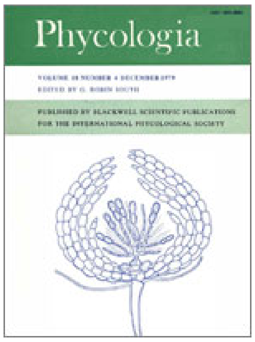

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The effect of depth on summer growth of *Laminaria saccharina* (Phaeophyta, Laminariales)

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Mature *Laminaria saccharina* sporophytes transplanted to seven depths between 1 and 21 m below mean low water showed different rates of blade growth during July. A maximum rate of 1·15 cm day^{-1} occurred at 9 m. Elongation proceeded about 40% as rapidly in transplants at 1 and 3 m and in undisturbed plants on shore at 0 m. Growth was much reduced below 17 m. Low levels of nitrate and high temperatures near the surface and attenuated illumination at depth are suggested as limiting factors. A quantitative survey of subtidal kelp beds around the study site showed that *L. saccharina* dominates *L. digitata* and *Agarum cribrosum* in abundance and biomass between 2 and 8 m.

Introduction

Kelp forests are among the most productive plant communities in the world (Mann, 1972) and may grow to considerable depths where waters are cool and clear. Several investigators have examined seasonal variations in productivity, but the influence of depth usually has been of secondary concern. Black (1950), however, analysed chemical constituents and John (1970) measured growth in young sporophytes specifically to determine the effects of depth. The present study quantifies the response of mature *Laminaria saccharina* (L.) Lamour. (considered conspecific with *L. longicruris* by Chapman, 1974) in New England waters to depth of immersion.

The site of this work, Appledore Island, Maine, U.S.A. (42° 59′ N, 70° 57′ W) is the largest (38·5 ha) of nine low glacially eroded, granite islands lying 10 km offshore in the southwestern Gulf of Maine. Depths in the immediate vicinity can exceed 35 m and bottom topography is highly irregular, consisting of ledges and scattered boulders. Local waters are exceptionally free from coastal pollution and are influenced by generally southward flowing currents. A strong thermocline typically becomes established in summer (Loder, Anderson & Shevenell, 1973).

Methods

Mature, healthy, uninjured sporophytes at mean low water (MLW) level were selected for the growth rate experiment and carefully removed from the substratum. Holdfasts were attached to plexiglass plates by rubber bands. Blades were amputated to standard lengths of 50, 75 and 100 cm in equal numbers to reduce variations in growth that might be caused by plants of non-uniform sizes (Mann, 1972). Four plants of each length class were suspended at 1, 3, 6, 9 and 12 m below MLW on buoyed anchor lines about 200 m from the protected western shore of the island. Constant depth with respect to MLW was maintained to simulate subtidal conditions. Sets of five 100-cm plants were transplanted to 17 and 21 m; ten plants (four 50-cm, three 75-cm, and three 100-cm) were tagged but left undisturbed on shore at 0 m.

Growth was determined as elongation of the blade following the method of Parke (1948) except that holes were punched at 20 cm rather than 10 cm above the juncture of blade and stipe when an initial experiment showed that about 27% as much growth occurs from 10 to 20 cm as from 0 to 10 cm in 100 cm plants. Growth during an experimental period of 24 days (12 July to 5 August 1975) was calculated in cm day^{-1} for all plants surviving at the end.

Temperature was monitored to 15 m below the surface at 1 m intervals approximately weekly with a YSI Model 51 O_2/temperature meter. Light penetration was measured five times near midday over the same period the following summer. Levels of light of wavelengths photosynthetically useful to brown algae (based on action spectra between 400 and 700 nm of *Coilodesme*, *Laminaria*, and *Ilea*

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fascia; Haxo & Blinks, 1950) were determined relative to illumination just below the surface with a simple submersible photometer. The instrument was constructed of a meter, selenium photocell, cosine collector, and filter with transmission maxima at 430 and 670 nm and a minimum from 550 to 600 nm. Nutrient analysis near the site is given in Norall (1976).

An underwater survey of the *L. saccharina* zone was conducted by means of SCUBA in 1976. Quadrats of 0·25 m^2 were harvested between 0 and 13 m to determine the vertical distribution of plant density, biomass, and length of stipe and blade. Depths below 13 m were not sampled because of the scarcity of *L. saccharina*.

Results

Growth of *L. saccharina* differed substantially among the several depths of immersion (Fig. 1) and proceeded most rapidly at 9 m below MLW. The mean rate was 1·15 cm day^{-1} and differed significantly from all other depths except 12 m. Elongation of other sets was less than 61% as fast. Although transplants could not be attached to the apparatus at 0 m, those at 1 m are most comparable to the shore plants. Growth rates of these two sets, and the one at 3 m as well, were virtually identical and transplantation appears to have had no observable detrimental influence on the rate of growth near MLW. Shallow transplants were epiphytized by a tube-forming colonial diatom and an *Ectocarpus*-like brown filament, but the undisturbed plants resisted epiphytes perhaps because of turbulence on shore (Sundene, 1962). Steadily flowing currents did not prevent settling on the transplants. Plants at 17 and 21 m grew at about the same rate and much slower than shallower ones. Correlation of growth to depth was good: $r = 0{\cdot}806$ between 1 and 9 m (95% confidence interval is $+0{\cdot}63 \leqslant P_r \leqslant +0{\cdot}89$) and $r = -0{\cdot}857$ between 9 and 21 m (95% confidence interval is $-0{\cdot}71 \leqslant P_r \leqslant -0{\cdot}91$). Analysis of variance revealed that differences of growth rate between size classes were significant at the 5% level only at 3 and 12 m. Differences became insignificant if rates were normalized to cm day^{-1} per 10 cm of blade length. Because each size class contained at most four specimens, these statistical results should be regarded cautiously.

Increase in blade width of transplants grown for 67 and 78 days demonstrated an equivalent response to depth. Shallow plants showed minor losses, but plants at 6, 9, and 12 m had mean increases (±2 s.e. mean) in width over original dimensions of 38 ± 8%, 78 ± 13%, and 53 ± 12% respectively.

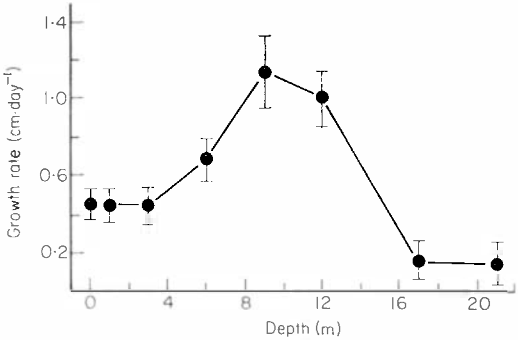

FIG. 1. Variation in growth of *L. saccharina* with depth. Mean rates and 95% confidence intervals.

Results of the subtidal survey are shown in Tables 1 and 2. The most abundant species over the range of

TABLE 1. Mean density (A) and kilograms of biomass (B) per quadrat at the study site; LS = *L. saccharina*, LD = *L. digitata*, AC = *A. cribrosum*

Depth interval (m)	Number of 0·25 m^2 quadrats	LS	LD	AC	Total
0–1	13	4·7^{A}	13·2	0·0	17·9
		0·555^{B}	1·016	—	1·571
2–4	6	7·3	0·0	0·0	7·3
		1·475	—	—	1·475
5–6	12	6·8	0·0	0·0	6·8
		1·110	—	—	1·110
7·5–8·5	6	2·8	0·3	2·0	5·1
		0·704	0·118	0·076	0·898
11–13	16	0·8	0·6	8·2	9·6
		0·414	0·041	0·302	0·757

TABLE 2. Mean size and mass of *L. saccharina* at several depth intervals

Depth interval (m)	Number of plants	Blade length (cm)	Stipe length (cm)	Hollow stipes (%)	Biomass of whole plants (g)
0–1	61	63·5	24·1	7	118·3
2–4	44	98·9	23·2	7	201·1
5–6	82	75·8	22·8	11	162·4
7·5–8·5	17	94·5	26·4	18	248·3
11–13	12	178·8	63·3	75	552·3

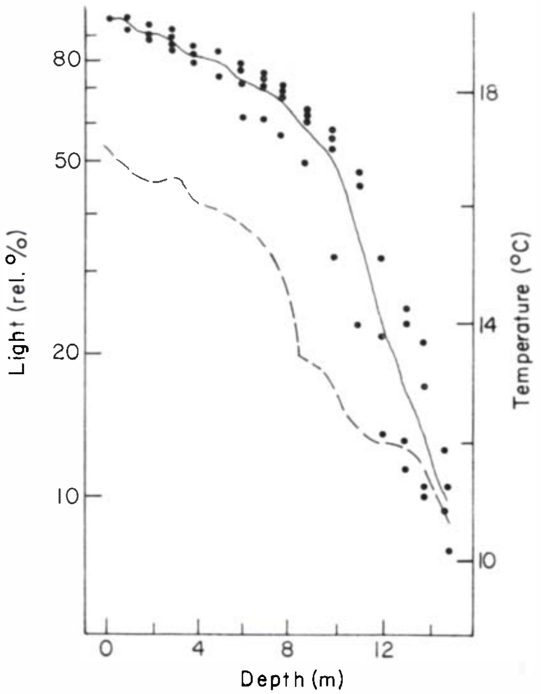

FIG. 2. Variation of temperature (dashed line) and light (solid line) with depth in July. Plots of mean values with data points shown for light penetration.

depths examined was *L. saccharina* at 48%. It dominated a zone from 2 to 8 m in both density and biomass. Above 2 m it was replaced by *L. digitata* and below 11 m by *Agarum cribrosum* which, although ten times more abundant, nevertheless maintained a slightly smaller biomass per unit area.

Penetration of photosynthetically useful light was good in late July with only about half of that entering the water column extinguished at 10 m and 10% reaching 15 m (Fig. 2). Water temperatures during the experimental period averaged 17·0°C at the surface and dropped to 10·6°C at 15 m. The steepest rate of change occurred between 6 and 8 m.

Discussion

Rates of summer growth for *L. saccharina* of 0·3–0·6 cm day^{-1} are reported for the northwest Atlantic coast (Reynolds, 1974; Chapman & Craigie, 1977). Results presented here agree well for plants at 6 m and shallower, while rates at 9 and 12 m are somewhat elevated and at 17 and 21 m depressed. A maximum rate at 9 m coincides with data of Chapman & Craigie who also found, however, nearly equal growth at 18 m. John (1970) records best growth at 1·5 m in Scotland, but he obtained results from only one other depth (13·7 m) and may have missed the optimal level.

Light, temperature, and nutrient concentration are major environmental parameters which affect the growth of algae and all varied with depth at Appledore Island. Sufficient light was available at 9 m to support the fastest rate of growth measured. Rapidly curtailed growth below that level probably resulted from diminishing illumination. Saturation may be assumed above 9 m and slower growth rates attributed to other factors. Kjeldsen & Phinney (1972) state that *L. saccharina* on the Oregon coast was 'very sensitive to high temperatures' (16–20°C) in field and laboratory studies. Surface temperatures rose into this range during my experiment and may have impaired growth to some extent although this species can tolerate such temperatures in the southernmost part of its distribution. Recent findings of Chapman & Craigie (1977) in Nova Scotia indicate that limited growth of *L. longicruris* beginning in July is linked to depletion of internal nitrogen reserves after external nitrate levels have dropped. Summer growth rate improved if plants were fertilized with $NaNO_3$. Nutrient analysis near the experimental site shows that more nitrate is available below 12 m than above, suggesting that growth was limited by very low concentrations (0–1 μg-at·L^{-1}) in the upper meters of thermally stratified waters while higher concentrations (2–3 μg-at·L^{-1}) at depth boosted rates of growth.

These results point out the very significant effect depth of immersion as an integrator of several parameters can have on growth in *L. saccharina*. It is an important consideration to bear in mind in calculations of productivity of kelp beds based on growth rates.

Acknowledgments

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