Populations of *Laminaria hyperborea* at various latitudes

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KURZFASSUNG: **Populationen von *Laminaria hyperborea* in verschiedenen geographischen Breiten.** Jahreszeitliche Wachstumsschwankungen bei *Laminaria hyperborea* prägen sich in der Anatomie des Stiels aus. Dadurch läßt sich das wahrscheinliche Alter einer Pflanze an einem Längsschnitt durch die Basis ihres Stiels bestimmen. *L. hyperborea* wächst im Sublitoral; vollständige Pflanzen kann man durch Tauchen erhalten. Die Art kommt an exponierten und halbexponierten Küsten Europas von 40° N bis 71° N vor, und zwar auf felsigem Untergrund oder festliegenden Blöcken von der Niedrigwasserlinie bis zu Tiefen von 4 bis 35 m. Je nach den örtlichen Gegebenheiten ist sie die dominierende Art, oder sie kommt vergesellschaftet mit *L. digitata, L. saccharina, L. ochroleuca, Saccorhiza polyschides* oder *Alaria esculenta* vor. Die untersuchten Pflanzen stammten aus Beständen von Standorten verschiedener geographischer Breite und abgestufter Exposition, hauptsächlich von der Isle of Man sowie von Süd- und Nordnorwegen. Gewicht und Länge des Stieles und der Lamina jeder Pflanze wurden gemessen und ihr wahrscheinliches Alter bestimmt. Am Ende der Periode des raschen Wachstums entspricht die Lamina einer Jahresproduktion; sie wird jährlich abgeworfen. Der Stiel dagegen ist mehrjährig und zeichnet den Wachstumsverlauf während der gesamten Lebensdauer einer Pflanze auf. Bei vergleichbarer Tiefe unter dem mittleren Meeresspiegel schwankt das Wachstum im allgemeinen an den untersuchten Standorten verschiedener geographischer Breite nicht mehr als unter den ökologischen Gegebenheiten eines Ortes. Jedoch pflegen an begünstigten Standorten der höheren Breiten die Pflanzen älter zu werden als bei Isle of Man. Bis zu einer Tiefe von 15 m nimmt das Wachstum nur wenig ab, in erheblich tieferem Wasser ist das Wachstum aber auffallend verringert. Die Pflanzen werden auch merklich kleiner, wenn sie am Eingang exponierter Höhlen wachsen. An Standorten, die ständig einer starken Strömung ausgesetzt sind, ist das Wachstum bei geringer Lebensdauer der Pflanzen intensiv. *L. cucullata*, vielleicht eine in ruhigem Wasser ausgebildete Form von *L. hyperborea*, erzeugt ein im Verhältnis zum Stiel schwereres Laub.

INTRODUCTION

Laminaria hyperborea (GUNN.) FOSLIE is probably the most important subtidal kelp in western Europe. Although it does not compare in size with plants such as *Macrocystis* it does form extensive forests in which it dominates over all other algae and many animals. The forests occur on rock or stable boulders in exposed or semi-exposed sites from about low water springs down to a variable depth depending on conditions. Geographically it extends from about 40° N in Portugal (SEOANE-CAMBA 1966) to 71° N in north Norway, and at least as far east as the U.S.S.R. border (BAARDSETH, private communication) (Fig. 1).

L. hyperborea is a perennial plant with a fast growing period which lasts in Britain from the end of December until June or July. During this season the transition zone between the frond and the stipe is active in producing primary stipe tissue below and frond tissue above. Secondary growth of the stipe increases its diameter and

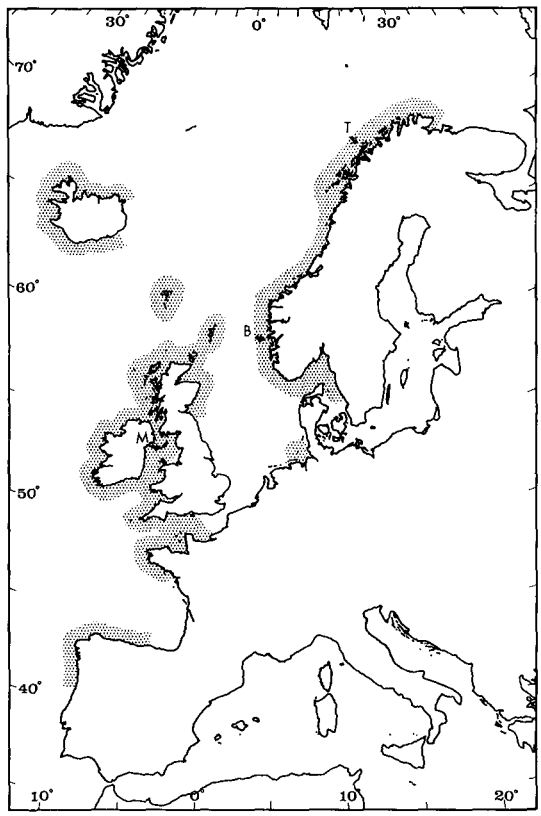

Fig. 1: Map of western Europe showing, as stippled area, coasts where *Laminaria hyperborea* occurs. Apparent gaps in the distribution are due to the unsuitability of coasts and isolated groups of plants may occur within these if there is rock present. Sampling areas: M (Isle of Man), B (near Bergen), T (near Tromsø)

occurs, as in trees, through the activity of a sub-surface meristem. Outside the fast growing season growth is extremely slow, expansion of the frond slight, and secondary growth in the stipe slight, laying down small dark cells. Because these are easily distinguished from cells produced during fast growth, the number of zones of these cells gives an indication of the age of the plant (KAIN 1963). In order to observe all the zones it is necessary to examine a median section of the whole of the base of the stipe, when the slow growth zones appear as pairs of lines, each pair often separated from the next by the enlarged bases of haptera (Fig. 2). The determination of a plant's age is complicated by a number of factors. Firstly interference lines are sometimes

formed as a result of some sort of disturbance other than season. Secondly, in some areas the limpet *Patina pellucida* (L.) grazes cavities in the holdfast, removing some of the tissue which should be examined. Thirdly, under favourable conditions, growth may not slow down sufficiently in some first year plants to show a growth line.

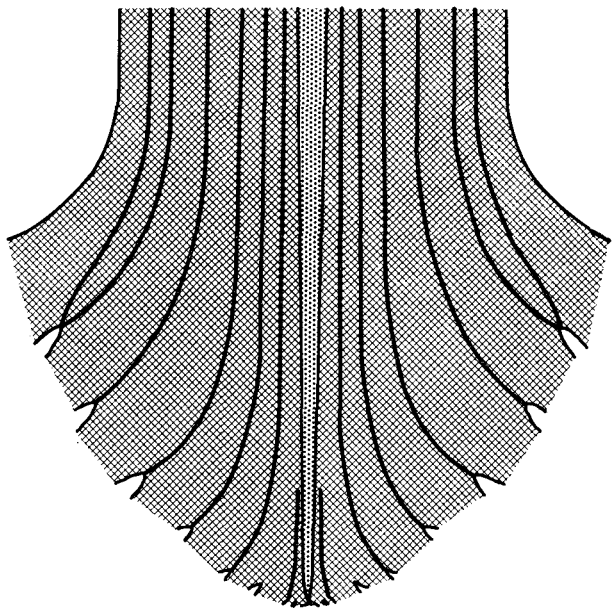

Fig. 2: Diagrammatic representation of a median section of the base of a stipe of *L. hyperborea*. Stippled area: primary tissue (including medulla and cortex); Cross-hatched area: secondary tissue (cortex); Thick lines: slow growth zones. The plant is at least 7 years old and produced two rings of haptera in its second year and none in its seventh

Fourthly it is possible (though not actually observed) that old plants may not produce discernable secondary tissue during fast growth, with the result that no line is made apparent for that year.

METHODS

L. hyperborea was sampled in sites where it was dominant, mainly in the Isle of Man and in south-west and north Norway. The Norwegian populations were sampled in June–July 1965 and those in the Isle of Man in June 1966. The collection of the plants was necessarily accomplished by divers as it is not possible to obtain the whole of the plant base by any remote method. No selection of plants was made: plants of all sizes were removed systematically from an area of rock.

In the laboratory samples were kept in wet sacks. The frond was cut off each plant and weighed. The stipe was weighed fresh after the haptera had been cut off.

The base was then split with a knife and a thick section cut from the centre. When this was wetted and viewed against the light the growth lines were usually visible.

Because the stipe is perennial, its size reflects the growth of the plant throughout its life. For the purpose of brevity, comparisons will be made here only between the stipe weights of different populations. It has been found that in all populations plant size for a given age is extremely variable. In addition, certain year groups in some populations seem comparatively advanced or retarded, presumably because of differing conditions from one year to the next. For this reason comparisons between populations can be made safely only by comparing age groups. The means and fiducial limits (at 5 %) of stipe weight have been plotted against age for each population.

RESULTS

The shaded area in Figure 3 shows the means and fiducial limits of stipe weight for a population in the Isle of Man at 1 m below extreme low water springs (ELWS) or 4 m below mid-tide. The site (54° 5.62′ N, 4° 46.7′ W) is exposed for the Isle of Man but not to full Atlantic swell. It is designated in the figure ME4 (for Man, Exposed,

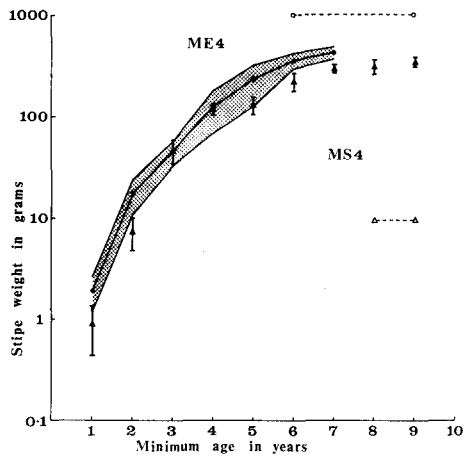

Fig. 3: Means and fiducial limits of stipe weights at different ages of two populations of *L. hyperborea*. ● and hatched area: population ME4; ▲: population MS4. The age range of the oldest 5 % of the plants: ○ - - - - ○: population ME4; △ - - - - △: population MS4. See text for further explanation

4 m below mid-tide). The fiducial limits have been calculated in the usual way but plotted on a logarithmic scale in order that the results for the small young plants can be seen as clearly as the old. The fiducial limits have been joined by lines between age groups in order to make comparisons with other populations possible. Also in this figure (not shaded) are shown similar results for a relatively sheltered population (MS4) at the same depth in the Isle of Man (54° 6.52′ N, 4° 45.0′ W). The two popu-

lations can be readily compared. Not too much importance should be attached to slight differences in first and second year old plants because these may largely reflect short term differences in site conditions. In addition, the fiducial limits may not be reliable here because the distribution of stipe weights may not be normal. Older plants, however, represent a longer growth period and it is clear from Figure 3 that 6 and 7 year

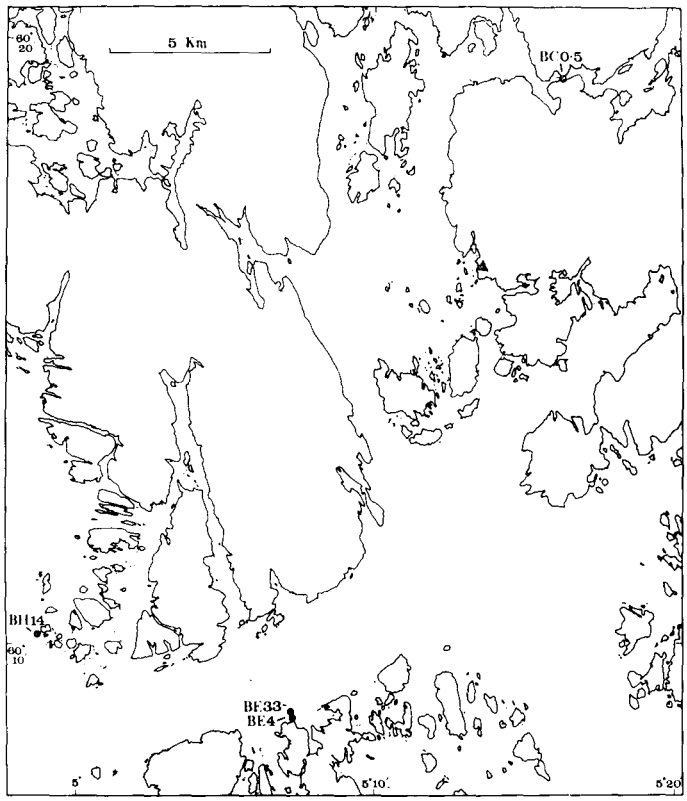

Fig. 4: Map of the coastal area south of Bergen showing sites of the populations of *L. hyperborea* sampled. ▲: Biological Station, Espegrend

plants were smaller in the sheltered site than the relatively exposed. As it might be expected that larger plants would be selected out by wave action in an exposed locality, particularly at this shallow depth, some unknown factor must have been inhibiting growth of the plants in sheltered water. It is possible that lack of water movement might sometimes reduce assimilation but this is speculation. Also shown in Figure 3 is the age range of the oldest 5 % of the plants in the samples. In the exposed site the oldest 5 % were between 6 and 9 years and in the sheltered between 8 and 9 years. Thus although the maximum age observed was the same there were proportionately more older plants in the sheltered population. This could be explained either by the effect of wave action or by the fact that *Patina* infection of the hold-

fast was greater in the exposed population. It has already been suggested (KAIN 1963) that this may be a frequent cause of plant dislodgement.

The site of a population in south-west Norway is shown as BE4 (Bergen area, exposed, 4 m below mid-tide) in Figure 4. It is an exposed site, 3.5 m below ELWS and 4 m below mid-tide. It is therefore comparable with the exposed Isle of Man site ME4.

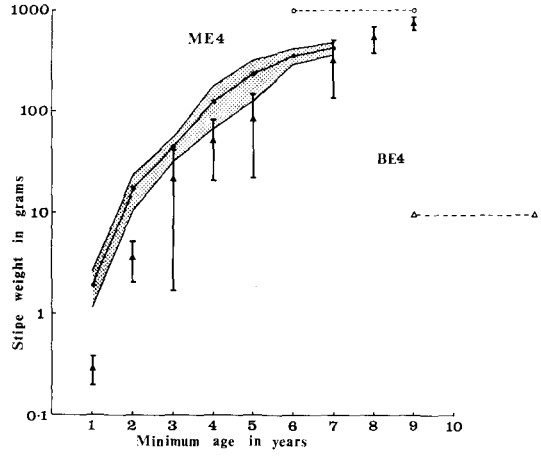

Fig. 5: Similar to Figure 3. ● and ○: ME4; ▲ and △: BE4

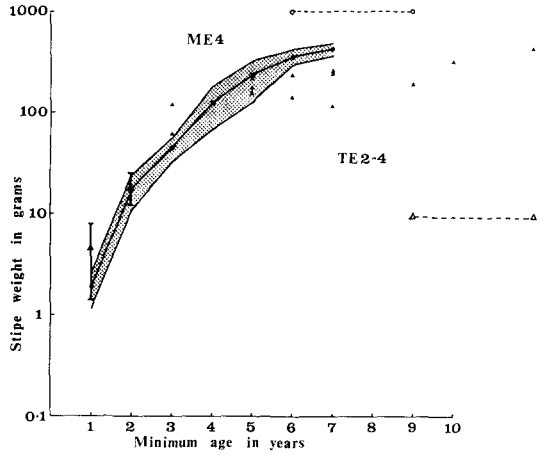

Fig. 6: Similar to Figure 3. ● and ○: ME4; ▲ and △: TE2-4

The stipe weights are compared in Figure 5. Although the younger plants had smaller stipes in the Norwegian population there was a much greater proportion of older plants and the maximum size attained was thus considerably greater. Although at a similar depth below mid-tide, this population would not be subjected to as much stress from breaking waves because the tidal range is smaller.

Figure 6 shows some stipe weights of a limited number of plants collected from two fairly exposed sites off Kvaløy (69° 35.8′ N, 18° 1.3′E) and Ringvassøy (69° 54.6′ N, 18° 43.7′ E) near Tromsø in northern Norway, at depths of 2 and 4.5 m below mid-tide (TE2–4). The stipes of the lower age groups were similar to those in the Isle of Man but there was a much higher proportion of older plants and these seemed small. This could be due to interference lines complicating the aging of the stipes or to persistence, without much growth, of mature plants in colder water. This latitude can probably be considered to be above the optimum in Norway as populations of this species seem sparse. This is supported by the spring grab results of GRENAGER (1958).

It thus seems that at the depth of 4 m below mid-tide in exposed or semi-exposed sites there is no more difference in the growth in established populations during the first 7 years between sites at the latitude of the Isle of Man 54° N and that of Tromsø 69° N than there is locally in the Isle of Man. Longevity is greater in Norway however.

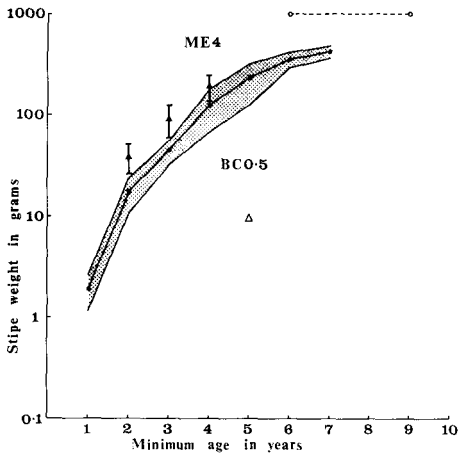

Fig. 7

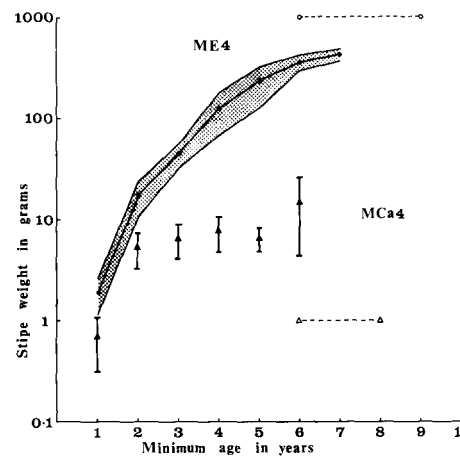

Fig. 8

Fig. 7: Similar to Figure 3. ● and ○: ME4; ▲ and △: BCO.5
Fig. 8: Similar to Figure 3. ● and ○: ME4; ▲ and △: MCa4

An interesting population was observed in the rapids at Nordåsstraumen (Fig. 4, BR0.5) at about 0.5 m below mid-tide. These plants were subjected to an almost continuous current running in and out of a pool. The stipe weight (Fig. 7) of 2 to 4 year olds was high, in fact that of either 3 or 4 year olds was higher than in any other observed population. The fronds were also unusually large. It seems extremely likely, therefore, that the rate of growth is increased by water movement, given adequate light. On the other hand longevity appeared low; the oldest 5 % were all 5 years old. Older plants may get swept away or the site may have been cleared 5 years previously.

Returning to the Isle of Man, Figure 8 shows the stipe weights of a population at the entrance to a cave (54° 6.3′ N, 4° 46.0′ W) at 4 m below mid-tide. The stipes were all particularly small for their ages and had an apparent limit to their size. It

is likely that this was due to the type of water movement encountered in this site rather than to diminished light firstly because of this limit and secondly because a high proportion of the plants had distorted fronds and stipes resulting from damage to the transition zone.

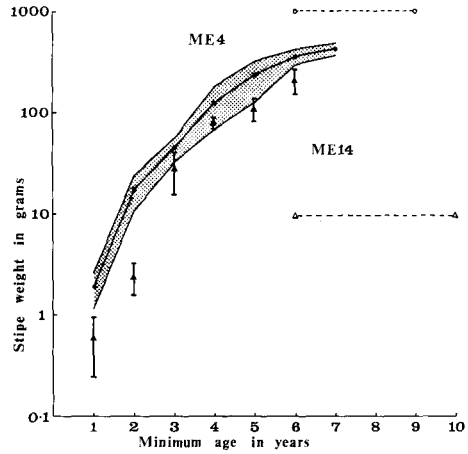

Fig. 9: Similar to Figure 3. ● and ○: ME4; ▲ and △: ME14

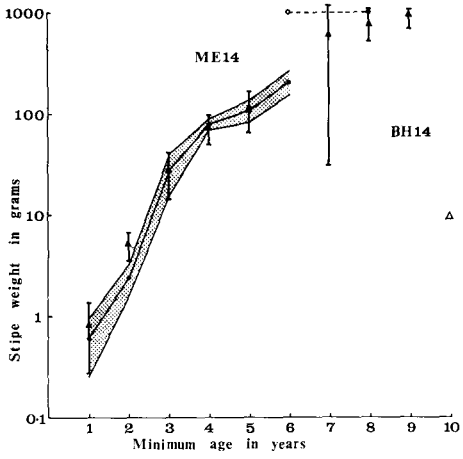

Fig. 10

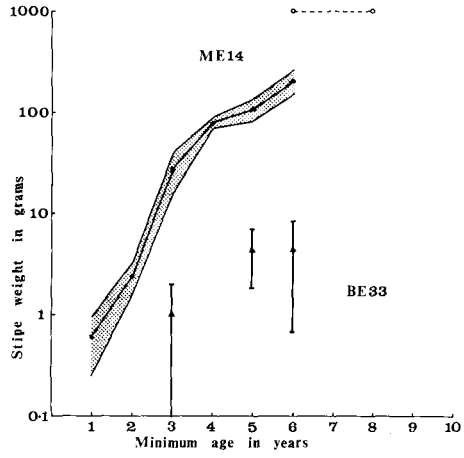

Fig. 11

Fig. 10: Similar to Figure 3. ● and ○: ME14; ▲ and △: BH14
Fig. 11: Similar to Figure 3. ● and ○: ME14; ▲ and △: BE33

Turning to deeper water, Figure 9 shows the stipe weights of an exposed population in the Isle of Man (54° 3.35′ N, 4° 46.4′ W) at 11 m below ELWS or 14 m below mid-tide (ME14). Although variable, the stipes were somewhat smaller than those in shallower water but the longevity was similar. This may be due to reduced light. In the following figures this population is taken as a basis for comparison.

Figure 10 shows a comparison with a population from a highly exposed locality near Bergen (Fig. 4, BH14), with no protection from full Atlantic swell, at 14 m below mid-tide. Up to the age of 5 the stipe weights show a marked similarity to the Isle of Man population at the same depth but whereas in the latter the oldest 5 % of the plants were 6 to 8 years, in these the oldest 5 % were all 10 years. The maximum size was correspondingly large.

Figure 11 shows the stipe weights of a small sample of *L. hyperborea* collected near the lower limit of the species near Bergen at an exposed site at 33 m below mid-tide (Fig. 4, BE33). The stipes were clearly very much smaller, the mean weight of 6 year olds was only one fiftieth of the population at 14 m. It would seem likely that light was limiting.

It can be concluded from these deeper populations that whereas there is little difference between the rate of growth in established populations at 4 m and 14 m below mid-tide either in the Isle of Man or near Bergen, there is a marked reduction over the next 19 m of depth.

Infestation of the holdfast of *L. hyperborea* by *Patina pellucida* has already been mentioned. This limpet spends the first part of its life on the frond and then may move down the stipe into the holdfast (GRAHAM & FRETTER 1947). Cavities in the holdfast are common in the Isle of Man and the English Channel but not a single one was encountered in Norway although the species was frequently found on the frond as far north as the Tromsø area. It therefore seems likely that Norwegian populations of the plant are not subjected to this hazard.

CONCLUSIONS

In conclusion it can be said that the rate of growth of stipes of *Laminaria hyperborea* in established populations under similar environmental conditions does not differ much over the range of latitude studied. Greater differences occur in the ability of the species to become established and in the age attained. In the Isle of Man, with the exception of the cave population, there is only a small difference in growth rate over the depth range where forests occur; thus the populations are limited by factors affecting establishment rather than growth. Near Tromsø forests are absent from apparently suitable sites, so it would seem that conditions for establishment are not particularly good there. In the Isle of Man longevity seems low compared with the Bergen area. No plants over 10 years old have been found and plants over 7 are comparatively rare. In south-west Norway plants from 9 to 12 years are common. In north Norway no large plants were found. It thus seems that in Europe the latitude of southern Norway is at or near the optimum for the establishment of this species and the attainment of large size.

SUMMARY

1. Populations of *Laminaria hyperborea* were sampled in the Isle of Man (54° N), the Bergen area (60° N) in south-west Norway and the Tromsø area (70° N) in north Norway.
2. The age of each plant was determined through the observation of a median section of the base of the stipe and the fresh weight of the stipe taken as a measure of the production of primary and secondary stipe tissue by the plant.
3. At 4 m below mid-tide there was a slight difference in stipe weights at a given age between exposed and relatively sheltered sites in the Isle of Man. Differences between those in the Isle of Man and those at exposed sites near Bergen and near Tromsø were also slight. The longevity of the plants was greater near Bergen however.
4. At 14 m below mid-tide plants were slightly smaller than at 4 m in the Isle of Man and a population from the same depth in a highly exposed site near Bergen had similar stipes. Again, however, the longevity was greater near Bergen, resulting in some very much larger plants.
5. At 33 m below mid-tide near Bergen plants were very much smaller than at 14 m.
6. Plants very small for their age were encountered in the Isle of Man only at the entrance to caves, where breaking waves seemed to cause damage.
7. The largest plants for their age were found in shallow water rapids near Bergen. The longevity of these was low, however.
8. It is concluded that local conditions have as much effect on early growth rate as latitude. Greater differences occur in the ability to become established and in longevity over the range of latitude studied and south-west Norway appears favourable for these.

ACKNOWLEDGEMENTS

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Discussion following the paper by KAIN

SVENDSEN: I am surprised that you find approximately the same rate of growth at 4 m and 14 m. I have some measurements of stipe lengths of tagged plants at 4 m and 7 m. Growth rate was much faster at 4 than at 7 m, but the locality was a little sheltered. Do you have any explanation for these differences in growth rate?

KAIN: Your results, I believe, applied to plants growing on areas of rock cleared previously. It is difficult to compare established populations with these. The different results may be due to the density of established populations; there may also be some other explanation.

BARNES: Is it not possible that the similar growth rates with position are due to a compensation between temperature and day-length?

KAIN: Yes, this may be so. We do not known when the fast growing period near Tromsø is, but because storage material is laid down in the summer, use could be made of the continuous light in summer for fast growth if this starts in winter when there is almost no light.

DELÉPINE: Un autre moyen d'étude serait peut-être de comparer les variations de la vitesse de croissance au moment du maximum de la croissance de ces algues et la température moyenne durant cette même période.

KAIN: The minimum temperature near Bergen is about 3 to 4° C below that near the Isle of Man, but the maximum is about the same. The minimum at Tromsø is about the same as near Bergen but the maximum is about 4° C lower. I agree that these differences are small and would like to obtain samples from farther south.

DELÉPINE: Il est connu que le mètabolisme des algues varie beaucoup avec la température (les mêmes algues ont des tailles différentes en fonction de la température). L'absence de différences entre les diverses latitudes est peut-être due à de faibles variations de température aux différents stations.

KAIN: Yes, laboratory experiments on this might be interesting, but the situation may be complicated by the fact that diving late summer when storage tissue is laid down, the temperature required is different.

DELÉPINE: Il est connu que le métabolisme des algues varie beaucoup avec la température (les manifestations solaires?

KAIN: WALKER's correlation with sunspots was based on density measurements repeated at various places over many years. I have worked on *L. hyperborea* for only 8 years and have made no density measurements.

SÖDERSTRÖM: At the Swedish west coast *Laminaria hyperborea* grow only in the northern half as small specimens at a depth of around 15 m. The explanation for these differences as compared with the Norwegian coast could be either the low winter temperature, the greatly diminished tide or the low salinity. Can you comment on the growth of *L. hyperborea* in low salinities?

KAIN: I have no experience with this species in reduced salinity but had the impression that the limitation on the Swedish west coast was associated with the reduction in salinity.

HEMPEL: Are there indications for mortality being selective with regard to growth rate of individuals favouring the fast growing or the slow growing individuals of an age group? This might cause differences in the apparent growth curves in populations of different habitats.

KAIN: I am aware that my measurements may not have resulted in the growth curves because of possible selection out of larger plants. However, one would expect this selection to be greater in an exposed site, while in fact it was the plants in the sheltered site which were small for their age.