Continuous underwater light measurement near Helgoland (North Sea) and its significance for characteristic light limits in the sublittoral region

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ABSTRACT: Underwater irradiance was measured at intervals of 20 min for one year at 2 water depths (2.5 and 3.5 m below M.L.W.S.) and in 3 spectral regions in the sublittoral region of the rocky island of Helgoland. Data are presented for spectral and total irradiance at water depths ranging from 2 to 15 m (below M.L.W.S.). 90 % of the total annual light reaching sublittoral habitats is received during the period from April to September, when Jerlov water type 7 (occasionally water type 5) dominates. During the other half of the year, the water is very turbid, and transparency is so low that long dark periods occur even at moderate water depths. The total annual light received at the lower kelp limit *(Laminaria hyperborea)*, at 8 m water depth, is 15 MJ m^{-2} year^{-1} or 70 E m^{-2} year^{-1}, which corresponds to 0.7 % of surface irradiance (visible). At the lower algal limit (15 m water depth) these values are 1 MJ m^{-2} year^{-1} or 6 E m^{-2} year^{-1}, corresponding to 0.05 % of surface irradiance. These data are similar to measurements at the same limits in several different geographical areas, and may determine the depth at which these limits occur.

INTRODUCTION

Detailed knowledge about the seasonal variation of underwater irradiance is needed by the phycologist mainly for two reasons. First, it aids understanding of the performance of a given alga in the field, since rates of photosynthesis, growth or photomorphogenetic reactions which were determined for this alga in the laboratory can be calculated for different depths in the field according to prevailing underwater irradiance. Second, it should be possible to arrive at "annual quantum budgets" for the major algal zones. For example, since red crustose corallines represent the deepest-occurring algal vegetation in many locations, where the lower algal limit is set by light and not by availability of hard substrate, the number of light quanta received per unit area in one year at the lower limit of algal vegetation should be of the same order in all oceans, from the Tropical to the Arctic or Antarctic zone.

In regions where spectral transmittance remains fairly constant over the year, such as many locations in the tropics, underwater irradiance can be estimated with reasonable

accuracy from continuous measurements of irradiance above the surface and occasional underwater measurements of spectral transmittance, using the water types established by Jerlov (1968) as a basis for calculation. Weinberg & Cortel-Breeman (1978) provide an example of such calculations. Where there are big changes in water type over the year, however, as can be expected at many locations outside the tropics, spectral transmittance must be determined more frequently, or underwater light must be measured continuously.

The optical oceanographer is normally not interested in the underwater optical climate near the margins of the oceans, where the benthic algae occur, and so the marine botanist has to perform his underwater light measurements himself. Optical oceanography has, however, provided sound recommendations for the measurement of underwater light (Jerlov, 1966, 1968, 1976; Jerlov & Nygård, 1969; Tyler, 1973; Tyler & Smith, 1970).

The present investigation was performed in a habitat where water clarity is very much influenced by storms stirring up the sediment which surrounds the rocky island of Helgoland. Since algal limits within the phytal zone of Helgoland had been determined earlier by diving (Lüning, 1970), an attempt can also be made in the present paper to correlate yearly integrals of energy or quanta with certain characteristic algal depth limits.

METHODS

Terminology

Terms and units of light measurement were used according to the recommendations of the Système International d'Unités (SI, see Incoll et al., 1977) and are listed along with some conversion factors, in Table 1.

Irradiance meter

Selenium photo elements (S 50 UV, 5 cm diameter; Lange, Berlin) were enclosed in watertight housings made from polyvinylchloride (PVC), as shown in Fig. 1. Frosted glass (2 mm thick Zeiss-Überfangglas) was used as cosine collector, as recommended by Jerlov

Table 1

Terms, units and conversions used for light measurements

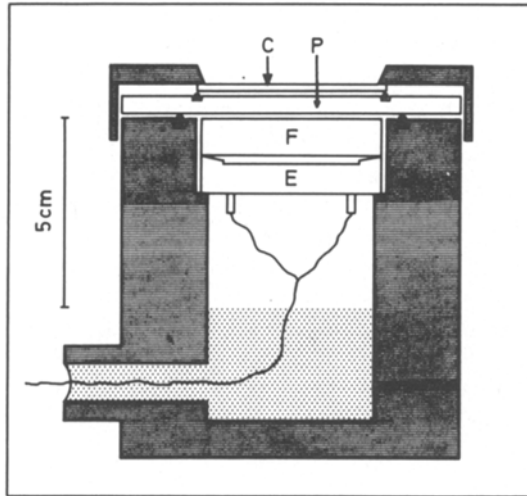| Term	Unit	Conversions
Irradiance	$W\ m^{-2}$	$1\ W\ m^{-2} = 1\ J\ m^{-2}\ s^{-1}$ $1\ cal = 4.19\ J$
Photon flux density	$\mu E\ m^{-2}\ s^{-1}$	$1\ \mu E\ m^{-2}\ s^{-1} = \dfrac{119.7}{\lambda\ (nm)}\ W\ m^{-2}$
		$1\ \mu E\ m^{-2}\ s^{-1} = 0.1\ nE\ cm^{-2}\ s^{-1}$ $1\ E = 6.02 \cdot 10^{23}\ quanta$ $1.66\ nE\ cm^{-2}\ s^{-1} = 10^{15}\ quanta\ cm^{-2}\ s^{-1}$

Fig. 1: Section through underwater light sensor. E = photo element, F = glass filter combination, P = Plexiglas cover, C = irradiance collector (Zeiss-Überfangglas), hatched area = underwater housing, made from PVC, dotted area = two-component glue
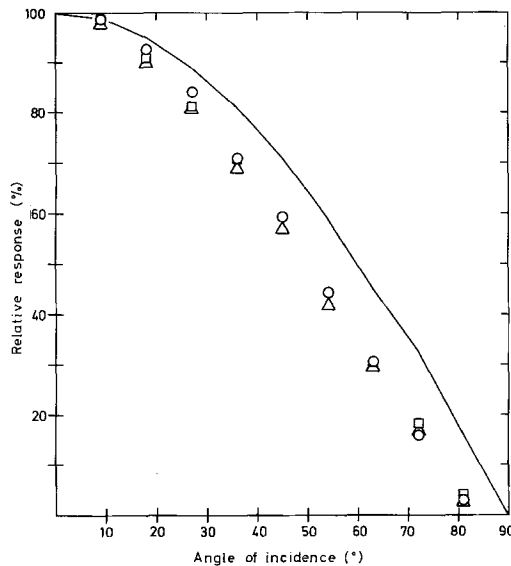

Fig. 2: Angular response of light meter, as measured for blue light (circles, SFK 20), green light (quadrats, SFK 11), and red light (triangles, SFK 15), compared with ideal cosine response (solid line)

& Nygård (1969). O-ring seals were used to combine cosine collector, Plexiglas cover and PVC housing into a watertight irradiance meter. The cable was embedded in a two-component glue (Rhenolit K/75; Kabel und Draht, Mannheim).

The angular dependence of light collection, as measured underwater, at 30 cm distance from a standard lamp (Model SRC, Spectroradiometer Calibrator; ISCO, Lincoln, Nebraska) is shown in Fig. 2. Deviations of 10–15 % from the ideal cosine response curve occur at incidence angles > 30 °. Spectral differences are negligibly small, as was found in corresponding tests of similar instruments (Jerlov & Nygård, 1969; Smith, 1969; Burr & Duncan, 1972).

Filters

The following glass filter combinations (Schott, Mainz) were used (spectral transmissions, Fig. 3): SFK 20 (transmission maximum, T-max: 439 nm; half-band width, HW: 35 nm), SFK 11 (T-max, 552 nm; HW, 25 nm), and SFK 15 (T-max, 655 nm; HW, 60 nm). Compared with uncombined Schott glass filters the combinations have the advantages of smaller half-band widths and of blocked-off transmission in unwanted spectral regions. Separate irradiance meters were used for each spectral region.
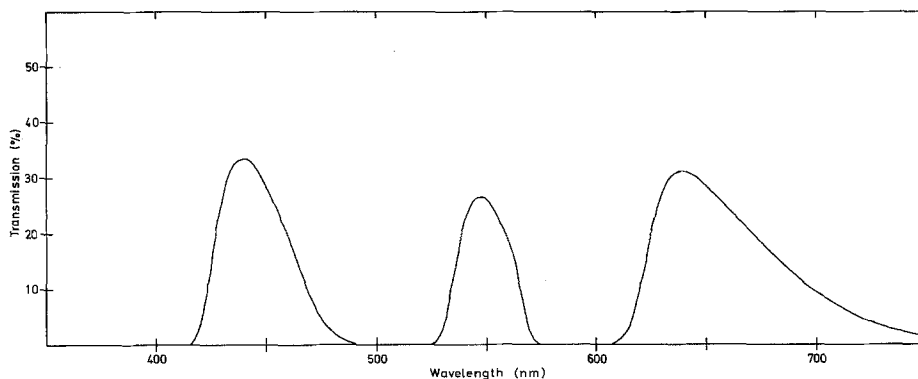

Fig. 3: Transmission curves (from left to right) for Schott glass filter combination SFK 20, SFK 11, and SFK 15, as measured in a recording spectral photometer

Since "band-width errors" occur when filters with such broad half-band widths are used in light of different spectral composition (Joseph, 1949; Jerlov, 1968), the spectral sensitivity of the different filter-photocell combinations was calculated for a range of underwater light fields. The greatest discrepancies were obtained when comparing measurements at 2 m depth in water type 5 under a cloudless sky with those at 6 m in type 9 under an overcast sky (Fig. 4). These calculations show that the maximum band-width error is only 3 nm for SFK 15 (red light) and 8 nm for SFK 11 (green), but is as much as 23 nm for SFK 20 (blue). This large shift in spectral sensitivity in blue light, however, only occurs in turbid waters (type 9), and, since irradiance in the blue region is very low in such waters, no attempt has been made to correct for it. The long "tail" which is to be seen in the transmission curve of the SFK 15 filter on its own (Fig. 3) is mainly compensated for by the sharp fall-off in the spectral sensitivity of the selenium photo element beyond 700 nm.

Outside the spectral ranges shown in Fig. 3 no transmission could be detected for SFK

20 and SFK 15, as measured with a Shimadzu recording spectral photometer (MPS-50L; accuracy 0.005 % transmission). A small "leakage" was detected for SFK 11 (0.05 % transmission at 603 nm, half-band width 15 nm), but this had a negligible effect on the present measurements.

Calibration

Two independent methods were used for calibration, but the calibration factors produced by the two methods differed by less than 10 %. (1) The irradiance meters were positioned 30 cm from a standard lamp (ISCO, see above) and were calibrated using data for photon flux density per nm obtained from the manufacturer of the standard lamp. (2) The meters were calibrated in a simulated underwater light field (Leitz Prado Universal projector with 24 V 250 W quartz-iodine lamp, 5 mm KG 3 heat filter, Schott glass filters 2 mm BG 38 and 2 mm GG 4; for spectral distribution see Lüning, 1980). Photon flux density per nm was determined with a quantum spectrometer (QSM 2400; IRD, Stockholm) in the simulated underwater light field. This instrument was re-calibrated in
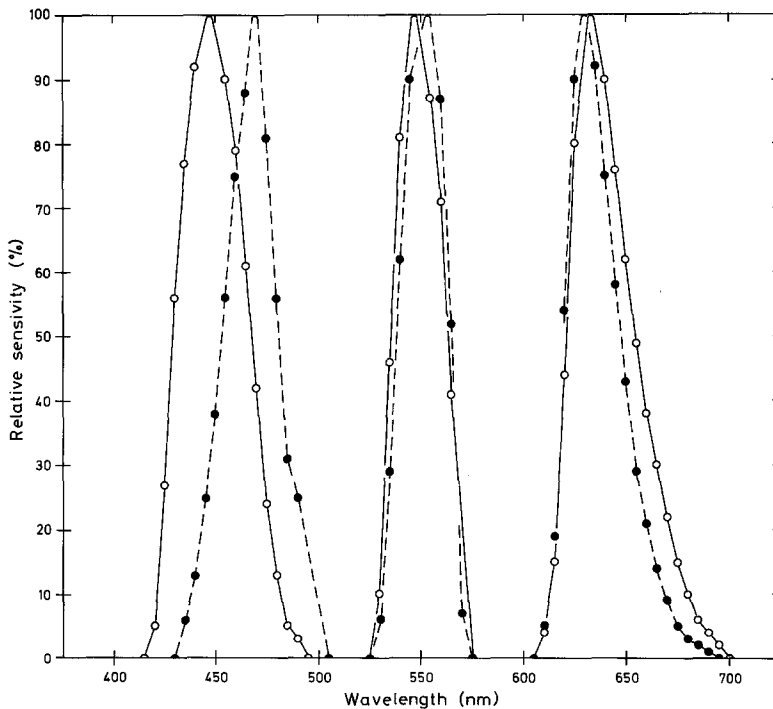

Fig. 4: Relative spectral sensitivity of irradiance meters (selenium photo element, combined with [from left to right] Schott glass filter combinations SFK 20, SFK 11, and SFK 15) in two calculated underwater light fields. Solid lines: cloudless sky (sun at 45 °), 2 m water depth, water type 5. Broken lines: overcast sky, 6 m water depth, water type 9. Data were obtained by multiplying spectral sensitivity of the photo element (as specified by manufacturer) by spectral distribution of quanta above surface (calculated from Jerlov, 1954) and spectral transmission according to water type (Jerlov, 1968)

interference filter light fields (half-band width 6–9 nm) against a thermopile (Kipp & Zonen, Delft).

The calibration factors K (λ_i) (symbols according to Burr & Duncan, 1972) result from:

$$K (\lambda_i) = H_c (\lambda_i) / G_c (\lambda_i), \text{ where}$$
$$H_c (\lambda_i) = \text{photon flux density } (\mu E \cdot m^{-2} \cdot s^{-1} \cdot 100 \text{ nm}^{-1})$$
$$G_c (\lambda_i) = \text{reading of measuring instrument } (\mu A)$$

Since the calibration factors were obtained in air, they had still to be corrected for the immersion effect (Westlake, 1965; Jerlov, 1968), which results in an underestimation of irradiance when measured underwater. The immersion factors f (λ_i), determined according
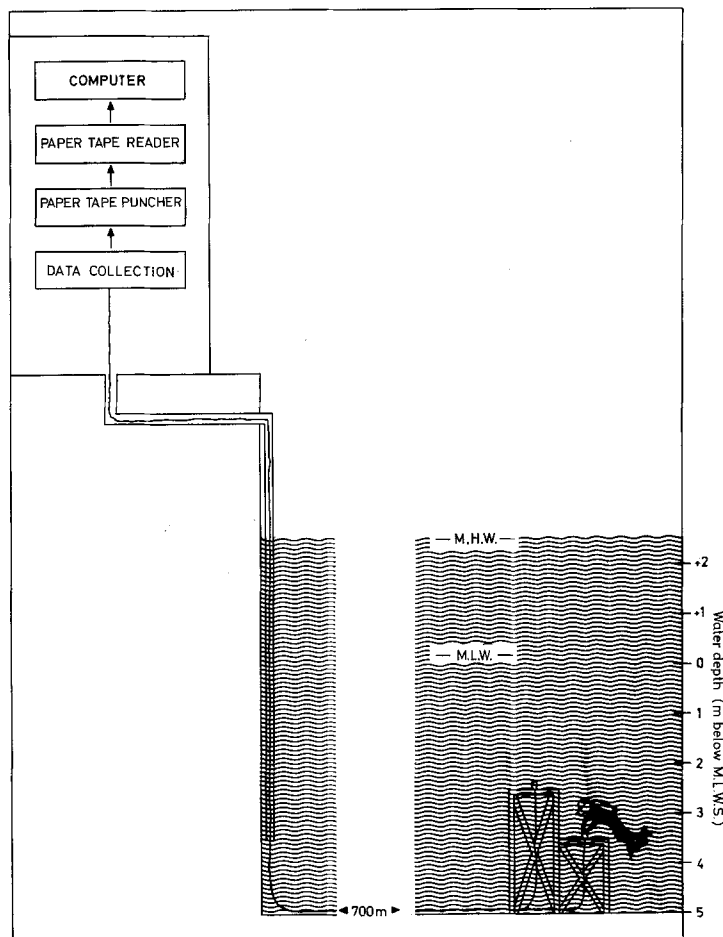

Fig. 5: Scheme of underwater light measuring station. Three irradiance meters are attached at each of two depths (2.5 and 3 m below M.L.W.S.) to an iron rack. Photocurrents are conducted by cable to a land station, where they are punched on tape every 20 min, and finally evaluated in a computer

to Smith (1969), were 0.77 (SFK 20), 0.80 (SFK 11), and 0.78 (SFK 15). The calibration factors were then calculated from:

$$K (\lambda_i) = H_c (\lambda_i) / G_c (\lambda_i) f (\lambda_i).$$

Underwater measuring station

The irradiance meters were attached to an iron rack, situated at 5 m water depth (all water depths quoted are measured from M.L.W.S.), near the southwest Helgoland Kabeltonne (Fig. 5). The 2.5 m high rack was secured by steel ropes fastened to railway wheels. Three irradiance meters (for measurement of blue, green, and red light) were placed at 2.5 m depth and another three at 3.5 m depth. Mean tide range near Helgoland is 2.3 m, the difference between Low Water and Low Water Spring is 0.2 m.

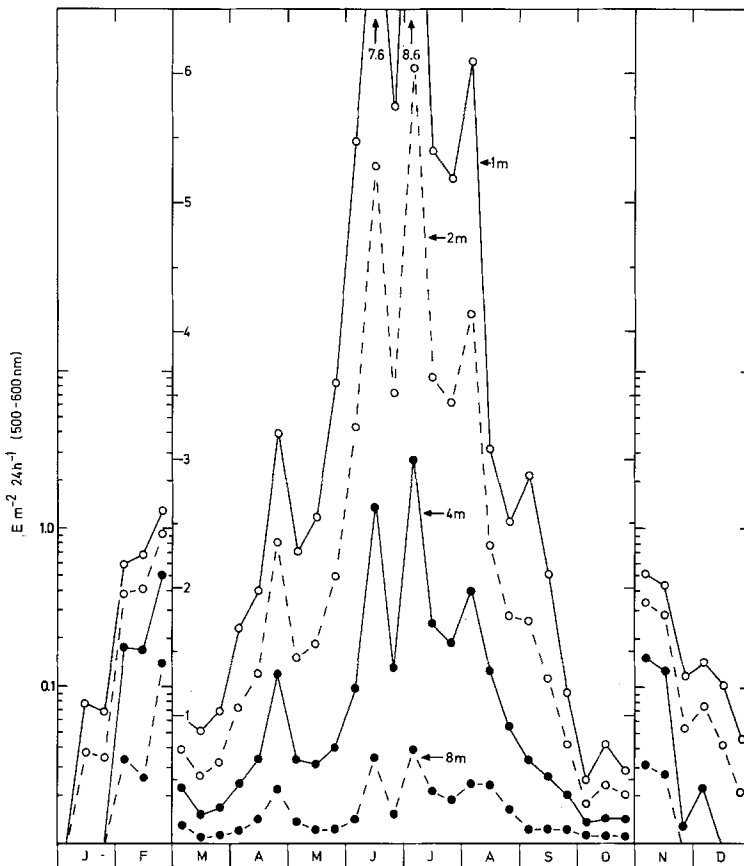Fig. 6: Helgoland, 1975. Photon flux density (daily integrals, mean of 10 days) in the green range (500–600 nm; 1 μE at 550 nm = 0.218 J). Values at different water depths were calculated from measurements recorded at 2.5 and 3.5 m water depth (below M.L.W.S.) every 20 min

The photo currents of the 6 irradiance meters were conducted to the laboratory across an 800 m long multiaxial cable (resistance about 10 Ohm). They were recorded by a data aquisition system (ADEM 100/1; Uhlig, Viersen, FRG) consisting of a multiplexer and a microampèremeter (internal resistance 0.3 Ohm). Full scale of the microampèremeter (200 μA = numerical value 9999) was reached when the green light sensors received a photon flux density of about 200 μE · m^{-2} · s^{-1}. Although this value was sometimes surpassed in summer the relationship between photon flux density and amperage was linear up to a numerical value of 15 000 and overflows could be easily detected and corrected. Data (numbers of irradiance meter and amperage) were punched on 8-channel paper tape every 20 min. There was a time interval of 1.5 s between the readings from successive meters. The collectors of the irradiance meters were cleaned by divers twice a week from February –September and once a week for the rest of the year. Long-term stability and temperature dependence (at the prevailing water temperatures) were checked 5 times per year by attaching an underwater lamp to each of the irradiance meters. The lamp was operated
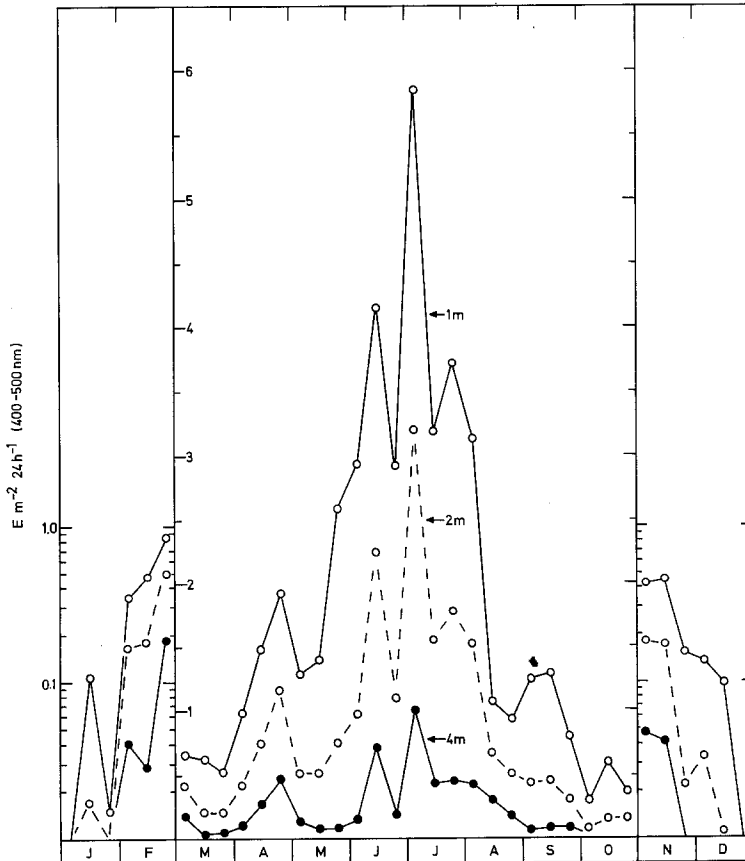

Fig. 7: Helgoland, 1975. Photon flux density (daily integrals, mean of 10 days) in the blue range (400–500 nm; 1 μE at 450 nm = 0.266 J). For further details see legend to Fig. 6

from an electronically stabilized battery, and its voltage was adjusted so that a photo element, stored in darkness, gave a standard current when exposed to the test lamp. No systematic long-term drift could be detected, the test values differing by not more than 4 % from the mean, over the period of 1 year.

Data were evaluated by means of a desk computer (Wang 2200, capacity 12 K). The raw data (instantaneous amperage, recorded every 20 min at 2 depths in 3 wavebands) were converted to spectral photon flux density in the following spectral ranges: 400–500 nm, 500–600 nm, 600–700 nm, and the sum of these, 400–700 nm. For each of these ranges, and for both depths, the instantaneous photon flux densities (in $\mu E \cdot m^{-2} \cdot s^{-1}$) for one day were classified into size classes, so that the total length of time at (or above) any given photon flux density could be determined. From this classification, the "daylength" – defined as the length of time for which the photon flux density in green (500–600 nm) exceeded 0.5 $\mu E \cdot m^{-2} \cdot s^{-1}$ – was estimated. The transmission of each waveband (in $\% \cdot m^{-1}$) was also calculated for every 20-minute interval by comparing the readings of corresponding photo elements at 2.5 and at 3.5 m depth. The following values were also calculated for each spectral range:

(1) 20-minute integrals ($E \cdot m^{-2} \cdot 0.33\ h^{-1}$ – instantaneous photon flux density x 1200 s);
(2) daily integrals ($E \cdot m^{-2} \cdot 24\ h^{-1}$ – the sum of 20-minute integrals for a whole day);
(3) daily means of photon flux density ($\mu E \cdot m^{-2} \cdot s^{-1}$ – daily integral divided by measured "daylength");
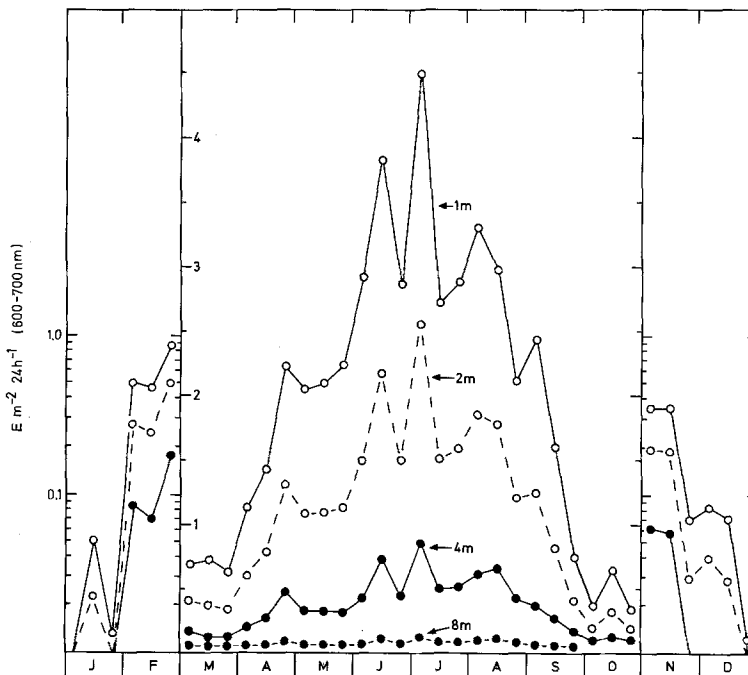(4) daily means of transmission ($\% \cdot m^{-1}$).

Fig. 8: Helgoland, 1975. Photon flux density (daily integrals, mean of 10 days) in the red range (600–700 nm; 1 μE at 650 nm = 0.184 J). For further details see legend to Fig. 6

The daily mean of transmission at 550 nm was compared with tabulated values for different water types (Jerlov, 1968), and thus the water type for the day was determined. Transmission values for all other wavelengths were taken as those tabulated for this water type, and these values were used to calculate the absolute photon flux density at a series of depths from the measurements made at 2.5 and 3.5 m.

RESULTS

The seasonal variation of photon flux density (daily integrals; $E \cdot m^{-2} \cdot 24 \, h^{-1}$), as calculated for different depths, can be seen from Figures 6–9. Corresponding values of mean photon flux density ($\mu E \cdot m^{-2} \cdot s^{-1}$) and irradiance ($W \cdot m^{-2}$), based on instantaneous readings from light measuring instruments, are presented for comparison in Table 2.
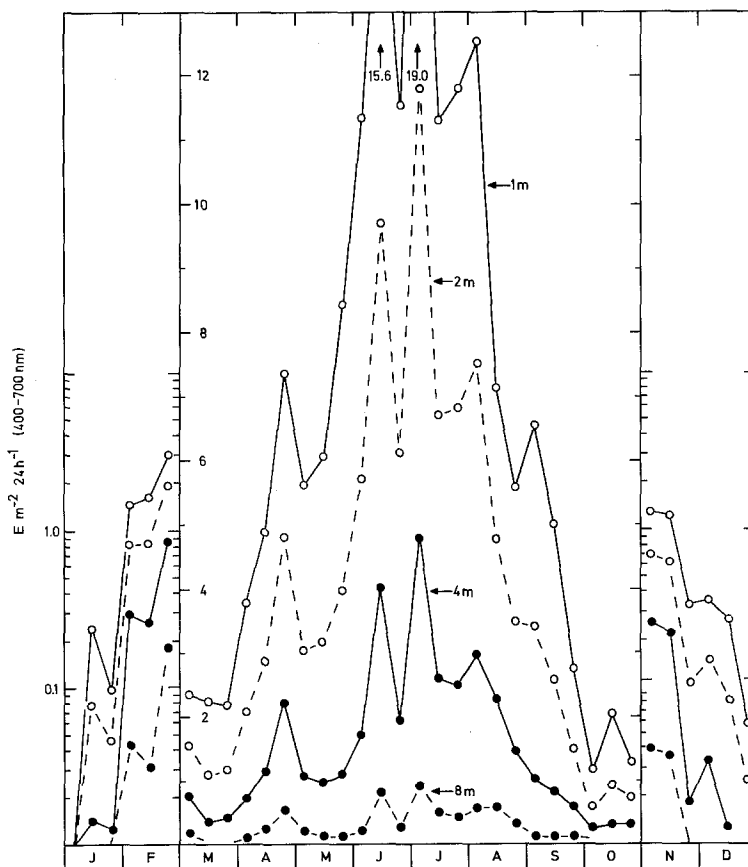

Fig. 9: Helgoland, 1975. Photon flux density (daily integrals, mean of 10 days) in the visible (400–700 nm; sum of three separately measured spectral ranges). For further details see legend to Figure 6

On some days during late autumn and in winter no light could be detected at all even at 2.5 m water depth, since prolonged storms had stirred up the sediment and the water had become extremely turbid. 22 of these "dark days" were recorded in January, 3 in October, 4 in November and 9 in December. The 10-day mean of the daily integrals of photon flux density (400–700 nm) at 2 m depth was lower than 0.1 E. $m^{-2} \cdot 24 \ h^{-1}$ in December and January, and lower than 2 E $\cdot \ m^{-2} \cdot 24 \ h^{-1}$ from February to March, and from October to November (Fig. 9). The monthly mean of photon flux density at the same depth for these months did not exceed 40 μE $\cdot \ m^{-2} \cdot s^{-1}$ (corresponding to an irradiance of 9 W $\cdot \ m^{-2}$), whereas a maximum of about 140 μE $\cdot \ m^{-2} \cdot s^{-1}$ (32 W $\cdot \ m^{-2}$) was attained in July. The brightest day underwater was July 2, with a daily mean of 240 μE $\cdot \ m^{-2} \cdot 5^1$ or a daily integral of 14.11 E $\cdot \ m^{-2} \cdot 24 \ h^{-1}$ (both 400–700 nm) at 2 m water depth.

The prevailing water type (Fig. 10) was similar to water type 7 (i.e. 63 % transmission at 550 nm). Under very calm weather conditions, and hence clearer water, water type 5 (72 % transmission at 550 nm) occurred occasionally. For the latter water type, the spectral distribution of quanta at moderate water depths is roughly: 25 % in the blue, 50 % in the green, and 25 % in the red region of the spectrum. For instance, in July, at 2 m water
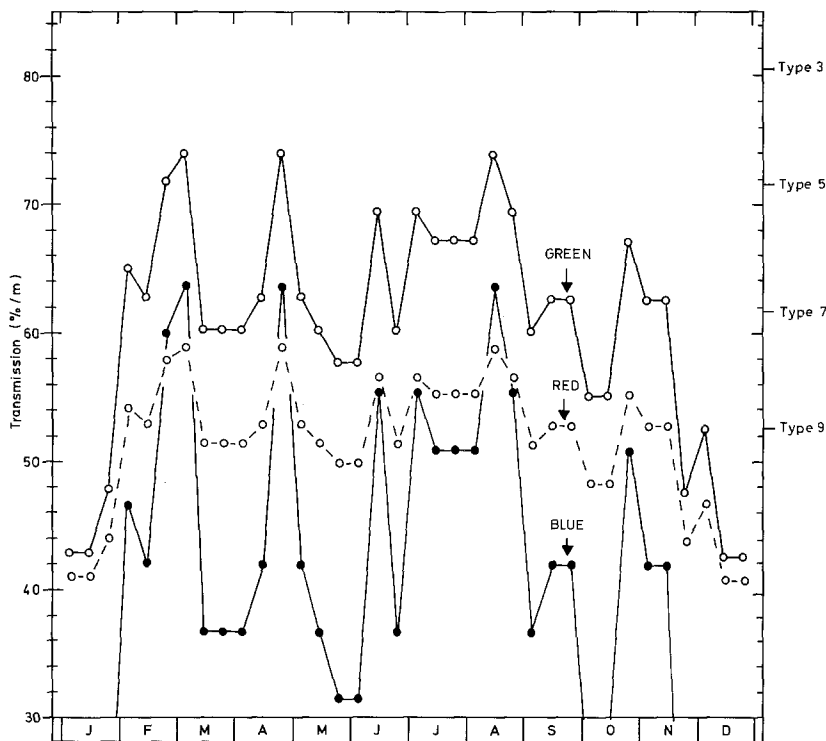
Fig. 10: Helgoland, 1975. Seasonal variation of transmission (mean of 10 days), as measured for green light (550 nm) and adopted from Jerlov (1968) for blue (450 nm) and red (630 nm) light, according to water type (characterized by measurements performed at 550 nm). Right-hand scale indicates transmission at 550 nm according to Jerlov's (1968) water types

Table 2

Monthly means of Q = photon flux density (in $\mu E\ m^{-2}s^{-1}$) and I = irradiance (in $W\ m^{-2}$) at different water depths D (in m below M.L.W.S. at Helgoland, 1975) in 4 different spectral ranges (blue: 400–500 nm, green: 500–600 nm, red: 600–700 nm, total: 400–700 nm). M = month, L1 = daylength above surface (according to latitude of 54°N, from Smithsonian tables), L2 = daylength in sublittoral region (as measured at 2.5 m below M.L.W.S.), W = monthly mean of Jerlov water type [scale given by Jerlov (1968) subdivided into intervals of 0.5], S1 = monthly integral of photon flux density (400–700 nm), S2 = monthly integral of irradiance (400–700 nm), P = irradiance as percentage of irradiance above surface (400–700 nm).

M	L1	L2	W	D	Blue Q	Blue I	Green Q	Green I	Red Q	Red I	Total Q	Total I	S1 $E\ m^{-2}\ month^{-1}$	S2 $kJ\ m^{-2}\ month^{-1}$	P %
1	8.0	1.1	9.0	2	1.9	(0.50)	6.0	(1.32)	2.4	(0.44)	10.3	(2.26)	1.27	278.4	1.11
				4	0.1	(0.02)	1.6	(0.35)	0.5	(0.09)	2.2	(0.47)	0.27	58.3	0.23
				8	0.0	(0.00)	0.1	(0.02)	0.0	(0.00)	0.1	(0.03)	0.01	4.1	0.02
				10	0.0	(0.00)	0.0	(0.00)	0.0	(0.00)	0.0	(0.00)	0.00	1.2	0.00
				15	0.0	(0.00)	0.0	(0.00)	0.0	(0.00)	0.0	(0.00)	0.00	0.0	0.00
2	9.8	8.7	6.5	2	8.5	(2.27)	17.4	(3.80)	10.1	(1.87)	36.1	(7.95)	31.72	6972.0	13.07
				4	2.5	(0.68)	8.2	(1.80)	3.1	(0.58)	14.0	(3.07)	12.29	2694.3	5.05
				8	0.3	(0.08)	1.9	(0.43)	0.3	(0.05)	2.6	(0.57)	2.30	505.5	0.95
				10	0.1	(0.03)	1.0	(0.21)	0.1	(0.01)	1.2	(0.26)	1.07	236.6	0.44
				15	0.0	(0.00)	0.1	(0.04)	0.0	(0.00)	0.2	(0.04)	0.18	41.1	0.08
3	11.8	9.0	6.5	2	8.7	(2.33)	19.7	(4.30)	11.3	(2.09)	39.9	(8.74)	40.11	8779.1	7.67
				4	2.6	(0.69)	8.8	(1.93)	3.4	(0.62)	14.8	(3.25)	14.94	3268.0	2.86
				8	0.3	(0.10)	2.0	(0.45)	0.3	(0.06)	2.7	(0.61)	2.80	617.7	0.54
				10	0.1	(0.04)	1.0	(0.23)	0.1	(0.01)	1.3	(0.29)	1.33	295.8	0.26
				15	0.0	(0.00)	0.2	(0.04)	0.0	(0.00)	0.2	(0.05)	0.25	55.6	0.05
4	14.0	11.7	6.5	2	18.7	(4.97)	37.7	(8.21)	21.2	(3.91)	77.6	(17.11)	98.17	21 623.2	11.87
				4	6.6	(1.77)	18.7	(4.09)	6.8	(1.25)	32.2	(7.12)	40.79	9 003.9	4.94
				8	1.1	(0.31)	5.2	(1.14)	0.7	(0.13)	7.2	(1.60)	9.10	2 025.8	1.11
				10	0.5	(0.14)	2.9	(0.63)	0.2	(0.04)	3.6	(0.82)	4.67	1 039.7	0.57
				15	0.0	(0.02)	0.7	(0.15)	0.0	(0.00)	0.7	(0.17)	1.00	223.8	0.12
5	15.9	14.7	7.5	2	11.5	(3.06)	32.3	(7.05)	20.7	(3.81)	64.6	(13.93)	106.04	22 867.2	8.73
				4	1.9	(0.53)	12.3	(2.68)	5.5	(1.02)	19.9	(4.24)	32.67	6 968.1	2.66
				8	0.1	(0.05)	2.1	(0.45)	0.4	(0.08)	2.7	(0.59)	4.48	968.7	0.37
				10	0.0	(0.02)	0.9	(0.20)	0.1	(0.02)	1.1	(0.25)	1.90	414.5	0.16
				15	0.0	(0.00)	0.1	(0.03)	0.0	(0.00)	0.1	(0.04)	0.30	67.8	0.03

Stn				Depth											
6	17.0	16.7	7.0	2	24.3 (6.47)	67.0 (14.60)	28.6 (5.27)	120.0 (26.36)	216.50	47 546.7	16.77
				4	5.9 (1.59)	28.6 (6.24)	8.3 (1.53)	42.9 (9.36)	77.48	16 898.2	5.96
				8	0.6 (0.16)	5.8 (1.27)	0.7 (0.13)	7.2 (1.58)	13.04	2 850.2	1.01
				10	0.2 (0.05)	2.7 (0.60)	0.2 (0.04)	3.2 (0.71)	5.85	1 281.6	0.45
				15	0.0 (0.00)	0.4 (0.10)	0.0 (0.00)	0.5 (0.11)	0.93	205.9	0.07
7	16.7	16.5	6.0	2	37.1 (9.88)	73.7 (16.08)	31.8 (5.86)	142.7 (31.83)	262.94	58 612.9	22.62
				4	10.7 (2.85)	34.9 (7.62)	10.0 (1.84)	55.7 (12.31)	102.56	22 679.1	8.75
				8	1.1 (0.30)	8.2 (1.79)	1.0 (0.18)	10.3 (2.27)	19.07	4 193.9	1.62
				10	0.4 (0.10)	4.0 (0.88)	0.3 (0.05)	4.7 (1.05)	8.83	1 940.3	0.75
				15	0.0 (0.00)	0.7 (0.16)	0.0 (0.00)	0.7 (0.17)	1.47	323.0	0.12
8	14.8	14.7	5.5	2	17.4 (4.65)	52.0 (11.35)	30.6 (5.63)	100.2 (21.64)	164.38	35 504.9	16.06
				4	5.8 (1.54)	26.4 (5.76)	10.2 (1.87)	42.4 (9.18)	69.63	15 069.8	6.82
				8	0.8 (0.22)	7.2 (1.57)	1.1 (0.21)	9.2 (2.01)	15.18	3 313.4	1.50
				10	0.3 (0.09)	3.8 (0.84)	0.3 (0.07)	4.6 (1.01)	7.90	1 664.1	0.75
				15	0.0 (0.01)	0.8 (0.18)	0.0 (0.00)	0.9 (0.20)	1.54	338.2	0.15
9	12.7	12.0	7.0	2	9.6 (2.55)	29.4 (6.43)	19.3 (3.56)	58.4 (12.55)	75.78	16 266.6	11.84
				4	1.7 (0.46)	11.5 (2.50)	5.2 (0.97)	18.5 (3.94)	24.02	5 112.3	3.72
				8	0.1 (0.02)	1.8 (0.41)	0.4 (0.07)	2.4 (0.51)	3.12	669.3	0.49
				10	0.0 (0.00)	0.7 (0.17)	0.1 (0.02)	0.9 (0.20)	1.22	263.8	0.19
				15	0.0 (0.00)	0.1 (0.02)	0.0 (0.00)	0.1 (0.02)	0.14	30.4	0.02
10	10.6	8.2	8.0	2	4.9 (1.32)	13.0 (2.83)	7.9 (1.45)	25.9 (5.62)	23.72	5 144.0	7.39
				4	1.0 (0.28)	5.2 (1.15)	2.1 (0.40)	8.5 (1.84)	7.82	1 686.5	2.42
				8	0.0 (0.02)	1.0 (0.23)	0.1 (0.03)	1.3 (0.29)	1.22	265.5	0.38
				10	0.0 (0.00)	0.4 (0.10)	0.0 (0.01)	0.5 (0.12)	0.53	117.0	0.17
				15	0.0 (0.00)	0.0 (0.01)	0.0 (0.00)	0.0 (0.01)	0.08	17.9	0.03
11	8.7	6.6	8.0	2	5.1 (1.38)	8.9 (1.94)	5.3 (0.99)	19.5 (4.31)	13.90	3 077.6	10.63
				4	1.2 (0.33)	3.7 (0.81)	1.5 (0.28)	6.5 (1.43)	4.68	1 026.2	3.55
				8	0.1 (0.03)	0.7 (0.17)	0.1 (0.02)	1.0 (0.23)	0.77	169.4	0.59
				10	0.0 (0.01)	0.3 (0.08)	0.0 (0.00)	0.4 (0.10)	0.34	76.3	0.26
				15	0.0 (0.00)	0.0 (0.01)	0.0 (0.00)	0.0 (0.01)	0.05	12.4	0.04
12	7.5	3.5	9.0	2	1.2 (0.32)	3.5 (0.77)	1.8 (0.34)	6.6 (1.44)	2.59	562.5	3.24
				4	0.0 (0.02)	0.8 (0.19)	0.3 (0.07)	1.3 (0.28)	0.52	111.3	0.64
				8	0.0 (0.00)	0.0 (0.01)	0.0 (0.00)	0.0 (0.00)	0.03	7.1	0.04
				10	0.0 (0.00)	0.0 (0.00)	0.0 (0.00)	0.0 (0.00)	0.00	2.0	0.01
				15	0.0 (0.00)	0.0 (0.00)	0.0 (0.00)	0.0 (0.00)	0.00	0.1	0.00

Table 3

Integrals of irradiance and photon flux density (both 400–700 nm) at different water depths (below M.L.W.S. at Helgoland, 1975)

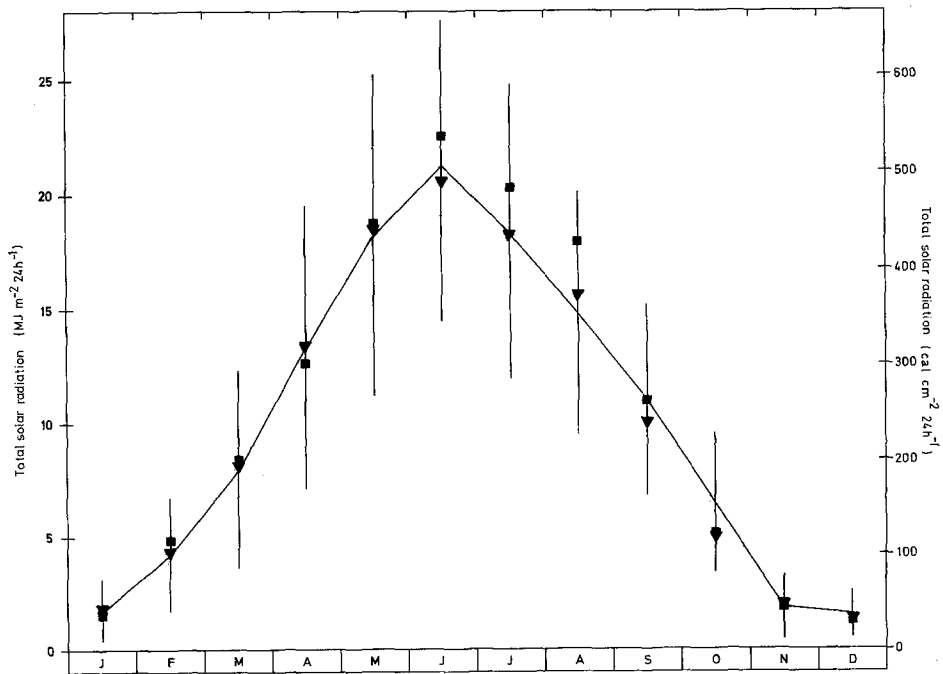| (A) 12 months (January to December)	Water depth (m)	Irradiance (MJ · m^{-2} · year^{-1})	Photon flux density (E · m^{-2} · year^{-1})	Percentage of surface irradiance
	2	227.2	1037.2	10.91
	4	84.6	387.7	3.96
	8	15.6	71.2	0.71
	10	7.3	33.4	0.33
	15	1.3	6.0	0.05
(B) 6 months (April to September)	(m)	(MJ · m^{-2} · 0.5 year^{-1})	(E · m^{-2} · 0.5 year^{-1})	
	2	202.4	923.8	14.64
	4	75.7	347.2	5.47
	8	14.0	64.0	1.01
	10	6.6	30.1	0.47
	15	1.2	5.4	0.08

Fig. 11: Total solar radiation (300–3000 nm) at Helgoland (Triangles: mean of measurements from July 1965 to June 1970, quadrats: measurements in 1975; Hagmeier, unpublished) and in Copenhagen (solid line, mean of 1959–1971, vertical bars: standard deviations; Gargas, 1975)

depth, the mean photon flux density was $74 \mu E \cdot m^{-2} \cdot s^{-1}$ in green (500–600 nm), $37 \mu E \cdot m^{-2} \cdot s^{-1}$ in the blue (400–500 nm), and $32 \mu E \cdot m^{-2} \cdot s^{-1}$ in the red part (600–700 nm) of the spectrum (Table 2). At 8 m, a monthly mean photon flux density greater than $10 \mu E \cdot m^{-2} \cdot s^{-1}$ was only achieved in July.

Monthly integrals of photon flux density and irradiance are also given in Table 2, together with irradiance as a percentage of surface irradiance (visible). At 10 m water depth the maximum values, occurring in July, were $8.8 \, E \cdot m^{-2} \, month^{-1}$, or $1940 \, kJ \, m^{-2} \, month^{-1}$ (both 400–700 nm), or 0.8 % of energy (visible) above the surface.

Finally, the total number of quanta and the total energy (both visible) received per unit area over the whole year (Table 3) have been calculated from the data given in Table 2. The yearly integrals, expressed as $E \cdot m^{-2} \cdot year^{-1}$ (or as $MJ \cdot m^{-2} \, year^{-1}$) are roughly: 1000 (230) at 2 m water depth, 70 (16) at 8 m, and 6 (1) at 15 m. Table 3 also shows the total light received during the 6 months from April to September. In the sublittoral zone, 90 % of the
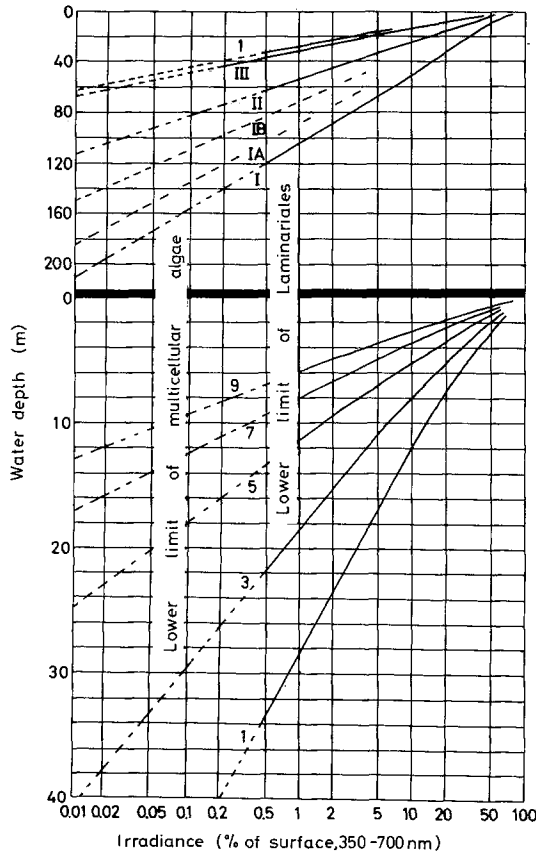

Fig. 12: Percentage of surface downward irradiance (350–700 nm) as function of water depth and Jerlov water types. Solid lines (range 100–0.5 %): according to Jerlov (1970). Broken lines (range 0.5–0.01 %): projections of Jerlov's curves into lower percentage ranges. Critical light levels of major importance are situated at 0.5 to 1 % of surface irradiance (lower limit of Laminariales) and at 0.05 to 0.1 % of surface irradiance (lower limit of multicellular marine algae)

yearly integral is received during this period, although the corresponding value for surface irradiance is 81 %. During the same period, 15 % of the irradiance above water (400–700 nm) penetrates to 2 m water depth, 1 % to 8 m, and only 0.1 % to 15 m. These percentages were calculated from measurements of total solar radiation at Helgoland (Fig. 11), multiplied by a factor of 0.5 to obtain photosynthetically active radiation ("visible") (Westlake, 1965; Szeicz, 1974).

DISCUSSION

The present calculations were performed only for the range 400–700 nm, instead of the range 350–700 nm which was recommended by the SCOR Working Group 15 (Tyler, 1975a, b). The discrepancy is not great however, since the range 350–400 nm contains a maximum of only 10 % of total quanta in "blue" waters (Morel & Smith, 1974), and makes up a negligible proportion of the total quanta in waters as turbid ("green waters"), as those near Helgoland.

The irradiance meters used in the present investigation have two major disadvantages: (1) Although the shift of spectral sensitivity can be tolerated in the green and red part of the spectrum, the maximum shift of 23 nm occurring in the combination of selenium photo element plus blue filter (SFK 20) precludes reliable determinations of transmission in the blue range. Interference filters with narrow bandwidths have been used in conjunction with photo elements (Gordon & Dera, 1969; Ivanoff et al., 1961), but the sensitivity of this system is very low, since the radiation coming to the collector must be limited to an incidence angle of 10–15 if the interference filter is to perform correctly. Photodiodes need to be combined with interference filters in order to overcome these problems, and a new underwater light-measuring system is now being developed which incorporates irradiance meters of this type. (2) The present system recorded the instantaneous value of photon flux density every 20 minutes, and transmission was calculated from the readings of 2 separate irradiance meters at 2.5 and 3.5 m depth. Although the time interval between the 2 readings was only 1.5 s, transmission values for a single day sometimes varied greatly, especially when wave action or broken cloud caused rapid changes in irradiance. This problem of the shortterm variability of irradiance measurements can be overcome, without increasing the total amount of data collected, by integrating irradiance readings over a 20-minute period, and recording the total number of incident quanta every 20 minutes. This modification is also being incorporated into the new light-measuring system.

The long-term stability of the photo elements was satisfactory. Similar stability was observed by Anderson (1971) and by Holmes & Snodgrass (1961) in selenium photo elements used permanently in the field over several years. According to Jerlov (1966), selenium photo elements should be exposed to not more than 1.5 % of full daylight, and should be operated with a shunt not greater than 50 Ohm. These conditions were fulfilled in the present measurements. Sensitivity drifts due to temperature changes are negligible, as long as small shunts are used (Kubin, 1971).

Since underwater irradiance was measured only in one location near Helgoland, the results may not be representative of the whole of the phytal zone around this island. However, in view of the large seasonal differences in transparency and of the strong mixing

Table 4

Irradiance as percentage of surface (350–700 nm) at the lower kelp limit and at the lower limit of multicellular algae

Species	Locality	Deepest record (m)	Irradiance (% of surface)	Jerlov water type	European system[1]	Stephensons' scheme[2]	French school[3]
Laminaria hyperborea	Helgoland[4]	8[5]	0.7[6]	7[7]	sublittoral region →	IF[30]	étage infra-littoral
Laminaria hyperborea	Isle of Man[8]	19[9]	0.8[10]	3[11]			
Laminaria hyperborea	Roscoff[12]	25[13]	1.2[14]	III[12]			
Laminaria hyperborea	Glénan[15]	26[13]	1.4[16]	1[16]			
Macrocystis pyrifera[17]	California[18]	–[19]	0.3–0.5[20]	–			
Pelagophycus porra[17]							
Laminaria farlowii						infra-littoral-zone	
Laminaria rodriguezii	Corsica[21]	95	0.6[10]	IA[22]			étage circa-littoral
Various red algae[23]	Helgoland[4]	10–15[5]	0.3–0.05[6]	7[7]			
Various algae[24]	Glénan[15, 25]	40–47[13]	0.2–0.05[10]	1[16]			
Maripelta rotata[26]	California[18]	–[19]	0.15–0.05[20]	–			
Litothamnia	Corsica[21, 27]	120	0.1[10]	IA[22]			
Litothamnia	Bahamas[28]	175	0.05[10]	I[29]			

1 den Hartog (1959)
2 Stephenson & Stephenson (1949)
3 Pérès & Picard (1956), Pérès & Molinier (1957)
4 this paper and Lüning (1970)
5 depth below M.L.W.S.
6 range 400–700 nm, yearly mean
7 mean from February to November
8 Kain (1971); Kain et al. (1976)
9 Spanish Head; below LAT
10 calculated according to Jerlov water type (see Fig. 12)
11 Jerlov water type calculated from data of authors
12 Boutler et al. (1974)
13 depth below E.L.W.S.
14 measured by thermopile
15 Castric-Fey et al. (1973)
16 Descatoire et al. (1969)

17 young plants
18 Neushul (1971)
19 below canopy of *Macrocystis pyrifera*
20 percent green light of subsurface was measured (= 2 times values indicated)
21 Fredj (1972)
22 Ivanoff (1957)
23 *Delesseria sanguinea*, *Phyllophora traillii*, litothamnia
24 *Carpomitra costata*, *Halopteris filicina*, *Rhodymenia pseudopalmata* var. *elisiae*, litothamnia
25 Lafargue (personal communication)
26 also *Prionitis* sp.
27 Molinier (1960a, 1960b)
28 Lang (1974)
29 Ivanoff et al. (1961)
30 IF denotes Infralittoral Fringe

due to tidal currents it seems unlikely that big local differences exist. Furthermore, vertical stratification develops extremely rarely so that the calculation of irradiance for all water depths from measurements performed at only 2 depths appears to be justified. Continuous underwater light measurements which are planned for the future near Helgoland will show how "typical" the year 1975 was, but they are unlikely to change the absolute values dramatically. Both the present measurements and those obtained near Helgoland in 1967 (Lüning, 1971) demonstrate that the period from October until March contributes very little (10 % in 1975, Table 3) to the yearly integral of light received in the sublittoral region.

How much light energy arrives at different biological boundaries in the sublittoral region, and how universal are the values obtained in the present investigation? An alga consists of a certain quantity of organic material which requires a minimum level of light energy or quanta to sustain it and to complete the life cycle of the species. This minimum light requirement can at present only be estimated by measuring or computing the light energy at the lowest depth recorded for the occurrence of the species, although this depth (and light energy) may be too low to permit the completion of the life cycle. More precise estimates can only be obtained if exact light-dependent depth "survival ranges" (Neushul, 1967) are determined in the field, as well as in the laboratory in simulated underwater light fields. In the following, two important lower boundaries will be discussed: the lower limit of kelp species (Laminariales), and the lower limit of any multicellular marine algae – which is also the lower limit of the phytal zone.

Various data have been assembled (Table 4) on lower depth limits of algae (established by diving or by direct observation from submersibles) from investigations which allow us at least to guess which Jerlov water type (Jerlov, 1968) occurred at the site. The lower limit of the Laminariales occurs at 0.7 to 1.4 % of surface irradiance (visible), regardless of wheather that limit is at a depth of 8 m (Helgoland) or 25 m (Roscoff) for *Laminaria hyperborea,* or 95 m (Corsica) for *L. rodriguezzi. L. ochroleuca* also penetrates as deeply as *L. rodriguezii* in the Mediterranean near Sicily (Mojo & Buta, 1970; Giaccone, 1972; Drew, 1974).

The deepest multicellular marine algae receive 0.05–0.1 % of surface irradiance (visible). This is 10–20 times less than the generally accepted value of 1 % of surface irradiance as the limit of the euphotic zone for phytoplankton. In very clear waters, such as the Sargasso Sea, the euphotic zone for phytoplankton reaches to about 120 m (Steeman Nielsen, 1974), but benthic marine algae have long been recorded in dredgings from greater depths (see Gessner, 1955). These records have to be treated with caution, since the algae may have been caught by the dredge at shallower depths, or they may be loose fragments of plants which only grow higher up. Observations made from submersibles are more reliable and these have revealed crustose corallines and green algae at 175 m water depth on deep fore reefs off Jamaica and the Bahamas (Lang, 1974). If Jerlov water type I (oceanic water) occurs at these locations, the light at 175 m will be 0.05 % of surface irradiance (Fig. 12), which agrees well with the values for much shallower algal limits in coastal waters (Table 4).

The minimum light requirements of marine algae growing in the interior of sea caves appear to be similar to those suggested by their vertical distribution. Red algae have been found in caves at minimum irradiances of 0.06 % (Malta; Larkum et al., 1967) and 0.2 % (Ireland; Norton et al., 1971) of irradiance in the open.

There seems, therefore, to be good agreement between a wide variety of records if the lower limit of either the Laminariales or the deepest benthic algae are defined in terms of the percentage of surface irradiance occurring at that depth. Such a definition in relative terms can only be accepted as a first approximation, however, since variations in surface irradiance may result in large differences in the absolute amount of light energy or quanta available at these biological boundaries. We should, therefore, aim to define the minimum light requirements of a complete algal life cycle in absolute terms. The magnitudes which may be expected can be seen from Table 3. A laminarian plant (Table 3: 8 m depth, i.e. the lower limit of kelp near Helgoland) needs at least a photon flux density of about 70 E $\cdot$ m^{-2} $\cdot$ year^{-1} or an irradiance of 15 MJ $\cdot$ m^{-2} $\cdot$ year^{-1}. Since brown algae are good converters of blue as well as of green light, it is to be expected that these values will not change very much in clear ("blue") or turbid ("green") waters. The deepest-occurring algae (Table 3: 15 m depth) need at least 6 E $\cdot$ m^{-2} $\cdot$ year^{-1} or about 1 MJ $\cdot$ m^{-2} $\cdot$ year^{-1}, and, if these plants are red coralline algae, which are known to grow better in green than in blue light, they can be expected to reach depths in "green" waters which have a lower percentage of surface irradiance than reached in "blue" waters. Green algae, on the other hand, are good candidates for deep-water algae in "blue" waters, as has been stressed by Levring (1969), Drew (1969) and Larkum et al. (1967).

The depth at which irradiance is reduced to 1 % of the surface value is also regarded as a rough boundary between the two sub-zones of the sublittoral zone which are distinguished by the French school, the "étage infralittorale" and the "étage circalittorale" (Pérès, 1957, 1967a, b; Pérès & Picard, 1964). The infralittoral harbours the photophilous plants (e.g. Laminariales at medium and high latitudes, marine phanerogams in the tropics), and the circalittoral, extending to the lower limit of algal vegetation, the sciaphilous algae. Feldmann distinguished these two plant groups as early as 1937. Interestingly, the "deep algal community" in the fringing coral reef of Curaçao exists as rich algal turf down to depths of 50–55 m (corresponding to 3 % of surface irradiance if water type I B is predominating; see Fig. 12) and reaches its lower limit at 60–65 m, again at about 1 % of surface irradiance (Hoek & Breeman, 1978). This depth marks the absolute minimum for survival of the constituents of the "deep algal community", and corresponds to the lower limit of the Laminaria "park", but not to that of the Laminaria "forest" (i.e. the closed vegetation of dominating and overshadowing macrophytes). Taking a leaf area index of 1 (1 m^2 of frond area per 1 m^2 of bottom area) as boundary of the Laminaria "forest", the lower limit occurs at 4 m near Helgoland (predominating water type 7) or at 9–14 m near Arisaig, Scotland (predominating water type 4; Jupp & Drew, 1974; Kain et al., 1976), so that the light requirements of a closed kelp community seem to lie in the range 2–7 % of surface irradiance.

Since Stephenson & Stephenson (1949) proposed their zonation scheme, the "infralittoral fringe" reaching from the uppermost limit of the laminarians to about E.L.W.S. (2 m below M.L.W.S. near Helgoland) has been recognized by more and more workers and regarded as the uppermost part of the sublittoral region (see Table 4). Laminaria digitata is a typical inhabitant of the infralittoral fringe (Castric-Fey et al., 1973) and is specially adapted for this habitat by its flexible stipe. Kain (1976) observed that this species, together with others, colonised cleared areas well below its usual zone, but was outcompeted after 4 years by L. hyperborea which finally overshadowed the other species due to its possession

of a stiff stipe. Although algae of the "infralittoral fringe", such as *L. digitata*, seem to have a higher light resistance (Drew, 1974b), they do not seem to have higher light requirements than other photophilous algae of the sublittoral region, such as *L. hyperborea*.

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