Vol. 104: 131–137, 1994 | MARINE ECOLOGY PROGRESS SERIES Mar. Ecol. Prog. Ser. | Published January 27

Influence of spring-neap tidal cycles on the light available for photosynthesis by benthic marine plants

Matthew J. Dring[1], Klaus Lüning[2]

[1]School of Biology and Biochemistry, Queen's University, Belfast BT7 1NN, Northern Ireland, UK
[2]Biologische Anstalt Helgoland, Notkestr. 31, D-22607 Hamburg, Germany

ABSTRACT: An underwater light-measuring station, consisting of 3 sensors at each of 2 depths (4.5 and 5.5 m below MLWS), was established off Helgoland (southern North Sea) to provide continuous measurements of underwater irradiance at 3 wavelengths (452, 552 and 653 nm, isolated by interference filters). The percentage transmittance of each wavelength through 1 m of seawater was calculated from the readings at the 2 depths. Irradiance and transmittance were recorded every 75 s during 3 periods of 2 mo between August 1990 and June 1991. During autumn and winter 1990, in spite of variations in weather conditions, there was a strong 2-weekly cycle of total daily irradiation, with peaks when low tide occurred at around midday (neap tides at Helgoland) and troughs when high tide occurred at this time (spring tides). The amplitude of this cycle was much greater than could be accounted for by the difference in tidal height at midday, but could be explained if light penetration through the water was greater during neap tide series than during spring tides. This hypothesis was supported by the transmittance measurements, and by wind speed data and Secchi disc depths from the same site. However, no association between water clarity and the spring-neap cycle was apparent in April–June 1991. Nevertheless, the variable relationship between underwater and surface irradiance through the spring-neap cycle needs to be taken into account in any attempt to estimate benthic primary productivity from surface light data.

KEY WORDS: Benthic algae · Light measurement · Light quality · Primary production · Sublittoral · Tidal cycles · Water type

INTRODUCTION

Because of the practical difficulties of measuring the photosynthesis of marine plants *in situ*, attempts have been made to predict photosynthetic rates from photosynthesis vs irradiance curves determined in the laboratory and estimates of the irradiance incident on plants in the field (e.g. Brinkhuis 1977, Campbell et al. 1988). Ideally, the irradiance measurements should be continuous, but this has rarely been achieved over extended periods in benthic marine habitats (Kain 1971, Lüning & Dring 1979), and it may be more practicable to estimate underwater light from continuous records of surface irradiance and knowledge of the optical properties of seawater (Jerlov 1976, Kirk 1983). This approach is relatively easy to apply if the plants are assumed to be in a constant depth of water (e.g. Dring 1981), but plants fixed by their holdfasts at any given position in the intertidal or upper subtidal zones will be covered by a continually changing depth of water as the tides ebb and flow. A theoretical analysis of the influence of such tidal variations in water depth on the light climate experienced by benthic plants (Dring 1987) was valuable in interpreting the depth distribution of macroalgae in sites with large tidal ranges (e.g. 14 m; Bristol Channel, England). However, in sites with more typical tidal ranges (2 to 4 m), changes in water level were predicted to exert a much smaller influence on underwater irradiance, which might be completely swamped by natural variations in surface irradiance caused by weather conditions. The models developed by Dring (1987), therefore, require validation by continuous underwater light measurements.

The underwater light record obtained at Helgoland (North Sea) in 1975 (Lüning & Dring 1979) cannot be used for this purpose because the data had been analysed as 10 d means, which obscure any variations associated with the 14 d spring-neap cycle of the tides. A new set of continuous measurements was, therefore, planned at the same site, using a light-measuring station which incorporated several improvements on the station used in 1975. The new light-measuring station is described in this paper, together with an analysis of some of the data obtained, which demonstrate an unexpectedly strong influence of the spring-neap cycle on the underwater light climate.

METHODS

Light sensors. Six light sensors were constructed by Meerestechnik-Electronik (Trappenkamp, Germany). Each sensor (Fig. 1) was covered by an air-filled glass dome, similar to those used on many pyrheliometers and other meteorological irradiance measuring instruments. The curvature of the dome was found to reduce silt deposition and algal colonisation. Frosted glass (2 mm thick Zeiss-Überfangglas) fixed to the underside of the glass dome was used as as opal glass cosine collector, as recommended by Jerlov & Nygård (1969). Light emerging from the opal glass collector passed through a 7 cm long collimator (40 blackened, 2 mm wide metal tubes), an interference filter (Schott, MA3-0.5, peak transmittance 452, 552 or 653 nm, half-band width 10 to 15 nm) and a focusing lens, and then was measured by a Pin diode. This optical system was encased in a rigid PVC cylinder.

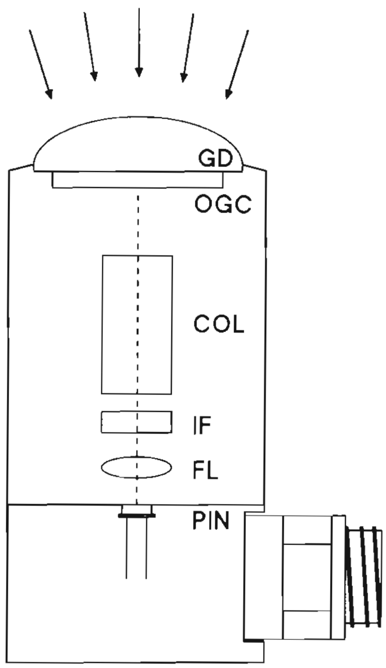

Fig. 1 Diagrammatic cross-section of light sensor. GD: glass dome; OGC: opal glass collector; COL: collimator; IF: interference filter; FL: focussing lens; PIN: pin diode

Calibration. The raw output from each sensor ranged from 0 to 255 units and increased linearly with increasing irradiance over at least 3 such ranges (i.e. up to 768 units). Since it was not possible to detect overflows of the base range automatically, however, the output had to be reduced by neutral density filters so that the maximum irradiance recorded yielded a raw output of less than 255 units. The sensors were then calibrated in simulated underwater light fields (Leitz Prado Universal projector with 24 V 250 W quartz-iodine lamp, 5 mm KG3 heat filter and Schott glass filters 2 mm BG38 and 2 mm GG4; for spectral distribution, see Lüning 1980) and in natural sky + sun light against the spectral photon irradiance measured by a Licor LI-1800 underwater spectroradiometer, integrated over the 100 nm waveband centred on each of the interference filters used (i.e. 400 to 500 nm for the 452 nm filter; 500 to 600 nm for the 552 nm filter; 600 to 700 nm for the 653 nm filter). The minimum sensitivity for the green sensors was about 1 μmol m^{-2} s^{-1} 100 nm^{-1}, whereas that for the blue and red sensors was about 0.4 and 0.7 μmol m^{-2} s^{-1} 100 nm^{-1}, respectively.

Immersion factors were determined according to Smith (1969), and were 0.68 at 452 nm, 0.69 at 552 nm, and 0.71 at 653 nm. The calibration factors obtained in air were corrected for these immersion factors to account for the immersion effect (Westlake 1965, Jerlov 1976).

Underwater measuring station. The 6 light sensors were attached to to an iron rack, situated in 7 m water depth (below MLWS at Helgoland) off the Jugendherberge jetty at the northeast corner of the island. The rack was 2.5 m high (see Lüning & Dring 1979) and was secured by steel ropes fastened to railway wheels. Three of the sensors (one for each wavelength) were placed at 4.5 m, and the other three at 5.5 m. The 6 sensors were connected by cables to a data acquisition module (Meerestechnik-Elektronik), which was also fixed to the iron rack. This module was linked by cable to a microcomputer in the laboratory of the Meeresstation Helgoland, which processed the data using Multipar software developed by Meerestechnik-Elektronik, and finally stored the data on floppy discs.

The glass domes of the light sensors were cleaned once a week by divers, and the long-term stability and calibration of the sensors was checked every 2 to 3 mo by testing their output in projector light fields in the laboratory against readings of a Lambda quantum meter (Licor, Lincoln, NB, USA). Deviations of individual sensors over 8 mo were within the range ±4%.

Recording and analysis. The photon irradiance at each light sensor was integrated over a period of 75 s and these integrals from all 6 sensors were then transmitted simultaneously to the computer. Since the sensors had been calibrated against a constant light source, each integrated output could be interpreted as a mean of the photon irradiance over 75 s in µmol m^{-2} s^{-1} 100 nm^{-1}. These data were transferred to a spreadsheet in order to compute the following:

(1) Transmittance (% m^{-1}) for each wavelength: calculated from corresponding irradiance readings at 4.5 and 5.5 m; to avoid spurious values when individual irradiance readings were low, transmittance was calculated only when irradiance at 5.5 m for any sensor was more than 5 times the minimum sensitivity of the sensor;

(2) Daily integrals (mol m^{-2} d^{-1} 100 nm^{-1}) for each waveband at each depth: the mean irradiances over 75 s recorded by each sensor were totalled for each day and multiplied by 75;

(3) Maximal daily irradiance (µmol m^{-2} s^{-1} 100 nm^{-1}) for each waveband at each depth: the largest 75 s mean recorded for each sensor on each day;

(4) Daylength (h) for each waveband at each depth: estimated as the number of non-zero 75 s means, divided by the number of readings per hour (48);

(5) Mean daily transmittance (% m^{-1}) for each waveband: mean of calculated transmittance values for each day.

Daily measurements of Secchi disc depths made by the Biological Oceanography group of the Biologische Anstalt Helgoland (data by courtesy of Dr W. Hickel & K. Treutner) and hourly measurements of wind speed at Helgoland (data by courtesy of Wasser- und Schiffahrtamt Tönning, Aussenbezirk Helgoland) were also analysed to give means over 3 to 4 d periods, for comparison with the irradiance measurements.

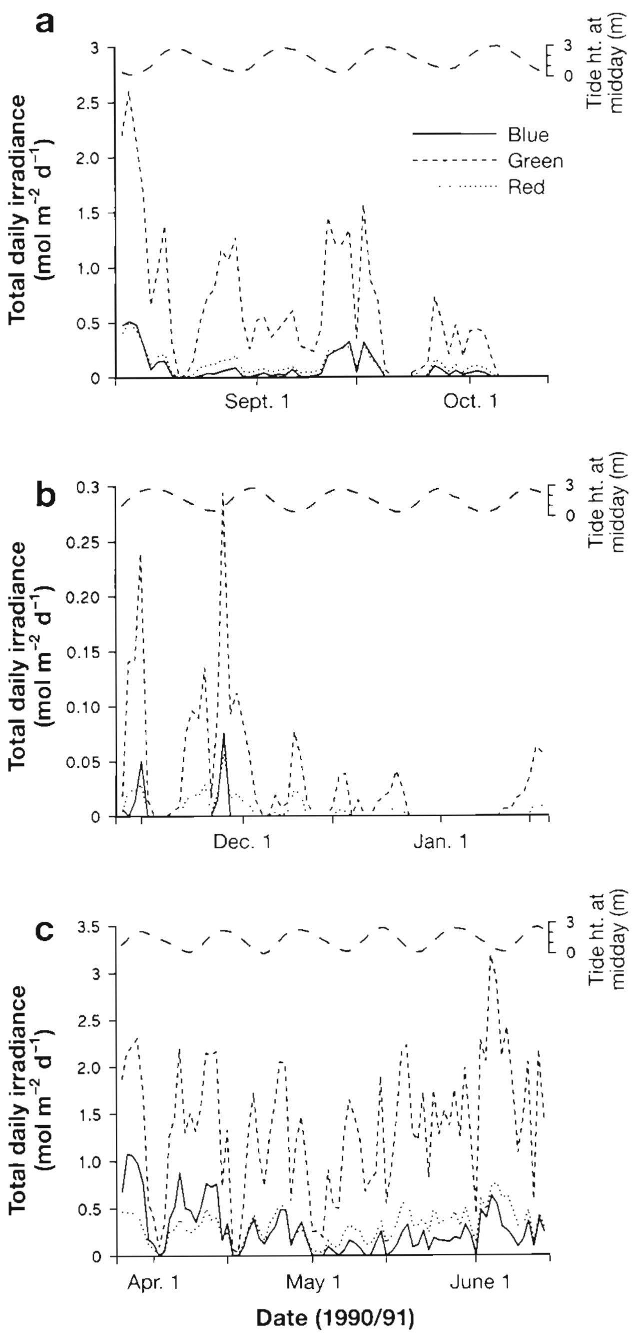

Fig. 2. Daily integrals of irradiance in blue, green and red wavebands at a fixed station 4.5 m below MLWS at Helgoland (North Sea) during the periods (a) 13 August to 11 October 1990, (b) 12 November 1990 to 7 February 1991, and (c) 26 March to 14 June 1991. The predicted water height above MLWS at midday is shown in the upper panel of each figure

RESULTS

Continuous records were obtained from the underwater light-measuring station for the periods 13 August to 11 October 1990, 12 November 1990 to 7 February 1991 and 26 March to 14 June 1991. The daily integrals of blue, green and red wavebands at 4.5 m water depth for each of these periods are presented in Fig. 2, and the monthly integrals of white light (400 to 700 nm) at 4.5 m are compared in Table 1 with similar data predicted for 4.0 m water depth from continuous underwater measurements at the same site in 1975 (Lüning & Dring 1979). It is clear that, allowing for year-to-year variations, the measurements in each month are of the same order of magnitude as those made in 1975.

Starting in late August 1990, there were several periods of 2 to 3 d during which no light was recorded, even in the green waveband, at 4.5 m (e.g. 21 August, 20 to 22 September, 8 to 10 October; Fig. 2a). These

Table 1. Monthly integrals of quantum irradiance of white light (400 to 700 nm) measured at 4.5 m below MLWS at Helgoland during 1990/91, compared with monthly integrals predicted for 4.0 m below MLWS from underwater measurements made at the same site in 1975 (Lüning & Dring 1979)

Month	Quantum irradiance of white light ($mol\ m^{-2}\ mo^{-1}$)	
	1990/91 (4.5 m)	1975 (4.0 m)
August	39.40[a]	69.63
September	20.49	24.02
October	nm	7.82
November	3.91	4.68
December	0.66	0.52
January	1.45	0.27
February	nm	12.29
March	nm	14.94
April	54.65	40.79
May	49.53	32.67
June	78.47[a]	77.48

[a]Data recorded for only part of month but corrected *pro rata* for missing days
nm: data not measured

periods all coincided with times when high tide occurred at around midday and, even when complete darkness was not recorded, the daily integrals tended to be lower on days on which high tide was around noon. Conversely, peaks in the irradiance record occurred during periods when low tide was close to noon. As overall irradiance levels decreased during the late autumn and winter of 1990/91, this pattern of peaks during periods of low tide at midday and troughs during periods of high tide became less pronounced, but it was still detectable (Fig. 2b). In spring 1991, there were no 'dark days', but the 3 deep troughs in the record in April and early May all coincide with periods of high tide at midday (Fig. 2c).

The data for maximal daily irradiance show a similar pattern of high values during periods when low tide occurred around midday and low values when high tide occurred at this time (Fig. 3).

In order to examine the relationship between underwater irradiance and tidal height at midday in more detail, and to reduce the influence of random weather-related variations in surface irradiance, the daily integrals and the maximal daily irradiances were averaged over 3 to 4 d periods when either low water or high water occurred between 12:00 and 14:00 h. The results of this analysis (Table 2) confirm the pattern revealed by the raw daily data, and reveal the magnitude of the influence of the spring-neap tidal cycle on the daily irradiance values. This influence has been quantified by expressing the values during each high tide series as a percentage of the corresponding values during each of the adjacent low tide series (Table 2).

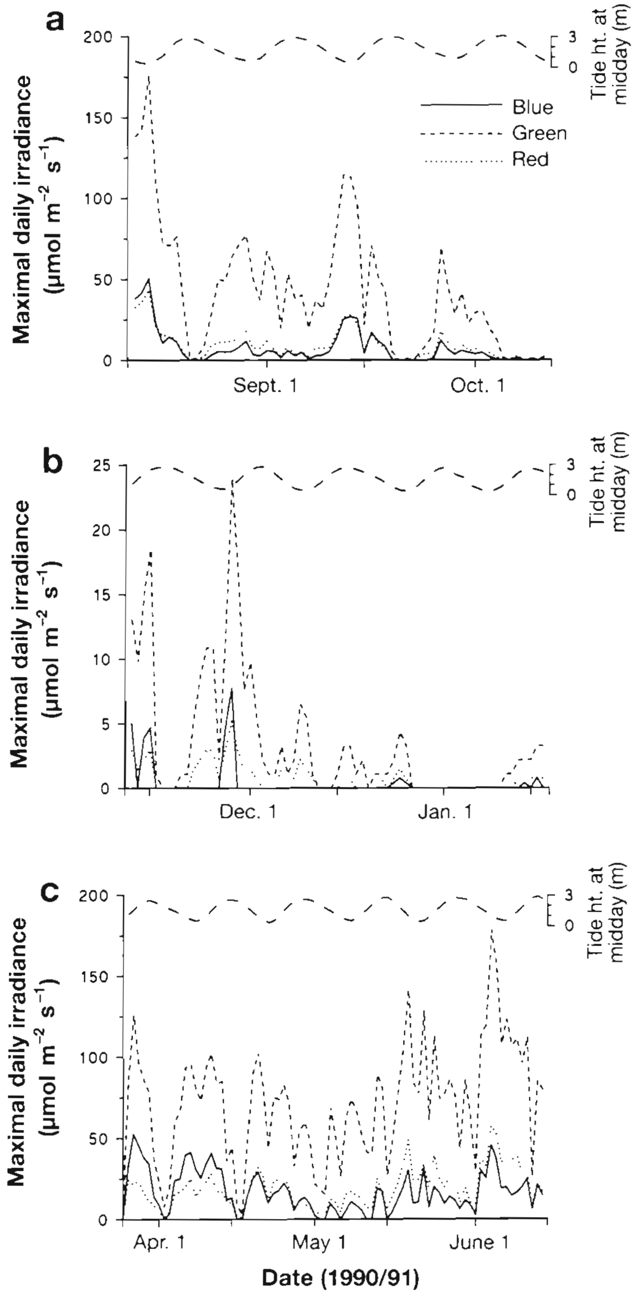

Fig. 3. Maximal irradiance recorded on each day in blue, green and red wavebands at a fixed station 4.5 m below MLWS at Helgoland (North Sea) during the periods (a) 13 August to 11 October 1990, (b) 12 November 1990 to 7 February 1991, and (c) 26 March to 14 June 1991. The predicted water height above MLWS at midday is shown in the upper panel of each figure

In the semi-diurnal tidal regime experienced at Helgoland, high waters occur at about midday only during spring tides (mean high water 2.7 m), whereas low waters occur at about midday only during neap tides (mean low water 0.4 m). Therefore, the sensors at 4.5 m

Table 2. Mean irradiance of green light (500 to 600 nm) during daylight and mean maximal daily irradiance of green light recorded at 4.5 m below MLWS over 3 to 4 d periods at Helgoland when the tide was either high or low between 12:00 and 14:00 h, together with mean wind speed and Secchi disc depths for these periods. Irradiance values for each high tide series are also given as a percentage of corresponding values for preceding or following low tide series

Date (1990/1991)	High (H) or low (L) tide at midday	Mean values over each 3 to 4 d period: Irradiance during daylight ($\mu mol\ m^{-2}\ s^{-1}$)		Maximal daily irradiance ($\mu mol\ m^{-2}\ s^{-1}$)		Transmittance at 550 nm (% m^{-1})	Mean wind speed ($m\ s^{-1}$)	Secchi disc depth (m)
14–16 Aug	L	40.49		142.9		73	5.17	4.83
			(8.3%)		(6.9%)			
21–24 Aug	H	3.38		9.8		56	12.60	1.13
			(24.0%)		(17.9%)			
29–31 Aug	L	14.09		54.8		67	5.17	2.97
			(62.1%)		(61.6%)			
5–8 Sep	H	8.75		33.7		63	7.98	3.23
			(29.3%)		(31.4%)			
12–14 Sep	L	29.83		107.4		75	6.70	5.13
			(1.3%)		(1.5%)			
19–22 Sep	H	0.40		1.6		nd	16.35	1.77
			(5.2%)		(5.3%)			
28–30 Sep	L	7.67		30.8		62	9.33	3.00
			(0.6%)		(2.6%)			
5–8 Oct	H	0.05		0.8		nd	14.10	1.55
18–21 Nov	H	0.11		0.5		nd	11.18	0.90
			(3.4%)		(6.5%)			
25–27 Nov	L	3.35		8.3		66	12.70	2.75
			(6.1%)		(17.4%)			
3–5 Dec	H	0.21		1.5		nd	10.03	1.63
			(8.7%)		(33.3%)			
9–11 Dec	L	2.36		4.4		nd	13.57	1.20
			(27.0%)		(37.5%)			
17–20 Dec	H	0.64		1.6		nd	6.15	2.38
			(55.2%)		(64.3%)			
25–27 Dec	L	1.15		2.5		nd	13.03	1.20
30 Mar–2 Apr	H	15.27		36.4		69	6.23	3.00
			(52.4%)		(43.9%)			
7–9 Apr	L	29.16		83.1		65	7.07	3.75
			(35.6%)		(32.1%)			
15–18 Apr	H	10.39		26.7		63	8.80	2.65
			(51.4%)		(40.2%)			
21–23 Apr	L	20.22		66.4		70	6.93	3.30
			(69.2%)		(56.1%)			
29 Apr–2 May	H	14.00		37.3		nd	5.73	5.33
			(52.8%)		(54.9%)			
7–9 May	L	26.50		67.8		nd	5.03	4.00
			(64.8%)		(75.9%)			
15–17 May	H	17.16		51.5		59	9.33	3.00
			(74.8%)		(58.0%)			
21–23 May	L	22.93		88.9		61	9.17	2.50
			(90.5%)		(62.4%)			
29 May–1 Jun	H	20.75		55.5		68	4.68	4.03
			(58.1%)		(49.4%)			
6–8 Jun	L	35.68		112.4		69	5.93	3.75
			(65.6%)		(56.4%)			
12–14 Jun	H	23.41		63.5		69	8.90	3.90

nd: transmittance values not determined, usually because light levels too low for reliable estimation

below MLWS would be covered by about 7.2 m of water at midday during the high tide series, but by only 4.9 m during the low tide series. Assuming that the water type was 'Coastal 7' (Jerlov 1976; transmittance at 550 nm, 63% m^{-1}; equivalent to an attenuation coefficient (k_{550}) of 0.462 m^{-1}), the extra 2.3 m of water during the high tide series would be expected to reduce the irradiance to about 35% of its value during the low tide series. During the spring of 1991, most values during the high tide series were 50 to 70% of the values during the adjacent low tide series (Table 2) but, in the late summer and autumn of 1990, the irradiance during the high tide series was nearly always reduced by a greater amount and it was frequently less than 10% of the values during low tide series (Table 2). These data suggest that, at least during the autumn season, light penetration through the water (and, hence, the water type) was poorer during the high tide series (i.e. spring tides) than during the low tide series (neap tides).

A direct measure of light penetration was available from the transmittance values calculated from the irradiance readings at 4.5 and 5.5 m in each waveband. The transmittance values for green light during the low tide series in August and September 1990 were reliable (95% confidence limits for most daily means were ± 0.3 to 0.4%) and were typical of either Coastal 7 (transmittance 63% m^{-1}) or Coastal 5 (74% m^{-1}; Table 2), but values are missing for many of the adjacent high tide series because insufficient light reached the sensors to permit a reliable estimate of transmittance to be calculated. Nevertheless, the few values that are available suggest that transmittance was poorer during these high tide series. Additional, if indirect, indications of water type were available from routine measurements of Secchi disc depths and wind speeds at Helgoland (Table 2). These data indicate that, during the 3 periods of very low light readings in August (21 to 24), September (19 to 22) and October (5 to 8) 1990, Secchi disc depths were low and mean wind speeds were high, whereas 2 of the intervening periods with high light readings (14 to 16 August, 12 to 14 September) coincided with light winds and greater Secchi disc depths. However, this pattern of high winds during high tide series and calmer conditions during low tide series began to break down during the more consistently stormy months of November and December 1990, and could not be detected in the spring of 1991.

The theoretical effect of change in water type, combined with the difference in water height at midday, on underwater irradiance was evaluated by calculating the surface irradiance required to give an irradiance of 100 units at 4.9 m, assuming one water type, and then calculating the penetration of this surface irradiance down to 7.2 m, assuming the same or a different water type (Table 3). If the water type did not change between the low tide (i.e. 4.9 m at midday) and the high tide (7.2 m at midday) series, the irradiance during the high tide series would be 50, 35 and 23% of that during the low tide series in water types Coastal 5, 7 and 9, respectively. If the water type improved between the low tide and the high tide series, the irradiance during the high tide series would be at least 80% of that during the low tide series, and it would be possible for *higher* irradiances to be recorded when high tide occurred at midday than when low tide occurred at this time (e.g. Coastal 9 during the low tide series, and Coastal 5 during the high tide series). If the water type worsened, however, as seems to have occurred on several occasions between August and December 1990, the irradiance during the high tide series could be reduced to 16, 10 or 5% of the corresponding values during the low tide series (Table 3). The large differences between irradiance values observed during adjacent spring and neap tide series could be explained, therefore, if the water type was consistently poorer during the spring tides than during the neap tides.

Table 3. Green (550 nm) irradiance at 7.2 m below the water surface as a percentage of corresponding irradiance at 4.9 m below the surface, assuming that optical water type may change between measurements at different depths. Calculations based on Jerlov transmittance values (i.e. 74% m^{-1} in Coastal 5, 63% m^{-1} in Coastal 7, 53% m^{-1} in Coastal 9; Jerlov 1976)

Water type for 7.2 m reading	Water type for 4.9 m reading		
	Coastal 5	Coastal 7	Coastal 9
Coastal 5	50.0	110.1	256.8
Coastal 7	15.7	34.6	80.6
Coastal 9	4.5	9.9	23.2

DISCUSSION

The new light-measuring station, which was tested underwater for the first time during this investigation, incorporated a number of improvements on the station used at the same site in 1975 (Lüning & Dring 1979). The use of interference filters instead of broad-band glass combination filters to define the waveband perceived by the sensors meant that these wavebands were more tightly defined and — more importantly — that the spectral sensitivity of the filter/sensor combination did not change with depth, water type and weather conditions (see discussion in Lüning & Dring 1979). Improvements to the electronics of the station enabled readings to be integrated over a given time period, instead of being instantaneous readings, so that rapid fluctuations in irradiance, due to wave action or broken cloud cover, were smoothed. The electronics and updated data storage system also permitted the irradiances to be read more frequently (every 75 s, instead of every 20 min), and all 6 sensors to be read simultaneously, instead of in sequence at 1.5 s intervals. The transmittance values calculated from readings at 2 depths were, therefore, more accurate than those obtained from the earlier station when irradiance levels were high.

The only disadvantage of the new system was the limitation imposed by the use of 8-bit data acquisition, since this required that the sensitivity of all sensors had to be reduced to prevent the maximal reading exceeding the base range (i.e. a maximum of 256 units). This problem will not have significantly affected the estimates of total daily irradiation or maximal daily irradiance reported in this paper, but the low sensitivity meant that, unfortunately, transmittance values were not available for days with poor light penetration. In addition, the estimates of underwater daylength (data not reported here) may be unduly pessimistic because the photoreceptor pigments effective in detecting daylength in plants are generally more sensitive than the sensors as used during these measurements (e.g. the short-day response of the brown alga *Scytosiphon* was inhibited by 0.25 µmol m^{-2} s^{-1} of blue light for 2 min, that of the red alga *Acrosymphyton* by 0.05 µmol m^{-2} s^{-1} of blue light or 0.25 µmol m^{-2} s^{-1} of red light for 8 h, and that of the flowering plant *Xanthium* by 0.02 µmol m^{-2} s^{-1} of red light at twilight; Dring & Lüning 1975, Breeman & ten Hoopen 1987, Salisbury 1981). Modifications to the system which will avoid this limitation are being considered. Nevertheless, the daylengths measured in this study will be reasonably accurate estimates of the length of the photosynthetic day, and will be used for calculations of *in situ* primary production in a subsequent, more detailed analysis of the spectral data obtained and of the variations in irradiance during the course of each day.

In spite of the low sensitivity of the station and day-to-day variations in surface irradiance, the influence of tidal variations in water height on the irradiance recorded at 4.5 m below MLWS was clearly observable. The mean values for total daily irradiation and for maximal daily irradiance over 3 to 4 d periods when high tide occurred around midday were consistently lower than the corresponding values during adjacent periods when low tide occurred at midday. During the autumn and winter of 1990, the differences between the irradiance values recorded in adjacent high tide and low tide series were greater than could be accounted for by the average difference in the depth of water overlying the sensors (2.3 m). Such large differences could be explained, however, if the light penetration (water type) was consistently poorer during spring tide series.

An apparent association between light penetration and spring tides could be explained by the stronger tidal flows that occur at spring tides. These strong flows might result in greater amounts of sediment in suspension, which would reduce the penetration of light. Mann & Lazier (1991) discuss the possible influence of the spring-neap cycle on the position of fronts in coastal systems, which could result in incursions of phytoplankton-rich water during spring tides and retraction during neap tides. This could cause higher phytoplankton densities in some sites during spring tides, which would also reduce light penetration. There is, however, no obvious reason for either of these effects to be stronger in autumn than in the spring, when no relationship was apparent in the present data. It is clear that more measurements of transmittance are needed over the spring-neap cycle to test the validity of the relationship that has been indicated in these data.

In any case, this study has shown that the variations in the timing of high tide through the spring-neap cycle have significant effects on the total daily irradiation available to benthic plants in the sublittoral zone. This factor needs to be allowed for in any attempts to model the primary productivity in this zone from measurements of surface irradiance.

This article was submitted to the editor

Acknowledgements. We are indebted to Hans Reichenberger for servicing the data acquisition system throughout the period of measurements, and for his careful underwater work, with the assistance of Uwe Schilling and Jimmy Lösche, in setting up and maintaining the station.

LITERATURE CITED

Breeman, A. M., ten Hoopen, A. (1987). The mechanism of daylength peception in the red alga *Acrosymphyton purpuriferum*. J. Phycol. 23: 36–42

Brinkhuis, B. H. (1977). Comparisons of salt-marsh fucoid production estimated from three different indices. J. Phycol. 13: 328–335

Campbell, E. E., du Preez, D. R., Bate, G. C. (1988). The light environment in a high energy surf-zone with high phytoplankton biomass. Botanica mar. 31: 329–335

Dring, M. J. (1981). Chromatic adaptation of photosynthesis in benthic marine algae: an examination of its ecological significance using a theoretical model. Limnol. Oceanogr. 26: 271–284

Dring, M. J. (1987). Light climate in intertidal and subtidal zones in relation to photosynthesis and growth of benthic algae: a theoretical model. In: Crawford, R. M. M. (ed.) Plant life in aquatic and amphibious habitats. Blackwell, Oxford, p. 23–34

Dring, M. J., Lüning, K. (1975). A photoperiodic effect mediated by blue light in the brown alga *Scytosiphon lomentaria*. Planta 125: 25–32

Jerlov, N. G. (1976). Marine optics. Elsevier, Amsterdam

Jerlov, N. G., Nygård, K. (1969). A quanta and energy meter for photosynthetic studies. Rep. Kjob. Univ. Inst. Fys. Oceanogr. 24: 1–7

Kain, J. M. (1971). Continuous recording of underwater light in relation to *Laminaria* distribution. In: Crisp, D. J. (ed.) Proc. 4th Eur. Mar. Biol. Symp. Cambridge University Press, Cambridge, p. 335–346

Kirk, J. T O. (1983). Light and photosynthesis in aquatic ecosystems. Cambridge University Press, Cambridge

Lüning, K. (1980). Critical levels of light and temperature regulating the gametogenesis of three *Laminaria* species (Phaeophyceae). J. Phycol. 16: 1–15

Lüning, K., Dring, M. J. (1979). Continuous underwater light measurements near Helgoland (North Sea) and its significance for characteristic light limits in the sublittoral region. Helgoländer wiss. Meeresunters. 32: 403–424

Mann, K. H., Lazier, J. R. N. (1991). Dynamics of marine ecosystems. Blackwell Scientific, Oxford

Salisbury, F. B. (1981). The twilight effect. Initiating dark measurement in photoperiodism of *Xanthium*. Plant Physiol. 67: 1230–1238

Smith, R. C. (1969). An underwater spectral irradiance collector. J. mar. Res. 27: 111–120

Westlake, D. F. (1965). Some problems in the measurement of radiation under water: a review. Photochem. Photobiol. 4: 849–868

Manuscript first received: April 26, 1993
Revised version accepted: October 25, 1993