SPOROPHYTE FORMATION OF *LAMINARIA HYPERBOREA* (LAMINARIALES, PHAEOPHYCEAE) RELATED TO PHOTON DOSES OF BLUE LIGHT IN THE SEA

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The sporophyte formation of *Laminaria hyperborea* (GUNNERUS) FOSLIE in the sea was studied from January till the end of May at a locality on the west coast of Norway. Three series of gametophytes, which had been cultured in red light to prevent sexual reproduction, were transferred to the sea at depths between 10 and 45 m. After about 30 or 70 days in the sea the frequency of sporophytes in each series was registered. From 14 January to 13 February sporophytes had developed at 10 m. From 14 February to 18 March sporophytes had developed at both 10 and 20 m, while from 20 March to 28 May sporophytes had developed at all examined depths. In the period from 20 March to 28 May sporophytes constituted 82 and 27 % of the examined specimens at 40 and 45 m, respectively. In all the other cases where sporophytes were registered, 100 % of the specimens examined had developed into sporophytes. Based on continuous recordings of photon irradiance (PAR) in air and measurements of blue and integrated irradiance transmittance at the locality, the photon doses of blue light at the experimental depths were calculated. The depths at which sporophytes developed corresponded with the depths at which the calculated photon dose of blue light exceeded the critical photon dose for reproduction of gametophytes.

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KEYWORDS:Depth distribution; *Laminaria hyperborea*; recruitment; sporophyte formation.

INTRODUCTION

Since the discovery of the heteromorphic life cycle of the Laminariales by Sauvageau in 1915, the gametophytic development of *Laminaria* spp. has mostly been investigated in the laboratory. The gametophytes may grow vegetatively and develop a filamentous morphology under suboptimal conditions (see refs. in KAIN 1979). The compensation point for photosynthesis in gametophytes and microscopic sporophytes of *Laminaria* spp. has been found to be about 0.2 µmol $m^{-2}s^{-1}$ (KAIN 1969, conversion factor from LÜNING 1981), while 1-2 µmol $m^{-2}s^{-1}$ represents the minimum photon irradiance allowing sustained growth in juvenile sporophytes (HAN & KAIN 1995). An important discovery was made by LÜNING & DRING (1972), who observed that red light promoted filamentous gametophytic growth and that a specific photon dose of blue light induced gametogenesis in the laboratory. LÜNING (1980) has demonstrated that the photon dose of blue light required for gametogenesis increases with increasing temperature.

Laminaria hyperborea releases around 200 000 zoospores per mm^2 of sorus during the fertile season (KAIN 1975). FREDRIKSEN & al. (1995) studied the dispersal of spores of *L. hyperborea* during winter and early spring, and found that spores could be found at least 50 m below the surface. Laminarian gametophytes have been found in a unicellular or multicellular stage in the sea on a few occasions (e.g. PARKE 1932; SAKAI & FUNANO 1964; FUNANO 1969). Little is known about the development of the laminarian gametophytes in the sea. The only direct field observations on the gametophytic development of *L. hyperborea* are of embryospores on glass slides in closed Plexiglas chambers containing nutrient enriched sea water and submerged at depths between 1 and 6 m near Helgoland (LÜNING 1980; DRING & LÜNING 1981). LÜNING (1980) showed that the gametophytes survived the winter months under poor light conditions in the unicellular stage, as primary cells, which matured within a few weeks in February when the light conditions improved. DRING & LÜNING (1981) showed that the reproduction of the gametophytes in the sea was medi-

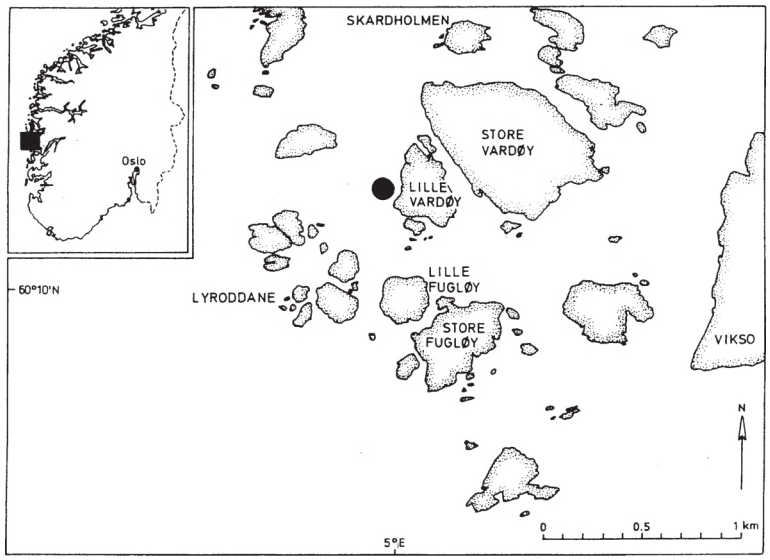

Fig. 1. A square marks the placing of the study site at the west coast of Norway. The circle marks the area where the three moorings were placed during the experimental period.

ated by a sufficient amount of blue photons. They also found that there was insufficient blue light for gametogenesis of *L. hyperborea* at depths of only 3-6 m at Helgoland.

Along the coast of Norway *L. hyperborea* is most abundant in coastal areas with clear water, and in the outer and wave exposed parts *L. hyperborea* extends to about 35 m depth (Kain 1971a). There is reason to believe that the gametophyte development and sporophyte formation in relation to depth at such sites is quite different from what has previously been observed at Helgoland. Here, results from a field experiment carried out on gametophytes of *L. hyperborea* at the west coast of Norway will be presented. The main purpose of the investigation was to observe the gametophytic development into sporophytes at a wide range of depths, after the sporulation period in late winter. Also, we wanted to examine if the critical photon dose needed to induce sporophyte formation in a range of depths at the study site was the same as observed in the laboratory. These doses were therefore calculated and correlated with the observed rate of sporophyte formation at the same depths.

MATERIAL AND METHODS

Hydrographic and optical observations

The locality where the experiment was carried out is situated on the west coast of Norway, at 60°10'N and 5°00'E, and is exposed to the North Sea (Fig. 1). Next to the locality *Alaria esculenta* (Linnaeus) Greville was found in the intertidal zone, which in south-western Norway indicates a high degree of wave exposure (Kain 1971a; Dalby & al. 1978).

Temperature and salinity were measured at the locality during the experimental period (14 January-29 May 1991) with a salinity and temperature measuring bridge (type M.C.5). Temperature has been demonstrated to influence gametogenesis in *Laminaria hyperborea* (Lüning 1980), while the salinity of the waters along the west coast of Norway may indicate whether the water masses are of Atlantic origin (Helland-Hansen & Nansen 1909).

During January-May photosynthetically active radiation in the spectral range 400-700 nm was measured above water, *P(PAR,air)*, every 5th second with a cosine sensor LI 190 S. The mean value for every hour was saved on the data log LI-COR 1000.

The *in situ* photon irradiance *P(PAR,z)* at the experimental depth *z* was measured at the locality at 7 dates with a cosine sensor LI-COR 185. The transmittance *T(z)* of the irradiance in air to the depth z was calculated. Similar *in situ* measurements with an added blue BG12 filter were also made, and this quantity, termed *P(BG12,z)*, was used to calculate the blue fraction of *P(PAR,z)*.

Cultivation

Fertile kelp specimens were collected in the field, brought to the laboratory and treated as described by Kain (1964) and Futsæter & Rueness (1985) in order to release the zoospores. Spores were seeded on sandpaper-rubbed Plexiglas plates (6×6 cm^2, marked in 36 squares of 1 cm^2) and cultured in IMR/2 medium (Eppley & al. 1967) in the laboratory at 6 °C.

Plexiglas plates with gametophyte cultures were placed in beakers which were wrapped in red cellophane paper in order to prevent exposure to blue light and thus sexual reproduction of gametophytes. These were placed under horizontally positioned daylight fluorescent lamps (Thorn EMI, T20W/28 Home Lite, with 75 % of the photons with wavelengths above 570 nm) which were covered with plankton net in order to reduce the light intensity (photoperiod 12:12 L:D). The beakers were rearranged under the lamps every week when medium was changed. When measured under the red cellophane in the beakers, photon irradiance varied between 10-13 µmol $m^{-2}s^{-1}$. Measurements of the light transmission through the red cellophane paper and the plankton net was made by a spectrophotometer (Shimadzu, UV 160), and the results showed that more than 99 % of the photons which reached the gametophytes had wavelengths above 570 nm. The largest photon dose of blue light (wavelengths 400-510 nm) the gametophytes could have received in the laboratory before they were transferred to the sea was calculated to be about 3.6×10^4 µmol m^{-2}. This is about 4 % of the assumed critical dose required to induce gametogenesis at a temperature of 6 °C (Lüning 1980).

A period of cultivation of the seeded spores in the laboratory made it possible to examine whether normal development

into gametophytes took place. Normal development of spores into gametophytes was observed. Also, normal gametogenesis and formation of sporophytes (within 12 days) was observed on a control plate in the laboratory when placed under daylight fluorescent lamps (photon irradiance 40 µmol $m^{-2}s^{-1}$), after each series had been transferred to the sea. Thus, cultivating the gametophytes under the described conditions did not affect their ability to germinate and produce sporophytes.

Field experiments

Three separate experiments were carried out in 1991. The first lasted from 14 January to 13 February, the second from 14 February to 18 March, and the third from 20 March to 28 May.

The gametophytes were in a one-celled stage (primary cells) and between 31 and 44 days old when transferred to the sea. Plexiglas plates carrying the gametophytes were transferred to the locality in an opaque seawater container. Transference to the sea was carried out at dusk, with photon irradiance always < 0.4 µmol $m^{-2}s^{-1}$(PAR), which is about the minimum value for vegetative growth of primary cells (Kain 1969, conversion factor from Lüning 1981). The Plexiglas plates were attached to opaque plates and fixed horizontally to stainless steel crosses. These were attached by ropes, and lowered to the experimental depths of 10, 20, 25, 30, 35, 40 and 45 m, and anchored to the bottom with a buoy at the surface. An extra buoy at 5 m depth kept the rope straight and the crosses in a horizontal position in the water column (Fig. 2). The described rope construction will later be referred to as a mooring. Three separate moorings were placed at distances of approximately 50 m from each other at the locality.

When terminating each time series all the moorings were hauled up and the Plexiglas plates were placed in dark containers with sea water and brought to the laboratory for examination under a microscope. Each stainless steel cross contained two Plexiglas plates from each series, of which one was analysed. On each Plexiglas plate between 16 and 133 specimens were examined within an area chosen at random on each plate. The lowest numbers were examined on the deepest plates, suggesting a low density of gametophytes here. However, we do not have data on densities and thus mortality rates of the gametophytes. Lengths of sporophytes were measured. Measurements on three Plexiglas plates (one from each of the three moorings) were pooled at each depth.

Calculation of blue photon doses

When Lüning (1980) determined the dose of blue light needed for gametogenesis in the laboratory, he worked with light in the spectral range 400-512 nm. To be able to compare the development of the primary cells in the present experiment with the results from Lüning's laboratory, it was necessary to know the corresponding photon doses of blue light.

The vertical irradiance transmittance $T(z,t)$ at the depth z and at the time t, of the irradiance in air, is defined by

$$T(z,t) = P(PAR,z,t) / P(PAR,air,t) \qquad (1)$$

where $P(PAR,z,t)$ is downward photon irradiance at the depth z and $P(PAR,air,t)$ the corresponding irradiance in air. From observations of $T(z,t)$ and the continuously recorded values of

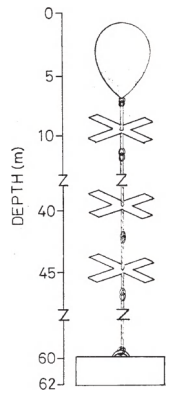

Fig. 2. Illustration of one of the moorings. Crosses were placed at 10, 20, 25, 30, 35, 40 and 45 m depth. The Plexiglas plates were placed horizontally at the crosses.

$P(PAR,air,t)$, continuous values of $P(PAR,z,t)$ could be calculated. The relative blue fraction $B(z,t)$ of $P(PAR,z,t)$ was found from irradiance measurements with an added BG12 filter, $P(BG12,z)$. The quantity $B(z,t)$ is defined for the blue range 400-510 nm by

$$B(z,t) = P(blue,z,t) / P(PAR,z,t) = \int_{400}^{510} P_\lambda(\lambda,z,t)\,d\lambda \Big/ \int_{400}^{700} P_\lambda(\lambda,z,t)\,d\lambda \qquad (2)$$

where $P_\lambda(\lambda,z,t)$ is the spectral irradiance of the daylight in the sea at the wavelength λ.

The photon dose of blue light, hereafter abbreviated PDBL, was then obtained by integration with time of the quantities $P(PAR,air,t)$, $T(z,t)$, and $B(z,t)$:

$$PDBL(z) = \int_0^{t_p} P(blue,z,t)\,dt = \int_0^{t_p} P(PAR,air,t)T(z,t)B(z,t)\,dt \qquad (3)$$

Here 0 and t_p indicate the start and the end of the experimental period, respectively. Eq. 3 contains the three time-dependent quantities $P(PAR,air,t)$, $T(z,t)$, and $B(z,t)$. The first quantity was observed every 5th second during the whole experimental period from January to May, while the two last quantities were obtained from observations around noon at only 7 dates.

The irradiance transmittance $T(z,t)$ (Eq. 1) may be written

$$T(z,t) = T_s(t)e^{-k(z,t)z} \qquad (4)$$

where $T_s(t)$ is the irradiance transmittance through the surface, and the exponential function expresses the transmittance between the surface and the depth z as a function of the mean vertical attenuation coefficient $k(z,t)$.

The diurnal variation of T_s depends on the solar altitude $h(t)$ and the cloudiness, and to a lesser extent on the surface roughness (Austin 1974). On clear days the largest contributions to PDBL will be obtained around noon, and it is to be expected

that the error by using the noon value of T_s for the whole day will be rather small. The error is expressed by the ratio γ, defined as

$$\gamma = \int_0^{24hrs} T_s(h)P(PAR,air,t)dt \,/\, T_s(h_n)\int_0^{24hrs} P(PAR,air,t)dt \quad (5)$$

where h is the solar altitude at the time t, and h_n is the solar altitude at noon. The values of $T_s(h)$ presented by JERLOV (1976, table XX) and observed values of $P(PAR,air,t)$ for clear days were used to calculate γ at the different field dates. The results showed that γ increased from 0.90 on the first date in January to 0.97 on the last date in May. The noon values of $T_s(t)$ were then multiplied with γ to produce better estimates of the mean diurnal values.

The diurnal variation of $k(z,t)$, due to the variation of the solar altitude, has been observed to be small in the Mediterranean (HØJERSLEV 1974) and in the Oslofjord (NILSEN & AAS 1977).

The relative blue irradiance fraction $B(z,t)$ (Eq. 2) was not observed directly, but could be estimated from the irradiance $P(BG12)$ measured with the blue filter BG12. The quantity A, defined as

$$A = P(BG12)/P(PAR) = \int_{400}^{700} T_f(BG12,\lambda)P_\lambda(\lambda)d\lambda \,/\, \int_{400}^{700} P_\lambda(\lambda)d\lambda \quad (6)$$

where $T_f(BG12,\lambda)$ is the transmittance of the BG12 filter in water at the wavelength λ, was obtained at all experimental depths at the locality. The quantities A and B are both determined by the shape of the spectral irradiance distribution.

AAS (1969) has presented 32 spectral irradiance distributions from four stations in the Norwegian Coastal Current, from the surface and down to 50 m depth. The quantities A and B were calculated for the different stations and depths, and the results showed that at each depth B was a unique function of A. This function was then applied to calculate B from the observed values of A at the present locality.

The vertical attenuation coefficient $k(z,t)$ was calculated from $T(z,t)$, by assuming that it varied linearly between the dates of the field observations. The product $\gamma T_s(t)B(z,t)$ was substituted by its mean value for the experimental period. Eq. 3 was then integrated by applying hourly means of $P(PAR,air,t)$.

RESULTS

The vertical water column at the study site was fairly well mixed during the period, with no apparent thermocline (Table 1) or halocline (Table 2). The studied area is characterized by coastal water masses with a salinity below 35 psu during most of the year, occasionally replaced with Atlantic water masses with a salinity above 35 psu (HELLAND-HANSEN & NANSEN 1909). Atlantic water was observed below 25 m on 19 April and at all the experimental depths on 29 May (Table 2).

The results from the measurements of transmittance of PAR at the experiment site are presented in Table 3. The transmittances at 1 m depth was omitted due to possible errors in the range 0.1-0.2 because of the influence of waves. The depth at which about 1 % of the photon irradiance measured in air could be found varied between 20 and 35 m during the investigation.

Within each experimental period the calculated values of photon irradiance decreased rapidly with increasing depth. At all depths the average number of hours per day with irradiance above 2 µmol $m^{-2}s^{-1}$ increased from January till the end of May (Table 4). Still, at 40 and 45 m depth the irradiance was found to be low even during the last experimental period. From 20 March to 28 May the average number of hours per day with irradiance > 2 µmol $m^{-2}s^{-1}$ was calculated to be 2.4 and 1.4 at 40 and 45 m, respectively (Table 4). In comparison, from 14 January to 13 February the average number of hours per day with irradiance > 2 µmol $m^{-2}s^{-1}$ was calculated to be 4 at 10 m depth. On the other hand the gametophytes received light with a photon rate > 0.2 µmol $m^{-2}s^{-1}$ for a much longer period per day at 40 and 45 m during March-May than at 10 m during January-February (Table 4).

In the present study the temperature at the locality varied around 5 °C during the investigation, with a minimum of 3.1 °C at 1 m in February and a maximum of 9.3 °C at 1 m in May (Table 1). At this temperature a PDBL of about 0.9 mol m^{-2} would induce gametogenesis in the laboratory (LÜNING 1980). The critical PDBL for sporophyte formation was consequently set to this value. Calculated values of $PDBL(z)$ for the three experimental

Table 1. Temperature (°C) at the depths 1-45 m, from 14 January to 29 May.

Date / Depth	14 Jan	13 Feb	18 Feb	25 Feb	5 Mar	27 Mar	5 Apr	19 Apr	29 Apr	10 May	29 May
1	5.4		3.1	4.0	3.8	5.8	4.8	5.4	6.5	7.2	9.3
10	5.9	3.8	3.3	4.1	3.8	5.0	4.8	5.4	6.0	7.2	7.8
20	6.3	4.1	3.5	4.3	3.8	5.2	4.8	5.7	5.6	6.3	7.5
25	6.4	3.4	3.6	4.4	3.8	5.2	4.8	6.0	5.6	6.1	7.5
30	6.5	3.5	3.9	4.6	3.8	5.4	4.8	6.2	5.6	6.1	7.4
35	6.5	3.9	4.0	4.7	3.8	5.3	4.8	6.3	5.5	6.1	7.3
40	6.6	5.1	4.0	4.9	3.9	5.4	4.8	6.3	5.5	6.1	7.5
45	6.8	5.1	4.2	5.2	4.0	5.0	4.8	6.3	5.6	6.1	

series are presented in Table 4. From 14 January to 13 February the calculated PDBL at 10 m was about twice as large as the critical PDBL, while at 20 m the calculated PDBL was below the critical value. Sporophytes were registered at 10 m only. From 14 February to 18 March the calculated PDBL exceeded the critical value also at 20 m, but not at 25 m. The primary cells developed sporophytes at both 10 and 20 m depth, but not deeper. During the last period, from 20 March to 28 May, the calculated PDBL exceeded the critical value at all experimental depths, and the primary cells also developed sporophytes at these depths. However, at 40 and 45 m depth 82 and 27 % respectively of the examined plants were observed in the sporophytic stage (Table 4), while the rest were observed in the gametophytic stage, mainly as unicellular gametophytes (primary cells). A few plants were observed as two-cellular gametophytes.

Table 3 shows, however, that although $T(z,t)$ is fairly constant during the two first experimental series, it varies significantly during the last series, from 20 March to 28 May, and this variation should be taken into account. The largest possible error in the calculated values of PDBL due to a varying $T(z,t)$ was estimated to be ±30 % or less for the first two experimental periods, and ±50 % or less for the last period. However, it can be seen from Table 4 that this possible variation does not influence the conclusions made above.

The average size of the observed sporophytes decreased with increasing depth within each experimental period and increased at each depth from the first to the last experimental period (Fig. 3). Gametophytes transferred to the sea in March and examined at the end of May had developed sporophytes which varied in length from about 1150 µm at 10 m depth to about 50 µm at 45 m depth (Fig. 3).

DISCUSSION

The phytoplankton spring bloom in the area occurred in the end of February in 1991, and was much less developed than normal (Jacobsen 1993). None of the results from the optical measurements carried out during February or the beginning of March suggests a high concentration of phytoplankton at the locality. The optical conditions on 13 February at the end of the first experimental series coincided well with the conditions on 25 February and 5 March during the second series. The irradiance transmittance corresponded to Coastal Water Type 3 in Jerlov's classification (Jerlov 1976). At the start of the third series (20 March) a clearer water type was present, which coincided with Ocean Water Type III. This water may have been brought into the area by the strong southerly winds which dominated the preceding two weeks. During the rest of the period the transmittance was slightly lower and corresponded to Coastal Water Types 1-2 (Jerlov 1976).

The sporophytes of *Laminaria hyperborea* are fertile during winter when the irradiance is low (Kain 1975). However, the spores can survive in total darkness for a long period (Kain 1964), and the laminarian gametophytes can survive in darkness for many months (Lüning 1980; tom Dieck 1989) and develop sporophytes when irradiance increases during spring. In the present investigation the successive development of sporophytes with time and depth during late winter and spring suggests that this takes place under natural conditions.

Sporophytes developed at all depths where the calculated photon doses of blue light exceeded the critical value for reproduction of gametophytes proposed by Lüning (1980). It should be noted that the cases where PDBL exceeded the critical value coincided with the cases where $P(PAR)$ exceeds the minimum value for sustained growth in juvenile sporophytes. Thus the present field experiment does not allow us to separate the effects of these two quantities. In our opinion however, the experiments by Lüning (1980) and Dring & Lüning (1981) have already shown that the PDBL is the limiting factor. Our intention was to investigate the sporophyte formation under *in situ* conditions and in relation to the time of the year when *L. hyperborea* produces spores. Previous studies of gametophytic development are of gametophytes growing inside nutrient-enriched, closed Plexiglas chambers (Lüning 1980; Dring & Lüning 1981), and the experiments of Dring & Lüning (1981)

Table 2. Salinity (psu) at the depths 1-45 m, from 14 January to 29 May.

Date 14 Jan Depth	18 Feb	25 Feb	5 Mar	5 Apr	19 Apr	29 Apr	29 May
1	32.3	32.3	32.7	33.3	33.0	33.1	32.5	35.6
10	32.8	32.6	32.8	33.3	33.2	33.2	32.8	35.3
20	33.2	32.7	33.2	33.3	33.3	34.0	33.2	35.5
25	33.4	32.8	33.3	33.3	33.4	34.6	33.3	35.6
30	33.6	32.9	33.4	33.3	33.4	35.2	33.4	35.6
35	33.8	33.0	33.4	33.4	33.4	35.3	33.6	35.5
40	33.8	33.1	33.5	33.4	33.5	35.3	34.0	35.5
45	34.1	33.1	33.7	33.5	33.5	35.3	34.3	

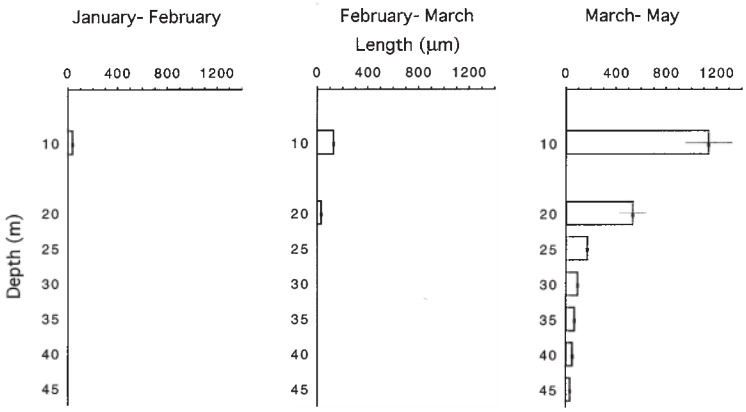

Fig. 3. The average length of the sporophytes (µm) with standard deviation at the end of the three experiments; from 14 January to 13 February, from 14 February to 18 March, and from 20 March to 28 May. n = 16-133.

were carried out between the end of April and the end of June. This is a considerable time period after the period of natural spore production of *L. hyperborea*. We also wanted to take the blue light effect into consideration, since this relationship has previously been examined under *in situ* conditions at Helgoland only, a site with very special irradiance conditions under water. Both spectral properties, attenuation and the depth range of the kelp bed are very different in the outer parts of the west coast of Norway compared to Helgoland. However, our results are consistent with no significant changes of the critical PDBL value.

From 20 March till 28 May a large portion of the surviving gametophytes at 45 m depth did not develop sporophytes, despite the fact that the calculated PDBL exceeded the critical value early in this period. However, while the PDBL acts as a trigger for gametogenesis, other environmental factors may inhibit the gametogenesis, such as high temperature (Lüning 1980), lack of nutrients (see refs. in Kain 1979) or the instantaneous rate at which gametophytes receive a specified photon dose (Deysher & Dean 1984). For *Macrocystis pyrifera* (Linnaeus) C. Agardh. Deysher & Dean (1984) found that gametogenesis was delayed if the photon fluence rate was below a critical level. We suggest that the photon fluence rate may be of importance in the present study. During March-May only a small part of the photon irradiance at 45 m exceeded the minimum value for sustained growth in juvenile sporophytes. It is possible that the low irradiance level may have hampered or delayed the gametogenesis of the primary cells, even though the PDBL should be sufficient for development according to the calculated values.

Fertilization of the laminarian egg cell will probably not take place unless the male and female gametophytes are situated relatively close to one another (Reed 1990). Low survival and low density of gametophytes will thus influence the degree of fertilization and formation of sporophytes. However, after the last experimental period all the gametophytes at 45 m were found to be in a vegetative stage. This suggests that the low portion of sporophytes observed here were connected to lack of fertility of the gametophytic stage.

When cultivated without blue light or in otherwise suboptimal conditions laminarian gametophytes can grow vegetatively as microscopic, filamentous gametophytes (Kain 1979; Lüning 1980). Filamentous growth of the gametophytes was not observed in the sea in the present study, in spite of the suboptimal light conditions under which the gametophytes must have grown during most of the time. However, other factors than light will also influence gametophytic development, such as temperature and nutrient conditions (Kain 1979). In culture studies Kain (1964) found that an unchanged medium brought about filamentous growth, and thus the fact that the gametophytes in the present *in situ* study were surrounded by continuously moving water may have been of importance. At 2-5 m depth at Helgoland Lüning (1980) also observed that the gametogenesis took place in an unicellular or few-celled stage of the gametophytes.

Table 3. Transmittance *T(z)* of downward quantum irradiance in percent of the value in air, at the depths 10-45 m, observed around noon from 13 February to 10 May. Numbers in parentheses are extrapolated.

Date	13 Feb	25 Jan	5 Mar	20 Mar	5 Apr	29 Apr	10 May
T(10)	5.8	5.6	5.6	14	8.4	12	9.4
T(20)	.96	.92	.93	4.6	2.1	2.8	2.3
T(25)	.48	.40	.42	2.7	1.1	1.3	1.2
T(30)	.19	.20	.21	1.6	.72	.74	.80
T(35)	.12	.11	.11	.92	.43	.33	.48
T(40)	.068	.050	.056	.56	(.3)	.18	(.3)
T(45)	(.04)	.025	.028	.33	(.2)	.092	(.2)

However, in both the study by LÜNING (1980) and in the present study the gametophytes developed in the open sea. Under normal conditions the recruitment to a kelp population takes place under a dense cover of canopy-forming plants, which offers different environmental conditions. The gametophytic development of primary cells within the kelp forests therefore needs to be investigated.

The results of the present study suggest that the lower limit for the development of microscopic *L. hyperborea* sporophytes probably is around 45-50 m at the examined locality. The observations of microscopic sporophytes in the present study are well below the observed lower depth limit for macroscopic *L. hyperborea* vegetation in western Norway, which formerly has been observed to be 35.5 m (below lowest astronomical tide) in the study area (KAIN 1971a). The general lack of observations of macroscopic sporophytes below 36 m (KAIN 1971b) suggests that the microscopic sporophytes developed at 40-45 m probably will perish before they become large enough to be observed. LÜNING (1990) has estimated that the microscopic sporophytes need a photon dose of about 70 mol m^{-2} per year to form a macrothallus, and results from several studies suggest that the depth at which the surface irradiance (350-700 nm) has been reduced to about 1 % is consistent with the lower limit of several Laminariales (LÜNING & DRING 1979). In clear coastal water the 1 % limit is found at about 30 m (JERLOV 1976). In the present investigation the depth receiving about 1 % of surface irradiance was found to vary between 20 and 35 m from January till the end of May. Thus, even though the irradiance during spring is sufficient for gametogenesis and development of microscopic sporophytes in a portion of the surviving gametophytes at 40 and 45 m, it may not be sufficient for a photosynthetic surplus for the plants on an annual basis. Respiration will possibly exceed photosynthesis in the microscopic sporophytes at 40 and 45 m during winter, thus making the sporophytes perish at these depths.

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Table 4. Observations of average hours per day with photon irradiance > 2 and > 0.2 µmol $m^{-2}s^{-1}$, photon doses of blue light (PDBL), and the relative amount of sporophytes (S) and gametophytes (G) at the experiment depths.

Series	Depth m	Hrs with *P(PAR,z)* > 2 µmol $m^{-2}s^{-1}$	Hrs with *P(PAR,z)* > 0.2 µmol $m^{-2}s^{-1}$	*PDBL* mol m^{-2}	S (%)	G (%)
14 Jan	10	4.0	7.2	1.8	100	0
to	20	0.2	5.5	0.34	0	100
13 Feb	25	0	2.9	0.18	0	100
(30 days)	30	0	0.4	0.07	0	100
	35	0	0	0.04	0	100
14 Feb	10	7.8	10	4.4	100	0
to	20	2.2	8.9	1.4	100	0
18 March	25	0.4	6.2	0.43	0	100
(33 days)	30	0.1	3.9	0.23	0	100
	35	0	1.7	0.13	0	100
	40	0	0.5	0.07	0	100
20 March	10	14	16	64	100	0
to	20	10	15	17	100	0
28 May	25	8.7	14	8.8	100	0
(69 days)	30	7.8	13	6.6	100	0
	35	3.9	13	4.2	100	0
	40	2.4	12	2.9	82	18
	45	1.4	11	1.8	27	73

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