Growth Strategies of Three *Laminaria* Species (Phaeophyceae) Inhabiting Different Depth Zones in the Sublittoral Region of Helgoland (North Sea)

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ABSTRACT: On European coasts, *Laminaria digitata* does not inhabit the deeper kelp zone; this is dominated by *L. hyperborea* and (locally) *L. saccharina*. Sporophytes of three *Laminaria* spp. were cultivated from unialgal gametophyte cultures in the laboratory and transplanted into the field in February, at depths of 2, 4.5 or 7 m below M.L.W.S. Near Helgoland, the deepest kelp (*L. hyperborea*) occurs at 8 m, and older plants of *L. digitata* are not found below 2 m depth. Photosynthesis was light-saturated in all three species, irrespective of cultivation depth, at photon flux densities above about 150 μE m^{-2}s^{-1} (corresponding to an irradiance of 30 W m^{-2}). The experimental plants of *L. digitata* and *L. saccharina* produced much bigger blade areas in spring and summer at all depths than *L. hyperborea*. In July, the latter species completely ceased blade growth and *L. saccharina* reduced its growth rate very much. *L. digitata*, however, first reduced its growth rate in September (by about 50 %), so that at the beginning of the dark season, from October onwards, its blades consisted of much younger tissue, resulting in a lower content of reserve materials per plant than in the case of the other two species. The long-persisting, high growth rate in *L. digitata* may be interpreted as adaptation to life in the sublittoral fringe; however, it obviously prevents the species from perennial colonization of the deepest parts of the kelp zone. The finding that the three *Laminaria* spp. reduced or ceased growth at different times during the year, under otherwise identical conditions of temperature, nutrients, light intensity or light quality, suggests the possibility that none of these factors actually trigger the seasonal growth behaviour of these species.

INTRODUCTION

On most European coasts *Laminaria digitata* inhabits the uppermost part of the sublittoral region, whereas *L. hyperborea* and (locally) *L. saccharina* dominate the middle and deeper parts of the kelp zone (Kain, 1962; Castric-Fey et al., 1973; Gayral & Cosson, 1973). *L. digitata* is well adapted for colonizing the upper sublittoral region, e.g. by possession of a flexible stipe due to which the thalli form a flat-lying mass when the population is exposed to drought or cold at extreme low water. The question is still open why adult sporophytes of *L. digitata* are excluded from the deeper kelp zone. It may be possible that this species is photosynthetically a 'sun plant', which is not able to produce sufficient photosynthate for growth in the 'shadow' regions of the deeper kelp zone. An alternative explanation might be sought in a genetically fixed allocation pattern of carbon into either growth, or formation of reserve materials. This pattern may be adequate for the upper, but not for the deeper parts of the kelp zone. In the present work the question was approached experimentally by transplanting laboratory-raised sporophytes to different water depths in the field, and investigating the photosynthetic and growth performance of the experimental plants.

MATERIALS AND METHODS

Cultivation in the Laboratory

Enriched seawater (PES; Provasoli, 1968) was used throughout for cultivation in the laboratory. Unialgal gametophyte cultures derived from wild Helgoland sporophytes were set up in red fluorescent light, as described in detail by Lüning et al. (1978). For obtaining sporophytes the filamentous gametophytes were gently ground with mortar and pestle. The few-celled gametophyte fragments were inoculated on white, roughened PVC plates (5 × 3 cm, 6 mm thick) which were situated in stagnant PES on the bottom of a plastic tank (50 × 50 cm, 20 cm high). The sticky gametophyte fragments settled on the PVC plates within a short time. In white fluorescent light (Osram 40 W/19; illuminance 2000–2500 lx) and at a tempera-

ture of 10 °C the gametophytes matured within 8–12 d (Lüning and Dring, 1975). Sporophytes, 1 mm long, were obtained 3 weeks after inoculation. At this stage most of the sporophytes were mechanically removed from their substrate, leaving 10–20 sporophytes per PVC plate. Subsequently, cultures were aerated and PES was changed every 4 d.

Six weeks after inoculation the sporophytes had reached lengths of 2–3 cm and were transferred into a seawater shower (Chapman, 1973a). Basically, this consisted of an Eternit tank (150 × 100 cm, 70 cm high; seawater volume, 185 l; seawater filtered through Seitz asbestos filter K 5, and renewed every 2 d) in which the
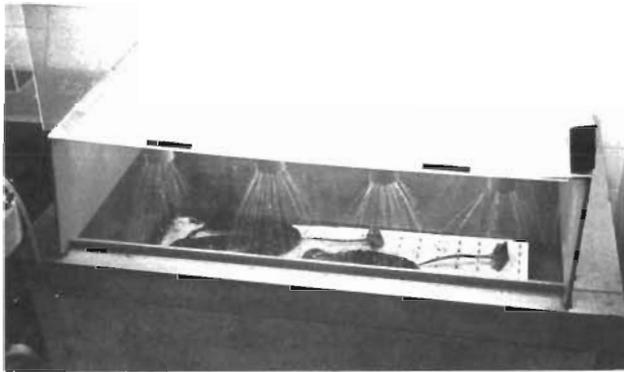

Fig. 1. Seawater shower used for cultivation of laminarian sporophytes

algae were sprayed by recirculated water from above (Fig. 1). For the first two weeks the algae were situated 2 cm below water level, but afterwards 5 cm above. After two months in the shower culture, the sporophytes had reached blade lengths of 5–25 cm and had formed rigid stipes and haptera. The plants on each PVC plate were thinned out again, leaving 3–5 plants per plate.

Cultivation in the Sea

By mid-February the experimental plants were transferred to an underwater station (iron grid, 2 × 1 m) situated in the sea near Helgoland at 2 m depth (all depths expressed as 'meter below Mean Low Water Spring Tide'). By the end of April the experimental plants were transferred to their final positions, i.e. to underwater stations at 7, 4.5 or 2 m water depth (45 PVC plates for each species and at each experimental depth). Growth measurements (see below) were performed from May until November, at seven dates. For this purpose the plants were surfaced by divers and 10 plants of each of the 9 experimental groups (3 species at 3 depths) photographed on board a ship. Measurements were taken from the photographs.

At 7 m depth the plants were lost by the end of July

due to heavy infestation by the bryozoan *Membranipora membranacea*. At the lower depths only small portions of the blades had been infested and were mechanically cleaned. A further loss of experimental plants was encountered by the beginning of October, when all individuals of *Laminaria digitata* disappeared from the underwater station at 2 m depth due to a storm.

Growth Measurements

The method of determining growth in blades of *Laminaria* spp. is based on the fact that elongation occurs within the lowermost 10 cm of the blade (Sundene, 1964). At each inspection date, a hole (6 mm diameter) was punched at 10 cm distance from the junction between stipe and blade in one experimental plant on each PVC plate. The hole marked the upper edge of the area $L1_{t-1}$ (Fig. 2). At the next inspection
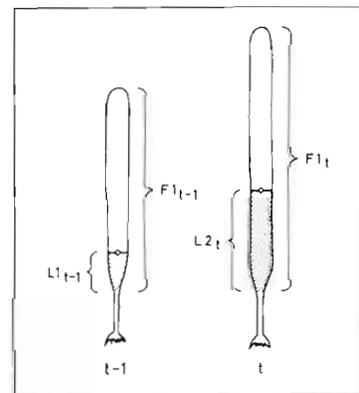

Fig. 2. Area parameters of *Laminaria* spp. used for calculation of growth rates (see text for further explanation)

date it marked the upper edge of the area $L2_t$. The increase in blade area (Z) which occurred in the interval from date $t-1$ to date t results from

$$Z = L2_t - L1_{t-1}$$

The total blade area $F1_{t-1}$ of a plant at date $t-1$ increases until date t according to

$$F2_t = F1_{t-1} + Z$$

where $F2_t$ denotes a fictive total area which is smaller than the actual total area $F1_t$ at date t, since not only growth has occurred, but also loss of tissue at the distal end of the blade due to erosion. The tissue lost (E) can be determined from

$$E = F2_t - F1_{t-1}$$

The relative growth rate R (Evans, 1972) was calculated on a monthly base (C = number of days between inspection dates) and refers to total blade area:

$$R = (\log_e F2_t - \log_e F1_{t-1}) \; 30 \cdot C^{-1}$$

Finally, an enlargement factor P was calculated from

$$P = antilog\, R$$

Gas Exchange Measurements

For determination of photosynthetic and dark respiration rates representative plants of the experimental groups were collected by divers one day prior to the measurements. Discs of 21 mm diameter were cut from the middle of the blades and kept dark overnight in flowing seawater (12 °C for measurements performed in May and June, 17 °C in August). Oxygen exchange of the disc was measured in a circular Plexiglas chamber (20 ml volume) supplied with an oxygen electrode (Hydrobios, Kiel). The seawater in the chamber was stirred by a magnetic bar. The oxygen electrode was calibrated both in airsaturated water and in a 1 % Na_2SO_3 solution, at constant temperature. Values for oxygen content in air-saturated seawater were taken from the tables presented by Green and Carritt (1967).

The oxygen measuring chamber was illuminated from above by a Leitz Prado Universal projector (quartz iodide lamp, 24 V, 250 W). The projector was combined with Schott colour glass filters BG 38 (2 mm thick) and GG 4 (1 mm thick) in order to imitate underwater spectral distribution at moderate water depths when Jerlov water Type 5 prevailed (see Lüning, 1980a). Ten different light intensities were achieved by Schott neutral glass filters. The latter were mounted in a filter wheel and changed automatically every 4 min. At the same time the measuring chamber was flushed with membrane-filtered seawater (Millipore, 0.45 μm). This procedure ensured that all measurements took place at 80–90 % of the oxygen content of airsaturated seawater. The signals from the oxygen electrode were monitored by a compensation recorder (Micrograpgh BD5, Kipp & Zonen, Delft, Holland). Photon flux density was measured by means of a Lambda quanta meter (Lambda Instruments Corp., Lincoln, Nebraska, USA). The conversion factors for the projector light field, as well as for the white fluorescent lamps used, were

$$10 \ \mu E \ m^{-2} \ s^{-1} \sim 2.0 \ W \ m^{-2} \sim 500 \ lx$$

Determination of Ash and Reserve Materials

By mid September up to 20 individuals from each experimental group (except the 7-m plants) were harvested for determination of area / dry weight (103 °C) relationships and of reserve materials. Parallel to this, plants (of unknown age) from the wild populations were harvested. The cultivated plants had an age of 1 year (7 months in the sea), when harvested. Dry blades were pulverized (Bühler homogenisator) and sieved (mesh width 80 × 80 μm), and the resulting algal powder was used for further analysis. The ash content was determined after combustion at 400 °C for 20 h

(Heraeus combustion furnace MR 170). The mannitol content was determined by oxidation for 1 min with periodate according to the method outlined by Cameron et al. (1948). Laminarin was assessed after neutralizing the hydrolyzate of 200 mg algal powder in 40 ml 1 N H_2SO_4 (4 h at 100 °C) using the glucose-oxidase test (Merck, GOD test).

RESULTS

From the beginning, the sporophytes of *Laminaria saccharina* exhibited the highest growth rate. At an age of 3 months (mid-February), when the experimental plants were transferred from the seawater shower into the field, maximum blade length was 25 cm in this species, but only 8–10 cm in the other two species. By mid-May, when growth measurements were started, mean values of blade area (at 2 m water depth) were 4.6 dm² in *L. saccharina*, and 2.9 or 1.5 dm² in *L. digitata* or *L. hyperborea*.

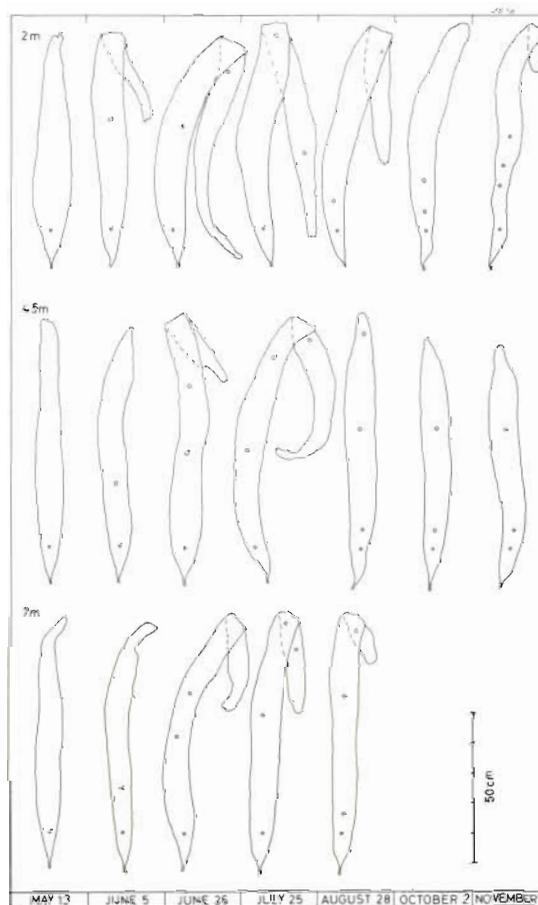From the growth records illustrated in Figures 3 and

Fig. 3. *Laminaria saccharina*. Records of the growth of experimental plants cultivated at 2 m, 4.5 m or 7 m water depth near Helgoland
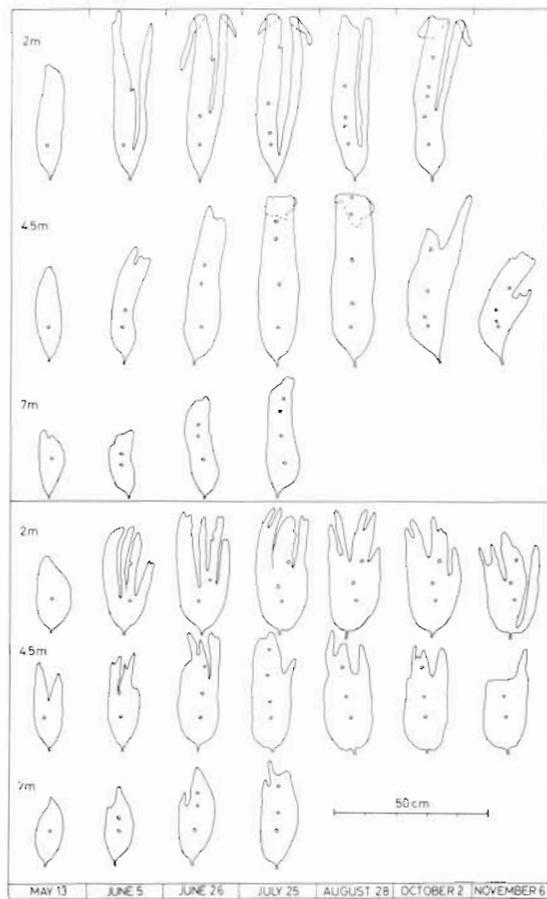
Fig. 4. *Laminaria digitata* (upper) and *L. hyperborea* (lower). Records of the growth of experimental plants cultivated at 2 m, 4.5 m or 7 m water depth near Helgoland

Fig. 5. *Laminaria* spp. Frond area at 2 m (○), 4.5 m (□) and 7 m (△) water depth. Vertical bars: confidence limits ($p = 0.05$, $n = 10$)

4, as well as from the seasonal changes of frond area (Fig. 5) the following features are obvious: (1) The maximum frond area occurred in July/August; it amounted to 9–11 dm² in *Laminaria saccharina*, but to only 5 and 3 dm² in *L. digitata* and *L. hyperborea*, respectively (all values at 2–4.5 m water depth). From September onwards the blade area decreased in all experimental plants, since loss at the distal end surmounted production of new tissue at the base. (2) Blade area at 2 and 4.5 m water depth was very similar, and only at 7 m significantly lower than at 2 m. (3) Splitting of the blade in the digitate species depended on cultivation depth. At 2 m, the blades exhibited deep splits by the beginning of June. At 4.5 m, 70 % of *L. digitata* and *L. hyperborea* were deeply split by the end of July. At 7 m only short splits were observed in *L. hyperborea* and no splits at all in *L. digitata*.

On October 2 about half the experimental plants of *Laminaria saccharina* had become sporogenous (irrespective of water depth); on November 6, all of them. The other two species had remained sterile until this date.
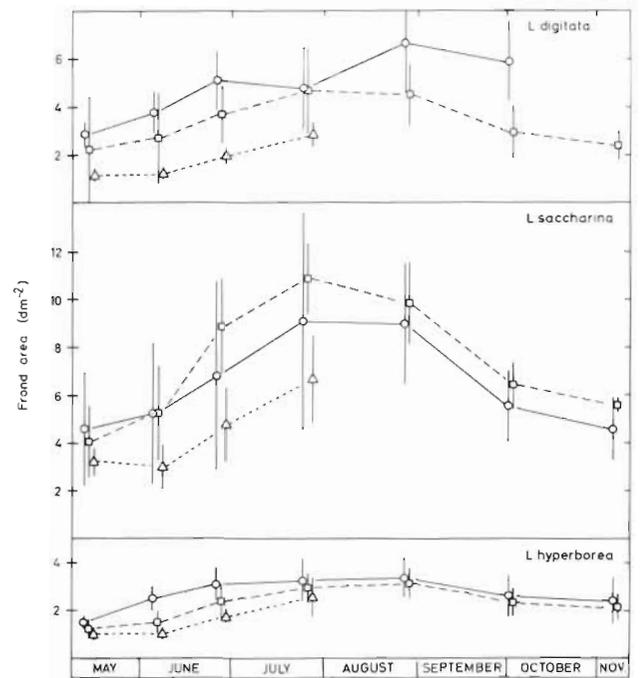
Significant differences in growth rate due to water depth could be most clearly detected in May (measuring date : June 5), and also during the summer in *Laminaria digitata* and *L. saccharina* (Figs 6 and 7). However the statistic resolution in the growth experiment was not sensitive enough to detect all depth effects on growth, and even some inconsistencies occurred. The relative growth rate (Fig. 7) reached its peak in May in *L. digitata* and *L. saccharina* at 2 m depth, or in June (measuring date: June 26) in all other experimental groups. The peak values of relative growth rate per month were in the range 0.5–0.8, corresponding to an enlargement of frond area by a factor of 1.7–2.2 within 30 d. Considerable increase in blade area occurred in July (measuring date: July 25) in all three species. By August, however, characteristic species-specific differences became obvious. In this month *L. hyperborea* ceased its increase in blade area completely, *L. saccharina* reduced its absolute growth rate by ca. 80 %, but *L. digitata* produced as much blade area as in the months before (Fig. 6). A decrease in growth rate (by 50 %, if compared with August) occurred in the latter species only in September (Figs 6 and 7).

During the period from mid-May until the beginning of October *Laminaria digitata* (2 and 4.5 m) and *L. saccharina* (2 m) enlarged their initial area (as present at May 13) by a factor $P = 4$. The corresponding value for *L. hyperborea* (2 and 4.5 m; also *L. saccharina* at 4

m) was $P = 3$ (Fig. 8). As stated above, P indicates the factor by which the initial area would have been enlarged if no losses of tissue at the distal end of the blade had occurred. The losses from May until October were in the range 42–70 %, with *L. hyperborea* exhibiting the lowest loss rate (Table 1). The loss rate was very variable from month to month and amounted to 10–40 % per month in *L. digitata* and *L. saccharina* and

to 10–30 % in *L. hyperborea*. No clear relation of loss rate with depth was discerned.

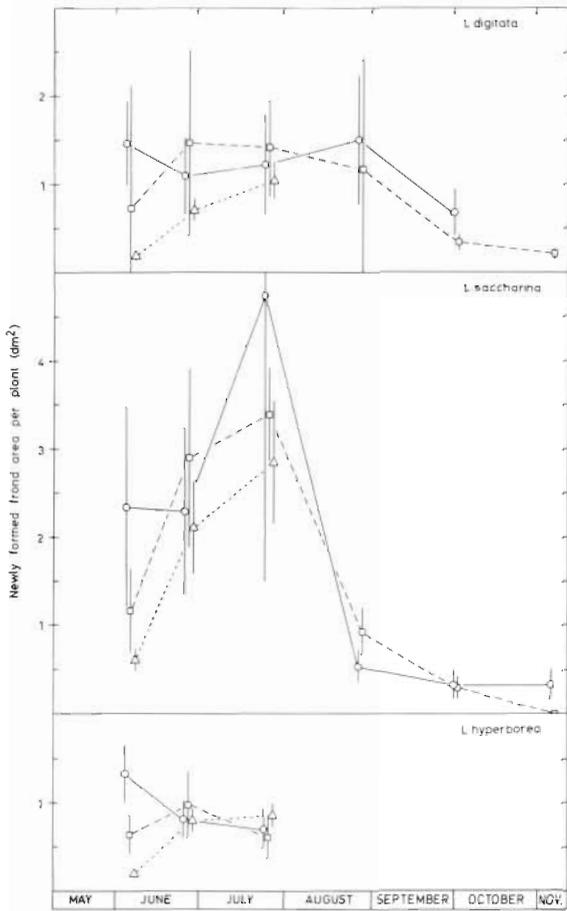Since the increase of blade area ceased compara-

Fig. 6. *Laminaria* spp. Newly formed frond area at 2 m (o), 4.5 m (□) or 7 m (△) water depth. Vertical bars: confidence limits ($p = 0.05$, $n = 10$)
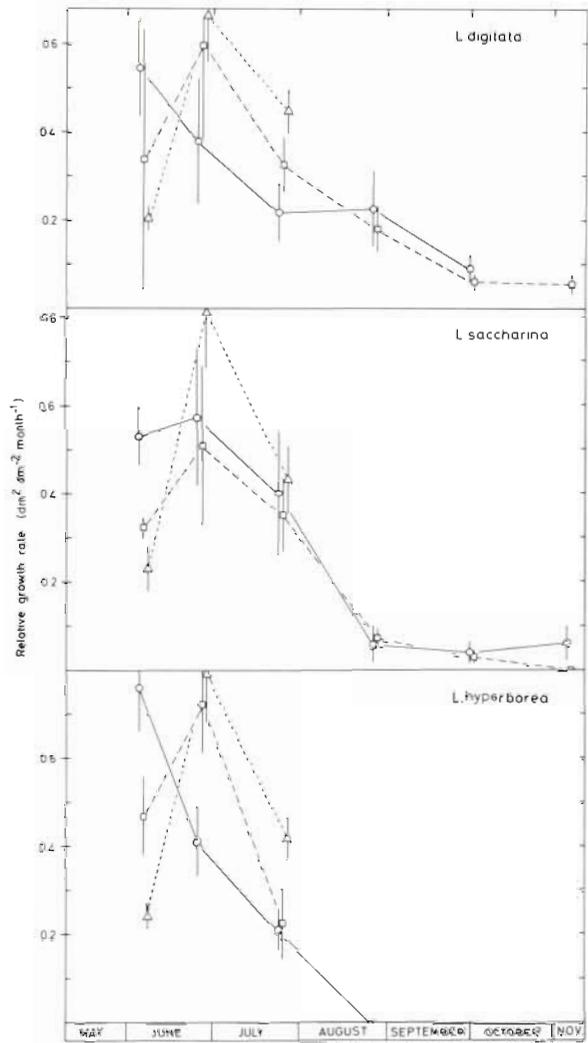

Fig. 7 *Laminaria* spp. Relative growth rate (per month) at 2 m (o), 4.5 m (□) or 7 m (△) water depth. Vertical bars: confidence limits ($p = 0.05$, $n = 10$)

Table 1. Total frond area per plant, produced from May 13 until October 2, and frond area lost during the same interval at two water depths (below M.L.W.S.). D: *Laminaria digitata*, S: *L. saccharina*, H: *L. hyperborea*

Species	Depth (m)	Frond area on May 13 (dm²)	Enlargement factor May 13–Oct. 2	Total frond area May 13–Oct. 2 (dm²)	Frond area Oct. 2 (dm²)	Frond area lost May 13–Oct. 2 (dm²)	(%)
D	2	2.9	3.8	11.0	5.9	5.1	46
	4.5	2.3	3.7	8.5	3.0	5.5	65
S	2	4.6	4.0	18.4	5.6	12.8	70
	4.5	4.1	2.9	11.9	6.4	5.5	46
H	2	1.5	3.0	4.5	2.6	1.9	42
	4.5	1.3	3.2	4.2	2.4	1.8	43

tively early and tissue losses were smallest in *Laminaria hyperborea*, the life span of the monthly formed blade portions was highest in this species. Figures 9 to 11 show the age of different portions of a blade in different experimental groups and the percentage of total blade area they made up at a given time. For example, the tissue formed until June 5 had completely disappeared by the beginning of October in *L. digitata* and *L. saccharina*, whereas it still made up 45 % of the blade area present in *L. hyperborea* at the beginning of November. About half of the blade area of the latter species consisted at this time of blade portions which were at least 5 months old. The age of 70–80 % of the blade area in early November was 2–3 months in *L. digitata*, 3–4 months in *L. saccharina* and 4–6 months in *L. hyperborea* (Figs 9 to 11).

By September the laminaran content in the blades of *Laminaria digitata*, cultivated at 2 m water depth, was

only 2 % of dry weight. The other two species, cultivated at the same depth, contained 5–9 times more laminaran (Table 2). Individuals of the wild population (more than one year old) which were investigated for comparison also exhibited a considerably lower laminaran content in *L. digitata* than in the other two species. The mannitol content was in the range 16–23 % (of dry weight) in all investigated groups, except a low value (8 %) in *L. digitata* cultivated at 4.5 m water depth. The highest ash and hence the lowest content in organic matter was found in *L. digitata*. Furthermore, there was a tendency for the ash content of the blades to decrease with increasing water depth (Table 2). The combined dry weight of stipe plus haptera amounted to 6 % (*L. saccharina*), 11 % (*L. digitata*) or 23 % (*L. hyperborea*). By September the stipes were 9–12 cm long (only 4 cm in *L. digitata* cultivated at 4.5 m water depth) in the experimental algae. Stipe diameter was 3–5 mm.

The relationship between net photosynthesis and

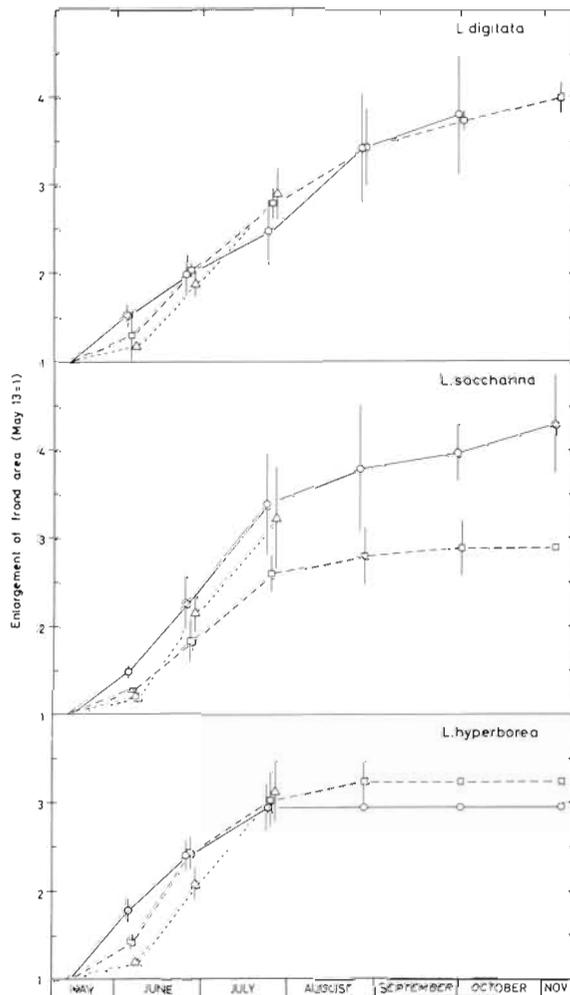Fig. 8. *Laminaria* spp. Enlargement of frond area at 2 m (○), 4.5 (□) or 7 m (△) water depth. The average area of the fronds attained on May 13th has been set as 1. Vertical bars: confidence limits (*p* = 0.05, *n* = 10)
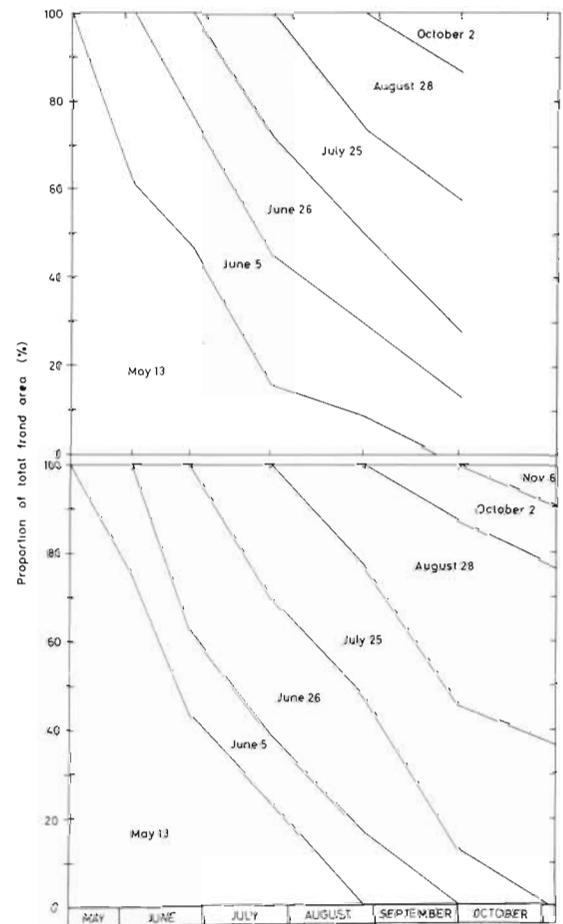

Fig. 9. *Laminaria digitata* at 2 m (upper) and 4.5 m water depth (lower). Proportion of frond area, newly formed between successive investigation dates, of actual frond area at dates given

light intensity (*P* vs *I* curve) was remarkably similar in all three *Laminaria* spp., and with respect to the water depth at which the algae had been cultivated. This was found in the experiments conducted in May/June at 12 °C (Fig. 12), as well as in August at 17 °C (Fig. 13). Net photosynthesis increased linearly with photon flux density up to 30 μE m^{-2} s^{-1}, and light saturation occurred above about 150 μE m^{-2} s^{-1}. It is obvious that no horizontal saturation plateau could be obtained in the range 100–200 μE m^{-2} s^{-1}. This must be due to the fact that in unilaterally illuminated blades of *Laminaria* spp. the photosynthetic layer on the opposite ('dark') side starts to contribute to the overall photosynthetic rate at concomitantly higher irradiances. Using a recording spectrophotometer (Shimadzu MPS-50L) it was found that a longitudinally halved blade (original thickness 1 mm) transmits 1 and 2 % at the absorption maxima (445 and 675 nm, respectively), or 25 % at the absorption minimum (605 nm). Assuming a transmission of 5 % over the whole visible spectrum, one can calculate that an intact blade, which is unilaterally

irradiated with 200 μE m^{-2} s^{-1}, receives 10 μE m^{-2} s^{-1} at the lower side, which is already above the compensation point (Figs 12 and 13). A correction for this effect has been made, and the resulting curves (dotted curves in Figs 12 and 13), which represent the net photosynthesis of the 'upper half' of the blade, indicate a much better saturation plateau. From the intersection of the corrected saturation plateau and the linear part of the *P* vs *I* curve an I_k-value (Talling, 1957) of about 50 μE m^{-2}·s^{-1} results.

For comparison, the *P* vs *I* curves of an eulittoral brown alga and of two sublittoral red algae were also investigated. In *Fucus serratus* net photosynthesis increased linearly with photon flux density up to 70 μE m^{-2} s^{-1} (Fig. 13), and saturation occurred at about 500 μE m^{-2} s^{-1}. The red algae *Delesseria sanguinea* and *Phycodrys sinuosa* were light saturated at 60 μE m^{-2} s^{-1}. Since the blades of the latter two species are for the most part one layered, a clear horizontal saturation plateau can be seen in these cases (Figs 12 and 13).

The rates of dark respiration, as calculated on an
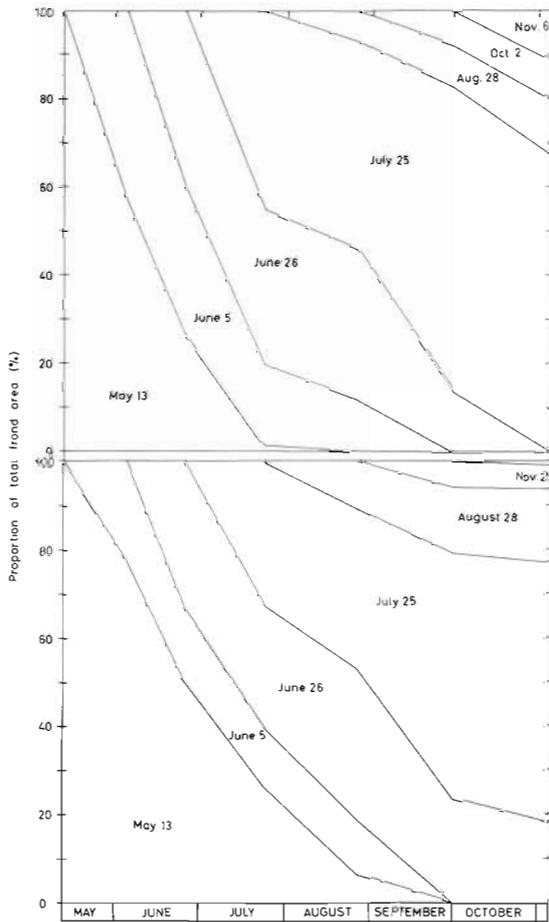

Fig. 10. *Laminaria saccharina* at 2 m (upper) and 4.5 m water depth (lower). Proportion of frond area, newly formed between successive investigation dates, of actual frond area at dates given

Fig. 11. *Laminaria hyperborea* at 2 m (upper) and 4.5 m water depth (lower). Proportion of frond area, newly formed between successice investigation dates, of actual frond area at dates given
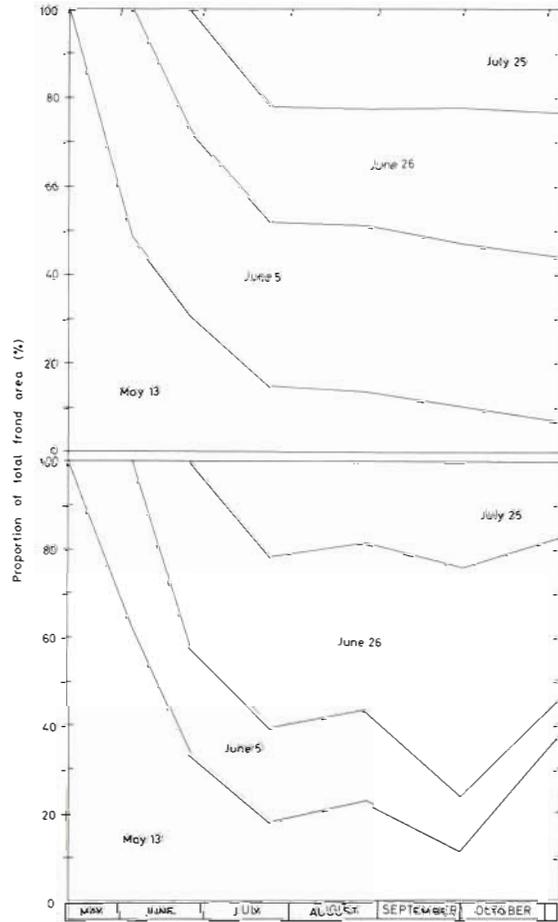
Table 2. Contents of ash, laminaran, mannitol, and conversion factors for fresh weight (FG) and dry weight (DW) (all mean values) in three *Laminaria* spp. at different water depths in September. D: *L. digitata*; S: *L. saccharina*; H: *L. hyperborea*; C: cultivated plants; W: wild plants. Number in code: water depth (m below M.L.W.S.); S.D.: standard deviation; N: number of analysed plants; TDW: total dry weight (frond plus stipe plus haptera)

Parameter	DC2	DC4	DW2	SC2	SC4	SW2	HC2	HC4	HW2	HW4
N	20	9	17	20	20	20	11	11	18	20
Ash (% of DW)	31.2	35.0	25.4	15.5	25.8	16.9	22.2	29.2	13.1	14.6
S.D.	3.4	1.1	3.3	2.5	4.3	2.7	4.6	4.3	2.9	2.6
Laminaran (% of DW)	2.4	1.4	8.1	21.2	5.1	21.1	10.8	3.8	26.0	19.4
S.D.	1.8	0.4	2.3	4.2	2.2	2.2	2.7	1.4	6.0	6.8
Mannitol (% of DW)	16.3	7.7	18.3	20.3	23.4	18.5	19.9	15.6	15.7	21.9
S.D.	2.6	1.9	2.0	2.1	3.6	1.3	3.9	4.2	2.9	2.7
Frond: DW (g g^{-1}FW)	16.2	15.0	17.1	23.0	16.2	20.6	19.8	16.3	27.2	24.2
S.D.	1.1	0.8	1.9	2.5	2.2	2.5	2.4	1.7	3.1	3.0
Frond: DW (g dm^{-2})	1.10	1.05	1.74	1.96	1.15	2.42	1.30	1.20	3.29	2.35
S.D.	0.15	0.08	0.28	0.31	0.34	0.24	0.28	0.19	0.64	0.61
TDW (g)	9.7	2.0	40.9	18.1	7.8	33.0	5.8	5.0	82.6	19.6
S.D.	5.3	1.2	17.0	8.8	6.5	14.5	2.4	2.1	31.3	7.4
Frond (% of TDW)	92.2	85.3		95.8	92.9		80.6	74.4		
S.D.	3.1	5.6		0.9	2.2		6.4	5.5		
Stipe (% of TDW)	4.9	5.9		2.3	3.2		8.3	8.1		
S.D.	2.7	2.7		0.8	1.2		2.4	2.0		
Laminaran plus mannitol (g dm^{-2})	0.17	0.09	0.15	0.21	0.25	0.16	0.24	0.16	0.13	0.18

area base, did not differ significantly according to species (Table 3). The lowest values were encountered in the plants cultivated at 7 m depth, which also had the thinnest blades. However, the latter aspect was not followed quantitatively.
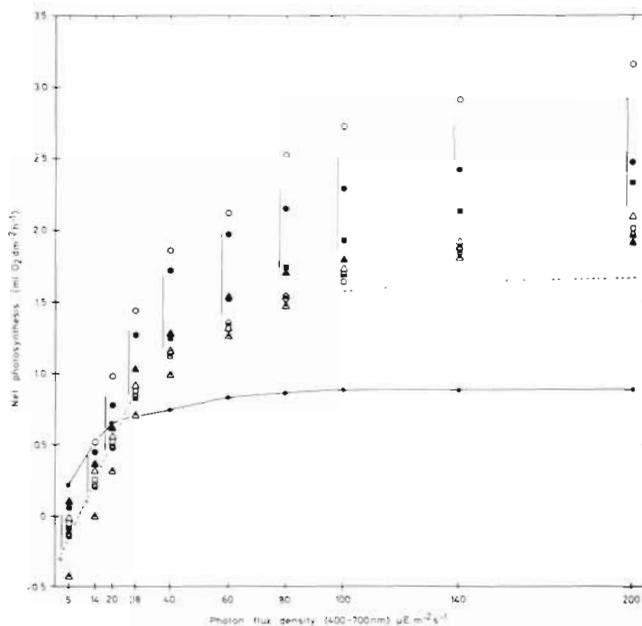
DISCUSSION

According to the results presented, no species-specific, genetically fixed traits in photosynthetic behaviour (in the sense of sun or shade adaptation) can account for the characteristic depth distribution of the three *Laminaria* spp. studied. Irrespective of species or depth, saturation of photosynthesis occurred at about 150 μE m^{-2} s^{-1} (equivalent to 30 W m^{-2} or about 7500 lx). It should be noted that these values were measured in late spring and summer. Saturation is likely to occur at somewhat deeper levels in winter (Lüning, 1971). Similar saturation levels have been found in other laminarian species: 10 800 lx in *Macrocystis pyrifera* (Clendenning, 1971), 10 000 lx in *L. japonica* (Niihara, 1975), 40 W m^{-2} in *Undaria pinnatifida* from low water

Fig. 12. *Laminaria digitata* (circles), *L. saccharina* (squares), *L. hyperborea* (triangles) and *Delesseria sanguinea* (small circles, solid line). Net photosynthesis at different light intensities, as measured from May to June (12 °C). All *Laminaria* spp. were cultivated at 2 m (open symbols), 4.5 m (half filled symbols) or 7 m (filled symbols) water depth. Regression equation for linear part of *P* vs *I* curve (dashed, in range 0–28 μE m^{-2} s^{-1}) : $y = 0.45x - 0.36$. Dashed line in range 100–200 μE m^{-2} s^{-1} represents *P* vs *I* curve, when corrected for transmission of 5 % of incident light (400–700 nm) by the upper half of the frond (see text for further explanation). Vertical bars: least significant ranges at $p = 0.05$
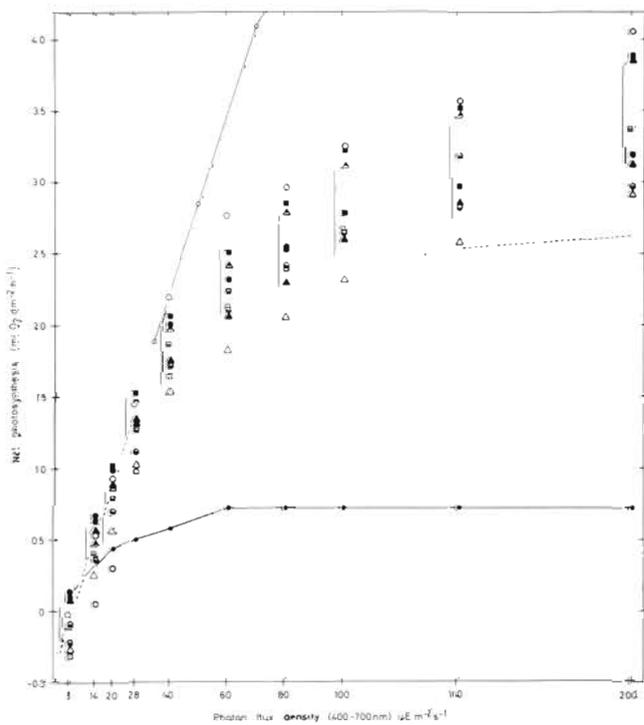
Fig. 13. *Laminaria digitata* (circles), *L. saccharina* (squares), *L. hyperborea* (triangles), *Phycodrys sinuosa* (small, filled circles; solid line) and *Fucus serratus* (small, open circles; solid line). Net photosynthesis at different light intensities, as measured in August (17 °C). Regression equation for linear part of P vs I curve (dashed, in range 0–28 μE m^{-2} s^{-1}) : $y = 0.59x - 0.38$. For further details see legend to Figure 12

Table 3. Dark respiration (ml O_2 dm^{-2} h^{-1}) of fronds of three *Laminaria* spp. cultivated at three water depths (below M.L.W.S.), and measured at two different times during the year. S.D.: standard deviation (N = 6)

Species	Depth	May/June (12 °C)		August (17 °C)	
	(m)	Mean	S.D.	Mean	S.D.
L. digitata	2	0.51	0.31	0.34	0.04
	4.5	0.53	0.22	0.39	0.09
	7	0.19	0.06	0.22	0.08
L. saccharina	2	0.54	0.22	0.70	0.19
	4.5	0.52	0.20	0.59	0.20
	7	0.50	0.28	0.25	0.06
L. hyperborea	2	0.42	0.16	0.69	0.23
	4.5	0.79	0.22	0.42	0.13
	7	0.21	0.07	0.25	0.07

can be classified as 'shade plants'. True 'sun plants', such as *Fucus* spp., are photosynthetically light saturated at about 100 W m^{-2} (Kanwisher, 1966; this study).

The range of maximum net photosynthesis, as determined in this study for the three *Laminaria* spp. (2–4 ml O_2 dm^{-2} h^{-1}) compares well with the rates reported for other laminarian species (Kain, 1979). In *L. saccharina* and *L. digitata* the growth rates found in this study can be compared with measurements of length increase of the blade performed by other authors. As can be seen from Table 4, during the first year the maximum increase in blade length is 7–11 cm week^{-1} in *L. saccharina* or 3–4 cm week^{-1} in *L. digitata* (see also Kain, 1979).

It is well known that in the European *Laminaria* spp. maximum blade growth occurs in late spring, and that adult sporophytes (older than 1 year) of *L. hyperborea* (Lüning, 1969) stop blade growth in June (except for 'collar' formation; Kain, 1975a), whereas adult sporophytes of *L. digitata* (Cosson, 1967; Pérez, 1969) and of *L. saccharina* (Parke, 1948) continue to grow during the second half of the year, although at a reduced rate. As the present study has shown, the differentiation between a 'rapid-growing period' (January to June) and a

mark and 30 W m^{-2} in *Undaria peterseniana* from 15 m water depth (Kageyama & Yokohama, 1974). Regarding light saturation of photosynthesis, the Laminariales investigated so far can be compared with shade-adapted phytoplankton (sampled at the depth at which 1 % of surface green light can be measured), which is light saturated at about 200 μE m^{-2} s^{-1} (equivalent to 44 W m^{-2}) according to Steemann Nielsen (1975). Together with deep-water red algae, which are light saturated at up to 50 % lower levels, i.e. 10–20 W m^{-2} (Mathieson and Norall, 1975; this study) and might be termed 'extreme shade plants'. The laminarian species

Table 4. Increase in frond length in two *Laminaria* spp. at the locations indicated (seasonal peak values)

Species	Location	Age (years)	Month	Growth rate (cm week^{-1})	Author
L. digitata	Helgoland	1	May	4.1	This study
	Tromsö	1	April	2.9	Sundene (1964)
	Calvados	2	May	8.0	Pérez (1969)
L. saccharina	Helgoland	1	June	10.6	This study
	Wales	1	May	7.0	Parke (1948)
	Wales	2	April	12.1	Parke (1948)
	NE-England	?	May	8.0	Burrows and Pybus (1971)

'slow-growing period' (July to December) – first made by Parke (1948) and afterwards adopted by Kain (1963) – must be modified for first-year plants of all three *Laminaria* spp. In the experimental plants of *L. hyperborea*, blade growth stopped completely by the end of July. The same phenomenon had been observed earlier in *L. saccharina* from the Isle of Man (Parke, 1948) and *L. digitata* from the coast of Brittany (Pérez, 1969). Also in these cases blade growth was reduced later in the year in first-year plants than in older plants.

It may be speculated that the long-lasting growth period during the first year is related to onset of formation of sporogenous tissue in such a way that the latter process reduces or stops vegetative growth of the blade. *Laminaria hyperborea* becomes sporogenous at a minimum age of 15 months (Kain, 1975a), *L. digitata* at 18–20 months (Gayral and Cosson, 1973). Both species were non-sporogenous at the end of the present experiment (in November), i.e. at an age of 14 months (9 months in the sea). *L. saccharina* from the Isle of Man formed sorus on 6-month-old blade portions (Parke, 1948), the experimental plants of *L. saccharina* in the present experiment on 4-month-old blade portions. The first-formed sorus, however, occupies only a relatively small area on the blade and is of a more patchy appearance, whereas in older *L. saccharina* plants the whole blade is covered with sorus, except for the wings. The amount of photosynthate required for sorus formation is, hence, probably small during the first year and, consequently, more photosynthate is available for vegetative growth than in later years. Probably, the allocation of photosynthate into either the formation of vegetative or reproductive tissue is not the cause, but only a consequence of the observed species-specific and age-specific seasonal growth patterns; this aspect deserves further investigation.

In summer, light intensity is sufficiently high to support photosynthesis of all three *Laminaria* spp. even at the lower limit of the *L. hyperborea* forest, which ends at 4 m water depth (below M. L. W. S.) near Helgoland. From June until August the mean photon flux density (400–700 nm) was in the range 42–56 $\mu E\,m^{-2}\,s^{-1}$ at this depth (Lüning and Dring, 1979). With this light supply the blades of the *Laminaria* spp. attain about 70 % of their maximum photosynthetic rate (Figs 12 and 13). The remarkably high growth rates of *L. digitata* and *L. saccharina* at 4.5 m (Fig. 6), well below the lower limit of their perennial vegetation, are hence not surprising.

From October until March only 10 % of total light available per year is received in the sublittoral region near Helgoland, and monthly means of photon flux density (400–700 nm) at 4 m water depth are as low as 1–14 $\mu E\,m^{-2}\,s^{-1}$ during this period (Lüning and Dring, 1979). Obviously, species inhabiting the deeper sublittoral must be capable of allocating a higher percentage of the carbon fixed in summer into pools of reserve material than species from the upper sublittoral. The dry weight content increases in all three *Laminaria* spp. in summer and early autumn due to the build-up of mannitol and laminaran, as shown by Black (1950a) for Scottish and by Haug and Jensen (1954) and Jensen and Haug (1956) for Norwegian populations. However, from the measurements of these authors it was also clear that the maximum laminaran content, occurring in September/October, is 50 % lower in *L. digitata* than in the other two species (Table 5). Similar results were obtained in the present investigation on plants harvested in the field (Table 2). In the plants cultivated this discrepancy was even more pronounced, since in *L. digitata* only 2 % of the dry weight was laminaran, but in the other two species 11–21 % (Table 2).

In the experimental plants the lowest content of combined mannitol and laminaran was found in *Laminaria digitata* cultivated at 4.5 m water depth (90 mg mannitol and laminaran per dm^2, or 14 % of organic weight). However, a few plants of this experimental group also survived the winter, so that the critical content of reserve materials for survival of a laminarian sporophyte near Helgoland must be somewhat lower It seems clear, however, that *L. digitata* cannot survive the period of limited light supply near

Table 5. *Laminaria digitata* (D), *L. saccharina* (S) and *L. hyperborea* (H). Contents of laminaran and mannitol in Norwegian populations, harvested in September. Values in brackets indicate seasonal maximum, where differing from September values by more than 1 %

Location	Laminaran (% of dry weight)			Mannitol (% of dry weight)		
	D	S	H	D	S	H
Reine, 1950*	10	31	24	17	15	17
Reine, 1951*	16	23	18	15	18	19
Reine, 1952**	12 (15; Oct.)	–	23 (32; Nov.)	15	–	17
Espevaer, 1952**	10 (13; Oct.)	–	17 (29; Nov.)	16	–	20

* According to Haug and Jensen (1954).
** According to Jensen and Haug (1956).

the lower limit of *L. hyperborea* (8 m depth near Helgoland) due to its restricted capability of building up reserve materials. This is not valid for *L. saccharina* which has a similar potential in this respect to *L. hyperborea* (Tables 2 and 5).

Laminaran and mannitol are interconvertible (Percival and McDowell, 1967), and the increase in laminaran content follows the increase in mannitol with a lag phase of about 2 months (Haug and Jensen, 1954). Several findings indicate that laminaran is formed from mannitol in the same part of the thallus where mannitol was built up due to current photosynthesis. For instance, no translocation occurs in adult sporophytes of *Laminaria hyperborea* in summer (Lüning et al., 1973). In the blade of *L. saccharina*, Black (1954) found 0 % laminaran at the base, 10 % at 60 cm distance, and 30 % at 180 cm distance. A similar gradient was detected in the blade of a Pacific *Laminaria* sp. (Powell and Meeuse, 1964). From these findings it can be inferred that the laminaran content present in autumn must be directly related to the longevity of the tissue which fixed carbon at maximum rate in summer. The finding that 80–90 % of the tissue present in June/July still existed in September in *L. hyperborea* and *L. saccharina*, whereas this percentage amounted only to 65 % in the case of *L. digitata*, again stresses that the main reason why this species does not exist in the deeper kelp region (the 'park' of *L. hyperborea* on European coasts) is to be sought in its genetically fixed seasonal growth and carbon allocation pattern.

From the middle part of the kelp region, the 'forest' of *Laminaria hyperborea*, *L. digitata* and *L. saccharina*, both adapted for colonization of the upper kelp region by possession of a flexible stipe, are excluded due to competition with *L. hyperborea*. This has clearly been demonstrated by Kain (1975b, 1976), who cleared rocky areas within the 'forest' of *L. hyperborea*. One year later, sporophytes of all three *Laminaria* spp. were present on the experimental areas, but four years later, the rigid stipes of *L. hyperborea* had grown to a sufficient length to allow the formation of a blade canopy of this species, which eliminated all competitors by cutting short their light supply. This is another example for the general rule that the depth survival range of an algal species, limited primarily by coincidence of the physiological and morphological adaptations with the abiotic environment, is furthermore limited and reduced by biological competition (Chapman, 1973b).

Black (1950b), as well as Chapman and Craigie (1978), found that the laminaran content of *Laminaria* spp. decreased with increasing water depth; a similar trend was observed in the present investigation (Table 2). Hence the build-up of reserve materials does not seem to be regulated in such a way that the sporophytes of a given *Laminaria* species allocate

more photosynthate into reserve materials the deeper they grow. On the contrary, the content in reserve materials at a given time seems to depend directly on photosynthetic production and hence decreases with water depth.

The seasonal variation of environmental factors in the sea near Helgoland can be inferred from Figure 14, which also shows the seasonal course of vegetative growth of the experimental plants for comparison. As reported by Chapman and Craigie (1977), the growth of *Laminaria longicruris* growing at the coast of Nova Scotia is severely NO_3^--limited in summer and can be substantially increased by artificial fertilization of the kelp beds. Near Helgoland nutrient concentrations in summer (Fig. 14) are higher than at Nova Scotia, although still below the saturation level for growth of *L. saccharina* which is ca. 10 μM NO_3^- (Chapman et al.,
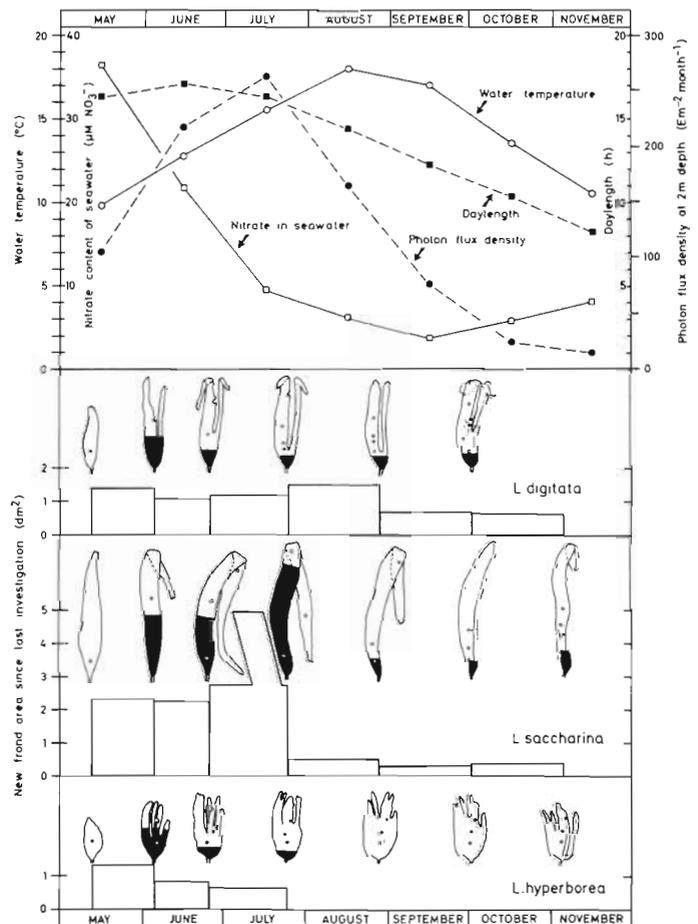

Fig. 14. Helgoland, 1975. Seasonal course of temperature, nitrate concentration of seawater (Harms and Hagmeier, 1976), photon flux density at 2 m water depth (Lüning and Dring, 1979), daylength (according to Smithsonian Meteorological Tables, 1951), and of frond area increase in experimental sporophytes of three *Laminaria* spp. (hatched areas), cultivated at 2 m water depth (filled area in outline drawings: new-formed tissue)

1978). The finding in the present work that during the first year of life *L. hyperborea* stopped its growth completely and *L. saccharina* reduced its growth rate considerably by the end of July (ambient NO_3^- concentration 8 μM), but *L. digitata* by 50 % only in September (ambient NO_3^- concentration 3–4 μM) suggests that nutrient concentration is only a secondary, but not the triggering, factor for termination or reduction of vegetative growth. The possibility that the seasonal course of reserve carbon accumulation per se might trigger the onset of late winter growth in *L. longicruris* had been ruled out by Chapman and Craigie (1978).

For microscopic laminarian gametophytes a broad temperature optimum has been recorded to occur above 10 °C, with inhibition acting near 20 °C (Kain, 1965, 1969; Pérez, 1971; Cosson, 1973). Since water temperature rises up to 18 °C near Helgoland, it might be possible that some of the reduction in growth rate is due to elevated temperatures. However, that *Laminaria hyperborea* did not resume growth in October, when water temperature fell below 15 °C (Fig. 14), makes it also unlikely that temperature, provided it is not near the lethal limit, is a triggering factor for vegetative growth. The same applies to photon flux density which in August, at 2 m water depth, was still as high as 164 E m^{-2} month^{-1} (Fig. 14) or 102 μE m^{-2} s^{-1} (conversion by use of daylength = 14.4 h). This means that the experimental plants of *L. hyperborea* and *L. saccharina*, which stopped or reduced their growth by the end of July, were still photosynthetically light-saturated in August (Figs 12 and 13).

One is then left with the theoretical possibility that either a circannual rhythm is involved in the regulation of seasonal growth, as suspected in the case of *Alaria esculenta* (Buggeln, 1978), or that photoperiodism is involved. The first possibility would be difficult to prove (Sweeney, 1969; Pengelly, 1974), and no experimental evidence has been produced so far to support the second hypothesis. The seasonal development of the gametophytes of the Laminariales investigated to date is definitely not under photoperiodic control (Lüning, 1980b). This does not exclude the possibility that photoperiod controls the development of the laminarian sporophyte, i.e. its vegetative growth behaviour and/or the onset of sporangia formation. This problem, which is also important for aquaculture prospectives with laminarian species, must now be tackled experimentally.

LITERATURE CITED

Black, W. A. P. (1950a). The seasonal variation in weight and chemical composition of the common British Laminariaceae. *J. mar. biol. Ass. U.K.*, 29, 45–72.

Black, W. A. P. (1950b). The effect of the depth of immersion on the chemical constitution of some of the sub-littoral seaweeds common to Scotland. *J. Soc. chem. Ind., Lond.*, 69, 161–165.

Black, W. A. P. (1954). Concentration gradients and their significance in *Laminaria saccharina* (L.) Lamour. *J. mar. biol. Ass. U.K.*, 33, 49–60.

Buggeln, R. G. (1978). Physiological investigations on *Alaria esculenta* (Laminariales, Phaeophyceae). IV Inorganic and organic nitrogen in the blade. *J. Phycol.*, 14, 156–160.

Burrows, E. M. and Pybus, C. (1971). *Laminaria saccharina* and marine pollution in north-east England. *Mar. Pollut. Bull.*, NS, 2, 53–56.

Cameron, M. C., Ross. A. G. and Percival, E. G. V (1948). Methods for the routine estimation of mannitol, alginic acid, and combined fucose in seaweeds. *J. Soc. chem. Ind., Lond.*, 67, 161–164.

Castric-Fey, A., Girard–Descatoire, A., Lafargue, F. and L'Hardy-Halos, M. T (1973). Étagement des algues et des invertébrés sessiles dans l'Archipel de Glénan. *Helgoländer wiss. Meeresunters.*, 24, 490–509.

Chapman, A. R. O. (1973a). Methods for macroscopic algae. In J. R. Stein (Ed.), *Handbook of Phycology*. University Press, Cambridge, pp. 87–104.

Chapman, A. R. O. (1973b). A critique of prevailing attitudes towards the control of seaweed zonation on the sea shore. *Botanica mar.*, 16, 80–82.

Chapman, A. R. O. and Craigie, J. S. (1977). Seasonal growth in *Laminaria longicruris*: relations with dissolved inorganic nutrients and internal reserves of nitrogen. *Mar. Biol.*, 40, 197–205.

Chapman, A. R. O. and Craigie, J. S. (1978). Seasonal growth in *Laminaria longicruris*: relations with reserve carbohydrate storage and production. *Mar. Biol.*, 46, 209–213.

Chapman, A. R. O., Markham, J. W and Lüning, K. (1978). Effects of nitrate concentration on the growth and physiology of *Laminaria saccharina* (Phaeophyta) in culture. *J. Phycol.*, 14, 195–198.

Clendenning, K. A. (1971). Photosynthesis and general development in *Macrocystis*. *Nova Hedwigia (Beih.)*, 32, 169–190.

Cosson, J. (1967). Étude d'une population de *Laminaria digitata* Lam. (biométrie, croissance, régénération). *Bull. Soc. linn. Normandie*, 8, 246–281.

Cosson, J. (1973). Influence des conditions de culture sur le développement de *Laminaria digitata* (L.) Lam. (Phèophycèes, Laminariales). *Bull. Soc. phycol. Fr.*, 18, 104–112.

Evans, G. C. (1972). *The Quantitative Analysis of Plant Growth*, Blackwell, Oxford.

Gayral, P. and Cosson, J. (1973). Exposé synoptique des données biologiques sur la laminaraire digitée *Laminaria digitata*. *Synop. Synop. FAO Pêches*, 89.

Green, E. J. and Carritt, D. E. (1967). New tables for oxygen saturation of seawater *J. mar. Res.*, 25, 140–147.

Harms, E. and Hagmeier, E. (1976). Hydrographie, Chemie und Planktongehalt des Wassers bei Helgoland. In *Jahresbericht 1975*. Biologische Anstalt Helgoland, Hamburg. pp. 21–27

Haug, A. and Jensen, A. (1954). Seasonal variations in the chemical composition of *Alaria esculenta*, *Laminaria saccharina*, *Laminaria hyperborea* and *Laminaria digitata* from Northern Norway. *Norsk institutt for tang- og tareforskning, rep.*, 4, 1–14.

Jensen, A. and Haug, A. (1956). Geographical and seasonal variation in the chemical composition of *Laminaria hyperborea* and *Laminaria digitata* from the Norwegian coast. *Norsk institutt for tang- og tareforskning, rep.*, 14, 1–8.

Kageyama, A. and Yokohama, Y (1974). Photosynthetic properties of marine benthic brown algae from different depths in coastal areas. *Bull. Jap. Soc. Phycol.*, *22*, 119–123.

Kain, J. M. (1962). Aspects of the biology of *Laminaria hyperborea*. I. Vertical distribution. *J. mar. biol. Ass. U. K.*, *42*, 377–385.

Kain, J. M. (Mrs. N. S. Jones) (1963). Aspects of the biology of *Laminaria hyperborea*. II. Age, weight and length. *J. mar. biol. Ass. U. K.*, *43*, 129–151

Kain, J. M. (Mrs. N. S. Jones) (1965). Aspects of the biology of *Laminaria hyperborea*. IV. Growth of early sporophytes. *J. mar. biol. Ass. U.K.*, *45*, 129–143.

Kain, J. M. (Mrs. N. S. Jones) (1969). The biology of *Laminaria hyperborea*. V Comparison with early stages of competitors. *J. mar. biol. Ass. U.K.*, *49*, 455–473.

Kain, J. M. (Mrs. N. S. Jones) (1975a). The biology of *Laminaria hyperborea*. VII. Reproduction of the sporophyte. *J. mar. biol. Ass. U.K.*, *55*, 567–582.

Kain, J. M. (Mrs. N. S. Jones) (1975b). Algal recolonization of some cleared subtidal areas. *J. Ecol. 63*, 739–765.

Kain, J. M. (Mrs. N. S. Jones) (1976). The biology of *Laminaria hyperborea*. VIII. Growth on cleared areas. *J. mar. biol. Ass. U.K.*, *56*, 267–290.

Kain, J. M. (Mrs. N. S. Jones) (1979). A view of the genus *Laminaria*. *Oceanogr. mar. Biol.*, in press.

Kanwisher, J. W (1966). Photosynthesis and respiration in some seaweeds. In H. Barnes (Ed.), *Some Contemporary Studies in Marine Sciences*. Allen & Unwin, London. pp. 407–420.

Lüning, K. (1969). Growth of amputated and dark-exposed individuals of the brown alga *Laminaria hyperborea*. *Mar. Biol.*, *2*, 218–223.

Lüning, K. (1971). Seasonal growth of *Laminaria hyperborea* under recorded underwater light conditions near Helgoland. In D. J. Crisp (Ed.), *Proceedings of the 4th European Marine Biology Symposium*. University Press, Cambridge. pp. 347–361

Lüning, K. (1980a). Critical levels of light and temperature regulating the gametogenesis of three *Laminaria* spp. (Phaeophyceae). *J. Phycol.*, in press.

Lüning, K. (1980b). Control of algal life history by daylength and temperature. In *Systematics Association Special Volume*, in press.

Lüning, K., Chapman, A. R. O. and Mann, K. H. (1978). Crossing experiments in the non-digitate complex of *Laminaria* from both sides of the Atlantic. *Phycologia*, *17*, 293–298.

Lüning, K. and Dring, M. J. (1975). Reproduction, growth and photosynthesis of gametophytes of *Laminaria saccharina* grown in blue and red light. *Mar. Biol.*, *29*, 195–200.

Lüning, K. and Dring, M. J. (1979). Continuous underwater light measurement near Helgoland (North Sea) and its significance for characteristic light limits in the sublittoral region. *Helgoländer wiss. Meeresunters.*, *32*, 403–424.

Lüning, K., Schmitz, K. and Willenbrink, J. (1973). CO_2 fixation and translocation in benthic marine algae. III. Rates and ecological significance of translocation in *Laminaria hyperborea* and *L. saccharina*. *Mar. Biol.*, *23*, 275–281.

Mathieson, A. C. and Norall, T L. (1975). Physiological studies of subtidal red algae. *J. exp. mar. Biol. Ecol.*, *20*, 237–247

Niihara, Y (1975). Physiological studies of *Laminaria japonica* var *ochotensis*. The effect of temperature, light intensity and salinity upon photosynthesis and respiration of young sporophytes. *Hokkaido-Ritsu Suisan Shikenjo. Yoichi, Jap.*, *17*, 11–17.

Parke, M. (1948). Studies on British Laminariaceae. I. Growth in *Laminaria saccharina* (L.) Lamour *J. mar. biol. Ass. U. K.*, *27*, 651–709.

Pengelly, E. T. (1974). *Circannual Clocks, Annual Biological Rhythms*, Academic Press, New York.

Percival, E. and McDowell, R. (1967). *Chemistry and Enzymology of Marine Algal Polysaccharides*, Academic Press.

Pérez, R. (1969). Étude biomètrique d'une population de *Laminaria digitata* Lamouroux de l'étage infralittoral profond. *Revue Trav. Inst. (scient. tech.) Pêch. marit.*, *33*, 117–135.

Pérez, R. (1971). Influence de quelques facteurs physiques sur le développement de *Laminaria digitata* (L.) Lamour. *Bull. Soc. phycol. Fr.*, *16*, 89–105.

Powell, J. H. and Meeuse, B. J. D. (1964). Laminarin in some Phaeophyta of the Pacific coast. *Econ. Bot.*, *18*, 164–166.

Provasoli, L. (1968). Media and prospects for the cultivation of marine algae. In A. Watanabe and A. Hattori (Eds), *Cultures and Collections of Algae*. (Proc. Jap. Conf. Hakone, 1966). Jap. Soc. Plant Physiol., Tokyo. pp. 63–75.

Smithsonian Meteorological Tables (1951). Duration of daylight. *Smithson. misc. Collns, 114*, 507–512.

Steemann-Nielsen, E. (1975). Marine photosynthesis, Elsevier, Amsterdam.

Sundene, O. (1964). The ecology of *Laminaria digitata* in Norway in view of transplant experiments. *Nytt. Mag. Bot.*, *11*, 83–107.

Sweeney, B. M. (1969). Rhythmic phenomena in plants, Academic Press, London.

Talling, J. F. (1957). The phytoplankton population as a compound photosynthetic system. *New Phytol.*, *56*, 133–149.