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Population studies of *Laminaria hyperborea* from its northern range of distribution in Norway

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Abstract

Eight populations of *Laminaria hyperborea* from wave-exposed localities in Finnmark (70–71 °N) were compared with two populations in Vega (65 °N). Standing stock in shallow water (3–5 m) was within the same range in the two areas (6–16 kg fr. wt. m^{-2}). Both the highest and lowest value of standing stock were registered in Finnmark. Degree of wave-exposure was determined by the numbers of sectors exposed to open sea at each locality, with each sector given a relative wind force value. The most wave-exposed locality in Vega had a slightly higher annual biomass production as a function of plant age compared with the populations from Finnmark within a similar range of wave exposure. Of the two localities in Vega the most wave-exposed one had a higher annual biomass production per plant than the more sheltered one. The most wave-exposed locality examined was situated in Finnmark and exhibited the lowest annual biomass production per plant. Recruits (one-year-old plants) were found at all the localities except at one locality in Finnmark. The plants reached a higher age in Finnmark (13–18 years) than in Vega (8–9 years).

Introduction

Laminaria hyperborea grows in the northeastern Atlantic, from Iceland, the North Cape of Norway and the Kola Penninsula to Portugal (Kain, 1971a). It is not clear why *L. hyperborea* does not penetrate further north into the Arctic. The southern limit of distribution is probably due to a growth and reproductive boundary (Lüning, 1986), and possible competition with *L. ochroleuca* and *Saccorhiza polyschides* (Kain, 1979).

Laminaria hyperborea plants may reach their maximum size between 55° N and 65° N (Kain, 1971a), although local conditions are generally demonstrated to have a greater influence on plant growth than latitude (Kain, 1967). Under sheltered conditions the plants develop a special morphology, *L. hyperborea* f. *cucullata* (Svendsen & Kain, 1971).

During the 1950s the standing crop of *Laminaria hyperborea* in northeastern Norway was estimated to be 7.4 kg fresh weight m^{-2} at 2–6 m depth (Grenager, 1956). However, these results were obtained by using a spring grab, which underestimates the standing crop (Kain, 1971a). Reliable biomass estimates of *L. hyperborea* in northern Norway have not been available.

This paper presents a study of *Laminaria hyperborea* populations from the northernmost part of its geographical range. The populations are compared with two more southern populations with regard to standing stock, biomass production and age distribution. The populations grow in the same range of depth in wave-exposed localities.

Materials and methods

Ten localities in North Norway have been examined; eight in Finnmark and two in the Vega archipelago (Fig. 1). Stations 1–8 (Finnmark) were visited during August and September 1985 and Stations 9 and 10 (Vega archipelago) during May and September 1991. In addition, three samples collected during March 1991 at Station 9 were included. The populations of *Laminaria hyperborea* examined were situated 3–5 m below ELWS.

Wave exposure at the examined localities was estimated according to a sector method developed by Baardseth (1970), in which each station is assumed to be a point with 36 × 10° sectors. The degree of wave exposure is determined by the numbers of sectors exposed to open sea. We used a modified method in which the relative influence of the local topography, a fjord or the open sea on the site, was reflected in the number of exposed sectors with radii of 0.5, 7 and 100 km from the station (Oug *et al.*, 1985). Each sector was also given a relative wind force value based on the mean force and frequency of wind (data kindly made available from The Norwegian Meteorological Institute).

Mean monthly water temperatures from 1936–1991 at 4 m depth in the open sea close to Station 6 (Finnmark) and off the Vega archipelago were provided by the Institute of Marine Research, Bergen.

At Stations 1–8 an area of 3 m^2 was sampled and at Stations 9 and 10 areas of 19 m^2 and 6 m^2 respectively were sampled. The sample areas were chosen by a diver who swam over the kelp forest and dropped a 1 m^2 frame haphazardly. At one instance an area of 14 adjoining 1 m^2 was sampled at Station 9, otherwise sample size was 1 m^2. Thus there were three samples at Stations 1–8 and six at Stations 9–10. The stations were not influenced by sea urchin grazing except Station 10, where patches with barren ground could be found. Only areas with kelp forest were sampled at this station. The plants were age-determined by counting cortex rings corresponding to growth annulae of the stipe (Kain, 1963). The plants were separated into lamina, stipe and hapteron, and weighed wet.

The samples were collected during a period when most of the lamina and stipe elongation had been completed (Lüning, 1971). The biomass measurements of the plants were converted to estimates of annual biomass production (fresh weight) per plant according to Bellamy *et al.* (1973). The three samples collected in March 1991 at Station 9 were excluded from the material describing biomass production.

Estimates of biomass production were obtained in two ways. The samples from Stations 1–8 contained few plants in each year class, the haptera were not included and small (<100 g) plants were not weighed. In order to correct for this, several calculations were made. We obtained estimates for hapteron production for Stations 1–8 by using the average ratio between hapteron and stipe biomass of plants older than 3 years at Station 9. The ratio varied between 0.35 and 0.5 in the age groups 4–8 years. Hapteron production is normally unimportant compared to the total plant production (Bellamy *et al.* 1973; Kain, 1977). Even a large deviation from the ratio between hapteron and stipe weight obtained at Station 9 would result in only a minor difference in the estimates of total biomass production per plant at Stations 1–8. The effect of variation in plant size in each year class was reduced by using polynomial regression of untransformed stipe weights, and applying the significant ($P<0.05$) regressions (Stations 1, 4–8) to estimate the stipe weight in each year class at these stations. A total production estimate was obtained for year classes comprising more than one plant by adding average lamina weight and estimated hapteron production to the estimated stipe biomass production.

Annual biomass production per plant at Stations 9 and 10 was based directly on converted

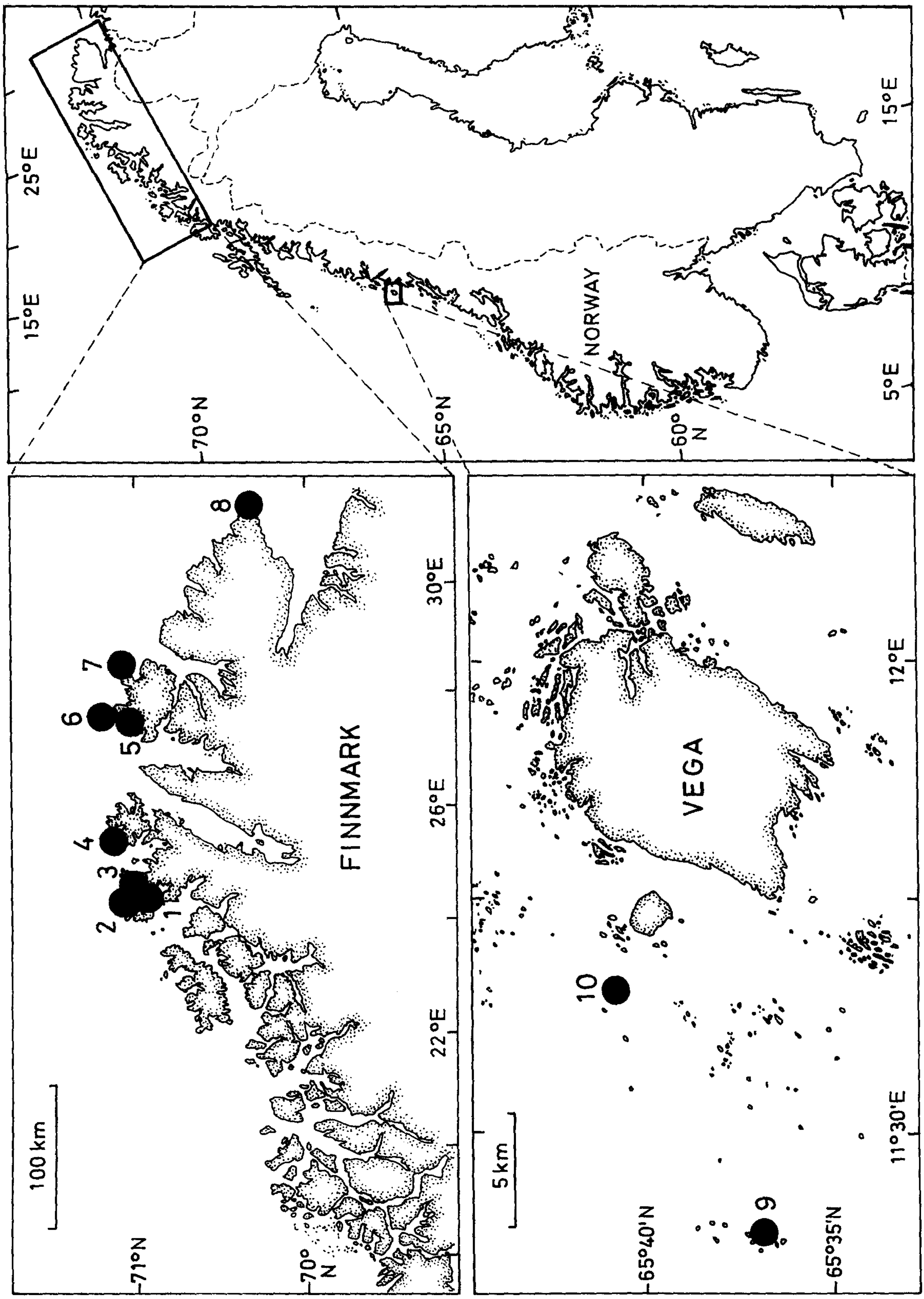

Fig. 1. Stations 1–8 in Finnmark and Stations 9 and 10 in the Vega archipelago.

biomass measurements. In addition a control calculation, based on 3×1 m^2 chosen at random from the sample of 14×1 m^2 at Station 9, was conducted to verify the validity of the estimation method used for Stations 1–8.

Results

The surface temperature is lower in Finnmark than in the Vega archipelago (Fig. 2). The maximum difference is in August when the average temperature reaches 9 °C in Finnmark and almost 13 °C in the Vega archipelago.

Station 10 is the most sheltered and Station 6 the most wave-exposed station (Table 1). Stations 3, 4, 7 and 6 have more than two sectors facing open sea and are extremely wave-exposed. Stations 8, 9, 2, 1 and 5 either have 1–2 sectors exposed to open sea or 6–12 sectors unaffected by land 7–100 km from the station. They may all be characterized as very wave-exposed.

Recruits (one-year-old plants) of *Laminaria hyperborea* were recorded at all stations except Station 8 (Fig. 3). In Finnmark the oldest plants at each station were between 13 and 18 years old. The oldest plants in the Vega archipelago were 9 years old.

Mean standing crops of the stations were between 6 and 16 kg fresh weight m^{-2}, with both the highest and lowest value recorded among the stations in Finnmark (Fig. 4).

The control calculations of estimated annual biomass production per plant at Station 9 are shown in Fig. 5. This method gave estimates similar to those resulting from biomass conversions of the whole sample, except that no 6-year-old plants were present in the small sample. The greatest deviation from the estimated values based on the whole sample was about 100 g in one age group.

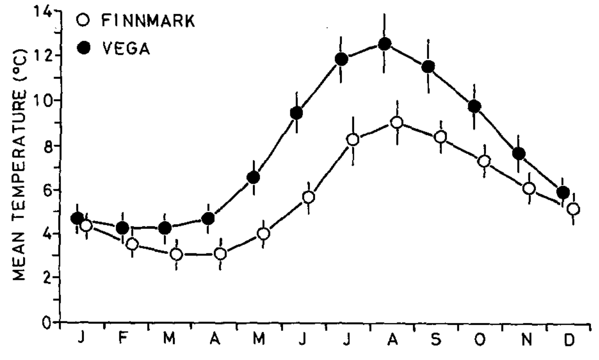

Fig. 2. Temperature at 4 m depth in the open sea in Finnmark and in the Vega archipelago. Mean monthly values (1936–1991) with standard deviation.

Table 1. Numbers of 10° sectors containing open sea only at a distance of 0.5 km (R_1), 7 km (R_2) and 100 km (R_3) from land at Stations 1–10. The stations are ranked according to their estimated value of wave-exposure (E).

Station	R_1	R_2	R_3	E
10	20	3	0	68
8	17	6	0	162
9	16	10	1	249
2	19	9	0	296
1	17	12	0	340
5	17	3	2	370
3	19	13	3	1594
4	19	7	7	1912
7	19	14	8	2112
6	18	17	11	3109

At Station 9, biomass production of the oldest year classes with more than one plant (6–8 years) was estimated to be between 0.9 and 1.1 kg fresh weight per plant per year (Fig. 5). At the other stations estimated annual biomass production of the oldest year classes with more than one plant (6–8 years at Station 10, 9–14 years at Station 1 and 5–8) ranged between 0.2 and 0.8 kg fresh weight per plant. Stations 1, 5, 8 (Finnmark) and Station 9 (Vega archipelago) are within the same range of estimated wave-exposure.

At the most sheltered locality (Station 10) the biomass production of the oldest plants was about 0.5–0.6 kg fresh weight per plant per year, and at the most wave-exposed stations (Stations 4, 7 and 6) it was about 0.2–0.75 kg fresh weight per plant per year, the most wave-exposed station (Station 6) exhibiting the lowest production (Fig. 5).

Discussion

Plants of 13 years or more were recorded at all stations in Finnmark. Grenager (1956) found 18-

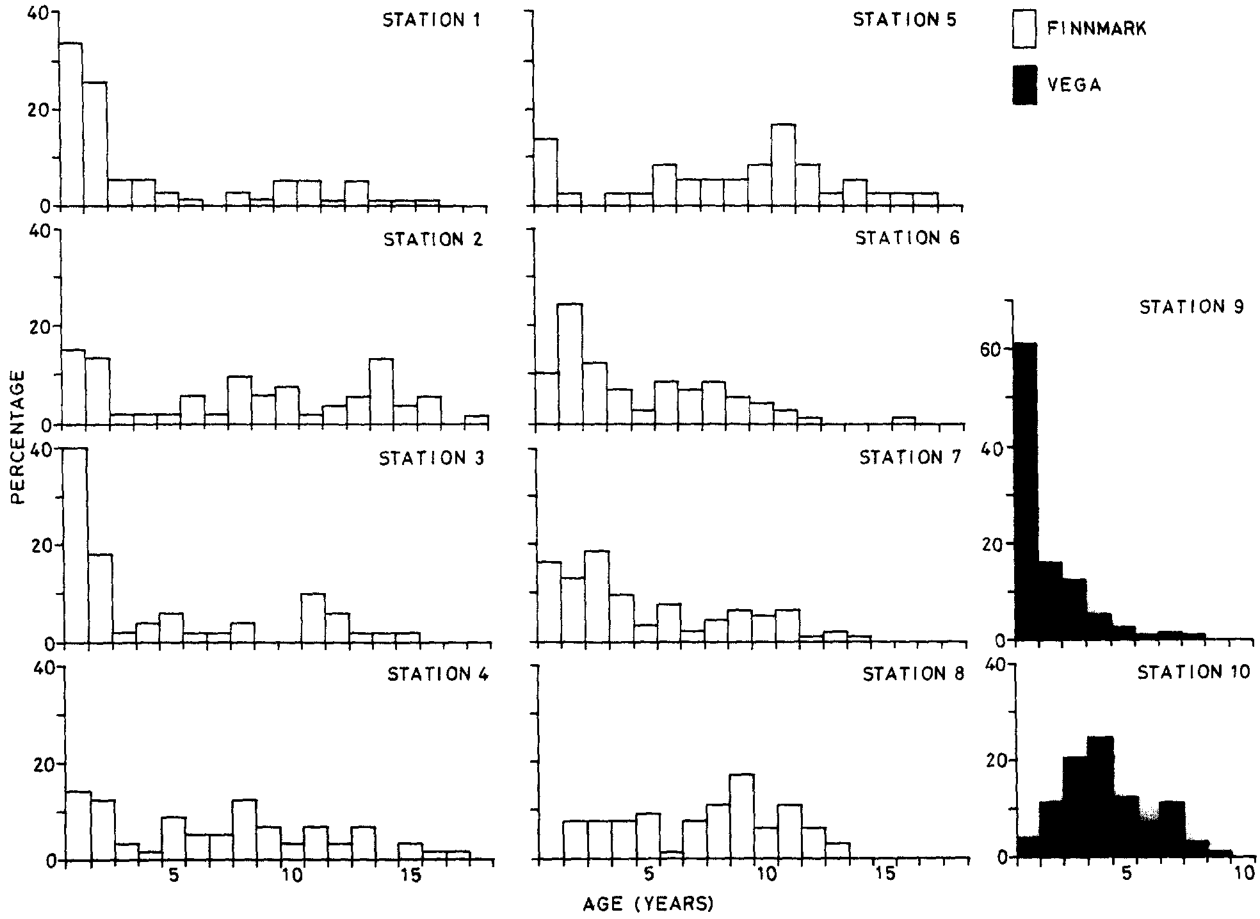

Fig. 3. Laminaria hyperborea. Age distribution at Stations 1–8 in Finnmark (1985) and Stations 9 and 10 in the Vega archipelago (1991).

year-old plants in eastern Finnmark, while Gunnarsson (1991) found plants reaching an age of 25 years in Iceland. Plants older than 10–11 years are otherwise seldom reported (Kain, 1971a), thus it seems that the longevity of *Laminaria hyperborea* is generally high in the northern part of its distribution area. The sea temperature is lower in Finnmark and Iceland (Gunnarsson, 1991) than in the Vega archipelago. Seaweeds may in general have greater longevity in the Arctic region, but the reasons for this are unknown (Lüning, 1990).

The mean standing crop is within the same range in Finnmark and in the Vega archipelago (6–16 kg fresh weight m^{-2}). This abundance is greater than that previously reported from northern Norway (Grenager, 1956; Kain, 1971b), but close to the range found in shallow water at various latitudes (11–20 kg fresh weight m^{-2}, cited in Kain, 1979). Kain (1971b) did not find *L. hyperborea* to be abundant in apparently suitable sites in northern Norway. However, this may have been due to a previous period of grazing in the area, as large populations of *Strongylocentrotus droebachiensis* and barren grounds have been reported from North Norway (Hagen, 1987).

Biomass production as a function of plant age is slightly lower in Finnmark than in the Vega archipelago at stations of comparable depth and wave exposure. This may be due to the environmental differences. Finnmark has not only lower annual temperatures but also lower irradiance

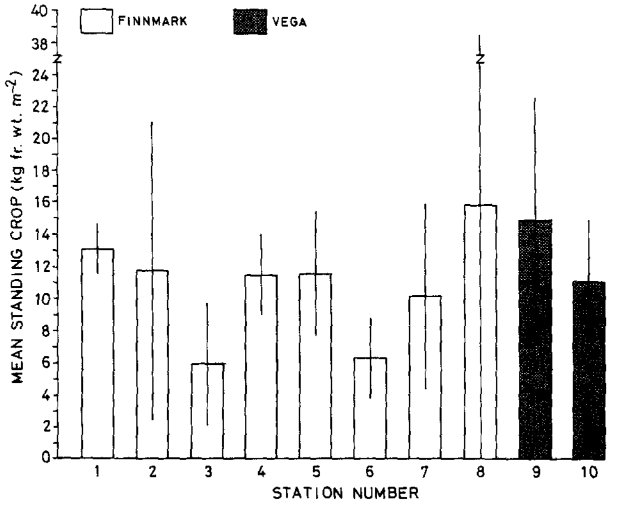

Fig. 4. Laminaria hyperborea. Mean standing crop (fresh weight) at Stations 1–8 in Finnmark (1985) and Stations 9 and 10 in the Vega archipelago (1991). Vertical bars represent 95% confidence limits, $n = 3$ at Stations 1–8 and $n = 6$ at Stations 9 and 10.

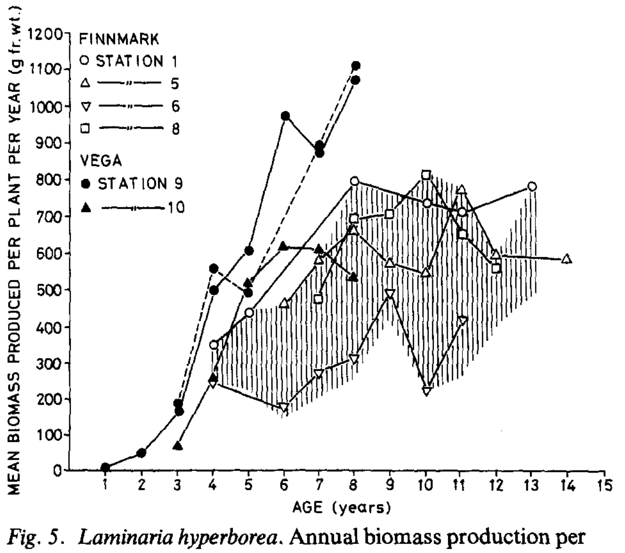

Fig. 5. Laminaria hyperborea. Annual biomass production per plant as a function of age. Stations 1–8 were examined in 1985 and Stations 9 and 10 in 1991. Shaded area: the results from all stations in Finnmark, with the curves of Station 1, 5, 6 and 8 lined out. Dotted line: the result of using a smaller sample and a polynomial regression line at station 9 (see text).

during the spring and autumn (Olseth & Skartveit, 1985). The biomass production of young plants growing in a dense canopy of *Laminaria hyperborea* may be light-limited (Kain, 1976). Among the oldest and canopy-forming individuals the effect of self-shading is probably reduced or absent, and the biomass production of these age groups represents the maximum at the station.

In the Vega archipelago the plants from the most sheltered locality (Station 10) had a lower biomass production per plant than plants in the more wave-exposed one (Station 9). The observation may be a result of enhanced nutrient supply via increased water movement and thus higher biomass production in *Laminaria hyperborea* (Kain, 1977).

On the other hand, there may be an optimal range of wave exposure favoring growth of *Laminaria hyperborea*. In extremely wave-exposed shallow sites the biggest plants are probably torn continuously (Kain, 1963), and the low annual production per plant in the most wave-exposed locality (Station 6) may be due to mainly small plants being left in the population. However, it is not known if annual production per plant in a year class is dependent on individual plant size.

At Station 9 a small sample gave similar estimates of annual biomass production per plant as that of a large sample, and the conclusion may be drawn that the smallest area sampled ($3 \times 1m^2$) is large enough to give an adequate estimate of the annual production of the oldest plants in the populations. However, the two areas were not investigated during the same year, and it is not known if local conditions for growth vary from one year to another in the examined areas.

It is not evident from the present study why *Laminaria hyperborea* does not penetrate further north into the Arctic. There is no indication of lack of recruitment in the populations in Finnmark, as one-year-old plants were found at seven stations. The result of the present study indicates that biomass production is somewhat lower in Finnmark than in the Vega archipelago, when comparing sites of similar degree of wave exposure. Still, the general conclusion is that at its northenmost limit of distribution *L. hyperborea* grows well, and forms dense canopies which dominate the sublittoral vegetation in wave-exposed sites.

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