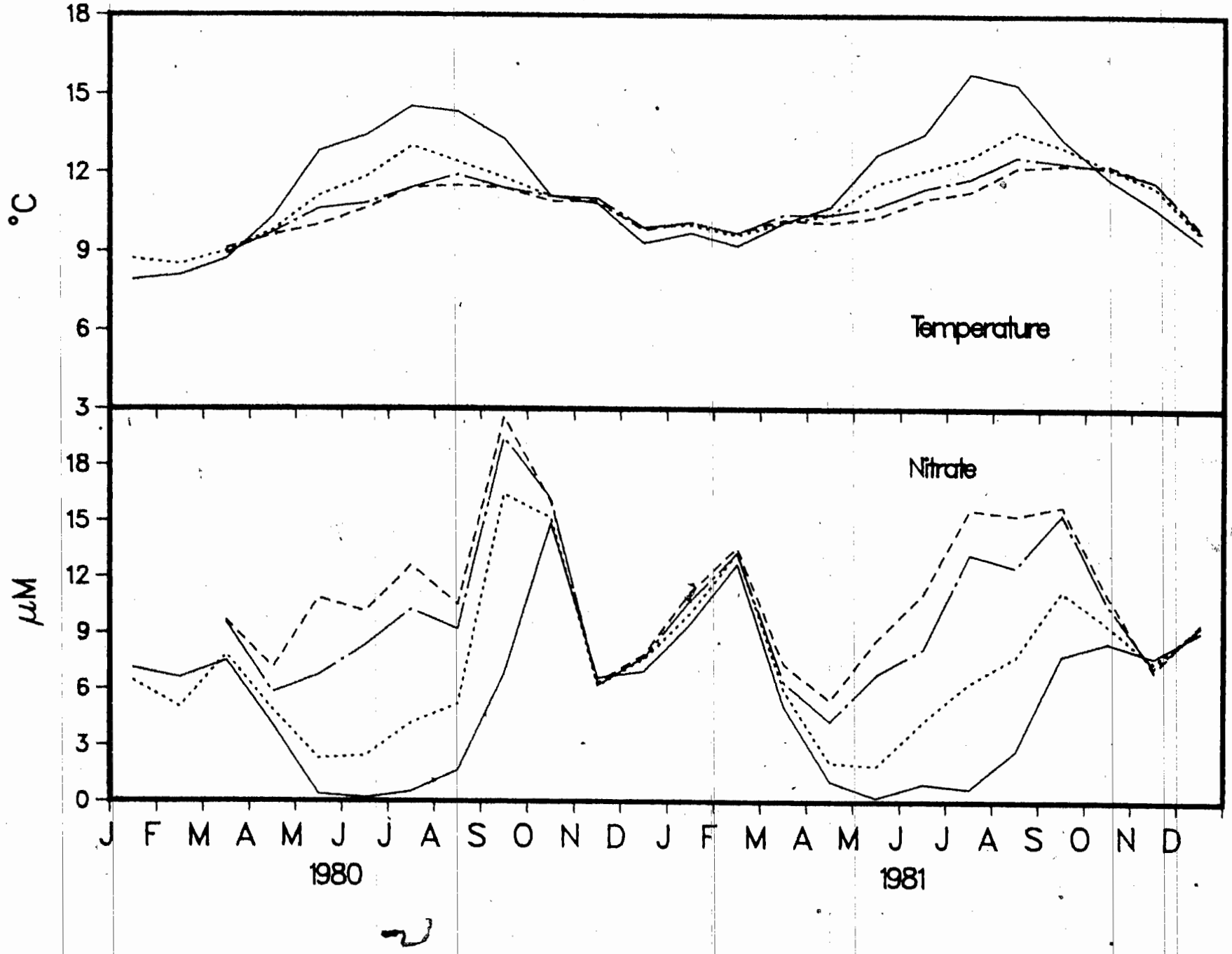
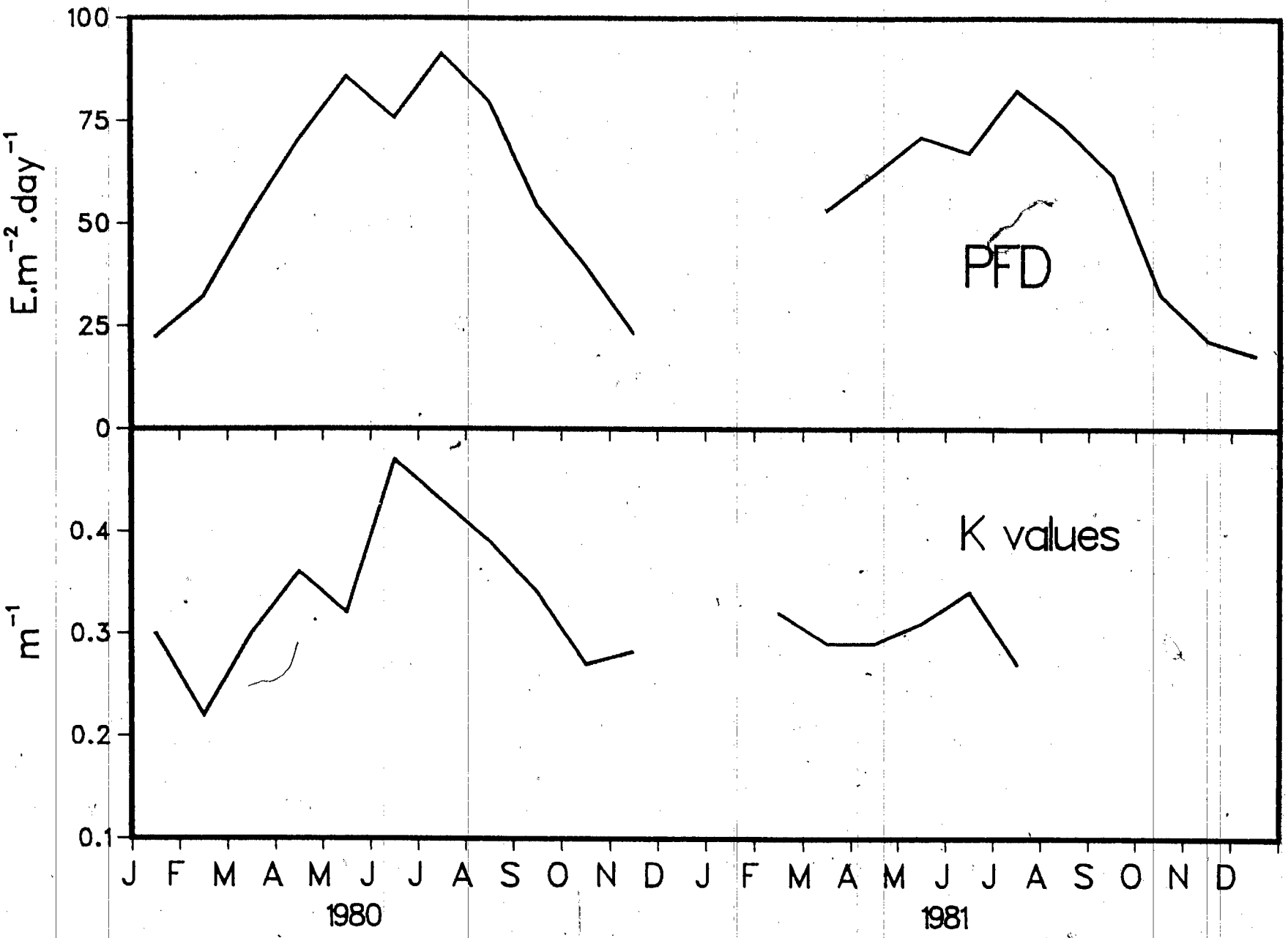

°C
18
15
12
9
6
3
Temperature
µM
18
15
12
9
6
3
0
Nitrate
J F M A M J J A S O N D J F M A M J J A S O N D
1980
1981

Figure 6. Seasonal variation in incident photon flux density (PFD) and extinction coefficients of the water column (K).

The pyrheliometer data, from Carnation Creek, were kindly provided by Dr. J.C. Scrivener (Pacific Biological Station, Nanaimo).

K values (monthly average) are computed from weekly light readings at 1 and 5m.


100
75
50
25
0
E.m^{-2}.day^{-1}
PFD
0.4
0.3
0.2
0.1
m^{-1}
K values
J F M A M J J A S O N D J F M A M J J A S O N D
1980
1981

measurements at 1 and 5m depth, followed a pattern similar to the surface illumination being maximum in summer and minimum in winter (Fig 6). Consequently, the high turbidity of the water in summer attenuated the seasonal submarine illumination peak. The highest light reading measured weekly at 12m was 60 $\mu E.m^{-2}.s^{-1}$ in July 1981 (Table 1); a value below the saturating PPFD for photosynthesis in *L. groenlandica* (see Fig 15). Only twice was this saturating level (85 $\mu E.m^{-2}.s^{-1}$) surpassed at 9m. In 50% of the cases, the PFD was higher than 400 $\mu E.m^{-2}.s^{-1}$ at 1m.

Potential blade length and blade elongation rate

Blade elongation was measured as the tissue increment in the first 10cm of the blade (from the transition zone). However, as pointed out by Parke (1948) and Sundene (1964), some growth may occur beyond this region. Therefore the actual blade length may at times exceed the value of the potential blade length, This was particularly true for the 2nd year plants where, in April 1980, growth beyond 10cm from the transition zone accounted for as much as 30% of the total increase in length (Fig 10).

1st year plants

The plants started to grow in March 1980. At this time, the blade elongation rate decreased with depth (Fig 7). In April, the 1m plants degenerated rapidly and their blade elongation

Table 1: Maximum monthly light readings ($\mu E.m^{-2}.s^{-1}$) measured weekly at midday.

DATE	DEPTH						
	Above Surf.	1m	3m	5m	7m	9m	12m
Jan'80	400	121	54	31	-[1]	-	-
Feb	500	228	127	74	-	-	-
Mar	870	402	268	160	-	-	-
Apr	1200	603	335	214	134	87	47
May	430	255	121	74	47	36	19
Jun	1075	630	255	100	55	43	34
Jul	750	201	79	43	21	11	6
Aug	700	402	134	72	48	34	21
Sep	760	335	121	58	34	25	19
Oct	720	402	201	120	75	54	34
Nov	-	-	-	-	-	-	-
Dec	-	-	-	-	-	-	-
Jan'81	-	-	-	-	-	-	-
Feb	480	281	121	60	40	30	16
Mar	940	536	228	147	80	51	30
Apr	850	261	98	71	50	36	28
May	1050	603	281	111	60	38	25
Jun	640	268	101	50	38	27	17
Jul	1500	670	375	188	134	91	60

[1]No data.

Figure 7. Seasonal and bathymetric variations in the blade elongation rate for 1st and 2nd year plants of *L. groenlandica* from the 1980 growth experiment.

(Initial N= 6)
In 1981, the plants were in their 2nd and 3rd year.

22b

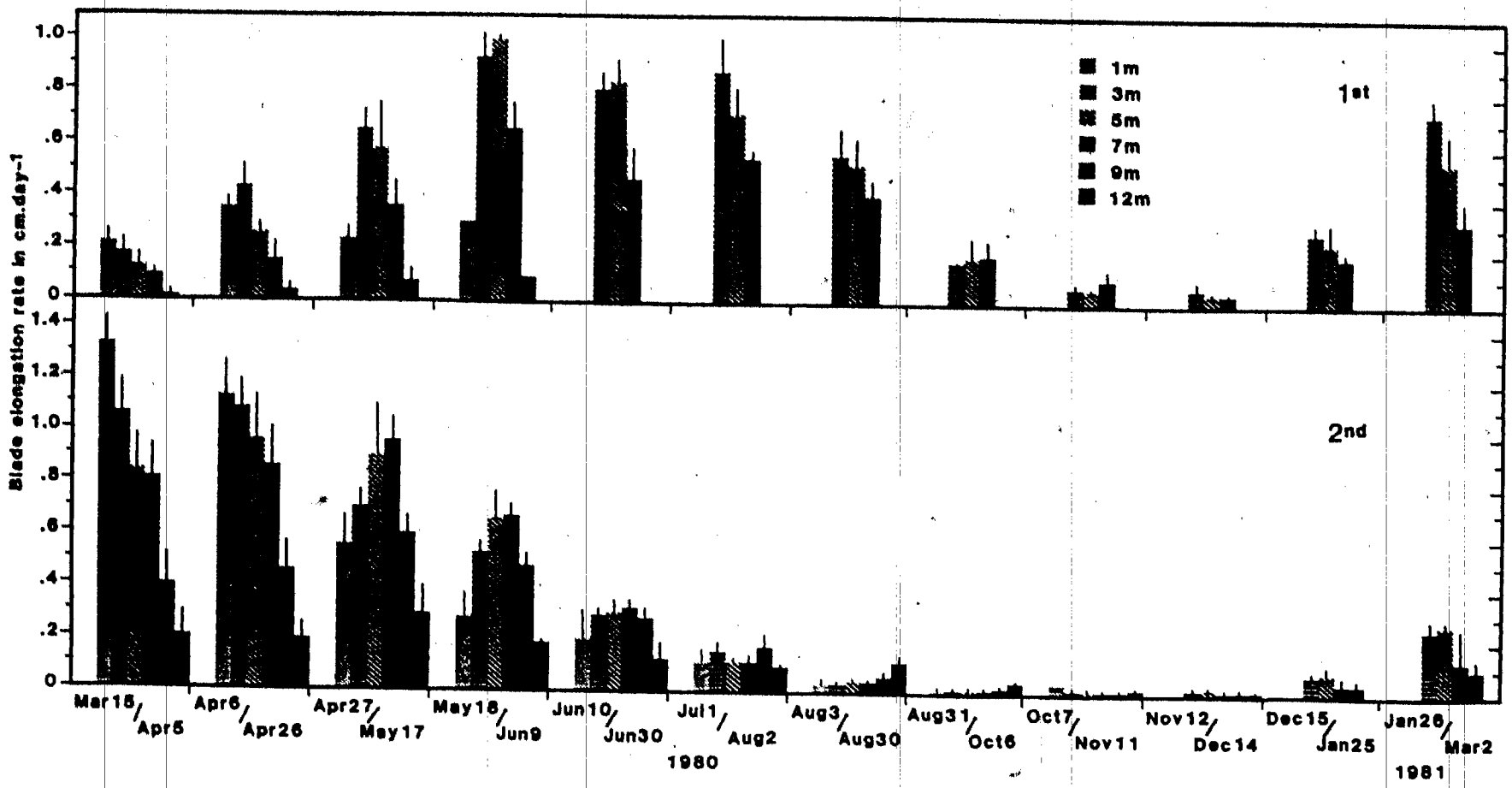

Blade elongation rate in cm.day-1
1.0
.8
.6
.4
.2
0
1m
3m
5m
7m
9m
12m
1st
1.4
1.2
1.0
.8
.6
.4
.2
0
2nd
Mar15/Apr5
Apr6/Apr26
Apr27/May17
May18/Jun9
Jun10/Jun30
Jul1/Aug2
Aug3/Aug30
Aug31/Oct6
Oct7/Nov11
Nov12/Dec14
Dec15/Jan25
Jan26/Mar2
1980
1981

Figure 8. Seasonal and bathymetric variations in blade length (bar) and potential blade length (curve) for the 1st year plants of *L. groenlandica* from the 1980 growth experiment.

(Initial N= 6)
In 1981, the plants were in their 2nd year.

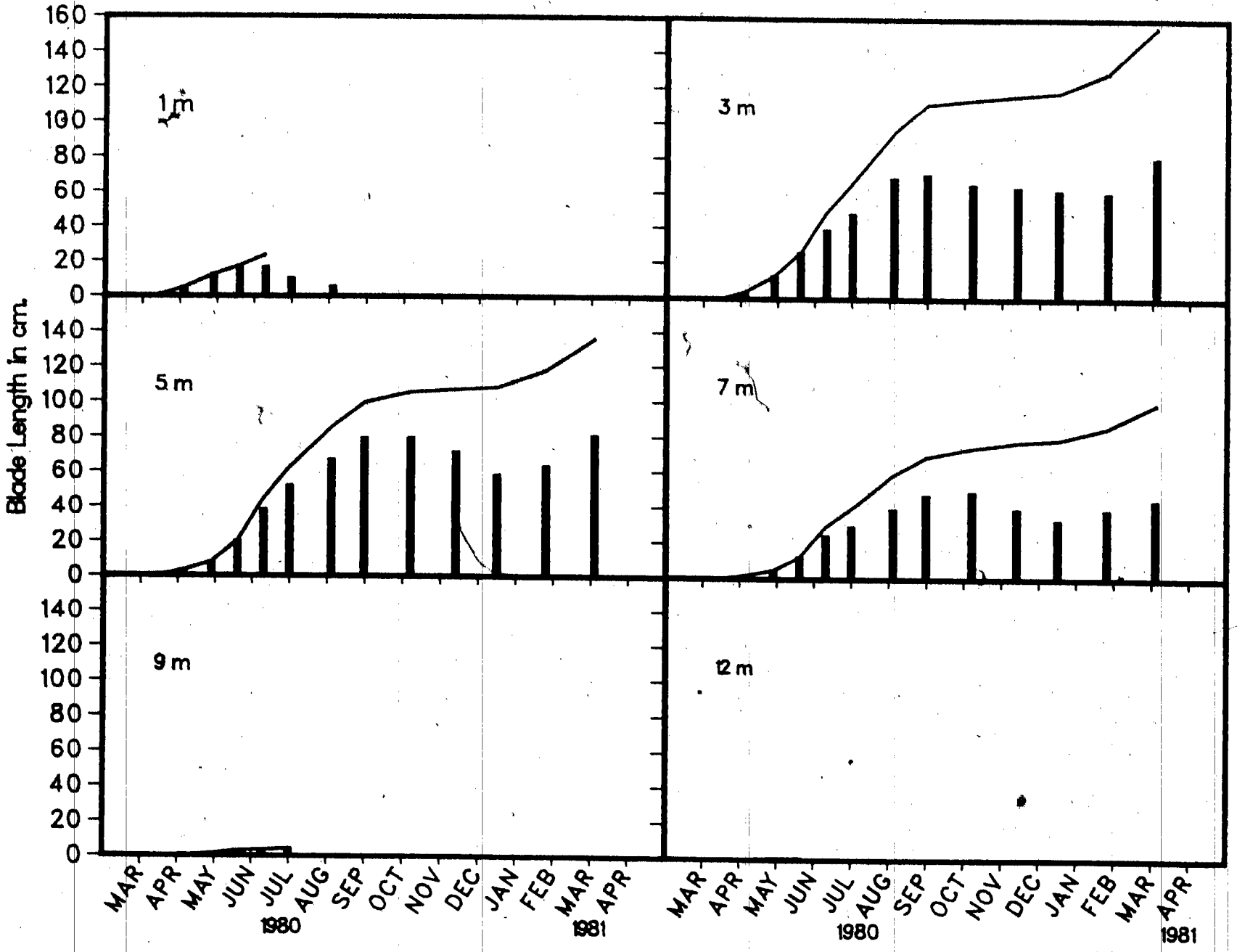
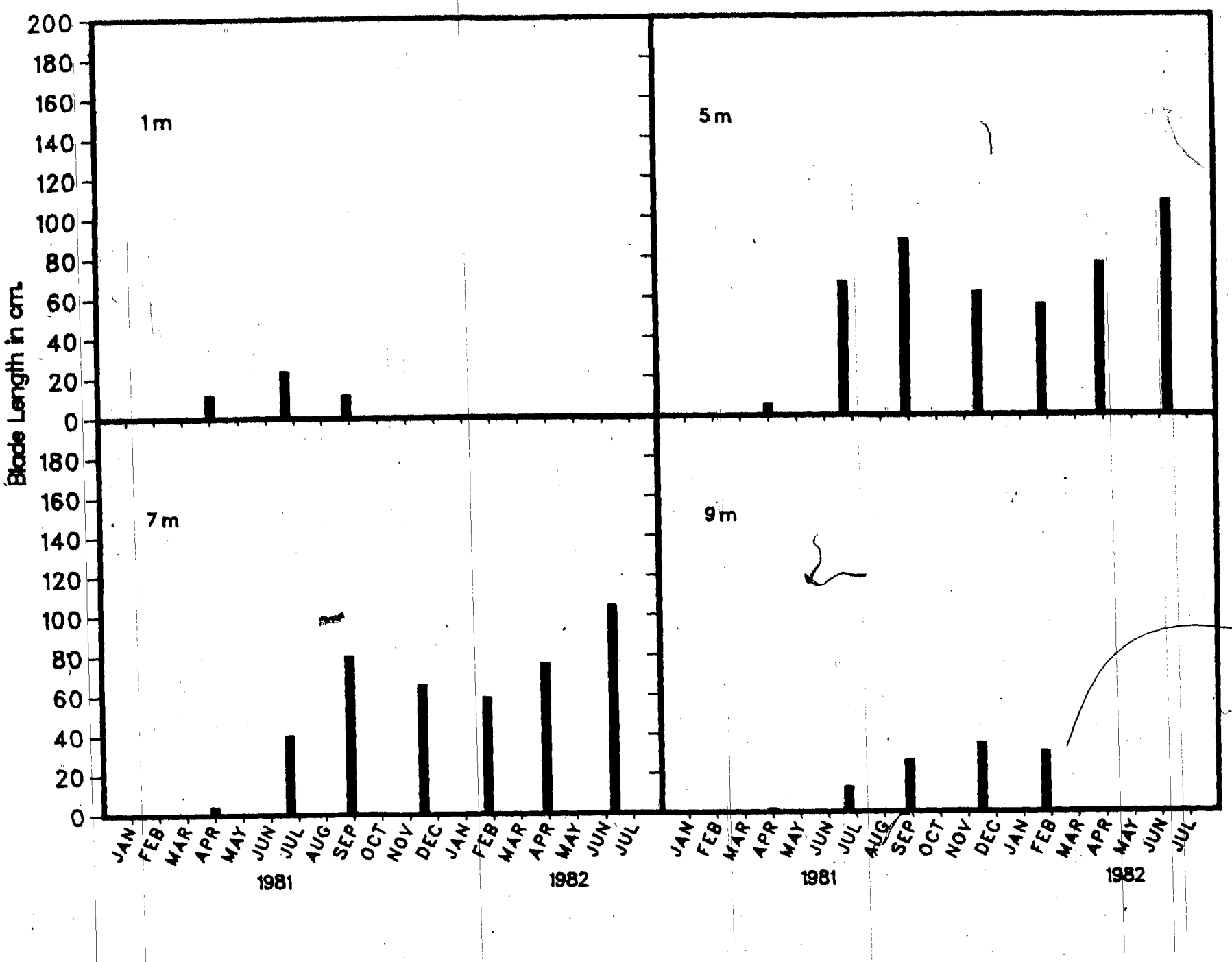

Blade Length in cm.
1 m
3 m
5 m
7 m
9 m
12 m
0
20
40
60
80
100
120
140
160
MAR
APR
MAY
JUN
JUL
AUG
SEP
OCT
NOV
DEC
JAN
FEB
MAR
APR
1980
1981

Figure 9. Seasonal and bathymetric variations in blade length for the 1st year plants of *L. groenlandica* from the 1981 growth experiment.

(Initial N= 60)
In 1982, the plants were in their 2nd year.


Blade Length in cm
200
180
160
140
120
100
80
60
40
20
0
1m
5m
7m
9m
JAN FEB MAR APR MAY JUN JUL AUG SEP OCT NOV DEC JAN FEB MAR APR MAY JUN JUL
1981
1982

rate declined gradually from then on. Consequently their potential blade length did not exceed 20-25cm (Fig 8). From 3 to 7m the blade elongation rate increased from March to the beginning of June where it ranged between 0.66 and 1.00 $cm.day^{-1}$. It maintained similar or slightly lower values until the end of July (0.55-0.88 $cm.day^{-1}$) and decreased steadily afterward. During the active growth period this rate was lower at 7m than at 3 and 5m where no substantial difference was detected (Fig 7). In the fall the blade elongation rate was minimal (<0.2 $cm.day^{-1}$) and did not vary with depth. In December, similar potential blade length values (108-118cm) were obtained at 3 and 5m, whereas 80cm of blade tissue were produced at 7m (Fig 8). The blade elongation rate at 9 and 12m was very low (<0.1 $cm.day^{-1}$); consequently these plants did not produce more than 5cm of blade tissue at 9m and 1cm at 12m (Fig 8) by August when the last plants had died at these two depths (Fig 8). The 12m plants and to a certain extent the 9m ones may have suffered when the kelp farm rubbed against an underwater cliff. Assuming a blade elongation rate of 0.1-0.2 $cm.day^{-1}$ as the minimal growth threshold, I arbitrarily defined March-September inclusively as the growth season for 1st year plants. The plants initiated active growth in January as they entered their second year. A decrease in blade elongation rate with depth was already evident by March; elongation rates ranged from 0.73 $cm.day^{-1}$ at 3m to 0.32 $cm.day^{-1}$ at 7m (Fig 7).

The potential blade lengths of 1st year plants were not evaluated for the 1981 growth season. However substantial increase in length between June and August indicated that their growth season was similar to that observed in 1980 (Fig 9).

2nd year plants

These plants displayed a marked difference in blade elongation rate ranging, in April 1980, from 1.3 to 0.2 cm.day^{-1} between 1 and 12m respectively (Fig. 7). The highest blade elongation rate shifted from 1-3m in April to 5-7m in May and June. At 1 and 3m the blade elongation rate remained high through April and decreased rapidly thereafter, while at 7 and 9m it increased slightly until May and then declined. In April, some of the 5m plants were damaged when handled; this may explain the lower rates at this depth in May. The blade elongation rate was greatly reduced at all depths in July and reached minimal values in the fall (Fig 7). As a result of this shift in highest blade elongation rate from shallow to deep water with time, the plants had produced, in December, similar length of blade tissue between 1 and 7m; the mean potential blade length at these depths varied between 110 and 116cm (Fig 10). The 9m plants showed a potential blade length of 85cm. At 12m the blade elongation rate remained low throughout the year and in December the potential blade length had attained 63cm (Fig 10). As stated earlier for the 1st year plants, the 12m

Figure 10. Seasonal and bathymetric variations in blade length (bar) and potential blade length (curve) for the 2nd year plants of *L. groenlandica* from the 1980 growth experiment.

(initial N= 6)
In 1981, the plants were in their 3rd year.

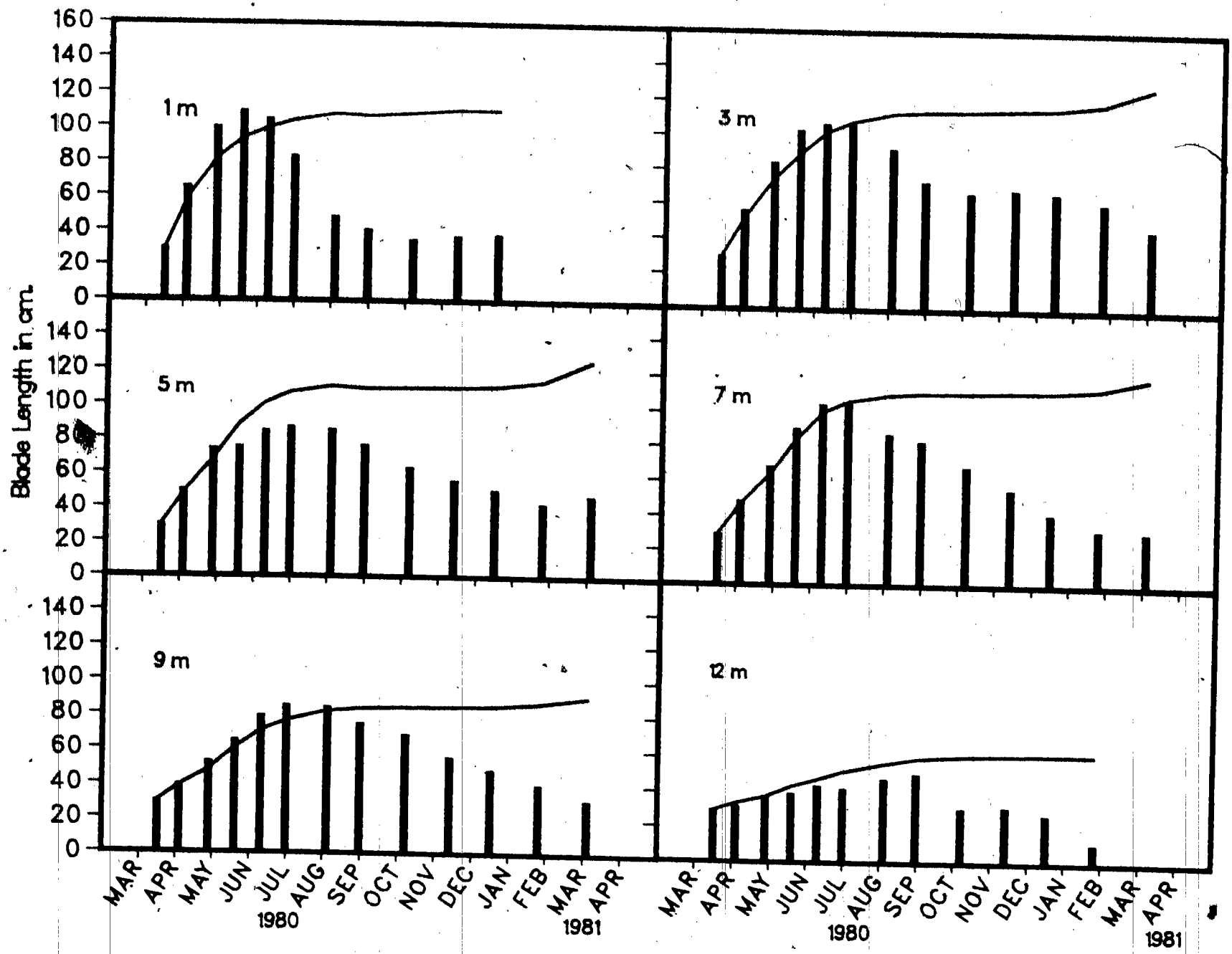
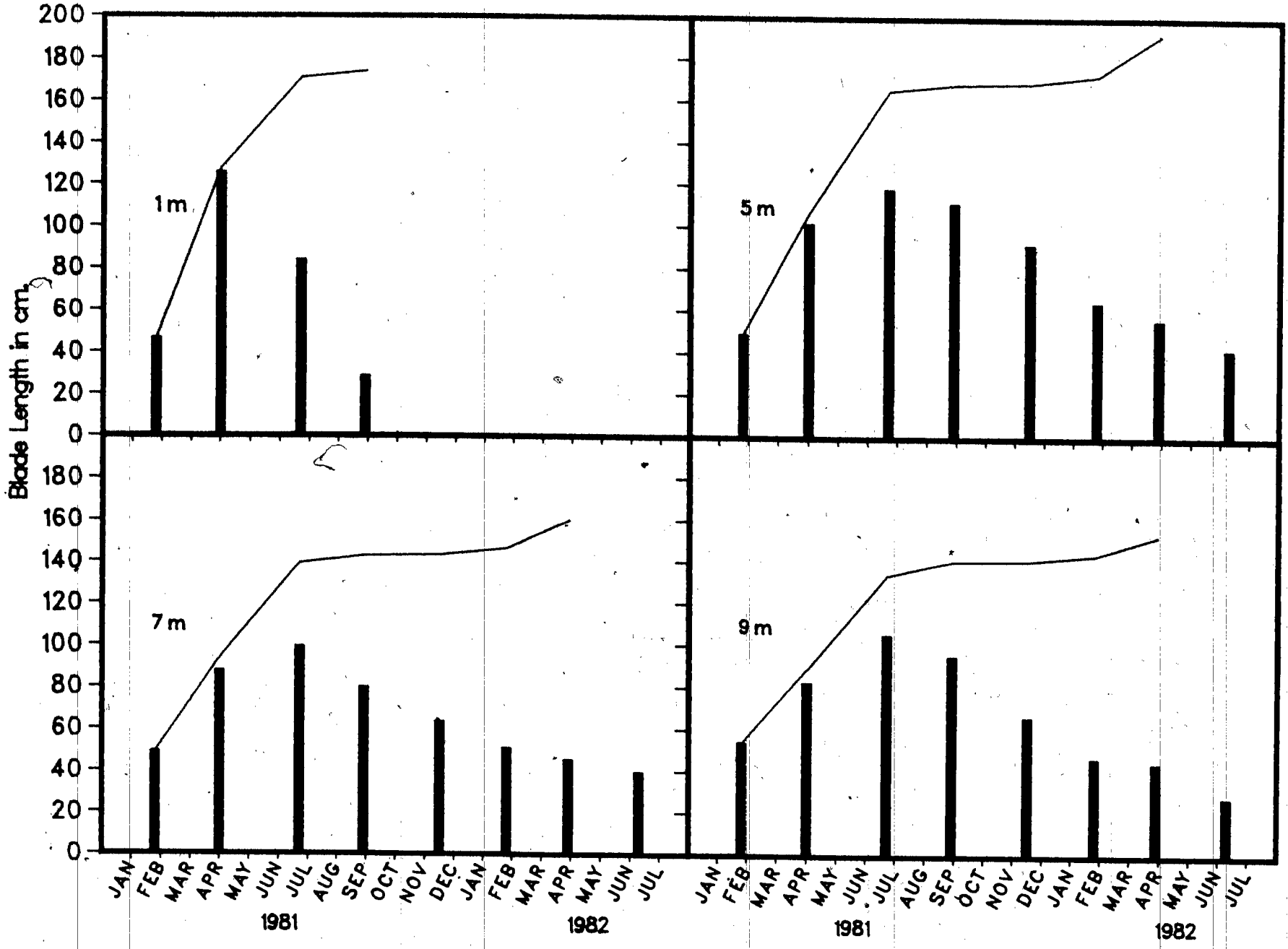

Blade Length in cm
1m
3m
5m
7m
9m
12m
0
20
40
60
80
100
120
140
160
MAR
APR
MAY
JUN
JUL
AUG
SEP
OCT
NOV
DEC
JAN
FEB
MAR
APR
1980
1981

Figure 11. Seasonal and bathymetric variations in blade length (bar) and potential blade length (curve) for the 2nd year plants of *L. groenlandica* from the 1981 growth experiment.

(Initial N= 60)
Bar=blade length
Curve=potential blade length
In 1982, the plants were in their 3rd year.


Blade Length in cm
200
180
160
140
120
100
80
60
40
20
0
1m
5m
7m
9m
JAN FEB MAR APR MAY JUN JUL AUG SEP OCT NOV DEC JAN FEB MAR APR MAY JUN JUL
1981
1982

plants and possibly the 9m ones suffered from physical disturbance. The 12m plants showed visible damage possibly caused by the purple sea urchin (*Strongylocentrotus purpuratus*) or the red sea urchin (*S. franciscanus*).

These potential blade length values for the 1980 growth experiment underestimate the blade growth potential. The experiment started in March, two months after this age class normally initiates growth, and the blades were trimmed at 30cm. From the 1981 growth experiment (Fig 11), it can be seen that the 1 and 5m plants had produced 170-173cm of blade tissue in November whereas 143cm were produced at 7 and 9m.

Using the same threshold of 0.1-0.2 cm.day^{-1}, the figure 7 data indicate that the active growth season of the 2nd year plants extended from January to July inclusively with a maximum rate in March in shallow water and lower maxima in May in deeper water. The onset of growth of these plants, now entering their 3rd year, occurred in January (Fig 7). In March 1981, after one year on the kelp farm, the 1st year plants (now in their second year) showed higher blade elongation rates than the 2nd year plants (now in their third year).

Blade length and erosion

1st year plants

The blade length data for the 1980 growth experiment are summarized in figure 8. The blade length was inversely related to depth in April; it ranged from 12-13cm at 1-3m to 1.1cm at 12m. The 1m plants reached their maximum blade length (17.2cm) in May. These plants were very pale and later became heavily epiphytized. By the end of August all plants had died at 1m. From 3 to 7m the plants attained their maximum blade length in August towards the end of their growth season. The 3 and 5m plants showed similar blade lengths, 71.6 and 79.3cm respectively, whereas the 7m plants were shorter (48.6cm) Afterward the distal erosion exceeded the intercalary growth and consequently the plants decreased in length. In December, the plants from 3 to 7m had lost some 45-48% of their blade tissue. Despite the fact that these plants initiated active growth in January, as they entered their second year, they did not show a substantial increase in blade length before the beginning of March due to the distal erosion of the previous year's tissue. The 9m plants reached 4.3cm at the end of June and the ones at 12m were 1.1cm long in May. By the beginning of August all plants had died at these two depths.

When the experiment was repeated in 1981, the growth pattern was similar seasonally but differed bathymetrically from 5 to 9m (Fig 9). No substantial difference in blade length was observed between the 5 and 7m plants. Many plants died at 9m but some plants (15%) survived until November when they reached their maximum blade length: 34.3cm.

2nd year plants

The blade length data for the 1980 growth experiment are summarized in figure 10. In April, blade length was inversely related to depth. The 1m plants reached their maximum blade length (109cm) in May; the length of the blade decreased rapidly afterwards due to a strong decline in blade elongation rate and a high distal erosion. From 3 to 12m, the plants attained their maximum blade length in June. As mentioned earlier, some of the 5m plants were damaged during manipulation; this may explain why their blade lengths were shorter than at 7m. From August to October the plants were of similar length between 3 and 9m. Only in November and December were the 3m plants longer than those from 5 to 9m. The 12m plants always had shorter blade lengths than at the other depths. By December, all plants regardless of depth, had lost between 40 and 65% of blade tissue produced during the preceding growth season. However in the summer months, the tissue loss tended to be greater in shallow (1-5m) than in deeper (7-12m) water; the reverse was true in fall (Fig 10).

The 1981 growth experiment produced data similar to the previous year (Fig 11). At the end of March, the blade length decreased with depth. The plants reached their maximum blade length in June except for the 1m plants which had a March peak in blade length. The longest blades occurred at 1m in the spring

and at 5m in the summer. Until the end of the year, the 5m plants retained a longer blades than did the 7 or 9m plants. By November 1981, some 46 to 53% of the blade tissue produced during that year was lost from the plants in the 5 to 9m range . At that time all plants had died at 1m.

Blade margin thickness

The blade thickness data for the 1981 growth experiment are summarized in Table 2. The 1st year plants were thinner than the 2nd year plants. The blade margin thickness for both age classes tended to decrease with depth and increase with time, being minimal in spring and maximal in fall. The bathymetric variation in blade thickness was not as pronounced by November. In March'82, the increase in blade thickness with depth reflected the lower blade elongation rate at the deeper levels (i.e. thick blade tissue from the previous year).

Substantiality and C-N content

The plant substantiality, on a fresh weight (Table 3) and on a dry weight (Table 4) basis, increased with time as indicated by the increases from August to November 1981 and from April to June 1982. There was no consistent change in substantiality with depth when viewed on a fresh weight basis. However, substantiality on a dry weight basis did decrease with

Table 2: Seasonal and bathymetric variations in blade margin thickness (mm) for the 1st and 2nd year plants of *L. groenlandica* (Initial N=60, $\bar{X} \pm$ S.D.).

	1st year plants				2nd year plants			
	1m	5m	7m	9m	1m	5m	7m	9m
Jun'81	0.10±0.00	0.12±0.04	0.10±0.00	<0.10	0.53±0.12	0.40±0.08	0.38±0.08	0.32±0.05
Aug'81	0.17±0.06	0.30±0.05	0.19±0.04	<0.10	0.57±0.11	0.51±0.07	0.47±0.09	0.41±0.09
Nov'81	- [1]	0.59±0.09	0.56±0.07	0.38±0.09	-	0.92±0.09	0.87±0.11	0.81±0.14
Jan'82 [2]	-	0.80±0.17	0.57±0.21	0.30	-	0.98±0.09	1.03±0.10	0.92±0.12
Mar'82 [2]	-	0.33±0.06	0.37±0.06	-	-	0.43±0.17	0.64±0.26	0.68±0.28

[1] No data.

[2] Plants now in their 2nd and 3rd year respectively.

Table 3: Seasonal and bathymetric variations in substantiality, on a fresh weight basis, (mg fw.cm^{-2}) for the 1st and 2nd year plants of *L. groenlandica* (N= 6, $\bar{X}$ ± S.D.).

	1st year plants				2nd year plants			
	1m	5m	7m	9m	1m	5m	7m	9m
Aug'81	-[1]	74.0± 8.5	64.5± 5.5	-	110.0± 5.1	107.5± 3.6	103.2± 8.3	115.2± 2.0
Nov'81	-	97.1± 8.9	94.3± 5.8	73.2±17.4	-	120.1± 8.2	110.3± 5.9	108.1± 5.2
Apr'82[2]	-	67.6± 1.8	71.7± 5.1	-	-	86.9±14.3	91.4±11.2	111.3±11.3
Apr'82[3]	41.9± 4.7	-	-	-	77.6± 3.6	69.6± 4.0	72.4± 5.0	70.9± 2.9
Jun'82[3]	77.6± 5.8	67.8± 3.1	61.2± 8.2	-	98.2± 9.8	102.2± 5.6	97.8± 5.0	84.8± 7.3

[1]No data.

[2]Plants now in their 2nd and 3rd year respectively.

[3]Plants from the 1982 growth experiment.

Table 4: Seasonal and bathymetric variations in substantiality, on a dry weight basis, (mg dw.cm^{-1}) for the 1st and 2nd year plants of *L. groenlandica* (N= 6, $\bar{X}$ ± S.D.).

	1st year plants				2nd year plants			
	1m	5m	7m	9m	1m	5m	7m	9m
Aug'81	-[1]	10.1± 1.2	8.4± 1.2	-	28.8± 3.3	25.4± 2.6	17.9± 2.4	16.2± 0.6
Nov'81	-	17.2± 2.0	16.5± 2.5	9.6± 4.7	-	21.5± 0.3	18.3± 1.6	16.7± 0.5
Apr'82[2]	-	6.4± 0.4	6.4± 0.6	-	-	8.4± 1.5	9.1± 1.6	12.6± 1.9
Apr'82[3]	3.9± 0.4	-	-		9.9± 0.7	6.9± 0.4	6.5± 0.7	6.2± 0.2
Jun'82[3]	9.1±0.6	8.0± 0.4	5.9± 1.0	-	24.8± 2.9	19.2± 2.1	14.8± 1.8	8.7± 1.0

[1]No data.

[2]Plants now in their 2nd and 3rd year respectively.

[3]Plants from the 1982 growth experiment.

Table 5: Seasonal and bathymetric variations in total carbon, as % of dry weight, for the 1st and 2nd year plants of *L. groenlandica* (N= 6, $\bar{X}$ ± S.D.).

	1st year plants				2nd year plants			
	1m	5m	7m	9m	1m	5m	7m	9m
Aug'81	-	29.17±1.79	26.23±2.29	-	38.29±1.54	37.53±0.73	33.45±1.77	30.45±1.51
Nov'81	-	33.08±1.35	33.20±2.16	27.70±3.18	-	34.79±1.25	33.04±1.97	32.57±1.82
Apr'82[2]	-	22.86±2.92	22.86±0.58	-	-	24.42±0.74	24.31±0.73	25.74±0.97
Apr'82[3]	27.28±1.40	-	-	-	31.21±0.76	26.12±0.95	23.58±0.87	22.97±0.55
Jun'82[3]	28.92±1.46	28.45±1.32	22.57±0.52	-	36.78±0.86	34.60±2.01	31.70±1.87	25.43±1.61

[1] No data.

[2] Plants now in their 2nd and 3rd year respectively.

[3] Plants from the 182 growth experiment.

Table 6: Seasonal and bathymetric variations in total nitrogen, as % of dry weight, for the 1st and 2nd year plants of *L. groenlandica* (N= 6, $\bar{X} \pm$ S.D.).

	1st year plants				2nd year plants			
	1m	5m	7m	9m	1m	5m	7m	9m
Aug'81	-[1]	2.45±0.15	2.30±0.18	-	1.28±0.26	2.36±0.12	2.45±0.04	2.31±0.11
Nov'81	-	2.81±0.11	2.70±0.23	2.49±0.21	-	2.41±0.20	2.44±0.19	2.42±0.20
Apr'82[2]	-	1.64±0.37	1.97±0.43	-	-	1.96±0.17	2.20±0.12	2.21±0.15
Apr'82[3]	0.88±0.07	-	-	-	1.42±0.09	1.79±0.10	2.03±0.12	2.33±0.17
Jun'82[3]	1.27±0.26	1.53±0.11	2.26±0.09	-	1.01±0.13	1.88±0.17	2.23±0.06	2.39±0.23

[1]No data.

[2]Plants now in their 2nd and 3rd year respectively.

[3]Plants from the 1982 growth experiment.

depth. Second year plants had higher substantiality than 1st year plants.

The total carbon content (as % of the dry weight) tended to increase with time and decrease with depth (Table 5). Although the total nitrogen content (as % of the dry weight) did not show a tendency towards seasonal or bathymetric variations, higher values were recorded in November than in April 1981 and in April than in June 1982 whereas the 1m plants showed lower values than the ones in the 5-9m range (Table 6).

Photosynthetic studies

Pigment variation

The chl *a* and fucoxanthin concentrations on a surface area basis followed a similar seasonal trend for both age classes: a minimum concentration in April followed by a rise in July to maximum concentrations in November (Fig 12). Chlorophyll *c* values increased from from April to July after which no substantial increase could be detected; no consistent bathymetric pattern could be observed for this pigment. The chl *c*:chl*a* and fx:chl *a* ratios did not vary seasonally and were similar for both age classes except in July when the 1st year plants exhibited higher ratios (Fig 13). Generally the pigment levels were higher for the 2nd year plants than for the 1st year plants in July and November 1981. Pigment concentrations were

Figure 12. Seasonal and bathymetric variations in chlorophyll *a* (chl *a*), chlorophyll *c* (chl *c*) and fucoxanthin (fx) concentrations for the 1st and 2nd year plants of *L. groenlandica* from the 1981 growth experiment.

(N= 5 ± S.D.)
In 1982, the plants were in their 2nd and 3rd year.

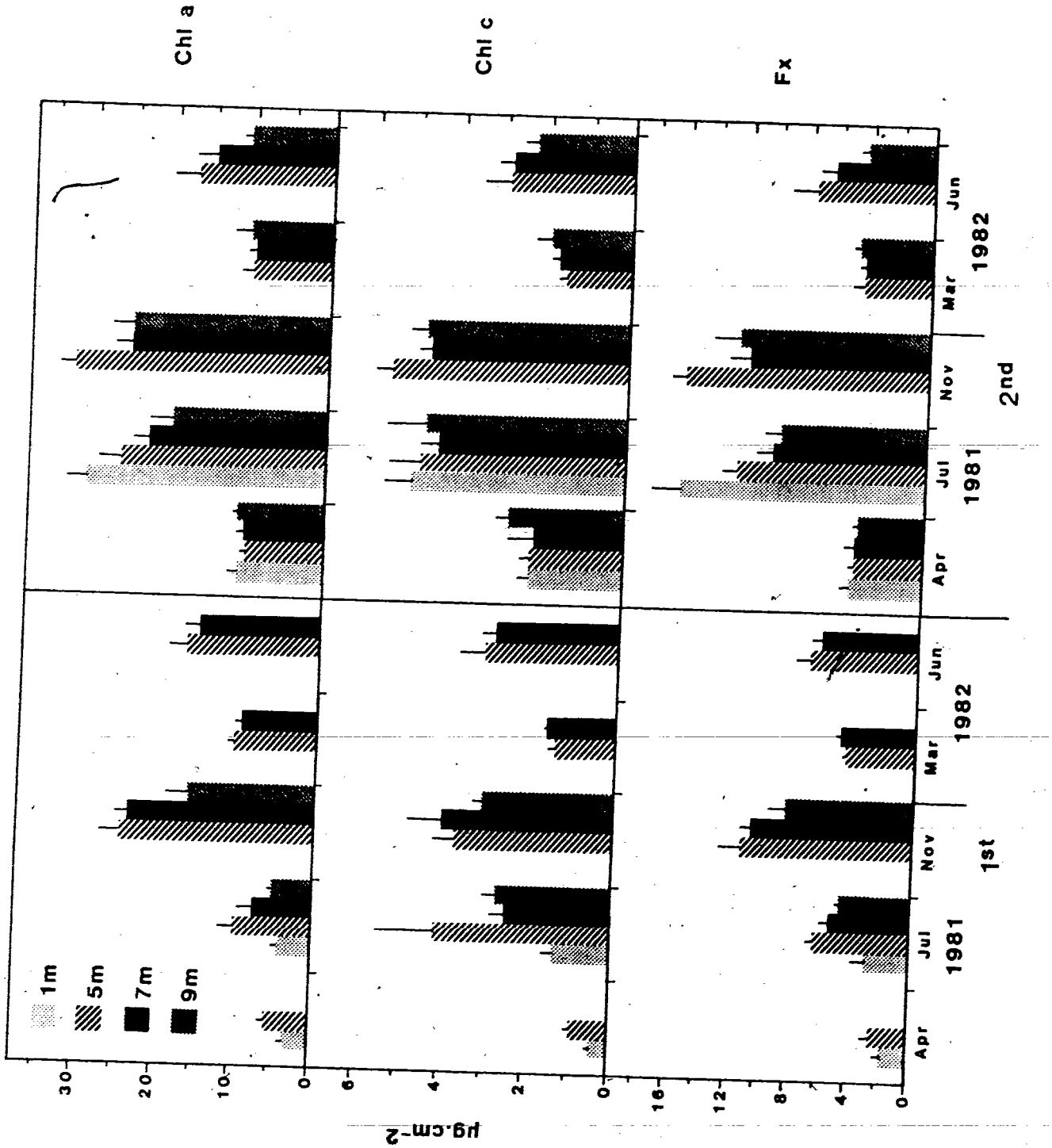
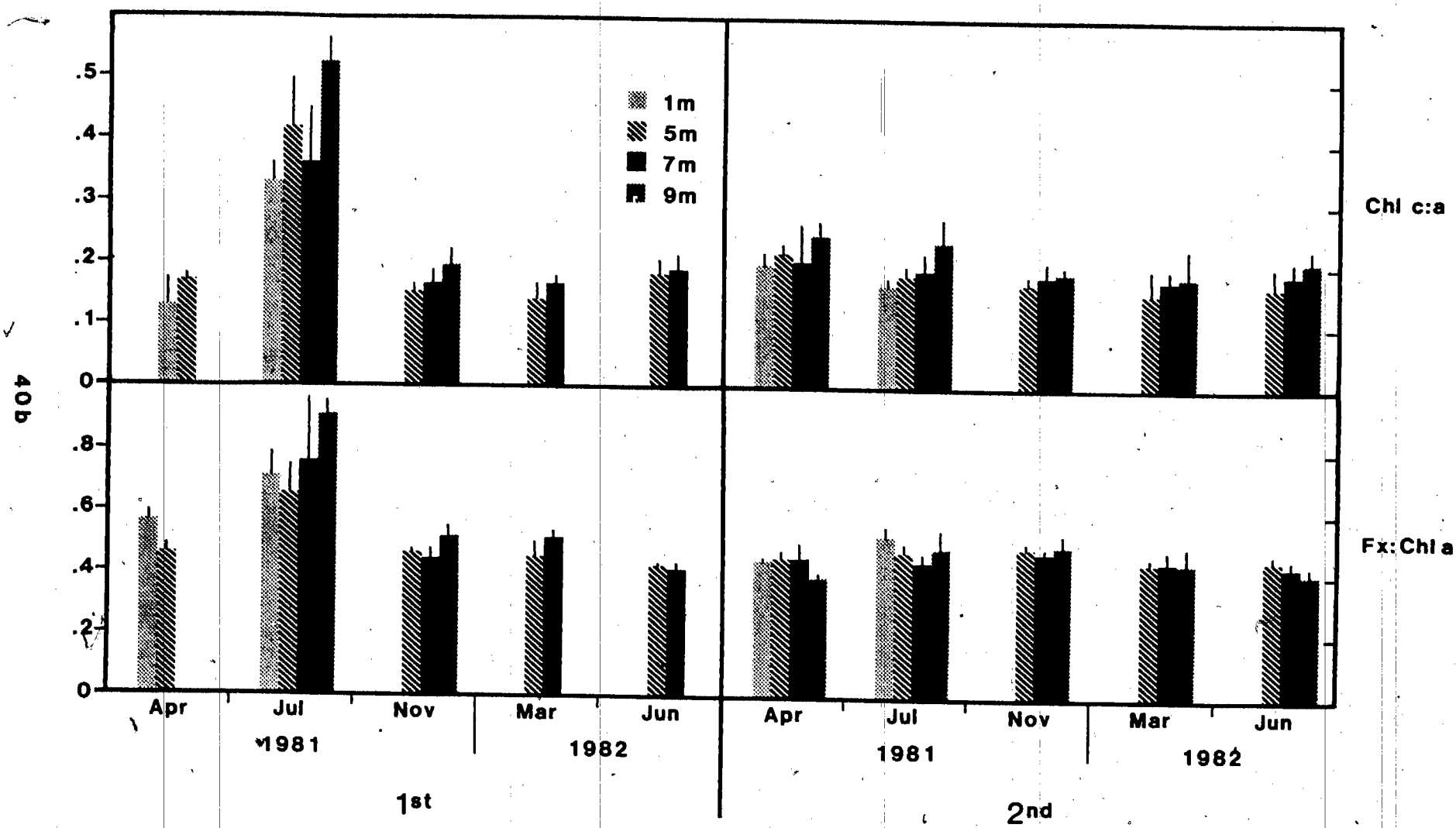

Chl a
Chl c
Fx
1m
5m
7m
9m
μg.cm-2
Apr
Jul
Nov
Mar
Jun
1981
1982
1st
2nd

Figure 13. Seasonal and bathymetric variations in chlorophyll *c* to chlorophyll *a* (Chl *c*:*a*) and fucoxanthin to chlorophyll *a* (Fx:chl *a*) ratios for the 1st and 2nd year plants of *L. groenlandica* from the 1981 growth experiment.

(N= 5 ± S.D.)
In 1982, the plants were in their 2nd and 3rd year.


1m
5m
7m
9m
.5
.4
.3
.2
.1
0
.8
.6
.4
.2
0
Chl c:a
Fx:Chl a
Apr
Jul
Nov
Mar
Jun
1981
1982
1st
2nd

40b

similar for all plants in March and June 1982.

On a bathymetric gradient, the chl *a* and fucoxanthin concentration increased from 1 to 5m and then declined at 7 and 9m for the 1st year plants (Fig 12, 1981 data). As for the 2nd and 3rd year plants, there was no bathymetric variation in pigment content in April (Fig 12, 1982 data). However, in July the chl *a* and fucoxanthin concentrations for the 2nd year plants were inversely related with depth on a surface area basis.

Oxygen exchange

The light panel used for the photosynthetic performance experiments illuminated the plants from above only. This stimulated the photosynthetic machinery of the upper surface of the plant at low PPFD. As the latter increased, it activated the photosynthetic machinery of the lower surface of the plant; the activity of which increased with increasing PPFD. This affected the shape of the upper portion of the P *vs* I curve and explains the absence of a plateau at saturating light intensities. Being related to the thickness of the plant and its pigment concentration, this effect varied with depth and time (Fig 14). The light-saturated rate of photosynthesis (Pmax) was estimated at 85 $\mu E.m^{-2}.s^{-1}$ approximatly. This saturating light intensity did not vary with depth or season except in November where it seems to be lower (*ca* 67 $\mu E.m^{-2}.s^{-1}$) at all depths (Fig 14). However this could have been caused by the reasons mentioned

Figure 14. Photosynthesis *vs* Irradiance curves for the 2nd year plants of *L. groenlandica*.

(N= 3 ± S.D.)

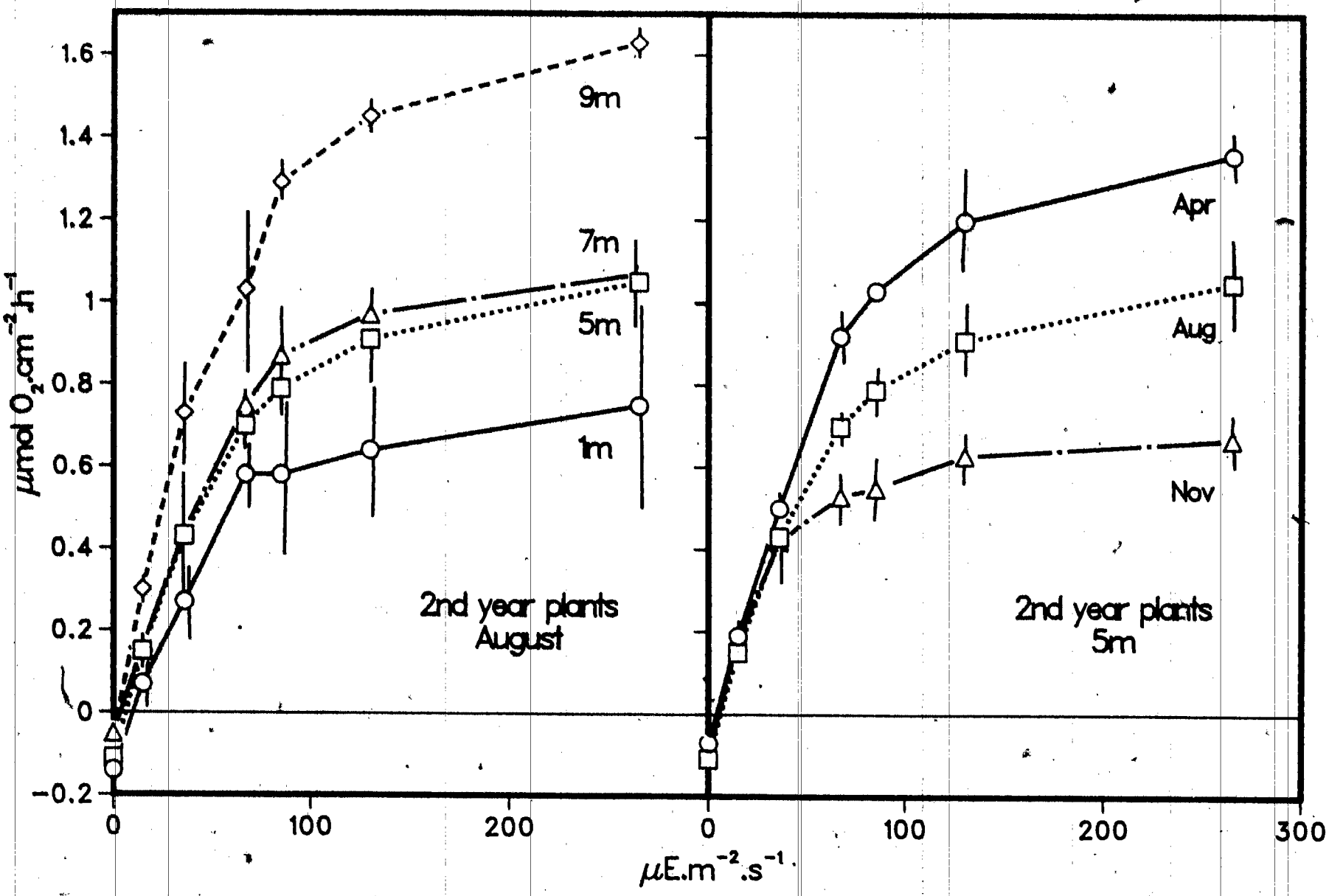
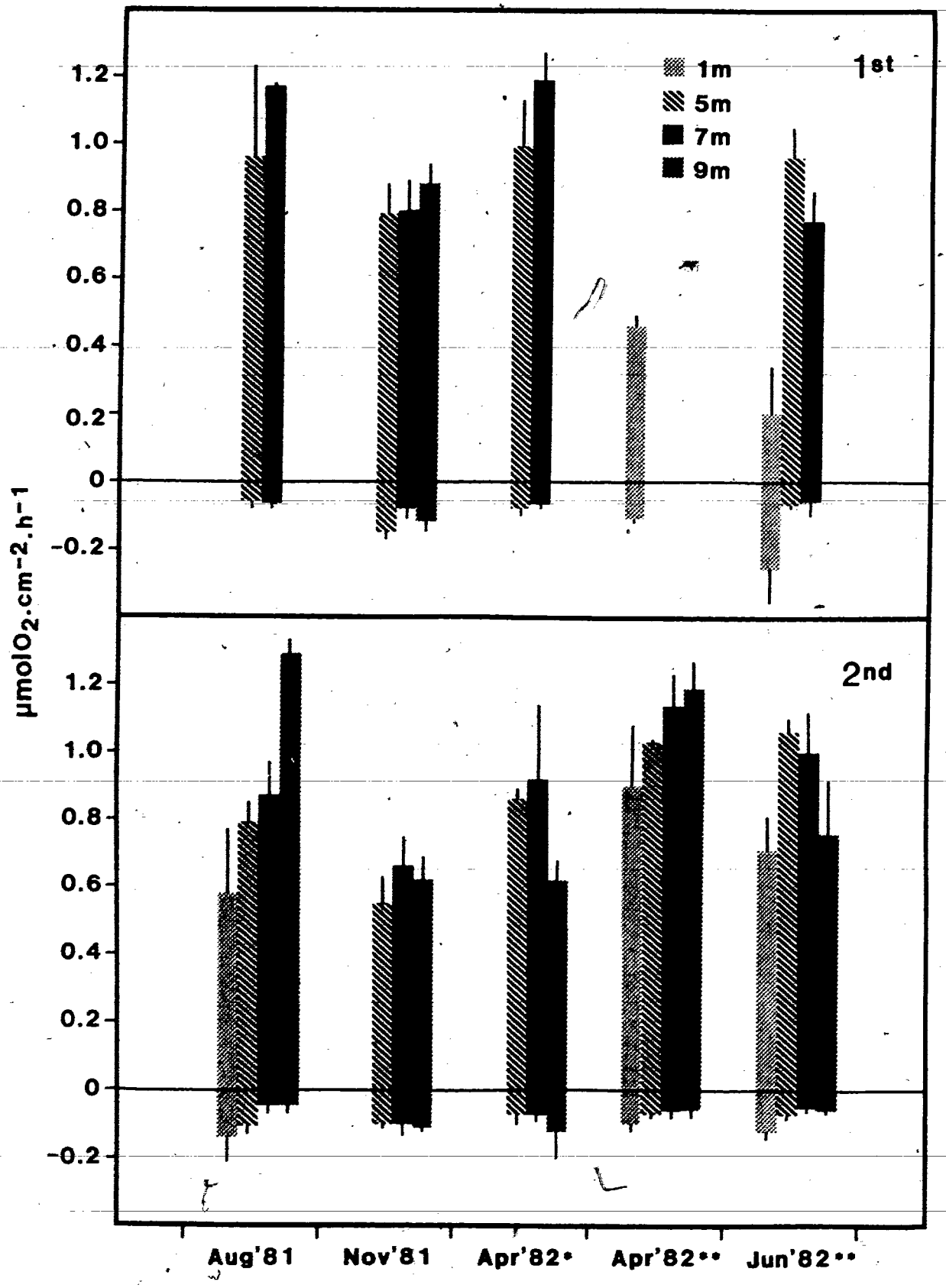

1.6
1.4
1.2
1
0.8
0.6
0.4
0.2
0
-0.2
μmol O2.cm-2.h-1
9m
7m
5m
1m
2nd year plants
August
0
100
200
Apr
Aug
Nov
2nd year plants
5m
0
100
200
300
μE.m-2.s-1

Figure 15. Seasónal and bathymetric variations in Pmax and dark respiration, on a surface area basis, for the 1st and 2nd year plants of *L. groenlandica* from the 1981 and 1982 growth experiment.

(N= 3 ± S.D.)
* Plants are in their 2nd and 3rd year.
** Plants from the 1982 growth experiment.


1m
5m
7m
9m
1st
2nd
1.2
1.0
0.8
0.6
0.4
0.2
0
-0.2
µmolO2.cm-2.h-1
Aug'81
Nov'81
Apr'82*
Apr'82**
Jun'82**

above.

The seasonal and bathymetric variations of Pmax are summarized in figure 15. Maximum values were recorded in April and June for the 2nd year plants and in August for the 1st year plants; minimum ones were observed in November for both age classes. In April and August, Pmax for 1st and 2nd year plants increased with increasing depth whereas no bathymetric differences were observed in November. In June, Pmax increased from 1 to 5m and then decreased with increasing depth for both age classes.

On a surface area basis, the initial slope of the photosynthesis-irradiance curve (α) was maximum in April and minimum in November, although the seasonal variation was not very pronounced for either year class (Table 7). No substantial bathymetric difference was observed for the 1st year plants within the depth range studied. For the 2nd year plants, α increased with increasing depth. The 1st year plants had higher α values than the 2nd year plants, in August and November, but the reverse was true in April. In April, the 3rd year plants at 9m had lower Pmax and α values than the shallower plants of the same age class. As mentioned earlier, these plants had barely resumed growth and consisted mostly of thick blade tissue from the previous year. Still in April, the 1st year plants from the 1981 growth experiment (now in their 2nd year) showed Pmax and α values similar to the ones of the 2nd year plants from the 1982 growth experiment.

Table 7: Seasonal and bathymetric variations of α, on a surface area basis, (μmol $O_2 \cdot cm^{-2} \cdot h^{-1} / \mu E \cdot m^{-2} \cdot s^{-1} \times 10^{-2}$) for the 1st and 2nd year plants of *L. groenlandica* (N= 3, $\bar{X} \pm$ S.D.).

	1st year plants				2nd year plants			
	1m	5m	7m	9m	1m	5m	7m	9m
Aug'81	-[1]	1.30±0.26	1.48±0.16	-	1.05±0.19	1.19±0.08	1.19±0.05	1.61±0.29
Nov'81	-	1.29±0.11	1.17±0.16	1.30±0.07	-	0.90±0.11	1.07±0.12	1.08±0.06
Apr'82[2]	-	1.52±0.12	1.52±0.10	-	-	1.22±0.06	1.32±0.22	1.05±0.13
Apr'82[3]	0.74±0.15	-	-	-	1.31±0.17	1.47±0.10	1.55±0.14	1.58±0.11

[1]No data.

[2]Plants now in their 2nd and 3rd year respectively.

[3]Plants from the 1982 growth experiment.

Table 8: Seasonal and bathymetric variations of α, on a chl *a* basis, (μmol O_2.μmol chl a^{-1}.h^{-1}/$\mu E.m^{-2}.s^{-1}$) for the 1st and 2nd year plants of *L. groenlandica* (N= 3, $\bar{X}$ ± S.D.).

	1st year plants				2nd year plants			
	1m	5m	7m	9m	1m	5m	7m	9m
Aug'81	-[1]	1.17±0.23	1.77±0.19	-	0.31±0.07	0.40±0.03	0.45±0.02	0.71±0.13
Nov'81	-[1]	0.46±0.04	0.43±0.06	0.71±0.04	-	0.25±0.03	0.37±0.04	0.38±0.02
Apr'82[2]	-	1.30±0.11	1.43±0.02	-	-	1.01±0.12	1.16±0.19	0.86±0.11
Apr'82[3]	1.85±0.38	-	-	-	0.82±0.11	1.07±0.08	1.38±0.12	1.40±0.10

[1]No data.

[2]Plants now in their 2nd and 3rd year respectively.

[3]Plants from the 1982 growth experiment.

A larger seasonal variation was found for *a* on a chl *a* basis, along with an accentuated difference between year classes and depth (Table 8). This was specially true for the 1st year plants which showed very low values in November compared to the ones in August. In April, the 1st year plants at 1m had a low *a* on a surface area basis but a much higher *a* on a chl *a* basis when compared with the other plants.

The respiration rates were similar for both year classes at all dates and depths studied with the exception of an elevated value for 1st year plants at 1m in June 1982 (Fig 15).

DISCUSSION

Growth studies

The highest blade elongation rate, recorded in this study, for *L. groenlandica* was 1.3 cm. day^{-1} for the 2nd year plants in April 1980 and in March 1981. This values fall in the range (0.8-1.5 cm.day^{-1}) observed by other investigators for *L. digitata* (Sundene, 1962, 1964; Pérez, 1970), *L. pallida* (Dieckmann, 1980), *L. religiosa* (Abe *et al*, 1983) and *L. saccharina* (Parke, 1948; Johnston *et al*, 1977; Brady-Campbell *et al*, 1984). Blade elongation rates of more than 3 cm.day^{-1} were reported for *L. angustata* (Hasegawa, 1962). *Laminaria longicruris* reached blade elongation rates in excess of 3.5 cm.day^{-1} (Anderson *et al*, 1981); Kain (1976) and Chapman and Lindley (1980) recorded blade elongation rates of more than 2 cm.day^{-1} for *L. hyperborea* and *L. solidungula* respectively. Sasaki (1969) and Kawashima (1972) observed rates as high as 6.8 and 13.2 cm.day^{-1} respectively for *L. angustata* var. *longissima*.

The lower blade elongation rate observed at depth in late winter-early spring has been ascribed to light limitation (Mann, 1972; Chapman and Craigie, 1977; Calvin and Ellis, 1981; Kain, 1963). I obtained similar results for *L. groenlandica* (Fig 7). This depth-related growth reduction may become more evident as

one takes into account more than one growth parameter. Kain (1976) pointed out the limitations in defining growth solely in terms of length increment. Blade thickness and substantiality on a dry weight basis decreased with depth; the behaviours of those morphological parameters coupled to the lower blade elongation rates accentuate the observed growth reduction with depth.

The late spring-early summer growth decline in shallow water for other *Laminaria* species has been attributed to ambient nutrient depletion (Chapman and Craigie, 1977; Johnston *et al*, 1977; Gagné *et al*, 1982). A similar growth decline has been observed in this study for both year classes of *L. groenlandica* at 1m and for 2nd year plants at 3m. The percentage of total tissue nitrogen (on a dry weight basis) of 1m plants is indeed lower than at the deeper levels and may indicate some degree of nitrogen starvation as observed for *Macrocystis pyrifera* (Gerard, 1982; Druehl, 1984) from low nutrient environments. The damaging effects of photoinhibition caused by high light intensity can not, however, be ruled out. Fortes and Lüning (1980) reported a 50 % reduction in the growth rate of *L. saccharina* grown in enriched culture medium at 250 $\mu E.cm^{-2}.s^{-1}$ compared to the optimum growth at 110 $\mu E.cm^{-2}.s^{-1}$. Similar growth reductions were observed for juvenile laminarian sporophytes (Pérez, 1971; Kain, 1965) grown in the same light range. Furthermore, the level of light intensity necessary to cause photoinhibition is known to decrease with decreasing temperature (Lapointe and Duke, 1984; Öquist *et al*, 1982). It is

plausible, therefore, that with increasing PPFD and still low temperature the plants may have suffered from photoinhibition, for some time during the day, as early as May. This effect can be enhanced by ambient nutrient depletion (Lapointe, 1981; Lapointe and Duke, 1984).

The amount of blade erosion distally did not vary markedly with depth as all plants lost between 40 and 65% of the tissue produced during the year (Fig 8, 10 and 11).

Mann and his co-workers (1980; Gagné and Mann, 1981) have put forward two strategies regarding the growth of *Laminaria*: a 'nutrient' and a 'light' limited seasonal cycle. In environments where ambient nitrate concentrations undergo large seasonal fluctuations with low summer values, the plants store nitrate at the onset of growth in winter. These nitrate reserves sustain the plant growth beyond the spring decline in ambient nitrate levels. Then, owing to the low availability of nutrients and high light levels, the plants accumulate carbon reserves in the form of mannitol and laminarin; these compounds being used in late fall-early winter to support growth when the light levels are below the compensation point for growth. In late winter, growth is maintained by photosynthetic activity (Chapman and Craigie, 1977, 1978; Johnston *et al*, 1977; Gerard and Mann, 1979; Chapman and Lindley, 1980; Gagné *et al*, 1982).

In environments with relatively high nitrate year-around, the plant growth follows the seasonal light cycle with substantial growth rates in summer followed by a fall decline.

Here the plants do not build up large reserves of nitrate in spring or carbohydrates in summer (Braud, 1974; Reynold, 1974; Dieckmann, 1980; Anderson *et al*, 1981; Gagné *et al*, 1982).

Lüning (1979) suggests that the growth pattern in the genus *Laminaria* is determined genetically and that the seasonal nutrient cycle plays only a secondary role. He followed the growth of three *Laminaria* species in a nitrate-rich environment in the North Sea. *Laminaria digitata*, a species restricted to shallow waters, maintained a high growth rate through the summer months and did not accumulate large carbon reserves. *L. hyperborea* and *L. saccharina*, which grow below *L. digitata* and are known to build large carbohydrate reserves, either ceased growth completely (*L. hyperborea*) or reduced its growth rate substantially (*L. saccharina*) by July. Gagné and his co-workers (1982) observed different growth patterns in reciprocal transplants of *L. longicruris* from nitrate-rich and nitrate-poor environments. These authors suggested some genetic differentiation amongst the different populations. This was later confirmed by Espinoza and Chapman (1983).

In May, there was a rapid decline in the 2nd year plant blade elongation rates at 1 and 3m (and for the 1st year plants at 1m) while substantial rates were maintained at the deeper levels. this could indicate an ambient nutrient limitation on growth (Fig 7). Although the possibility of photoinhibition can not be ruled out (Drew, 1974; Fortes and Lüning, 1980). Despite the low ambient nitrate levels, the 1st year plants maintained

relatively high blade elongation rates until the end of July. Whereas the 2nd year plant growth pattern resembles the 'nutrient' limited cycle typical of nutrient-poor areas, the growth pattern of the 1st year plants matches the 'light' limited cycle typical of nutrient rich areas. To that effect, the 1st year plants behave like *Chorda filum* (South and Burrows, 1967) or *Sacchoriza polyschides* (Norton and Burrows, 1969) both annual laminariacean species.

Although there is evidence that nutrients, light or temperature influence the growth pattern of *L. groenlandica*, they do not provide a complete answer to the overall situation. It is suggested that the growth pattern of *L. groenlandica* is largely genetically determined and that it differs between the 1st and 2nd year plants.

Photosynthesis studies

Pigment variation

The general response of higher plants or macroalgae to shade or depth is to increase their pigment content (Solazzi and Tolomio, 1976; Ramus, 1976a, 1976b, 1977; Boardman, 1977; Li and Titlyanov, 1978; Wheeler, 1980; Perez-Bermudez *et al*, 1981; Prézelin, 1981). The pigment concentrations of the 1st year plants increased from 1 to 5m and then decreased with depth. When the 2nd year plants did show a bathymetric pigment

variation, it was inversely correlated with depth. Both year classes of *L. groenlandica* did not show any substantial changes in ratios of accessory pigments to chlorophyll *a* on a bathymetric gradient (Fig 13). In July 1981, the 2nd year plants at 1m that were heavily epiphytized showed a high pigment concentration. However the ones that were not epiphytized appeared pale. Rhee and Briggs (1977) reported similar results with epiphytized *Chondrus crispus*. The pigment concentration has been found to increase with nitrate concentration (Chapman *et al*, 1978; Lapointe and Duke, 1984). In this study, the capacity of the 2nd year plants from shallow water to maintain a high pigment concentration seems more related to dense epiphyte cover than to low ambient nitrate concentration. As for the lower pigment content observed at depth, it could be related in part to thallus morphology: the plants being thinner with increasing depth; although I do not have the evidence that the reduced thickness observed at depth is due to a reduction in the thickness of the pigmented layer or a reduction of the inner non-photosynthetic layer. Morphological responses such as the ones discussed above have been reported for higher plants growing in the shade, fresh water macrophytes and macroalgae growing at depth (Spence and Christal, 1970; Spence, 1976; Mariani Colombo *et al*, 1976; Van *et al*, 1977; Oquist *et al*, 1982). It is interesting to note the different responses of 2nd year plants to shade (epiphytized plants at 1m) and depth, although no explanation can be advanced at this point on this

phenomenon. Lower pigment concentrations have been reported for phytoplankton cultures maintained under low light conditions compared to high light ones (Prézelin and Sweeney, 1978; Falkowski and Owens, 1980); Perry *et al*, 1981). A plant may increase its pigment concentration up to a certain point where it may be more economical to choose in favour of morphological, biochemical or (molecular) conformational adjustments such as a reduction in the thickness of the photosynthetic layer, a lower turnover of pigments or an increase in energy transfer efficiency between or within pigment protein complexes (Shimura and Fujita, 1975; Ley and Buttler, 1980; Larkum and Barrett, 1983; Richardson *et al*, 1983).

Different strategies may be adopted by plants of different morphologies, i.e. thin *vs* optically thick thalli, regarding the regulation of pigment concentrations. Ramus (1978) demonstrated that for the optically translucent *Ulva*, thallus absorptance was positively correlated with pigment concentration, whereas for the optically opaque *Codium*, thallus absorptance was independent of pigment concentration. To use Ramus's terminology (1976a) *L. groenlandica* growing at depth seems to 'optimize' rather than 'maximize' its pigment content. The pigments increased from from 1 to 5m, a depth at which photosynthetically saturating light levels were attained, but lower pigment content were found down to 9m where plants rarely encounter saturating light levels (Table 1). At 9 and 12m, the deepest levels used in this study, the plants were faced with few options, morphologically, in

order to capture more light: they could minimized their growth in surface area and invest in a large pigment content or maintain a lower pigment concentration and maximize their growth. The results obtained in this study point to the second solution.

Photosynthetic performance

The saturating PPFD for *L. groenlandica*, determined at 85 $\mu E.m^{-2}.s^{-1}$ (Fig 14), is lower than values reported for other species of this genus: 120-130 $\mu E.m^{-2}.s^{-1}$ for *L. saccharina* (Johnston *et al*, 1977; Lüning, 1979), 130-150 $\mu E.m^{-2}.s^{-1}$ for *L. hyperborea* (Kain *et al*, 1976; Lüning, 1979) and similar to values reported for other Laminariales: 25-80 $\mu E.m^{-2}.s^{-1}$ for *Macrocystis integrifolia* and *Nereocystis luetkeana* (Smith *et al*, 1983; Wheeler *et al*, 1984).

The seasonal variation in Pmax, reported in this study, is not very pronounced for both age classes (Fig 15). It has been shown that Pmax may vary substantially on a monthly basis (Smith *et al*, 1983; Wheeler *et al*, 1984); therefore the few determinations presented here may not represent the total potential for the seasonal Pmax variation in *L. groenlandica*. However, Pmax does reflect the seasonal growth of *L. groenlandica* with high values in June and August (1st year plants), April and June (2nd year plants) and low values in November for both age classes.

On a surface area basis, α increased slightly with depth and decreased as the seasons progressed (Table 7). This effect was enhanced both seasonally and bathymetrically when α was expressed on a chl *a* basis (Table 8).

The variations in Pmax and α have been used to describe the 'activity' or 'efficiency' of the photosynthetic apparatus in terms of variation in the size or number of photosynthetic units (PSU) and of variation in the size or activity of the pool of ribulose biphosphate carboxylase (RuBP-C) (Prézelin, 1981; Ramus, 1981; Richardson *et al*, 1983). The situation becomes rapidly confusing as more than one parameter may vary at the same time. To complicate the situation further, other adjustments related to the photosynthetic machinery (changes in the ratio of light harvesting pigments or reaction centers, changes in the electron transport capacity and in photosynthetic enzyme activities) or of a physiological or ultrastructural nature may contribute to the overall photoadaptation strategy of a particular organism (Richardson *et al*, 1983). It seems unlikely that *L. groenlandica* growing at depth increased the size of its PSUs owing to the fact that no substantial increase in the ratios of accessory pigments to chlorophyll *a* was observed with depth (Fig 13).

Generally, 'shade' plants are characterized by a higher α and a lower saturating PPFD or a lower Pmax. This has been interpreted as a greater and/or a more active pool of RuBP-C for plants grown at high light intensity (Boardman, 1977). Yadykin

and Titlyanov (1980) showed for a variety of seaweeds that the ones growing in the shade of grottos maintained higher levels of RuBP-C and other photosynthetic enzymes than the same species growing nearby in brightly illuminated habitats. However, plants growing at depth would not likely invest in a large pool of RuBP-C as they rarely encounter high light levels. The activity of RuBP-C has been observed to vary seasonally and in relation to ambient nitrate concentrations. (Küppers and Weidner, 1980; Wheeler and Weidner, 1983).

The photosynthetic performance was measured under white light. It is possible that the deeper plants might have been more disadvantaged than the shallower ones, since the light spectrum at depth is greatly reduced in the blue and red band. Beer and Levy (1983) have demonstrated that plants grown in green or blue light had higher Pmax under the same color of light they had been grown in, than in white light; these changes were brought about without changes in pigment concentrations. This led the authors to suggest that conformational changes in the pigment protein complexes might be involved.

From the results of this study, it can be concluded that *L. groenlandica* does not seem to show a large degree of photoadaptation on a depth gradient. Unicellular algae (Dinoflagellates) which show photosynthetic responses similar to those exhibited by *L. groenlandica* are thought to poorly adapt to high light levels and grow better at relatively low light intensities (Richardson *et al*, 1983). Much work needs to be done

regarding the molecular structure of photosynthetic lamellae as well as the interactions between the light transmitting (light harvesting components) and light transducing (reaction center components) systems of such important primary producers.

The major findings of this study may be summarized as follows: *L. groenlandica* exhibits a determined seasonal growth cycle; this seasonal growth cycle is different for the 1st and 2nd year plants of this species; the pigment content may increase with depth (from the surface down to *ca* 5m) but decreases at the deeper levels and Pmax increases with depth.

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