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Effect of canopy biomass and wave exposure on growth in *Laminaria hyperborea* (Laminariaceae: Phaeophyta)

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Annual growth per plant and allocation of growth to the stipe were measured in 2- to 4-year-old plants of *Laminaria hyperborea* from five stations with different degrees of wave exposure and different amounts of canopy biomass. Low growth in plants with initial stipe lengths of less than about 40 cm suggested that the presence of canopy-forming plants suppresses growth of understorey plants, and this was supported by the high lamina growth rate of understorey plants after removal of the canopy-forming plants. Canopy biomass and wave exposure were found to exert a differential effect on the growth of the age groups examined. Average annual growth per plant in 2- to 3-year-old plants decreased with increasing canopy biomass; growth of 4 year-old plants was not significantly influenced by canopy biomass, but increased with increasing wave exposure of the sites, suggesting an influence of some factor connected with wave exposure. The allocation of annual growth to stipe and lamina was also found to be influenced by canopy biomass and wave exposure. In 2- to 3-year-old plants the amount of annual growth allocated to the stipe increased with increasing canopy biomass while a positive linear regression between allocation of growth to the stipe and wave exposure was found in 4-year-old plants. Individual measurements carried out at a wave-exposed locality showed that the maximum allocation of growth to the stipe in the intermediate-sized plants occurred simultaneously with a period of rapid stipe elongation. Thus, rapid stipe growth in *L. hyperborea* can be associated with high allocation of annual growth to the stipe when the plants are about to grow into the canopy-forming layer. We suggest that this is due to the combined effects of suboptimal light levels within the kelp forest and high wave exposure.

Key words: adaptation, canopy effect, kelp forest, *Laminaria hyperborea*, stipe growth, wave exposure

Introduction

Laminaria hyperborea grows in the northeastern part of the Atlantic from northern Portugal to the eastern part of the Kola peninsula (Kain, 1971a; Schoschina, 1997). When influenced by swell and strong currents, *L. hyperborea* forms nearly monospecific kelp stands, with reported standing crops between 5 and 40 kg fresh weight m⁻² in shallow water (e.g. Jupp & Drew, 1974; Kain, 1977; Gunnarsson, 1991; Sivertsen, 1991; Sjøtun *et al.*, 1993, 1995). The plants grow a long stipe (Svendsen & Kain, 1971), and the laminae form a canopy layer between 1 and 3 m above the bottom. In sheltered areas and in deep water, the plants grow a smaller stipe and larger lamina and the plants attain a different morphology: *L. hyperborea* f. *cucullata sensu* Svendsen & Kain (1971).

In macroalgal stands individual growth may either decrease (Reed, 1990) or increase (Schiel & Choat, 1980) with increasing density. The large size of individual plants in dense populations has been ascribed to fast growth and to a reduction of physical battering in high-energy environments by dense vegetation (Schiel & Choat, 1980). Low growth rates in dense populations have been

explained by increased interspecific competition, for example for light (Reed, 1990). Results from previous studies of *L. hyperborea* indicate that the growth of small plants in a population can be suppressed by the presence of large canopy-forming plants that absorb much of the light (Kain, 1976, 1977).

Growth and production of *Laminaria* spp. may vary considerably on a small spatial scale (Gerard & Mann, 1979; Conolly & Drew, 1985). Kain (1977) observed high production of *L. hyperborea* in an area with a high degree of wave exposure, which indicates that some factor connected with the degree of water movement may influence production in *L. hyperborea*. Different rates of macroalgal production in wave-exposed and sheltered areas can be attributed to a number of factors, for example different algal nutrient acquisition under different rates of water movement (Hurd *et al.*, 1996) or reduced irradiance at the thallus surface due to siltation in sheltered areas (Norton *et al.*, 1982).

During the seasonal growth period tissue is added to both lamina and stipe in *L. hyperborea*. The lamina is the main site for photosynthesis, and also for storing carbohydrates and for spore production (Kain, 1971a). The long and relatively flexible stipe which *L. hyperborea* develops in wave-exposed areas is probably a functional adaptation to strong water movement. However, because the stipe

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carries the lamina in an upright position in the water column, the amount of stipe growth will also regulate how much light reaches individuals growing within a dense kelp forest. Sjøtun & Fredriksen (1995) suggested that the allocation of growth to stipe and lamina in *L. hyperborea* could be influenced by the canopy density.

In the present paper, the average annual growth and the relative allocation of growth to the stipe in 2- to 4-year-old *L. hyperborea* plants are related to canopy biomass and wave exposure at five stations. The wave exposure at a site may impose a general influence on growth of all age groups in *L. hyperborea*. Canopy biomass is potentially the most important factor influencing growth of small plants in a kelp forest, by regulating the light penetration through the canopy layer. At one station the canopy-forming plants were removed in order to test the effect of removal on growth of understory plants. Growth may be better correlated with size than with age (Kain, 1975; Chapman, 1986). For that reason individual growth measurements of 2- to 4-year-old plants from one of the stations were included.

Materials and methods

Canopy biomass and wave exposure at the localities

Samples of *Laminaria hyperborea* (Gunnerus) Foslie were collected in Norway from two localities situated approximately at 65° 40' N, 11° 30' E (stations 1 and 2), and from three localities approximately at 60° 10' N, 5° 0' E (stations 3–5), during 1991–1992. The exact location of the stations is given in fig. 1 in Sjøtun & Fredriksen (1995).

Several samples were taken from each locality. A diver swam over the kelp forest and repeatedly dropped a frame, covering 0.5 or 1 m² substratum. All plants within the frame were collected. The samples were taken at random in the kelp forest, except at station 1 in 1991, when 14 adjoining square metres were sampled. Between 68 and 451 plants were collected from a total area of between 2 and 14 m² at the localities. Station 4 was characterized by a low density of small plants, and an additional sample of small plants was therefore collected. At station 5, *L. hyperborea* f. *cucullata* grew in patches within a kelp bed of *L. saccharina* at 5 m depth, and the sampling was done within one large patch of *L. hyperborea* f. *cucullata*. At the other stations only *L. hyperborea* was found. All samples were collected between May and September at a depth of 5 m (below chart datum). In *L. hyperborea* most of the annual growth is completed prior to this period (Lüning, 1970; Kain, 1976; Sjøtun *et al.*, 1996).

Growth was related to the canopy cover at each locality. Measuring lamina area of large kelp plants is very time-consuming, and instead we used measurements of lamina weights obtained from the samples. When relating average growth in different age groups to canopy biomass, the average lamina biomass per square metre of sea bed of plants older than each of the age groups examined was

chosen to estimate canopy density at each locality. The age of the plants was determined by counting cortex rings corresponding to growth rings of the stipe, as described by Kain (1963). In addition, the relationship between lamina weight and lamina area was examined at four of the localities during May and June by cutting discs of a fixed size (34.2 cm²) in laminae of 15–19 large, canopy-forming plants. Between 4 and 10 subsamples of each plant, evenly distributed over the laminae, were collected and weighed, and lamina wet weight per unit lamina area was calculated.

The degree of wave exposure at the stations was calculated according to a sector method developed by Baardseth (1970) and Oug *et al.* (1985). The method has earlier been used to describe wave exposure in kelp investigations (Sjøtun *et al.*, 1993; Sjøtun & Fredriksen, 1995). By using a map (scale 1:50 000) the number of 10° sectors exposed to open sea was determined at each station. A relative wind force value (e) was calculated, based on the mean force and frequency of wind during the last 5 years, the wind data being given for 12 directions:

$$e = \left(\frac{n_1 F_1}{100}\right) S_1 + \left(\frac{n_2 F_2}{100}\right) S_2 + \dots + \left(\frac{n_{12} F_{12}}{100}\right) S_{12}$$

where S is the number of open sectors in a given direction, n is the number of wind observations from a given direction with the average strength F (in Beaufort units). (Note that there is an error in this equation in Sjøtun & Fredriksen (1995).) An estimated value of total wave exposure at each station was calculated, where the relative influence of local topography was reflected in the number of exposed sectors with radii of 0.5, 7 and 100 km from the station. The procedure is given in Sjøtun & Fredriksen (1995).

Growth of 2- to 4-year-old plants calculated from biomass data

Lamina, stipe and hapteron of all plants in the samples from stations 1–5 were weighed independently, after removing epiphytes, and the age of each plant was determined. The biomass data were converted to estimates of average annual weight increase per plant in each age group using a method developed by Bellamy *et al.* (1973). According to this method, the annual weight increase of stipe and hapteron can be calculated as the difference between average stipe and hapteron weights in successive age groups in a sample, while the weight of the fully grown lamina represents annual lamina growth.

One-year-old plants were present in all samples except that from station 2. The lamina is renewed each year and may contribute most of the annual production in 2-year-old *L. hyperborea* (Sjøtun & Fredriksen, 1995). At station 2 the stipe growth of 2-year-old plants was estimated by multiplying lamina weight by a factor of 0.23 (Kain, 1977), to obtain an estimate of total annual production. Plants up to 6–9 years old were present at all stations except station 5, where no plants older than 4 years were found. Consequently, growth in the age groups 2 to 4 years

(n varied between 4 and 112) could be calculated at all the localities examined.

Individual growth measurements at one station

In 1991–1992 a field experiment to test the canopy effect on growth of understorey plants was carried out at 5 m depth at station 4. In August 1991 all plants with stipes longer than about 15 cm were removed in an area of about 7 m², leaving the understorey plants unshaded. The control area was situated beside the cleared area, with a buffer zone of about 1 m. In both the control and the experimental area, 30 plants with stipe lengths between 2 and 12 cm were tagged during August and October 1991 by means of adjustable lock-tight plastic strips. Negligible growth was observed from August to October. Also, 15 plants with stipe lengths between 3 and 15 cm were collected from the experimental site and the age of the plants determined. The length increase of the laminae of the tagged plants was measured at each visit to the locality from October 1991 to September 1992, while stipe lengths were only measured occasionally. When the new laminae were longer than about 10 cm, holes were punched in the laminae at 5 and 10 cm from the transition zone between stipe and lamina, and the distance these holes subsequently moved from this zone was measured.

To measure weight increase of *L. hyperborea* at an unmanipulated site, 140 specimens were tagged at 5 m depth at station 4 at the beginning of February 1993. The stipe lengths of the tagged plants varied between 9 and 130 cm. In June the plants were collected. Lamina, stipe and hapteron of the plants were weighed independently, after epiphytes had been removed. The stipe length was measured and the age of each plant was determined. The percentage dry weight of stipe and lamina fresh weight of each individual was also determined. The stipes were dried at about 40 °C, and subsamples taken every 10 cm along the middle of each lamina were dried at 70 °C to constant weight.

Stipe weights of 2- to 4-year-old plants were estimated from an equation relating stipe length and weight. A second-degree polynomial regression of log-log transformed values of stipe length (x) and weight (y) provided the best fit for the harvested plants ($n = 91$, $p = 0.0001$, $r^2 = 0.98$, equation: $y = 0.071 - 0.169x + 0.712x^2$). The stipe weights of 2- to 4-year-old plants were calculated from length measurements, and stipe growth was estimated as the difference between calculated stipe weight in February and June. Lamina weight of each plant in June represented lamina growth.

Results

Growth of 2- to 4-year-old plants related to canopy biomass and wave exposure

Station 3 was the most wave-exposed, followed by stations 4 and 1 (Table 1). Station 2 and especially station 5 were relatively sheltered. Wave exposure and lamina

Table 1. Average lamina biomass (kg fresh weight lamina per m² substratum) of *Laminaria hyperborea* older than each age group examined

| Station | Lamina biomass of plants more than | | | Lamina fresh weight (kg) per lamina area (m ²) | <i>E</i> |
|----------|------------------------------------|-----------|-----------|--|----------|
| | 2 years | 3 years | 4 years | | |
| 1 (1991) | 3.6 ± 1.0 | 2.7 ± 1.0 | 1.6 ± 1.1 | — | 249 |
| 1 (1992) | 5.6 ± 0.4 | 5.2 ± 0.5 | 4.9 ± 0.9 | 1.09 ± 0.05 | |
| 2 (1991) | 6.7 ± 1.9 | 6.5 ± 2.1 | 5.3 ± 3.6 | — | 68 |
| 3 (1992) | 4.3 ± 1.9 | 3.3 ± 1.9 | 2.2 ± 1.5 | 1.29 ± 0.06 | 888 |
| 4 (1992) | 6.5 ± 0.9 | 6.4 ± 1.0 | 4.5 ± 1.3 | 1.01 ± 0.03 | 478 |
| 5 (1992) | 1.5 ± 0.3 | 0.3 ± 0.3 | 0.0 ± 0.0 | 0.70 ± 0.03 | 7 |

Average lamina weight per unit lamina area (kg fresh weight m⁻²) is included for some samples. All values are the average ± 95% confidence intervals. Estimated values of the total relative wave exposure (*E*) of the stations are given (from Sjøtun & Fredriksen, 1995).

biomass at the stations were not significantly correlated (Pearson's product-moment correlation coefficient, $r = 0.7$, $p > 0.05$). The highest average lamina biomass was found at station 2, and the lowest at station 5 (Table 1). Plants with maximum stipe lengths between 90 and 140 cm were found at stations 1–4, while no plants with stipes longer than 42 cm were found at station 5.

Since *Laminaria hyperborea* has thicker laminae in wave-exposed areas than in sheltered ones (Kain, 1977), the lamina weight per square metre is not directly proportional to lamina area per square metre. Lamina fresh weight per lamina area was measured in large, canopy-forming plants collected from four of the stations. The lamina weight per unit lamina area was around 1 kg m⁻² at stations 4 and 1, and 1.29 kg m⁻² and 0.70 kg m⁻² at stations 3 and 5, respectively (Table 1). Thus, converting lamina biomass (kg per m² substratum) to lamina area (m²) per square metre of substratum will result in higher values for station 3 and lower values for station 5, compared with the values for lamina biomass in Table 1. However, the ranking of the stations will be the same.

The annual growth of 2- and 3-year-old plants decreased with increasing canopy biomass (Fig. 1). The annual growth of 4-year-old plants could not be related to canopy biomass, but showed a significant increase with increasing wave exposure (Fig. 1).

A higher proportion of annual growth was allocated to the stipe in 3- and 4-year-old plants than in 2-year-old plants at wave-exposed localities. In 3- and 4-year-old plants up to about 60% and 45% respectively of the annual growth occurred as stipe growth, while the amount of stipe growth did not exceed 30% of total annual growth in 2-year-old plants. After arcsine-transforming the data, the average annual portion of stipe growth per plant was correlated with canopy density and wave exposure at the localities. For 2- and 3-year-old plants a significant positive regression between allocation of growth to the stipe and canopy density was found, while no significant regression was found for 4-year-old plants

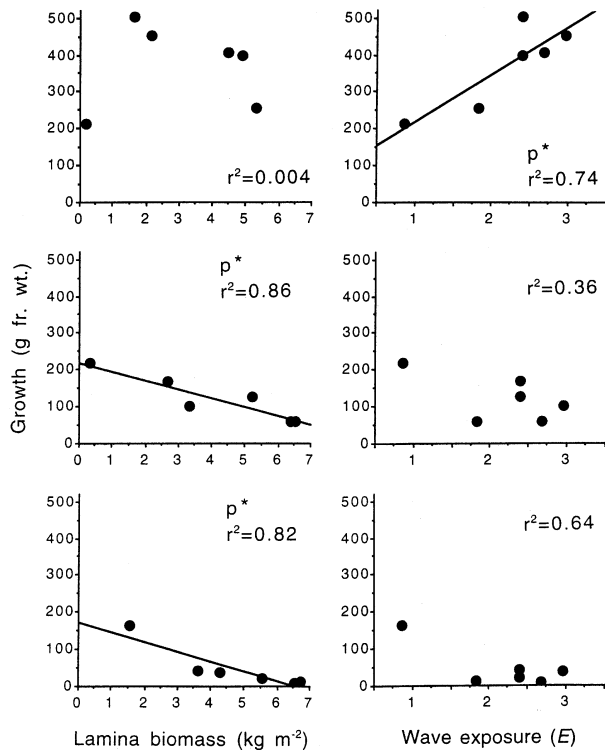


Fig. 1. *Laminaria hyperborea*. Average annual growth (g fresh weight) per plant of 2-year-old plants (upper graphs), 3-year-old plants (middle graphs) and 4-year-old plants (lower graphs) in relation to lamina biomass (kg m^{-2}) and wave exposure (log-transformed values) at the stations examined (data from Table 1). p^* indicates a significant linear relationship at $p < 0.05$.

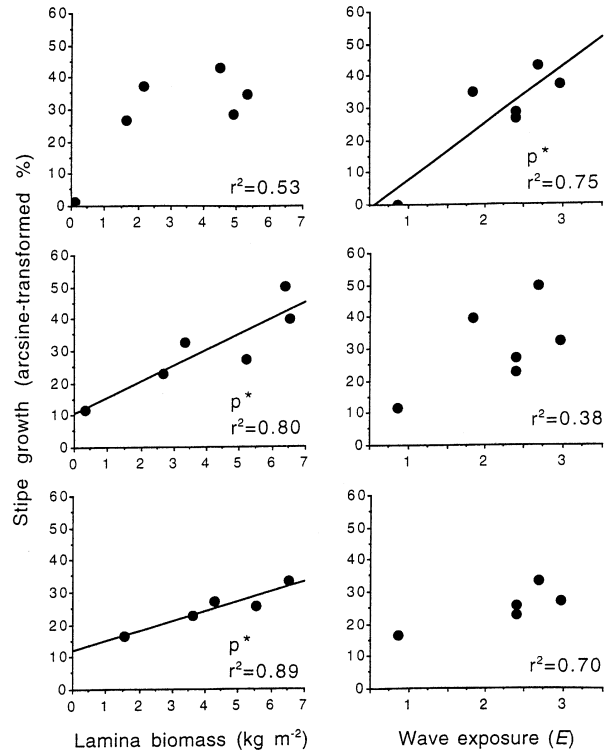


Fig. 2. *Laminaria hyperborea*. Arcsine-transformed values of the average portion of the annual growth allocated to the stipe (% of fresh weight total production) per plant of 2-year-old plants (upper graphs), 3-year-old plants (middle graphs) and 4-year-old plants (lower graphs) in relation to lamina biomass (kg m^{-2}) and wave exposure (log-transformed values) at the stations examined (data from Table 1). p^* indicates a significant linear relationship at $p < 0.05$.

(Fig. 2). A significant positive regression between allocation of growth to the stipe and wave exposure could be found for 4-year-old plants, but not for 2- and 3-year-old ones (Fig. 2).

Growth of understorey plants after removal of canopy-forming plants

Station 4, where the experiment took place, is relatively wave-exposed and is characterized by a high lamina density, with an average lamina biomass of about 6 kg fresh weight lamina per square metre during summer (Table 1). Average elongation rate of laminae was higher in the cleared area than in the control area from November to May (Fig. 3). The maximum lamina growth rate was about 23 mm per week in May in the cleared area, and about 8 mm per week in March in the control area (Fig. 3). In August lamina elongation was very low in both areas.

The plants collected prior to the experiment and belonging to the same size group as the tagged plants were found to be 2 or 3 years old. This indicates that most of the tagged plants belonged to these age groups.

Individual growth of 2- to 4-year-old plants in an unmanipulated kelp forest

At station 4 the individual dry weight increase of tagged plants was calculated from the beginning of February until

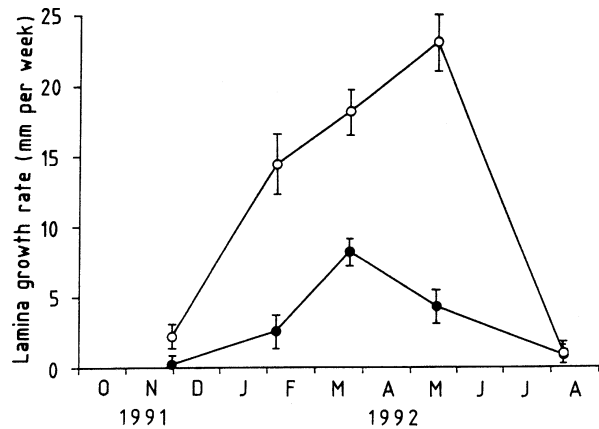


Fig. 3. *Laminaria hyperborea*. Average lamina elongation (mm per week with 95% confidence intervals) of tagged plants from control area (filled circles, $n = 7-20$) and cleared area (open circles, $n = 7-25$) at station 4.

June. The average dry weight of the stipes was about 12% of the fresh weight in all age groups, while for laminae the dry weight increased from about 12% of fresh weight in 2- and 3-year-old plants to about 14.5% in 4-year-old ones. Growth was found to be less than 5 g dry weight per year in plants with initial stipe lengths less than about 40 cm (Fig. 4). Most of the 2-year-old plants belonged to this group. In larger plants, growth gradually increased with increasing initial stipe length, with the highest

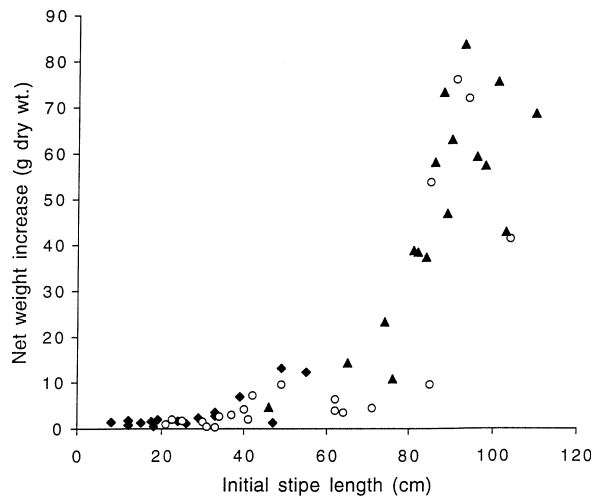


Fig. 4. *Laminaria hyperborea*. Total weight increase (g dry weight) from February to June in relation to initial stipe length of 2-year-old (diamonds), 3-year-old (circles) and 4-year-old (triangles) plants at station 4.

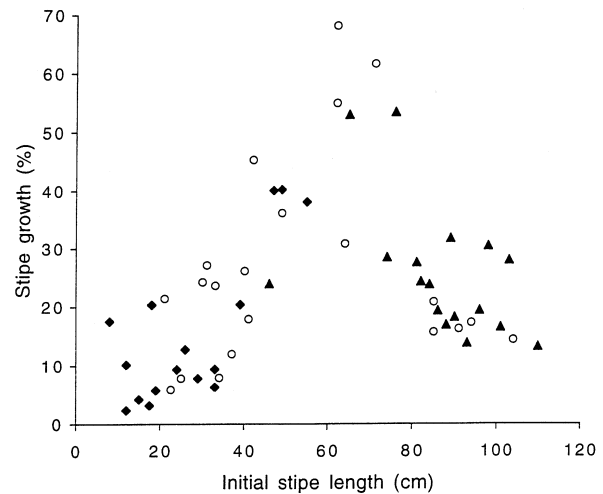


Fig. 6. *Laminaria hyperborea*. Allocation of growth to stipe (% of dry weight total production) from February to June plotted against initial stipe length of 2-year-old (diamonds), 3-year-old (circles) and 4-year-old (triangles) plants at station 4.

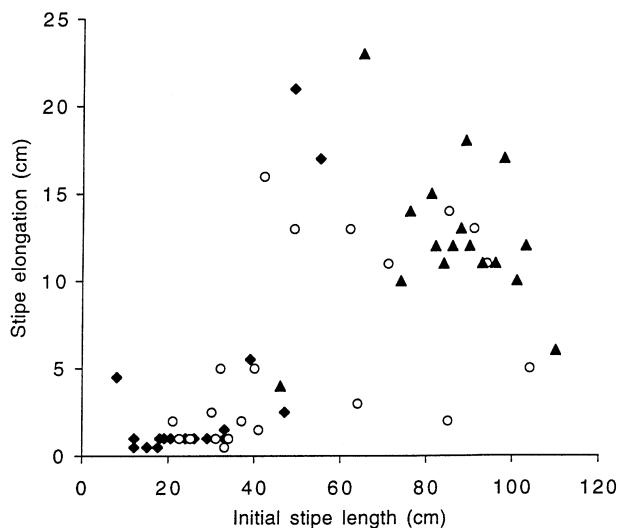


Fig. 5. *Laminaria hyperborea*. Stipe elongation (cm) from February to June plotted against initial stipe length of 2-year-old (diamonds), 3-year-old (circles) and 4-year-old (triangles) plants at station 4.

growth taking place in plants with initial stipe lengths between 80 and 110 cm. Initial stipe lengths varied between 8 and 55 cm in 2-year-old plants, between 21 and 104 cm in 3-year-old plants and between 46 and 110 cm in 4-year-old plants.

Both stipe elongation and allocation of growth to stipe and lamina showed a clear variation with initial stipe length (Figs 5, 6). Maxima in both stipe elongation and the allocation of growth to the stipe were found in plants with initial stipe lengths around 60 cm. A relatively high correlation between arcsine-transformed values of the proportion of growth in the stipe (% of total growth) and stipe elongation (cm) ($r = 0.74$, $p < 0.001$) suggests that the rapid stipe elongation in the intermediate-sized plants is mainly due to a high allocation of growth to the stipe.

In the smallest plants, there was a tendency for the proportion of growth in the stipe to increase with increasing initial stipe length. All 2-year-old plants and

more than half the 3-year-old plants belonged to this group (Fig. 6). In plants with an initial stipe size longer than about 60 cm the allocation of growth to the stipe decreased with increasing initial stipe size. Nearly all 4-year-old plants belonged to this group (Fig. 6).

Discussion

Growth in relation to canopy biomass and wave exposure

The method developed by Bellamy *et al.* (1973) for measuring annual biomass growth is based on the assumption that average growth in each age group shows no year-to-year variation at a site. Little is known about these relationships in *Laminaria hyperborea*. However, in the present investigation the growth results obtained by the biomass method were supported by those obtained by individual measurements. Both methods demonstrated suppressed growth of understorey plants in dense kelp forests.

The higher the canopy biomass was at a site, the less the growth in 2- and 3-year-old plants. This agrees with the observations of Kain (1976) that 1- to 3-year-old plants were larger when growing in initially cleared areas than when growing below the canopy-forming plants in a natural kelp forest. Suppressed growth of understorey *L. hyperborea* is probably due to the shading effect from the canopy-forming plants. Norton *et al.* (1977) found that as much as 90% of the incoming light can be absorbed by the canopy layer.

In the unmanipulated kelp forest, individual growth was found to be more closely related to size than to age of the plants, and increased with increasing initial stipe length. This is natural, since a large individual normally has a greater capacity for growth than a small one. However, very little growth was measured in plants with initial stipe lengths less than about 40 cm, and we suggest that this is due to strongly suppressed growth in this size group. Interestingly, total growth and stipe growth followed

different patterns in relation to initial size. The observed pattern of rapid stipe elongation in plants of intermediate size will result in a bimodal size distribution of stipe lengths in the population, as suggested by Kain (1977), for dense populations of *L. hyperborea*.

The results of the present study indicate that some factor connected with high wave exposure enhances growth in *L. hyperborea*. Water movement is highly variable at a site, and very difficult to quantify over long time periods. The sector method does not reflect a number of factors that may influence wave exposure, for example the underwater topography at a site. However, Sevrinsen (1997) found a good correlation between an exposure scale based on a sector method and an exposure scale based on biological response of littoral organisms. We therefore suggest that the sector method we have applied gives an adequate ranking of the stations according to wave exposure and represents a reasonable method to use.

High macroalgal production in wave-exposed areas is often reported (Lobban & Harrison, 1994), but the reason for this high production is not always clear. Low water movement may result in increased thickness of the boundary layer over the lamina surface, and thus reduced nutrient acquisition by the kelp plants (Wheeler, 1988). However, Hurd & Stevens (1997) suggested that flow around kelps is mostly turbulent, and that diffusion-limited growth thus rarely occurs in kelp. The presence of a canopy layer can reduce the water movement within a kelp bed (Eckman *et al.*, 1989), but there are no indications of this in *L. hyperborea* kelp forests (Mork, 1996).

A differential effect of canopy density and wave exposure on the age groups examined was found at the different sites. Growth of 4-year-old plants was higher in the most wave-exposed localities than in the sheltered ones, while growth of 2- and 3-year-old plants was not significantly influenced by wave exposure. On the other hand the annual growth of 4-year-old plants was not found to be significantly influenced by canopy density, while that of younger age groups was. This suggests that most of the 4-year-old plants had reached the layer of canopy-forming plants and were not overshadowed by larger plants at the sites examined.

Allocation of annual growth to the stipe

Allocation of growth to the stipe and lamina may vary with age in *Laminaria hyperborea* (Sjøtun & Fredriksen, 1995). The highest allocation of growth to the stipe has been found in 3- to 4-year-old plants. However, while it is known that high wave exposure results in higher stipe growth in *L. hyperborea* (Kain, 1971*b*; Sjøtun & Fredriksen, 1995), the present study demonstrates a combined influence of canopy density and degree of wave exposure on the amount of allocation of growth to the stipe. High canopy density promoted the highest allocation of growth to the stipe in 2- to 3-year-old plants, while high stipe growth in 4-year-old plants was associated with high wave exposure. These results are contrary to those of Kain

(1976), who found a fixed ratio between stipe and lamina growth in small *L. hyperborea*. However, Kain (1976) examined a regrowth situation, which means that a canopy effect was not present.

Dense canopies also suppressed the growth of understorey plants in the present study, but a straightforward relationship between suppressed growth and allocation of growth to the stipe was not found. The allocation of growth to the stipe was found to be relatively low in the smallest and potentially most light-limited plants. The thin and flat lamina structure is a functional morphology for effective light capture in algae (Norton *et al.*, 1982), and high lamina growth in small and young plants may enable the sporophytes to maximize photosynthesis at a developmental stage in which growth can be strongly suppressed by low light levels. On the other hand it is clearly advantageous for the plants to reach the canopy layer as fast as possible, and thus receive more light for photosynthetic activity. The results of the present study indicate that a prolonged period of suppressed growth may result in a higher allocation of growth to the stipe. A higher stipe growth in dense kelp populations than in more open ones has also been found in other kelp species (Reed, 1990; Hymanson *et al.*, 1990; Holbrook *et al.*, 1991).

The individual measurements in a dense kelp forest at a wave-exposed locality showed that the degree of allocation of growth to the stipe was better correlated with the size of the plants than with age. Maximum stipe elongation and allocation of growth to the stipe was found to occur simultaneously in plants with 50–70 cm long stipes. Rapid stipe elongation in *L. hyperborea* of intermediate size has earlier been interpreted as a response to loss of mature plants in a kelp forest, allowing rapid growth of understorey plants that previously were held back by shading by the canopy-forming plants (Kain, 1971*b*). The following reduction in stipe elongation in larger plants has been interpreted as an age-specific reduction in growth rate (Gunnarsson, 1991). However, the results of the present investigation suggest that the period of maximum stipe elongation of intermediate-sized plants is mainly due to a period of maximum allocation of total growth to the stipe.

The concurrent maxima of stipe elongation and allocation of growth to the stipe were found in the size group where total growth in relation to initial stipe length started to increase. We suggest that the height within the canopy corresponding to this size group represents a turning-point with regard to growth distribution in the plants. We also suggest that this turning-point is associated with the light environment within the kelp forest. Plants that have grown past this height within the canopy may be less influenced by the canopy effect. This suggestion is supported by comparison of the individual measurements with those of growth in different age groups. The individual measurements showed that nearly all plants showing increasing or maximum allocation of growth to the stipe with increasing initial stipe length

were 2- and 3-year-old plants. When comparing all the localities examined it is seen that both total growth and allocation of growth to the stipe were significantly influenced by canopy density in 2- and 3-year-old plants, while most of the plants showing decreasing allocation of growth to the stipe with increasing stipe lengths were 4-year-old ones. In 4-year-old plants neither total growth nor average allocation of growth to the stipe could be related to the canopy density, in contrast to what was observed for 2- and 3-year-old plants. Thus, for sporophytes growing in dense kelp forests in wave-exposed areas the highest degree of allocation of growth to the stipe will occur when the plants are about to grow into the canopy-forming layer. The high allocation of growth to the stipe in this size-group is probably due to a combined effect of high wave-exposure and suboptimal light levels for growth.

This study shows that the amount of allocation of growth to the stipe is dependent on both wave exposure and the light environment within the *L. hyperborea* kelp forest. A complicated picture with regard to morphological responses to the environment thus emerges in *L. hyperborea*, and the issue needs further study. In particular the physiological and morphological responses of subcanopy plants to the light environment in dense populations need to be examined more closely.

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