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Tidal amplification of seabed light

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[1] Because solar irradiance decreases approximately exponentially with depth in the sea, the increase in irradiance at the seabed from mid to low tide is greater than the decrease from mid to high tide. Summed over a day, this can lead to a net amplification of seabed irradiance in tidal waters compared to nontidal waters with the same mean depth and transparency. In this paper, this effect is quantified by numerical and analytical integration of the Lambert-Beer equation to derive the ratio of daily total seabed irradiance with and without a tide. Greatest amplification occurs in turbid water with large tidal range and low tide occurring at noon. The theoretical prediction is tested against observations of seabed irradiance in the coastal waters of North Wales where tidal amplification of seabed light by up to a factor of 7 is both observed and predicted. Increasing the strength of tidal currents tends to increase the turbidity of the water and hence reduce the light reaching the seabed, but this effect is made less by increasing tidal amplification, especially when low water is in the middle of the day. The ecological implications of tidal amplification are discussed. The productivity of benthic algae will be greater than that predicted by simple models which calculate seabed irradiance using the mean depth of water alone. Benthic algae are also able to live at greater depths in tidal waters than in nontidal waters with the same transparency.

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1. Introduction

[2] Seabed light, in sufficient quantity, is an essential requirement for the growth of benthic macroalgae and microalgae, both of which make significant contributions to the productivity of shallow waters [*Mann*, 1972; *Kirk*, 1994; *Gazeau et al.*, 2004; *Sarker et al.*, 2009]. Evidence for the importance of seabed light in these ecosystems is provided by studies showing that the maximum depth at which algae are found is proportional to the water clarity [*Duarte*, 1991, and references therein; *Nielsen et al.*, 2002]. In a nontidal sea or lake, the irradiance arriving at the algal surface depends only on the surface irradiance, the depth of water, and the water clarity. However, in tidal waters, it is known that the tide produces patterns in seabed irradiance which depend on the tidal range and the time of low tide [*Topliss et al.*, 1990; *Dring and Luning*, 1994; *Dring et al.*, 1995; *Koch and Beer*, 1996; *Bowers et al.*, 1997]. In these circumstances, it becomes pertinent to ask how the tide affects seabed irradiance averaged over the long time scales likely to be important in controlling algal growth.

[3] It might be thought that the tide will make little difference to the long-term average seabed irradiance as the gain in light when the optical depth of the water is reduced at low tide will be cancelled by the reduction in light when the optical depth is increased at high tide. However, this is not the case, as we illustrate in Figure 1. Because daylight decreases approximately exponentially with increasing depth below the surface, the increase in seabed irradiance from mid to low tide is greater than the decrease from mid to high tide. For this reason, the tide will tend to amplify the daily total light on the seabed compared to the situation with no tide but the same mean depth and the same water transparency. It is clear from Figure 1 that the exact magnitude of this amplification will depend on the tidal range and water transparency, which affects the shape of the curve. When the surface photon flux is changing with time, as the Sun rises and falls, the time of low tide relative to noon and the length of the day will also be important. A useful way to quantify the effect of the tide is to consider the ratio of the daily total seabed light in the presence of a tide to that which would be observed with no tide but the same mean depth of water and the same water transparency. We can consider this ratio as a tidal amplification factor. The usefulness of such a parameter is that, first, it can be used to give a quick assessment of whether the tide needs to be taken into account in models of benthic primary production. Second, it can be used to assess the effect of changes in tidal range or water transparency on seabed light: do benthic plants receive more light at spring or neap tides, for example. Third, there are a number of programs aimed at reintroducing sea grass beds to the environment [*Thorhaug*, 1987; *Park and Lee*,

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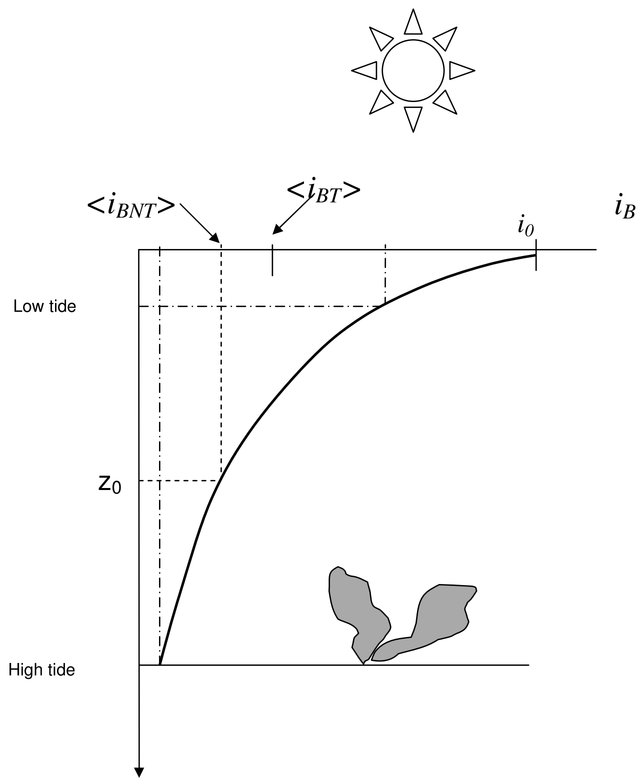

Figure 1. Illustration of the tidal amplification of light reaching the seabed for constant surface illumination i_0. The curve represents the exponential decay of solar irradiance with depth in the sea predicted by the Lambert-Beer law. The attenuation coefficient is considered to be time invariant. In a nontidal sea of depth z_0, the irradiance reaching the seabed (represented by $\langle i_{BNT}\rangle$) is a constant fraction of the surface irradiance. In a tidal sea, the increase in seabed irradiance at low tide is greater than the decrease at high tide, so the mean seabed irradiance over a tidal cycle (represented by $\langle i_{BT}\rangle$) is greater than $\langle i_{BNT}\rangle$. In these circumstances, the tidal amplification factor $\langle i_{BT}\rangle/\langle i_{BNT}\rangle$ depends only on tidal range and water transparency. When i_0 changes during the day, the amplification will also depend on the daylength and the time of low water as described in the text.

2007]. A better understanding of the role of the tide in moderating seabed light could help to identify optimum sites for these programs.

2. An Example Data Set

[4] The nature of the process is illustrated in Figure 2, which shows the variation of sea surface and seabed irradiance in a tidal seaway, the Menai Strait in Wales, on 9 June 2006 (for experimental methods and data processing techniques, see section 4.1). The tidal range on this day was 5.0 m and low tide occurred at 1510 GMT. Measured seabed irradiance is shown as the curve marked i_{BT} and this peaks at a time between noon and low tide. We have also drawn, as the curve marked i_{BNT}, the seabed irradiance that we estimate would have occurred in the absence of a tide at this site. This has been calculated from equation (1), given below, using the surface irradiance, the mean depth of water, and the average diffuse attenuation coefficient for PAR in this water on that day, which was 0.51 m^{-1}.

[5] The daily total seabed irradiance with and without a tide is given by the area under the respective curve. For this data set, these values are 18.5 E m^{-2} with a tide and 11.1 E m^{-2} without, giving an amplification of seabed light by the tide by a factor F = 1.7. In this case, the amplification is modest, although it could nevertheless make a significant difference to the growth rate of benthic algae, particularly those living at light levels close to the compensation irradiance.

3. Theory

[6] For monochromatic light of constant angular distribution, the instantaneous irradiance at the seabed i_B is given by the Lambert-Beer law,

$$i_B = i_0 \exp(-kz), \tag{1}$$

where i_0 is the irradiance at the surface, k is the diffuse attenuation coefficient for downwelling irradiance, and z is the water depth. On a given day, the variation of z with the tide can be represented most simply by $z = z_0 - b\cos(\omega(t - t_L))$, where z_0 is the mean depth, b is the tidal amplitude, ω is the angular frequency of the tide, t is time, and t_L is the time of

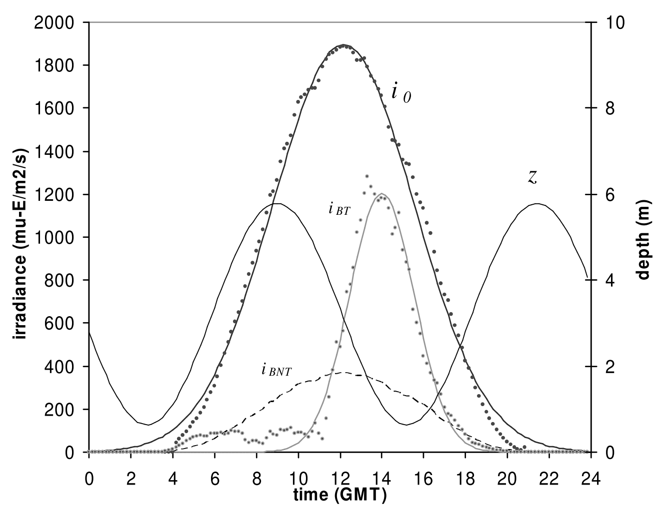

Figure 2. Surface (i_0) and bed irradiance (i_{BT}) measured in the Menai Strait, North Wales on 9 June 2006. The observations are shown as individual points and the curves represent the Gaussian fit to the data described in the text. Mean depth of water at the observing site was 3.2 m and the mean value of the diffuse attenuation coefficient k on this day was 0.51 m^{-1}. The dashed curve marked i_{BNT} is an estimate of the bed irradiance that would have occurred in the absence of a tide, calculated from i_0, the mean depth of water, and k. The tidal amplification factor is the ratio of the areas under the curves marked i_{BT} and i_{BNT}. The tidal curve is marked as z shows the depth of water above the bed sensor.

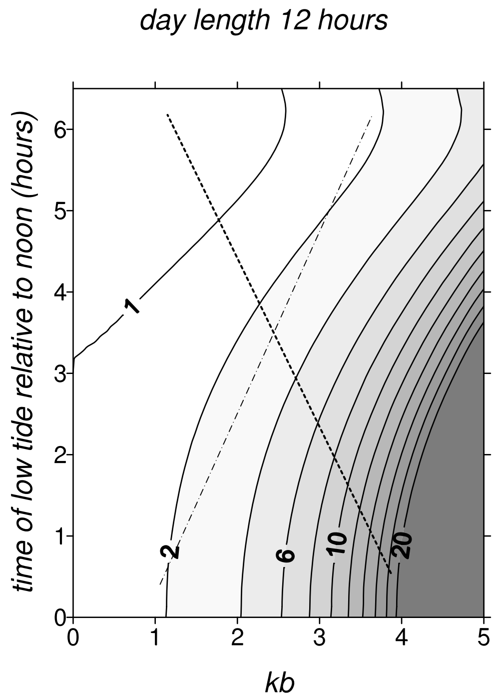

Figure 3. Numerical solution for the tidal amplification factor F (equation (2)) for a Gaussian surface irradiance, constant diffuse attenuation coefficient k, and daylength 12 h. The lines imposed illustrate the change in F over a springs neaps cycle, for a location where low water spring tides occurs at midday (dashed line) and for a location where high-water springs is at midday (dash-dotted line). For example, following the dashed line from spring tides (bottom right end of line where kb is maximum) to neaps (top left end of line) it can be seen that there is a large change in F over the springs neaps cycle, in contrast to the dash-dotted line, which shows little variation in F for constant k over the springs-neaps cycle.

low water. The ratio of the daily total seabed irradiance with a tide and with no tide (b = 0) is then

$$F = \frac{\langle i_{\mathrm{BT}} \rangle}{\langle i_{\mathrm{BNT}} \rangle} = \frac{\int_{-L/2}^{L/2} i_0 \exp(-k\{z_0 - b\cos(\omega(t - t_{\mathrm{L}})\}\mathrm{d}t}{\int_{-L/2}^{L/2} i_0 \exp(-kz_0)\mathrm{d}t}, \tag{2}$$

where the subscripts T and NT represent with and without a tide, respectively, and quantities within angle brackets are daily totals. Equation (2) has been written such that the limits of integration are from $-L/2$ to $L/2$, where L is the daylength and therefore both t and t_{L} are measured from noon. Equation (2) can be solved numerically for any variation of i_0 and k during the day. A special case is when k can be considered constant during the day, in which event $\exp(-kz_0)$ cancels in the numerator and denominator of equation (2) and F becomes independent of the mean depth of water.

[7] On cloudless days, i_0 can be derived using equations given in the work of *Kirk* [1994]. The variation can also be approximated by a Gaussian curve peaking at noon and this simplification makes an analytical solution to the problem possible. The Gaussian curve for surface irradiance can be written $i_0 = i_{\mathrm{M}} \exp - (t/q)^2$ (see Figure 2), where i_{M} is the maximum surface irradiance at noon, t is time (measured from noon) and q is a parameter that controls the length of the day. A suitable relationship is $q = 0.29L$, which gives 5% noon irradiance at dawn and dusk. The numerical solution to equation (2) with this form of i_0 and k = constant during the day is shown in Figure 3. The solution depends only on the length of the day (L), the time of low water relative to noon (t_{L}), and the product (kb) of the diffuse attenuation coefficient and the tidal amplitude. The dimensionless product kb recurs throughout this paper and is an important parameter in controlling seabed light in tidal waters. It can be seen from Figure 3 that if low water is within 3 h of noon, $F > 1$ for any $kb > 0$ and that F increases with kb rapidly if $t_{\mathrm{L}} \approx 0$ and more slowly as t_{L} moves away from noon.

[8] An analytical solution to equation (2) will help us to understand this behaviour. In turbid water an approximate analytical solution can be obtained using the fact that seabed irradiance takes the form of an approximately Gaussian "pulse" of light energy close to the time of low tide (see Figure 2). Close to low water, the cosine term in equation (2) can be expanded as a series of powers of the argument of the cosine. Taking the first two terms only in this series, the cosine term can be approximated close to low water as a parabola $(1 - \omega t'^2/2)$ where $t' = t - t_{\mathrm{L}}$ is time relative to low water. The third term in the expansion of the cosine can be neglected if $x^2 = (\omega t')^2 \ll 12$ or $t' \ll 7$ h for the semidiurnal tide for which $\omega = 0.5\ \mathrm{h}^{-1}$. We shall see that this places a constraint on the product kb. Substituting this approximation, the form of the bed irradiance becomes, after some rearranging,

$$i_{\mathrm{BT}} = A\exp(-\varphi)\exp\left[-a(t - t_{\mathrm{P}})^2\right], \tag{3}$$

where $A = i_{\mathrm{M}}\exp(-kz_0)\exp(kb)$, $\varphi = [x/(x + 1)](t_{\mathrm{L}}/q)^2$, $a = (1/q^2)(x + 1)$, $t_{\mathrm{p}} = [x/(x + 1)]t_{\mathrm{L}}$, and $x = 0.5\ kb\omega^2q^2$.

[9] Since A, φ, a, t_{P}, and x are all constant on a given day, equation (3) represents a Gaussian curve which peaks at time $t = t_{\mathrm{P}}$ measured from noon and has an amplitude equal to $A\exp(-\varphi)$. The amplitude will therefore increase exponentially with the product kb and decrease exponentially with the square of the time difference between low water and noon. The time difference between the peak in bed irradiance and low tide is $t' = t_{\mathrm{L}} - (x/(x + 1))t_{\mathrm{L}} = t_{\mathrm{L}}(1/(x + 1))$. For the peak to lie, say, within 3 h of low water to justify the approximation of the tidal curve around low water as a parabola, we require $x + 1 \geq t_{\mathrm{L}}/3$. This is easily achieved when $t_{\mathrm{L}} \approx 0$ but for high water at noon and $t_{\mathrm{L}} \approx 6$, we require $x \geq 1$. This is most easily achieved on long days when q is greatest. At the equinoxes when $\omega^2q^2 = 3$ for a semidiurnal tide we require the product $kb \geq 2/3$ for peak bed irradiance to occur within 3 h of low water for all times of low tide. This condition on kb will be met in many coastal seas with a reasonable tidal range and turbid water. The expression for the timing of the seabed irradiance maximum, $t_{\mathrm{P}} = (x/(x + 1)t_{\mathrm{L}}$ is the same as that given in the work of *Bowers and Brubaker* [2004] although derived by a different method.

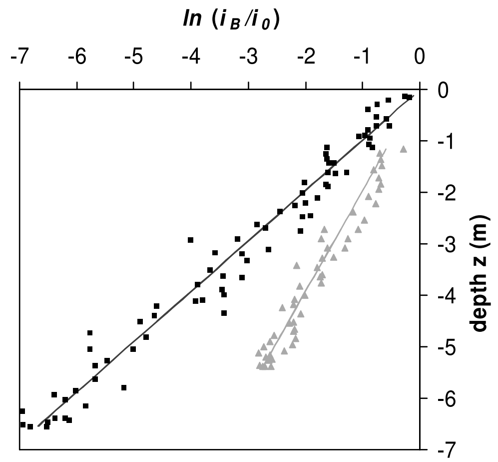

Figure 4. Graphs of the natural logarithm of the ratio of measured bed irradiance i_B to surface irradiance i_0 against the total depth of water z above the bed instrument at the time of measurement. Data are from the Menai Strait at spring tides on 26 May 2006 (dark squares) and neap tides (8 June 2006) lighter triangles. The lines show the line of best fit. The slope of the line gives the mean attenuation coefficient for the day, which was used in calculating the daily total bed irradiance in the absence of a tide. Daily total bed irradiance in the presence of a tide was calculated by integrating the values of i_B over the day. Tidal amplification factor F was taken as the ratio of daily total bed irradiance in the presence of a tide to that in the absence of a tide but with the same mean depth and attenuation coefficient.

[10] Equation (3) can be integrated to give $\langle i_{BT} \rangle$ using the definite integral of a Gaussian curve over all time. The same procedure can be used to integrate the denominator in equation (2) when surface irradiance is a Gaussian curve. Taking the ratio of these two integrals gives an analytical solution for the tidal amplification factor,

$$F = \sqrt{\frac{1}{x+1}} \exp(kb - \varphi). \tag{4}$$

This expression has the desired property that when the tidal amplitude b tends to 0 (and hence x and φ also tend to 0), F tends to 1. Equation (4) explains the main features of Figure 3. In many real situations, x will be of order 1 and so F will increase exponentially with the product kb, the increase becoming muted as φ increases as low tide moves away from midday. On longer days when it is possible to have two peaks in seabed irradiance produced by two low waters, one at the beginning and one at the end of the day, a more accurate expression for F, given that $b > 0$, is

$$F = \sqrt{\frac{1}{x+1}} \exp(kb)\{\exp(-\phi_1) + \exp(-\phi_2)\} \tag{5}$$

where φ_1 and φ_2 are calculated from the timing of the two low tides. Equation (5) can in fact always be used to calculate the tidal amplification factor on any day because only values of φ associated with peaks during daylight will make a significant contribution to the magnitude of F. Calculated values of F using equation (5) are indistinguishable, for practical purposes, from the numerical solution shown in Figure 3, over the range of kb and t_L in that diagram. Regression of the analytical solution (5) against the numerical solution (2) for kb in the range 0.2–4.0 and t_L in the range 0–6 h gives a slope of 1 and R^2 greater than 0.99.

4. Experimental Verification

[11] In order to test the ideas of section 3, simultaneous measurements of seabed and surface irradiance are required in shallow, tidal, coastal water in which the water transparency stays constant during the day. Effectively, this last requirement means that there should be no strong gradient of turbidity which will be advected past the observation site by the tide and that resuspension and settling of sediments by the tidal streams should be small.

4.1. Observational Methods

[12] Three data sets have been used to test the theory:

[13] 1. Observations in Royal Charter Bight on the coast of North Wales described by *Topliss et al.* [1980] and *Topliss* [1977]. The measurements were made in a mean depth of water of 7 m with an intercalibrated pair of irradiance meters with a cosine collector, one in a fixed frame on the seabed the other mounted on a frame at the coast and operating over the wavelength range 540–560 nm. A pressure transducer fixed to the frame was used to give the water depth.

[14] 2. Observations over a 2 week period described by *Bowers et al.* [1997] in the Menai Strait, North Wales in July 1994. Measurements were made with an intercalibrated pair of irradiance meters (described by *Kratzer et al.* [2000]), one fixed to the base of Menai Bridge pier and the other on the roof of a nearby building. These instruments, which have cosine collectors, record irradiance measurements at four wavelengths; only data from the most penetrating wave band in these waters, the green channel (560–580 nm), was used in this work. Depth data during this deployment were obtained from tide tables.

[15] 3. Measurements made over a 2 week period in the Menai Strait in May and June 2006. Seabed measurements were made with a HOBO self-logging light and temperature sensor in a mean depth of water of 3.2 m and surface irradiance measurements with the irradiance meter described above and in the work of *Kratzer et al.* [2000]. Each instrument had been calibrated against a Li-Cor PAR irradiance meter. Depth data were provided by a YSI 6600 EDS extended deployment "sonde" fixed to the same frame as the underwater light sensor.

[16] Attenuation coefficients were calculated by plotting the natural logarithm of i_B/i_0 against the depth of the bed sensor below sea level on each day. Examples of this procedure on 2 days during the 2006 deployment are shown in Figure 4. The linear relationship between $\ln(i_B/i_0)$ and z indicates that there were no systematic deviations from the assumption of constant k during the day. The slope of the line fitted to these data gives the attenuation coefficient (equation (1)). Only data from days when the correlation coefficient for this fit exceeded 0.8 were used in further analysis. In a total data set of 35 days, 5 days were discarded for this reason.

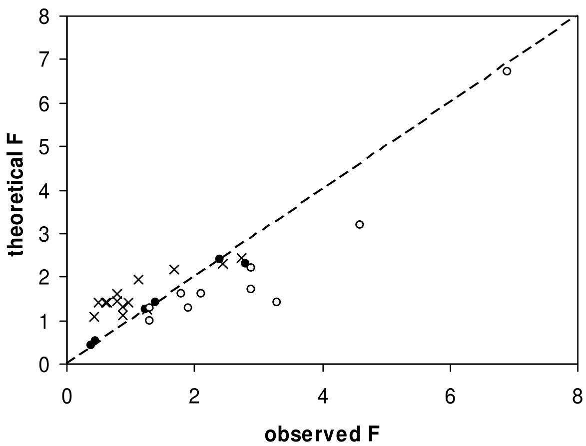

Figure 5. Theoretical tidal amplification factor predicted by equation (6) plotted against observed amplification for three separate data sets: Menai Strait 2006 (open circles), Royal Charter Bight (dark circles), and Menai Strait 1994 (crosses). The dashed line represents the line of perfect fit.

[17] The daily total bed irradiance in the absence of a tide was calculated by integrating $i_0\exp(-kz_0)$, where z_0 is the mean depth of water, over the day, and the total bed irradiance in the presence of a tide was then calculated by integrating observed i_B over the day. The amplification factor F was calculated as the ratio of these two integrals. Theoretical amplification factors were determined using equation (6) and the attenuation coefficient, day length, tidal range, and times of low water for each day.

[18] Figure 5 shows a plot of the observed and predicted tidal amplification factors for these data and the corresponding 1:1 line. Considering that the theory assumes cloud-free days, constant k and that it approximates the tide curve near low water as a parabola, the result is encouragingly good. The points cluster around the 1:1 line. Much of the scatter about this line is likely to be accounted for by the effects of variations in cloud cover during the day.

5. Springs-Neaps Cycle

[19] At a given location, the time of low-water advances by approximately 50 min each day and the tidal range changes with the springs-neaps cycle. The amplification factor F will therefore vary from day to day in response to these changes, and we have illustrated two possible scenarios as straight lines running across Figure 3. The dashed line indicates how F might vary at a place where low-water spring tides occur at midday. In this illustration, the tidal amplification factor increases from a value less than 1 at neaps to about 14 at springs. The reason for this dramatic increase can be seen in equation (5); kb increases and φ decreases in this situation as we move from neaps to springs. The second (dash-dotted) line illustrates the situation at a place where high-water springs occurs at noon. Now kb increases from neaps to springs but φ also increases as low water moves away from noon. The net effect is that there is little variation in F over the springs-neaps cycle; in fact the maximum value of F occurs in Figure 3 at a time between neaps and springs.

[20] The question then arises if there is any advantage, in light amplification terms, in having high-water springs at a particular time. At a given location, high-water spring tides tend to occur at the same time of day (this is called the tidal establishment [*Cartwright*, 1999]). It may be therefore that some places would be favored in the sense that their establishment produces the maximum amplification averaged over the springs-neaps cycle. To answer this question, we have used equation (2) to calculate the average value of F over a 14 day cycle in which the time of high-tide advances by 50 min each day and the value of kb changes from a maximum kb_S at spring tides to half this value at neap tides. This range of kb is fairly arbitrary: tidal ranges in the Irish Sea tend to be about twice as great at spring tides than at neaps, but there may also be changes in k associated with greater sediment resuspension at spring tides. These results should therefore be taken as illustrative only.

[21] The mean amplification over a springs-neaps cycle F_{SN} determined in this way depends on the day length, the value of kb at spring tides (kb_S), and the tidal establishment t_E. F_{SN} increases approximately exponentially with the value of kb_S and maximum F_{SN} occurs when t_E is 6 h before or after noon (that is, at spring tides, low water occurs at noon). The calculation of F_{SN} has been applied to a selection of places along the coastline of Great Britain and Ireland, and the results are shown in Table 1. It can be seen that at none of these places does the tide reduce the daily total light at the seabed (compared to the value with no tide and same water clarity) and in several places there is a significant amplification. In calculating the values in this table, the

Table 1. Mean Amplification Factor FSN Over the Springs-Neaps Cycle at Places Along the Coast of Great Britain and Ireland, Calculated for a 12 h Day

Place	Tidal Establishment t_E (h Relative to Noon)	Tidal Amplitude b at Spring Tides (m)	Attenuation Coefficient k (m^{-1})	kb at Spring Tides	F_{SN}
Invergordon	0.5	2.0	0.2	0.4	1.0
Whitby	4.5	2.5	1.7	4.3	7.3
Harwich	0.3	1.7	1.7	2.9	2.5
Dover	−0.25	3.2	0.8	2.6	2.3
Penzance	5.3	2.4	0.2	0.5	1.9
Fishguard	−4.3	2.0	0.2	0.4	1.9
Menai Strait	0	3.8	1.0	3.8	3.8
Barrow	−0.2	4.0	0.8	3.2	2.7
Londonderry	−3.5	1.2	0.4	0.5	1.0
Cobh	5.5	2.8	0.4	1.1	1.2

Table 2. Result of Calculation of the Likely Effect of Increasing Tidal Amplitude (b) and Current Speed U on the Concentration of Suspended Sediment Load C and Hence the Diffuse Attenuation Coefficient k[a]

b (m)	U (m s^{-1})	C (mg L^{-1})	k (m^{-1})	$\langle i_{BNT}\rangle/\langle i_0\rangle$ $t_L = 0$ (%)	$\langle i_{BT}\rangle/\langle i_0\rangle$ $t_L = 0$ (%)	F $t_L = 0$	$\langle i_{BNT}\rangle/\langle i_0\rangle$ $t_L = 6$ (%)	$\langle i_{BT}\rangle/\langle i_0\rangle$ $t_L = 6$ (%)	F $t_L = 6$
0	0	0	0.03	74	74	1	74	74	1
1	0.2	0.11	0.04	70	71	1.02	70	69	0.98
2	0.4	0.85	0.08	46	49	1.08	46	42	0.93
3	0.6	2.87	0.19	14	20	1.39	14	11.4	0.80
4	0.8	6.81	0.42	1.5	4.6	3.02	1.5	1.11	0.74
5	1.0	13.30	0.79	0.03	0.76	20.47	0.03	0.08	2.20

[a]The daily total bed irradiance in the absence $\langle i_{BNT}\rangle$ and presence of a tide $\langle i_{BT}\rangle$ is expressed as a percentage of daily total surface irradiance $\langle i_0\rangle$ in a case where low water occurs at noon ($t_L = 0$) and high water occurs around noon ($t_L = 6$) and the tidal amplification factor F is shown in each case.

attenuation coefficient was obtained from the classified water types set out in the European Union Water Framework Directive and the mean attenuation coefficients associated with these types reported by *Devlin et al.* [2008]. Values of the tidal range and time of high water at springs were taken from tide tables.

6. Effect of Variations in Light Atttenuation

[22] Tides often increase turbidity by suspending particles from the seabed into the water column. This has a negative impact on submarine light, in contrast to the normally positive impact of the tidal amplification effect. In order to compare these two tidal effects, one positive, the other negative, on underwater irradiance, we have estimated the suspended sediment load C in shallow tidally mixed water using the potential energy model of *Bowers* [2003]. This model assumes that a small, fixed fraction of the tide and wind energy dissipated in the sea is used to hold particles in suspension. The tidal current amplitude, required in this model, has been taken as proportional to the amplitude of the tidal elevation amplitude b and other values in this model have been taken from the work of *Bowers* [2003]. We have then calculated the diffuse attenuation coefficient for downwelling irradiance using $k = k_0 + (1/\mu)a^*C$, where a^* is the absorption coefficient per unit concentration of suspended sediment (a spectrally averaged value of 0.04 m^2 g^{-1} has been taken after *Bowers and Binding* [2006]) and μ is the mean cosine of the angle the downwelling photons make with the vertical (taken as 0.7, a typical value for turbid waters [*Kirk*, 1994]); k_0 is a background attenuation, the value in the absence of any suspended sediment, which we have taken as 0.03 m^{-1}. The daily total seabed light in the presence and absence of a tide has then been calculated from the expressions in the numerator and denominator of equation (2) and expressed as a percentage of the daily total irradiance falling on the sea surface.

[23] The results of these calculations are shown in Table 2 for a mean water depth of 10 m, day length 12 h, and a situation where first low water and then high water occurs at noon. It can be seen in this table that increasing the tidal current amplitude stirs up sediment, increases the attenuation coefficient, and hence reduces the proportion of surface irradiance reaching the seabed. The tidal amplification effect is small when the water is clear but becomes increasingly significant as the water becomes more turbid and the tidal range increases. This is particularly the case when low water is at noon. When high water is at noon, amplification does not occur, in this scenario, until the highest tidal range, most turbid conditions. The conclusion that can be drawn from this analysis is that tidal amplification is likely to be most important for benthic algae living close to critically low irradiance levels in turbid water with a large tidal range. The effect of the amplification in this case could make the difference between the algae receiving insufficient and just sufficient irradiance to survive.

[24] The results in Table 2 emphasize the importance of the springs-neaps cycle on the light received by benthic algae. If we consider, for example, a case where the tidal currents are 0.4 m s^{-1} at neaps and 0.8 m s^{-1} at springs and high-water spring tides is at noon then the ratio of daily total bed to surface irradiance changes from 1.11% at springs to 49% at neaps, largely because of the change in light attenuation but enhanced by the tidal amplification effect. If low-water spring is at noon, the effect of tidal amplification is to reduce the amplitude of the spring-neaps variation to extremes of 4.6% and 42%. The importance of the springs-neaps cycle is supported by the observations of daily total seabed irradiance reported by *Dring and Luning* [1994], who found a strong 2 weekly cycle in seabed daily total irradiance in the sublittoral zone of Helgoland.

7. Ecological Implications

[25] The tidal amplification process described here is a comparative one: more light will arrive at the seabed during the day in a tidal sea compared with a nontidal sea (or a sea with a smaller tidal range) of the same mean depth and transparency. One implication of this is that models of benthic primary productivity that ignore the tide and use the mean depth of water will underestimate the irradiance at the seabed, averaged over a period of a day or more, and hence will probably underestimate primary productivity. A second implication is that benthic algae should be able to live at greater depths in a tidal sea than in a nontidal one (or lake) without any change in the water clarity (Figure 6).

[26] A number of studies, mostly in lakes [*Vant et al.*, 1986; *Chambers and Kalff*, 1985; *Middelboe and Markager*, 1997] but also in coastal marine waters [*Duarte*, 1991; *Nielsen et al.*, 2002] have shown that the maximum depth at which macrolgae are found is proportional to a measure of the water clarity, either the Secchi depth or the inverse of the attenuation coefficient. This observation is consistent with the algae living at a compensation depth z_C at which the irradiance, averaged over a suitably long time interval, is a fixed fraction r of the surface irradiance. In a nontidal

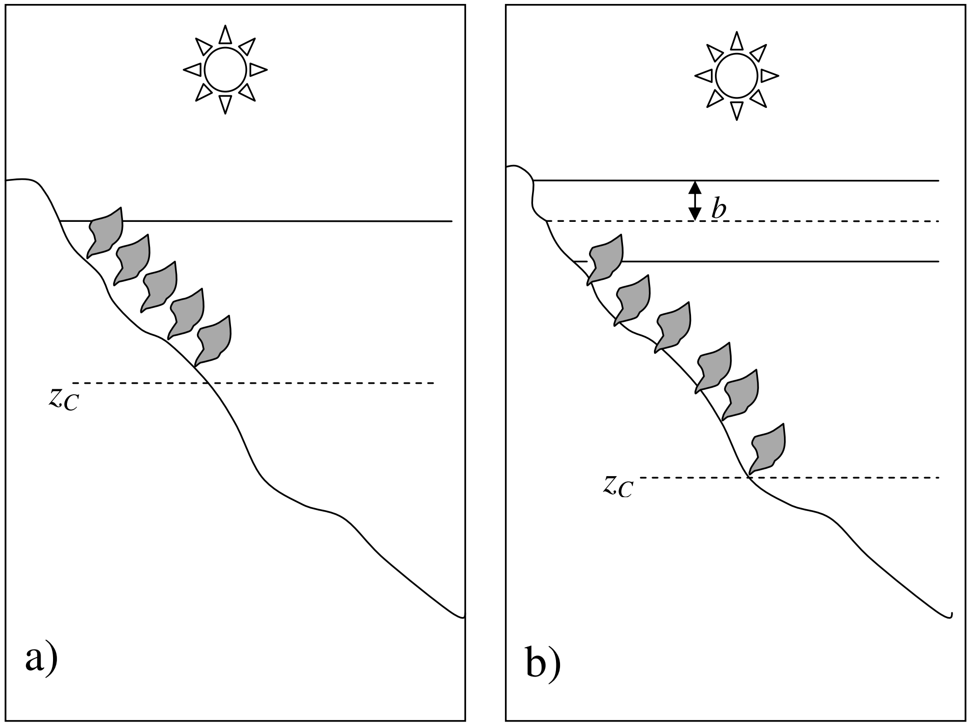

Figure 6. Illustration of how the tidal amplitude effect may enable benthic macroalgae to colonize greater depths in (b) tidal seas compared to (a) nontidal seas of the same water transparency. In each case, the macroalgae grow down to a critical level z_C where the irradiance, averaged over a suitably long time scale of a number of days, is the minimum required to sustain growth. Because of the tidal amplification effect, this depth will be greater, for a given water transparency, in a tidal sea than in a nontidal one.

sea $r = \langle i_{BNT} \rangle / \langle i_0 \rangle$. It follows from the Lambert-Beer law that

$$z_C = -\frac{1}{k}\log(r). \tag{6}$$

If the water becomes clearer and so k decreases, the algae will be able to colonize greater depths, provided their requirement for light r remains the same.

[27] In tidal waters, over time scales of one or more springs-neaps cycles the ratio $r = \langle i_{BNT} \rangle / \langle i_0 \rangle$ is increased by a factor F_{SN} due to the tidal amplification effect. The compensation depth is therefore also increased to

$$z_C = -\frac{1}{k}\log(r/F_{SN}) = \frac{1}{k}(\log F_{SN} - \log r) \tag{7}$$

And a graph of maximum algal depth against water transparency $1/k$ will have a slope which depends upon the tidal amplification factor. In support of this idea we have plotted in Figure 7 observations made by divers showing how the observed maximum depth of benthic algae changes with water clarity in two locations. In one data set, in the Menai Strait, the maximum depth of Laminaria has been measured over a number of years and is plotted against the mean Secchi depth for that year (data replotted from the work of *Lumb* [1990]). In the second data set (using data kindly supplied by S. L. Nielsen and published in the work of *Nielsen et al.* [2002]) the maximum depth of brown algae, including Laminaria, in Danish east coast waters is plotted against the observed Secchi depth at that location.

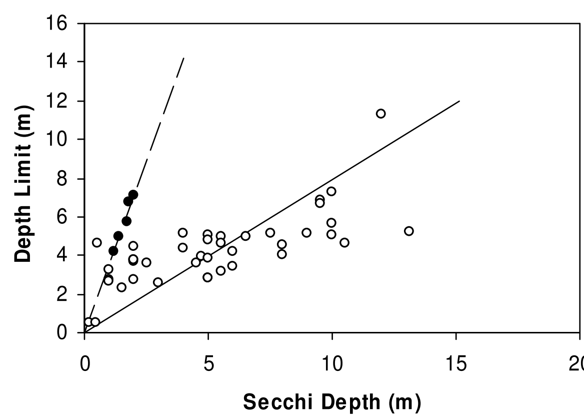

Figure 7. Observed depth limit for benthic macroalgae in two sea areas plotted against the water transparency as measured by the Secchi depth. Open circles are for brown algae, including Laminaria, in Danish east coastal waters (data taken from the work of *Nielsen et al.* [2002]). Closed circles are for Laminaria in the Menai Strait, North Wales (data taken from the work of *Lumb* [1990]). In each case the line shows the trend of increasing depth limit with increasing water clarity. The datum for measurements is not stated for the Danish data but is assumed to be at or near mean sea level, since the tides are small. The datum for the depth limit in the Menai Strait has been adjusted to mean sea level.

[28] It can be seen that for the same water transparency, Laminaria are found at greater depths in the Menai Strait than in Danish waters. In the Menai Strait, the light at the seabed will be enhanced by tidal amplification (F_{SN} = 3.8, Table 1), whereas along the Danish east coast, the tides are small and $F_{SN} \approx 1$. According to equation (7), this should lead to an increase in the slope of the relationship between z_C and water clarity (assuming the relationship between 1/k and Secchi depth and the light requirement factor r is the same in the two places) by a factor of (log(3.8) - log(r))/(-log(r)). If we take the algal light requirement as a proportion of surface irradiance r to be 11% [*Duarte*, 1991] then the ratio of slopes should be 2.7. The observed increase in slope shown in Figure 7 is by a factor of 4.6. The discrepancy may be due to differences in the light requirement factor r at the two locations. Although this comparison cannot therefore be considered conclusive in any way, it would be interesting to make further investigation into the influence of tidal amplification on maximum algal depth.

8. Discussion

[29] Our aim in this paper was to quantify the effect of the tide on solar irradiance received at the seabed. We have achieved this through analytical and numerical analysis of the effect of a periodic change in water depth on the light received at a fixed depth according to the Lambert-Beer law. The essential physics is that, because the decay of irradiance with depth in the sea is exponential, the light gained at low tide exceeds the loss at high tide. The analysis suggests that the amplification factor will scale as exp(kb), where k is the diffuse attenuation coefficient and b the tidal amplitude; this factor will be modified by the time of low water relative to noon and the day length. There would be no equivalent tidal amplification effect if, say, light decayed linearly with depth in the sea.

[30] The main consequence is that estimates of the daily total number of photons falling on the seabed based on the mean depth of water, ignoring the tide, will be incorrect in tidal waters. In most cases, the tide will increase Figure 7. We have shown that the amplification factor can be significant, up to a factor of 7 in the observations presented here and we would expect greater values in more turbid water with a larger tidal range. In many, perhaps most cases, this amplification will be beneficial to the algae, especially those that are experiencing light-limited growth. For algae that would be enjoying optimal light levels with no tide, the amplification will produce photoinhibition and reduced production. In either case, the tide will have an effect which should be taken into account.

[31] As well as influencing the total number of photons that reach the seabed, the tide will also change the spectral distribution of the light. Because the amplification depends on the product kb for a given tidal amplitude, the most attenuated colors will be amplified most. In green coastal waters, this means that red and blue light will be amplified more than green and the tide will tend to flatten the spectrum of seabed light. Multispectral measurements of seabed irradiance could be used to test this prediction. The flattening of the spectrum should be to the further advantage of algae in which the absorption spectrum is dominated by that of chlorophyll and hence which absorb more blue and red light than they do green. The effect may not be so important for brown algae which absorb green light strongly.

[32] We referred in the introduction to programs for re-introducing benthic macroalgae to places where they have become depleted, such as Chesapeake Bay. The lesson from this work is that, in turbid water where the algae are likely to be light-limited, greatest benefit from the tidal amplification effect will be gained in water with the largest tidal range. In equally turbid water with equal tidal range, greatest amplification will occur in places where low-water spring tides occur near midday.

[33] Our results and the discussion of them apply to the semidiurnal tide, which is the most common, but not ubiquitous. Tides with diurnal periods are found in Australia's Gulf of Carpenteria, parts of the Persian Gulf, Gulf of Mexico, and part of the South China Sea. Our theory would have to be adapted for these places. Some idea can be gleaned from equation (6), which contains the tidal period in the parameter x; this is the only place where it occurs. If the tidal period is increased by a factor of 2, x will decrease by a factor of 2, and we might expect an enhancement of the tidal amplification effect.

[34] An important problem is the effect of the tide on the light received by phytoplankton. These microscopic algae tend to be dispersed through the water column, and throughout tidal waters, not just in water shallow enough for benthic algae to live. The theoretical ideas presented here could be adapted for this case, but it is harder to gather experimental evidence to test it. Notwithstanding this difficulty, if production by phytoplankton in shelf seas is being underestimated because the effect of the tide on the submarine light has been neglected, this will have an important impact on our understanding of carbon uptake by shelf seas. It is therefore imperative to design an experimental program for measuring the tidal effect on daily total photon absorption in a layer of water.

[35] Finally, we have assumed that the attenuation coefficient is constant during the day and during the tide. In estuaries where there is a longitudinal gradient of turbidity, k can change in a way that is related to the rise and fall of the tide, possibly with a phase lag that depends on the nature of the tidal wave in the estuary [*Pilgrim and Millward*, 1989]. The analysis of this situation will be given in a forthcoming paper.

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References

Bowers, D. G. (2003), A simple turbulent energy-based model of fine suspended sediments in the Irish Sea, *Cont. Shelf Res.*, *23*(16), 1495–1505, doi:10.1016/j.csr.2003.08.006.

Bowers, D. G., and C. E. Binding (2006), The optical properties of mineral suspended particles: A review and synthesis, *Estuarine Coastal Shelf Sci.*, *67*, 219–230, doi:10.1016/j.ecss.2005.11.010.

Bowers, D. G., and J. M. Brubaker (2004), Underwater sunlight maxima in the Menai Strait, *J. Opt. A, Pure Appl. Opt.*, *6*, 685–689, doi:10.1088/1464-4258/6/7/005.

Bowers, D. G., P. Tett, and A. W. Walne (1997), A note on seabed irradiance in shallow tidal seas, *J. Mar. Biol. Assoc. U. K.*, *77*, 921–928, doi:10.1017/S0025315400038534.

Cartwright, D. E. (1999), *Tides: A Scientific History*, Cambridge Univ. Press, New York.

Chambers, P. A., and J. Kalff (1985), Depth distribution and biomass of submerged aquatic macrophyte communities in relation to Secchi depth, *Can. J. Fish. Aquat. Sci.*, *42*, 701–709, doi:10.1139/f85-090.

Devlin, M. J., D. K. Mills, R. J. Gowen, J. Barry, J. Foden, D. Sivyer, and P. Tett (2008), Relationships between suspended particulate material, light attenuation and Secchi depth in UK marine waters, *Estuarine Coastal Shelf Sci.*, *79*, 429–439, doi:10.1016/j.ecss.2008.04.024.

Dring, M. J., and K. Luning (1994), Influence of spring-neap tidal cycles on the light available for photosynthesis by benthic marine plants, *Mar. Ecol. Prog. Ser.*, *104*, 131–137, doi:10.3354/meps104131.

Dring, M. J., R. Schmid, and K. Luning (1995), Influence of blue light, UV-B radiation and tidal phasing on seaweed photosynthesis in sublittoral coastal ecosystems, in *Photosynthesis: From Light to Biosphere*, vol. 5, edited by P. Mathis, pp. 749–754, Kluwer Acad., Dordrect, Netherlands.

Duarte, C. M. (1991), Seagrass depth limits, *Aquat. Bot.*, *40*, 363–377, doi:10.1016/0304-3770(91)90081-F.

Gazeau, F., S. V. Smith, B. Gentili, M. Frankignoulle, and J. P. Gattuso (2004), The European coastal zone: Characterisation and first assessment of ecosystem metabolism, *Estuarine Coastal Shelf Sci.*, *60*, 673–694, doi:10.1016/j.ecss.2004.03.007.

Koch, E. W., and S. Beer (1996), Tides, light and the distribution of *Zostera marina* in Long Island Sound, USA, *Aquat. Bot.*, *53*, 97–107, doi:10.1016/0304-3770(95)01015-7.

Kirk, J. T. O. (1994), *Light and Photosynthesis in Aquatic Ecosystems*, 2nd ed., doi:10.1017/CBO9780511623370, Cambridge Univ. Press, Cambridge, U. K.

Kratzer, S., D. G. Bowers, and P. B. Tett (2000), The annual cycle of water colour and its interpretation in optical case-2 waters, *Int. J. Remote Sens.*, *21*, 2225–2246.

Lumb, C. M. (1990), Algal depth distribution and long-term turbidity changes in the Menai Strait, North Wales, *Prog. Underwater Sci.*, *15*, 85–99.

Mann, K. H. (1972), Ecological energetics of the seaweed zone in a marine bay on the Atlantic coast of Canada II productivity of the seaweeds, *Mar. Biol. Berlin*, *14*, 199–209.

Middelboe, A. L., and S. Markager (1997), Depth limits and minimum light requirements of freshwater macrophytes, *Freshwater Biol.*, *37*, 553–568, doi:10.1046/j.1365-2427.1997.00183.x.

Nielsen, S. L., K. Sand-Jensen, J. Borum, and O. Geertz-Hansen (2002), Depth colonisation of Eelgrass (*Zostera marina*) and macroalgae as determined by water transparency in Danish coastal waters, *Estuaries*, *25*(5), 1025–1032, doi:10.1007/BF02691349.

Park, J. I., and K. S. Lee (2007), Site specific success of 3 transplanting methods and the effect of planting time on the establishment of *Zostera marina* transplants, *Mar. Pollut. Bull.*, *54*, 1238–1248, doi:10.1016/j.marpolbul.2007.03.020.

Pilgrim, D. A., and G. E. Millward (1989), Variation in the diffuse optical depth of the bed of a tidal estuary, in *Developments in Estuarine and Coastal Study Techniques*, edited by J. McManus and M. Elliott, pp. 101–107, Olsen and Olsen, Fredensborg, Denmark.

Sarker, M. J., T. Yamamoto, and T. Hashimoto (2009), Contribution of Benthic Microalgae to the whole water algal biomass and primary production in Suo Nada, the Seto Inland Sea, Japan, *J. Oceanogr.*, *65*, 311–323, doi:10.1007/s10872-009-0029-5.

Thorhaug, A. (1987), Large-scale seagrass restoration in a damaged estuary, *Mar. Pollut. Bull.*, *18*, 442–446, doi:10.1016/0025-326X(87)90621-7.

Topliss, B. J. (1977), A study of optical irradiance in coastal waters, Ph.D. thesis, Univ. of Wales, Cardiff, U. K.

Topliss, B. J., J. R. Hunter, and J. H. Simpson (1980), Simultaneous measurements of transparency and irradiance in the coastal waters of North Wales, *Mar. Environ. Res.*, *4*, 65–79, doi:10.1016/0141-1136(80)90060-4.

Vant, W. N., R. J. Davies-Colley, J. S. Clayton, and B. T. Coffey (1986), Macrophyte depth limits in North Island (New Zealand) lakes of differing clarity, *Hydrobiologia*, *137*, 55–60, doi:10.1007/BF00004172.

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