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Tidal modulation of seabed light and its implications for benthic algae

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Running head: Tidal modulation of seabed light

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Abstract

1 The temporal behaviour of seabed light in a shallow, tidal sea is set largely
2 by the interaction of the solar elevation cycle with tidal cycles in water
3 depth and temporal variability in water clarity. The effect of tidal
4 modulation on seabed light often does not simply average out, producing
5 instead a net effect (either an amplification or a reduction of seabed light,
6 integrated over time) compared to a tideless, but otherwise equivalent,
7 scenario. Observations of this phenomenon from the Bay of Brest (France)
8 show reasonable agreement with predictions based on an earlier theoretical
9 framework, confirming that the key physics has been understood and that
10 the important parameters are tidal amplitude, timing of low waters, diffuse
11 attenuation coefficient, and daylength. Implications for benthic macroalgae
12 living in the bay's shallow subtidal zone are investigated using a simple
13 numerical model. The effects of the tide on time-integrated seabed light
14 and, in turn, time-integrated macroalgal community photosynthesis in the
15 Bay of Brest correspond closely at three timescales: annual, springs-neaps
16 (i.e., approximately fortnightly), and daily. Tidal amplification of both
17 parameters occurs over the year, during winter months generally, and at
18 spring tides during winter specifically (slight reduction occurs at neaps
19 during winter). For an individual, isolated thallus, the relationship between
20 tidal modulation of seabed light and photosynthesis is complicated by more
21 pronounced light-saturation and photoinhibition effects. Demonstrated here
22 for the first time, neglecting tidal effects on seabed light is likely to result in

²³ erroneous estimates (and, for many sites, underestimation) of subtidal
²⁴ benthic productivity.

Introduction

25 Shallow-water benthic ecosystems, such as kelp forests and seagrass
26 meadows, can be highly productive (Mann, 1972). They also serve as
27 nurseries, habitats, and refugia for many species of marine fauna (Steneck
28 et al., 2002; Heck et al., 2003). Light availability is often the most
29 important abiotic factor regulating the growth patterns, distribution, and
30 primary productivity of benthic algae and plants (Zimmerman et al., 1994,
31 and references therein). As noted by Ackleson (2003), we must continue to
32 refine our understanding of the influence of seabed light on these
33 ecosystems if we are to better predict their response to short-term changes
34 (e.g., storms and pollution events) and long-term changes (e.g., climate and
35 sea-level), and if we are to better quantify their role within the global ocean
36 carbon cycle.

37 In a tideless (or ‘non-tidal’) sea, irradiance at the seabed is controlled
38 largely by the daily and seasonal cycles of solar elevation, which govern sea
39 surface irradiation, and by the water depth and clarity, which together
40 determine the extent to which incident light is attenuated before it reaches
41 the bed (Bowers and Brubaker, 2010). In a ‘tidal’ sea, cycles in water depth
42 (and any associated cycles in water clarity) produce more complicated
43 temporal patterns in seabed irradiance (e.g., Topliss et al., 1980; Pilgrim
44 and Millward, 1989; Bowers et al., 1997; Bowers and Brubaker, 2004).
45 Whilst these patterns may influence the behaviour of benthic animals
46 (Naylor, 2010) and the time course of benthic photosynthesis (Gévaert et

al., 2002, 2003), the principal value of such tidal modulation lies in its potential to result in a net effect on seabed irradiance (and photosynthesis) integrated over time (Bowers and Brubaker, 2010).

Bowers and Brubaker (2010) hypothesised that the tide will tend to amplify the daily total seabed irradiance compared to a scenario with no tide, but with the same mean depth and clarity. They reasoned that light is attenuated in an approximately exponential manner with increasing water depth, and so the ‘gains’ in irradiance around low-waters should exceed the ‘losses’ around high-waters (see Fig. 1), leading to a net gain, or amplification, over time (relative to the ‘non-tidal’ scenario). They went on to demonstrate that the effect is more complicated than the initial premise. The tide can also reduce the daily total seabed irradiance, and the magnitude of the effect depends upon four key parameters: the time of low water, the tidal amplitude (or range), the diffuse attenuation coefficient (a measure of the turbidity of the water), and the daylength.

The ecological implications of the study by Bowers and Brubaker (2010) were potentially very significant, and warrant further investigation. In particular, models that ignore the tide (and use instead a mean water depth) were claimed to underestimate seabed irradiance and may, therefore, also underestimate benthic primary production. Given that the relationship between irradiance and photosynthesis is non-linear (see ‘Theory’ below and standard texts such as Hurd et al. (2014)), it is unclear whether a large tidal amplification of seabed light will cause a similar amplification of photosynthesis in benthic algae: gains in irradiance at low water will not

71 necessarily result in equivalent gains in photosynthesis if saturation or
72 photoinhibition occur.

73 The purpose of the present paper is twofold: (1) to test the original
74 theory against irradiance observations from a new site, the Bay of Brest in
75 France (n.b., the theory has thus far been validated using data from one
76 site only, the Menai Strait in Wales, UK), and (2) to further investigate the
77 ecological implications of Bowers and Brubaker (2010) by the construction
78 of a simple numerical model.

79 The Bay of Brest was selected on the basis that it is a macrotidal site
80 with tidal and turbidity characteristics that differ from those of the Menai
81 Strait. The Bay of Brest is less turbid, and low waters of spring tides
82 (LWST) always occur at about midday and midnight (i.e., opposite to the
83 case at the Menai Strait, where high waters of spring tides (HWST) occur
84 at these times). Large tidal ranges at spring tides and the coincidence of
85 LWST with the midday peak in sea surface irradiance create a potential for
86 large tidal irradiance amplification. A novel mooring design was employed
87 to measure, rather than infer (as in the original study), ‘non-tidal’
88 irradiance. The numerical model has been used to investigate the likely
89 effect of the tide on seabed irradiance and benthic photosynthesis in the
90 Bay of Brest over three timescales (i.e., daily, springs-neaps cycle, and
91 annual) and for two ecological entities (i.e., the individual, isolated kelp
92 thallus, and the established macroalgal community).

Theory

Tidal irradiance amplification

93 Irradiance at the seabed, I_B , is given by the Lambert-Beer Law,

$$I_B(t) = I_0(t) \exp[-k_{PAR}(t)z(t)], \quad (1)$$

94 where I_0 is the sea surface irradiance, k_{PAR} is the diffuse attenuation
 95 coefficient of photosynthetically active radiation (PAR), z is the water
 96 depth, and t is time. The law typically applies to monochromatic light, but
 97 it also applies approximately to irradiance integrated over the PAR
 98 waveband (i.e., approximately 400-700 nm) (Kirk, 1994), as required here.
 99 Daily total seabed irradiance is determined by integrating the expression
 100 above over time.

101 Bowers and Brubaker (2010) defined a daily tidal irradiance
 102 amplification factor, F , as the ratio of the daily total seabed irradiance in a
 103 ‘tidal’ scenario to that in an equivalent ‘non-tidal’ scenario. Initially, they
 104 represented tidal variation in water depth as $z_T = z_0 - b \cos(\omega(t - t_{lw}))$,
 105 where z_0 is the mean water depth, b is the tidal amplitude, ω is the angular
 106 frequency of the tide (approximately 0.5 rad h⁻¹ for a semi-diurnal tide), t
 107 is time and t_{lw} is the time of low water (both measured relative to midday).
 108 Water depth in the equivalent non-tidal scenario, z_{NT} , was taken to be z_0 .
 109 F was therefore given as

$$F = \frac{\langle I_{BT} \rangle}{\langle I_{BNT} \rangle} \quad (2)$$

$$= \frac{\int_{-L/2}^{L/2} I_0(t) \exp[-k_{PAR}(t)(z_0 - b \cos(\omega(t - t_{lw})))] dt}{\int_{-L/2}^{L/2} I_0(t) \exp[-k_{PAR}(t)z_0] dt}, \quad (3)$$

where the subscripts T and NT represent ‘tidal’ and ‘non-tidal’ parameters respectively, and angular brackets denote daily totals. Since times are measured relative to midday and L is the daylength, the limits of integration are from $-L/2$ (dawn) to $L/2$ (dusk). $F > 1$ indicates tidal amplification of seabed light, $F < 1$ indicates tidal reduction, and $F = 1$ indicates that the tide makes no discernible difference.

Eq. 3 can be solved numerically regardless of how I_0 and k_{PAR} are varied over the day. However, Bowers and Brubaker (2010) found that an approximate analytical solution can be obtained by making a number of simplifying assumptions. Firstly, k_{PAR} is treated as a constant over the day; to this end, a daily mean value, \bar{k}_{PAR} , suffices. Secondly, sea surface irradiance is approximated using a Gaussian curve, $I_0(t) = I_M \exp[-(t/q)^2]$, where I_M is the maximum (i.e., midday) surface irradiance, t is time (again measured relative to midday), and q is a parameter that controls the width of the Gaussian curve ($q \approx L/3$ offers a reasonable fit to observations of I_0 (Bowers and Brubaker, 2004)). Finally, tidally-varying water depth, z_T , is (re-)approximated as a parabola about low water by expanding the cosine term into its equivalent power series and retaining the first two terms only.

128 That is, $z_T = z_0 - b(1 - \omega^2(t - t_{lw})^2/2)$.

129 Substituting the above approximations into Eq. 3 ensures that both the
 130 integral in the numerator and that in the denominator have solvable forms,
 131 leading to the following analytical solution:

$$F = \sqrt{\frac{1}{x+1}} \exp[\bar{k}_{PAR}b](\exp[-\phi_1] + \exp[-\phi_2]), \quad (4)$$

132 where $x = 0.5\bar{k}_{PAR}b\omega^2q^2$, and $\phi = (x/(x+1))(t_{lw}/q)^2$. Subscripts 1 and 2
 133 on ϕ refer to its calculation using the time of either the first or second low
 134 water occurring in a day, respectively.

135 We have not reproduced here all intermediate steps in the derivation of
 136 this analytical solution. For these, the interested reader is referred to
 137 Bowers and Brubaker (2010).

Tidal photosynthesis amplification

138 A daily tidal photosynthesis amplification factor, Ψ , may be defined such
 139 that it is analogous to the daily tidal irradiance amplification factor, F .

$$\Psi = \frac{\langle P_{BT} \rangle}{\langle P_{BNT} \rangle} \quad (5)$$

$$= \frac{\int_{-L/2}^{L/2} P_{BT}(t) dt}{\int_{-L/2}^{L/2} P_{BNT}(t) dt}, \quad (6)$$

140 where P is the rate of (benthic algal) photosynthesis, subscripts denote
 141 either a ‘tidal’ or a ‘non-tidal’ parameter, angular brackets denote daily

142 totals of the enclosed parameters, and L is daylength. $\Psi > 1$ indicates tidal
 143 amplification of daily total seabed photosynthesis, $\Psi < 1$ indicates a tidal
 144 reduction, and $\Psi = 1$ indicates that the tide produces no discernible
 145 difference.

Photosynthesis-irradiance ($P-I$) curve equations

146 Data analysis and modelling aspects of this work are repeated using two
 147 different $P-I$ curve parameterisations (Fig. 2): (1) the Peeters and Eilers
 148 (1978) Model, and (2) the Lederman and Tett (1981) Model.

149 The Peeters and Eilers (1978) $P-I$ Model is appropriate at the thallus
 150 scale. It is mechanistic (rather than empirically derived) and includes the
 151 effect of photoinhibition. It has been used successfully to fit observed $P-I$
 152 curves for a common subtidal kelp species (*Saccharina latissima*) near our
 153 study site in Brittany (Gévaert et al., 2003). *Saccharina latissima* is found
 154 in the Bay of Brest (Hily et al., 1992) and is an excellent subject for the
 155 purpose of inferring / modelling photosynthesis in the subtidal zone.

156 Middelboe et al. (2006) found that, unlike for isolated thalli, the
 157 photosynthetic production of established macroalgal communities in
 158 shallow water tends not to become fully light-saturated or photoinhibited
 159 at the highest incident irradiances. The authors attributed this to a
 160 number of reasons associated with the species richness / composition of the
 161 community, and with canopy structure and density. We therefore repeat
 162 our analyses using the Lederman and Tett (1981) ‘Rectangular Hyperbola’

163 *P-I* Model (i.e., no true saturation, no photoinhibition), which Middelboe
 164 et al. (2006) used successfully to fit the *P-I* responses of shallow-water
 165 macroalgal communities off Denmark.

166 Both equations are given below, and we use the subscripts *t* and *c* to
 167 denote ‘thallus-scale’ and ‘community-scale’ parameters, respectively. Note
 168 that throughout the present work we have effectively normalised rates of
 169 thallus and community photosynthesis by their respective maxima. Thus,
 170 the maximum (‘normalised’) photosynthesis achievable has a value of 1 in
 171 both cases. This has the benefit that both thallus and community
 172 photosynthesis can be plotted on the same axis or using the same scale for
 173 straightforward comparison. We have expressed this ‘normalised’
 174 photosynthesis in arbitrary units, which are dimensionless. Values input
 175 into the equations are given in Table 1. The Peeters and Eilers (1978)
 176 equation is as follows:

$$P_t = \frac{I}{aI^2 + bI + c}, \quad (7)$$

177 where the coefficients *a*, *b*, and *c* dictate the precise shape of the curve.
 178 These are, in turn, functions of key photosynthesis parameters, as follows:

$$a = \frac{1}{\alpha_t I_{m,t}^2},$$

$$b = \frac{1}{P_{m,t}} - \frac{2}{\alpha_t I_{m,t}},$$

and

$$c = \frac{1}{\alpha_t},$$

179 where $\alpha_t = P_{m,t}/I_{k,t}$ (i.e., the initial slope of the P - I curve, or light use
 180 efficiency), $P_{m,t}$ is the maximum possible rate of photosynthesis (n.b., in
 181 this study, P_t is the ‘normalised’ thallus photosynthesis discussed above,
 182 expressed in dimensionless arbitrary units, and thus we assign to $P_{m,t}$ a
 183 value of 1), $I_{k,t}$ is the saturation onset irradiance (i.e., the irradiance
 184 threshold beyond which photosynthesis begins to become light-saturated,
 185 or, more formally, the irradiance at which the initial slope of the P - I curve
 186 (extrapolated) intersects the maximum rate of photosynthesis, $P_{m,t}$), and
 187 $I_{m,t}$ is the optimum irradiance (i.e., the irradiance at which $P_{m,t}$ is
 188 achieved).

189 The Lederman and Tett (1981) equation is as follows:

$$P_c = \frac{\alpha_c P_{m,c} I}{P_{m,c} + \alpha_c I}, \quad (8)$$

190 where $\alpha_c = P_{m,c}/I_{k,c}$ (i.e., the initial slope of the P - I curve, or community
 191 light use efficiency), $P_{m,c}$ is the maximum photosynthesis achievable (n.b.,
 192 P_c is the ‘normalised’ community photosynthesis discussed above, expressed
 193 in dimensionless arbitrary units, and thus we assign to $P_{m,c}$ a value of 1),
 194 and $I_{k,c}$ is the saturation onset irradiance for the community.

Materials and methods

Study site

195 The Bay of Brest (Fig. 3) is located at the westernmost extremity of the
 196 Brittany Peninsula in Northwest France, and has an area of approximately
 197 180 km². It is connected to the Iroise Sea and the Atlantic Ocean beyond
 198 via a narrow, shallow channel (about 1.8 km wide, 4 km long, and, at its
 199 deepest, 50 m deep), known locally as ‘Le Goulet’. The bay itself is
 200 shallower, with wide shoals and a mean depth of 10 m (Monbet and
 201 Bassoullet, 1989; Thouzeau et al., 2000).

202 The hydrodynamics of the Bay of Brest are dominated by tidal forcing.
 203 The average tidal range is 4.2 m, and ranges of up to 7.5 m are reached at
 204 large spring tides (Monbet and Bassoullet, 1989). Consequently, large
 205 exchanges of water occur through Le Goulet, and tidal currents there reach
 206 speeds of up to 2 m s⁻¹ (Salomon and Breton, 1991). Freshwater input to
 207 the Bay of Brest (through the Élorne and Aulne Rivers) is small compared
 208 to the tidal exchanges with the Iroise Sea (Monbet and Bassoullet, 1989),
 209 and the bay is typically well-mixed (Delmas and Tréguer, 1983).

210 The phase of the solar semi-diurnal (or S_2) tidal constituent at the Bay
 211 of Brest is approximately 180° (expressed as a phase lag behind the
 212 corresponding constituent of the equilibrium tide at Greenwich) (Pingree
 213 and Griffiths, 1981). Consequently, the low waters of spring tides (LWST)
 214 always occur at about midday and midnight; at neaps, high waters occur at
 215 these times. Daylength at the site varies from approximately 8 h in winter

216 to 16 h in summer (calculated for the latitude of the study site using
 217 equations from Kirk (1994)). The Bay of Brest is less turbid than the
 218 Menai Strait (G. Chapalain, pers. comm.; Roberts et al., 2014). It can,
 219 however, still be considered ‘coastal’ in optical water type.

Observational campaigns

220 Fieldwork campaigns were undertaken in summer (July 2011) and winter
 221 (December 2011), and were approximately 2 and 3 weeks in length,
 222 respectively. During each campaign, two moorings were deployed
 223 simultaneously (as illustrated in Fig. 4) in the southern part of the Bay of
 224 Brest, near the town of Lanvéoc (see Fig. 3).

225 Tidally-modulated seabed irradiance, I_{BT} , was measured using an
 226 irradiance sensor in a bed frame (Fig. 4). This we will refer to as the ‘tidal’
 227 mooring or condition. The sensor was fixed at 1.5 m above the seabed, and
 228 the frame was deployed in sufficiently deep water that it remained
 229 submerged at all stages of the tide. Its position was $48^{\circ} 17.55'N$ $4^{\circ} 26.96'W$
 230 (see Fig. 3). A pressure sensor was fixed to the frame to allow the
 231 (tidally-varying) water depth, z_T , above the irradiance sensor to be
 232 monitored.

233 Irradiance beneath a fixed depth of water, I_{BNT} , was measured by
 234 suspending an identical irradiance sensor beneath a surface buoy (Fig. 4).
 235 The buoy and instrument were free to move vertically up and down with
 236 the sea surface, but the sensor remained submerged beneath a relatively

constant depth of water, z_{NT} . We will refer to this as the ‘non-tidal’ mooring or condition. Its position was $48^{\circ} 17.79'N$ $4^{\circ} 26.92'W$ (see Fig. 3). A pressure sensor was fitted to this mooring also, to check that variability in z_{NT} remained acceptably low. Several novel features were incorporated into the design of the ‘non-tidal’ mooring. These features helped to reduce instrument line swing/lean, to prevent excessive slack in the tether, and to permit the mooring to align freely with changing current directions. They are described fully in Roberts (2015). The combined effect was to maintain a relatively constant instrument depth and to prevent mooring self-entanglement.

Sea surface irradiance, I_0 , was monitored using a third sensor positioned on the roof of the Centre d’Études Techniques Maritimes et Fluviales (CETMEF) at the Brest-Iroise Technopôle ($48^{\circ} 21.52'N$ $4^{\circ} 34.01'W$, Fig. 3). Prior to each fieldwork campaign, all sensors (i.e., irradiance and pressure sensors) were set to log measurements synchronously every 2 minutes.

We required that the contrived ‘non-tidal’ condition be comparable with the ‘tidal’ condition in terms of both mean water depth and clarity. The instrument on the ‘non-tidal’ mooring was positioned at a depth equal to the mean depth experienced by the ‘tidal’ instrument. This was determined in advance of deployment using tide tables, and verified after recovery using the pressure (depth) records. Both moorings were positioned as close together as was practically possible, so that they might experience similar conditions of water clarity. The ‘non-tidal’ mooring, however, was necessarily deployed in deeper water (i.e., further offshore) so that its

instrument was not grounded at low water.

A Lambert-Beer Law-based correction was applied to the I_{BNT} data to account for the fact that daily mean attenuation coefficients, \bar{k}_{PAR} , at the site of the ‘non-tidal’ mooring were consistently lower than at the site of the ‘tidal’ bed frame (in shallower, more turbid water). Time series of instantaneous k_{PAR} were calculated for both the ‘tidal’ and ‘non-tidal’ scenarios by using observations of sea surface irradiance, seabed irradiance, and water depth to solve Eq. 1 for k_{PAR} . Daily means, \bar{k}_{PAR} , were determined for both scenarios and the differences between corresponding daily means, $\Delta\bar{k}_{PAR}$ ($= \bar{k}_{PAR,tidal} - \bar{k}_{PAR,non-tidal}$), were used to correct (reduce) the appropriate instantaneous I_{BNT} values, according to $I_{BNT,corrected}(t) = I_{BNT,original}(t) \exp[-\Delta\bar{k}_{PAR}z_{NT}(t)]$. This correction effectively equates the daily mean attenuation coefficients of the two scenarios, whilst preserving the natural variability of the records.

The irradiance sensors were of type MDS-MkV/L (JFE Advantech, Kobe, Japan), which measure, and log internally, quantum scalar irradiance in the PAR waveband. Quantum scalar irradiance is the integral of the radiance distribution at a point, over all directions about that point (Kirk, 1994). Each instrument had been calibrated by the manufacturer against an LI-189 (LI-COR Biotechnology, Lincoln, Nebraska, USA) reference sensor, using a halogen light source. The manufacturers claim an accuracy of $\pm 4\%$ (full scale). Instrument resolution is $1 \mu\text{mol quanta m}^{-2} \text{s}^{-1}$. The irradiance sensors used for this study were intercalibrated over a typical daily irradiance range at the School of Ocean Sciences (Bangor University,

285 Wales).

286 Additional corrections were applied to the irradiance data: (1) the
 287 typical dark current reading was deducted from all measurements before
 288 further analysis (after Topliss et al., 1980); (2) measurements from the two
 289 submerged sensors were multiplied by an ‘immersion coefficient’ to account
 290 for the so-called ‘immersion effect’ (Kirk, 1994); and (3) linear
 291 intercalibration equations (with coefficients that were averages of those
 292 determined pre- and post-fieldwork) were applied to account for slight
 293 differences in instrument sensitivities. Furthermore, a green-brown biofilm
 294 began to develop on the irradiance collectors after 2 weeks of summertime
 295 (July) deployment. The affected records were curtailed (post-recovery) at a
 296 length of 13 days to negate this concern.

297 Pressure sensors used were of the type DST Centi TD (Star Oddi Ltd.,
 298 Reykjavík, Iceland). These are also internally-logging, and measure
 299 pressure with a resolution of 0.1 kPa (i.e., they can resolve approximately 1
 300 cm changes of depth) and an accuracy of ± 1 kPa (i.e., approximately ± 10
 301 cm water depth accuracy). The sensors were intercalibrated over a depth
 302 range of 0 - 8 m.

303 Atmospheric pressures were obtained from METAR (Meteorological
 304 Terminal Aviation Routine) reports generated hourly by the meteorological
 305 station at Lanvéoc-Poulmic Airbase ($48^{\circ} 16.93'N$ $4^{\circ} 26.50'W$). A time series
 306 with 2 minute intervals was produced by interpolation. Atmospheric
 307 pressure was deducted from each measured pressure to isolate the
 308 component resulting from the overlying head of water alone. These values

309 were converted to water depths by dividing by the product of water density
 310 and acceleration due to gravity. Water density was calculated according to
 311 the International Equation of State of Sea Water (IES-80) using measured
 312 pressures and temperatures (recorded by the DST Centi sensors as a
 313 secondary parameter), and an estimate of mean salinity at the site (34 psu
 314 is appropriate (Delmas, 1981)). Acceleration due to gravity was calculated
 315 to be 9.81 m s^{-2} at the latitude of the Bay of Brest, using the International
 316 Gravity Formula (IGF).

Numerical model

317 Numerical model input values (Table 1) were selected to represent the Bay
 318 of Brest, and an individual thallus of *Saccharina latissima* or an established
 319 macroalgal community growing there. A 1 h time step was used.

320 Sea surface irradiance, $I_0(t)$, was modelled over a year using the
 321 following equation (from Gates (1980)):

$$I_0(N, t) = I_{Atmos}(N) \sin(\alpha(N, t)) \exp[-k_{Atmos} m_{Air}(N, t)], \quad (9)$$

322 where I_{Atmos} is the solar irradiance incident upon a surface perpendicular to
 323 the Sun's rays just outside Earth's atmosphere (in this study we are
 324 interested only in the PAR component - see Table 1 footnote), α is the solar
 325 altitude, k_{Atmos} is an atmospheric attenuation coefficient (which we have
 326 assumed to be a constant and have treated as a tunable parameter, and
 327 which represents a spectral average), m_{Air} is the air mass ratio, N is the
 328 day number ($N=0$ on January 1st), and t is time, measured in hours from

the start of the day.

I_{Atmos} varies over the year, as a result of the elliptical orbit of the Earth about the Sun, according to $I_{Atmos}(N) = I_{SC}(1 + 0.0344 \cos(360^\circ N/365))$ (Kreith and Kreider, 1978; Duffie and Beckman, 2013), where I_{SC} is the solar constant - the irradiance (in this case, the PAR component only) received by a surface perpendicular to the Sun's rays just outside Earth's atmosphere at the mean Earth-Sun distance (see Table 1).

Solar altitude, α , is the angular elevation of the Sun above the horizon, and was calculated using the equation first developed by Milankovitch (1930): $\sin(\alpha(N, t)) = \sin(\gamma) \sin(\delta(N)) - \cos(\gamma) \cos(\delta(N)) \cos(360^\circ t/24)$, where γ is the latitude (in degrees), and δ is the solar declination (in degrees), the angle through which a given hemisphere is tilted towards (or away from) the Sun. δ was, in turn, calculated using $\delta(N) = 23.45 \sin(360^\circ(N + 284)/365)$ (Cooper, 1969; Brock, 1981).

The air mass ratio, m_{Air} , is the ratio of the optical path length through the atmosphere in the direction of the Sun, at an angle of α , to the path length in the vertical direction (i.e., with the Sun directly overhead at the zenith position) (Gates, 1980). We employed the commonly used approximation (Gates, 1980; Kumar et al., 1997) of $m_{Air} = 1/\sin(\alpha)$.

Eq. 9 is essentially a restatement of the Lambert-Beer Law, with the irradiance arriving at the outer atmosphere being attenuated exponentially as it propagates towards the sea surface. The additional $\sin(\alpha)$ factor, not found in the Lambert-Beer Law, represents an adjustment to I_{Atmos} (which is defined for a surface perpendicular to the Sun's rays) to account for the

fact that extraterrestrial solar radiation may be obliquely incident upon the local zenith (see Gates (1980) for diagrams illustrating geometric considerations). The form of Eq. 9 results in a continuous sine wave output, from which only the non-negative values are of relevance to our northern hemisphere site. Negative values were set to zero by the model script to represent night-time irradiances, which may be considered negligible for our purposes.

Seabed irradiance time series (i.e., $I_{BT}(t)$ and $I_{BNT}(t)$) were computed as $I_0(t)$ attenuated exponentially by the product of water depth, $z(t)$, and diffuse attenuation coefficient of PAR, $k_{PAR}(t)$, again in accordance with the Lambert-Beer Law (Eq. 1).

To obtain ‘tidal’ seabed irradiance, $I_{BT}(t)$, a tidally-varying water depth was used. This was modelled as the sum of a lunar and a solar semi-diurnal tide (i.e., the M_2 and S_2 tidal constituents respectively), to produce a semi-diurnal and a springs-neaps cycle. The phase of the S_2 constituent was set to 180° to ensure the low waters of spring tides always occurred at midday and midnight, as is approximately the case at the Bay of Brest.

$k_{PAR}(t)$ was modelled as daily mean values (i.e., \bar{k}_{PAR}) varying from day to day with daily mean tidal range, \bar{R} , as follows

$$\bar{k}_{PAR}(N) = \left(\frac{1}{2} + \frac{1}{2} \cos \frac{2\pi N}{365}\right) m \bar{R}(N) + c \quad (10)$$

where N is again day of the year, and m and c are constants. We return to the form of this equation below. $\bar{R}(N)$ was modelled as a cosine function with a springs-neaps periodicity; the mean, amplitude, period and phase

375 was set precisely by the M_2 and S_2 parameters in Table 1. k_{PAR} was not
 376 varied on shorter timescales (e.g., during the day with the semi-diurnal
 377 tide).

378 Irradiance and depth observations (see ‘Observational campaigns’)
 379 together permitted the calculation of \bar{k}_{PAR} values for each day of the two
 380 campaigns (not shown). In winter, a scattered but statistically significant
 381 (at the 95% confidence level) positive linear relationship between \bar{k}_{PAR} and
 382 \bar{R} was observed. In summer, however, the relationship was not statistically
 383 significant (at the 95% confidence level). Hence, we modelled the variation
 384 of \bar{k}_{PAR} with \bar{R} over a year using Eq. 10, which is that of a straight line
 385 with an intercept, c , representing a baseline value of \bar{k}_{PAR} , and a gradient
 386 that varies incrementally throughout the year, from m in mid-winter (i.e.,
 387 $\bar{k}_{PAR} = m\bar{R} + c$) to 0 in mid-summer (i.e., $\bar{k}_{PAR} = c$ for all \bar{R}). The
 388 gradient variation between m and 0 is achieved by means of the bracketed
 389 ‘gradient modifier’, a cosinusoidal function of annual periodicity, varying
 390 between 1 in mid-winter and 0 in mid-summer. m and c values used in the
 391 model are based on the winter observations, and are given in Table 1.

392 To obtain ‘non-tidal’ seabed irradiance, $I_{BNT}(t)$, the mean water depth
 393 was applied at all times, t . The choice of $k_{PAR}(t)$ parameterisation was
 394 determined by the desired output. For daily amplification factors, daily
 395 mean values of k_{PAR} (\bar{k}_{PAR}) were used here also (i.e., $k_{PAR}(t)$ was
 396 modelled, as for the ‘tidal’ case, using Eq. 10). This is because the Bowers
 397 and Brubaker (2010) definition of daily tidal irradiance amplification
 398 requires that \bar{k}_{PAR} values used in both ‘tidal’ and ‘non-tidal’ cases be equal

on any given day. For the output of springs-neaps amplification factors and for annual calculations, the ‘non-tidal’ k_{PAR} was held constant (i.e., set to the mean of the \bar{k}_{PAR} values generated by Eq. 10) over each springs-neaps cycle or over the year, respectively.

Modelled $I_{BT}(t)$ and $I_{BNT}(t)$ were initially input into the Peeters and Eilers (1978) P - I Equation (7) to provide $P_{BT}(t)$ and $P_{BNT}(t)$ appropriate at the thallus scale. Similarly, modelled $I_{BT}(t)$ and $I_{BNT}(t)$ were input into the Lederman and Tett (1981) P - I Equation (8) to provide $P_{BT}(t)$ and $P_{BNT}(t)$ appropriate at the community scale. Daily, springs-neaps, and annual totals of these outputs, for use in calculating amplification factors, were determined by numerical integration (i.e., trapezium rule) with respect to time. Daily tidal amplification factors for irradiance, F , and photosynthesis, Ψ , were calculated according to Equations 2 and 5, respectively. Springs-neaps and annual irradiance and photosynthesis amplification factors (i.e., F_{SN} , Ψ_{SN} , F_{ANN} , and Ψ_{ANN}) were determined similarly:

$$F_{SN} = \frac{\langle I_{BT} \rangle_{SN}}{\langle I_{BNT} \rangle_{SN}}, \quad (11)$$

$$\Psi_{SN} = \frac{\langle P_{BT} \rangle_{SN}}{\langle P_{BNT} \rangle_{SN}}, \quad (12)$$

$$F_{ANN} = \frac{\langle I_{BT} \rangle_{ANN}}{\langle I_{BNT} \rangle_{ANN}}, \quad (13)$$

and

$$\Psi_{ANN} = \frac{\langle P_{BT} \rangle_{ANN}}{\langle P_{BNT} \rangle_{ANN}}, \quad (14)$$

where angular brackets with the subscripts SN or ANN denote
springs-neaps or annual totals of the enclosed parameters, respectively.

Results

Tidal irradiance amplification determined from observations

Time series observations and daily tidal irradiance amplification factors, F ,
from the summer and winter campaigns are presented in Figures 5 and 6,
respectively. Throughout the summer campaign, observed F values were
close to unity (Fig. 5(d)), ranging from 1.0 to 1.3. No clear springs-neaps
cycle in F was apparent. In the winter dataset, however, F values exhibited
a strong springs-neaps cycle (Fig. 6(d)), being much larger at spring tides
(up to 31.5) than at neap tides (as low as 0.4).

Agreement between observed and theoretically predicted tidal irradiance
amplification (using Eq. 4) is demonstrated graphically in Figure 7. The
analytical solution appears to perform well for the Bay of Brest. Model II
regression (i.e., the major axis method (Ricker, 1973)) performed on the
combined summer and winter data gave a slope of 1.311 ± 0.050 and an
intercept of -0.63 ± 0.15 . t -tests (two-tailed) were conducted to compare
these values with the slope and intercept that would be expected in the
case of perfect agreement between observations and predictions (i.e., 1 and
0, respectively). There were statistically significant differences (at the 95%

confidence level) between both the slopes ($t = 6.25$, $df = 32$, $p < 0.001$) and the intercepts ($t = -4.10$, $df = 32$, $p < 0.001$). This departure from ‘perfect agreement’ reflects the relatively modest shortcomings of an analytical solution in which several assumptions were employed (see Bowers and Brubaker, 2010). The solution shows a tendency to overpredict at larger amplifications.

Tidal photosynthesis amplification determined from inferred photosynthesis

Fig. 8 illustrates (using a subset of our irradiance time series observations, and rates of photosynthesis inferred from these observations), some conditions under which photosynthesis amplification factors, Ψ , and irradiance amplification factors, F , may converge or differ.

On 12th July (left hand panels, Fig. 8), overcast conditions ensure irradiances in both ‘tidal’ and ‘non-tidal’ scenarios remain below the saturation onset irradiance of an individual thallus for much of the day, and below that of an established community for the entire day. Consequently, photosynthesis responds approximately linearly to irradiance throughout the day (in both ‘tidal’ and ‘non-tidal’ cases, and for both thallus and community). Computed thallus and community Ψ values are therefore both similar to the prevailing F value ($F=1.16$, cf. $\Psi(\text{thallus})=1.08$ and $\Psi(\text{community})=1.11$).

On 13th July (right hand panels, Fig. 8) the sky was relatively

cloud-free, and the day correspondingly brighter. Tidal irradiance amplification is clearly apparent by comparing the areas beneath the ‘tidal’ and ‘non-tidal’ irradiance curves. Thallus photosynthesis is light-saturated (and even photoinhibited) in both ‘tidal’ and ‘non-tidal’ scenarios for much of the day (note how P_B approximately flatlines in both scenarios between about 8am and 5pm). There is no appreciable photosynthesis amplification at the thallus scale, and thus $\Psi(\text{thallus})$ departs from F ($F=1.23$, cf. $\Psi(\text{thallus})=1.02$). In contrast, the P - I curve parameterisation adopted here to describe community photosynthesis does not truly saturate, and inferred community photosynthesis continues to respond at these elevated irradiances. In the ‘tidal’ community photosynthesis curve a local maximum can be seen at low water ($\sim 9\text{am}$), and the curve is somewhat depressed around high water ($\sim 3\text{pm}$). Consequently, some tidal photosynthesis amplification occurs at the community scale, such that F and $\Psi(\text{community})$ are closer in value ($F=1.23$, cf. $\Psi(\text{community})=1.11$).

Exploring the F - Ψ relationship with a numerical model

In Fig. 8, differences in sea surface irradiation from one day to the next, owing to differences in cloud cover, provided a convenient way to illustrate how F and Ψ may converge or differ. However, cloud cover is often ephemeral and changes with little temporal regularity. Here, we explore the more regular, predictable aspects of the F - Ψ relationship using the simple numerical model described earlier (see Materials and methods).

475 Output in which daily changes are resolved is shown in Fig. 9 for a mean
 476 water depth of 4.1 m (i.e., 1 m below the level of LWST) in the Bay of
 477 Brest. This corresponds approximately to the mean depth of our
 478 observations. Modelled F behaviour (Fig. 9(b)) compares favourably with
 479 the winter and summer observations. A springs-neaps pattern in F is
 480 present throughout the year; peaks are at spring tides (when low water is at
 481 midday) and troughs are at neaps (when high water is at midday). The
 482 amplitude of the cycle is large in winter (modelled F varies from 0.66 to
 483 11.72), when short daylengths exaggerate the difference between springs
 484 and neaps. It is considerably reduced in summer (modelled F varies from
 485 0.97 to 1.64), when the days are longer.

486 Modelled Ψ behaviour at the thallus scale (Fig. 9(c)) corresponds with
 487 that of F in winter, but a ‘switch’ in the sense of the springs-neaps pattern
 488 occurs near the equinoxes. Longer summer daylengths permit the morning
 489 and evening low waters of neap tides to occur within daylight hours. This
 490 boosts the tidally-modulated photosynthesis (i.e., P_{BT}) at neaps.
 491 Consequently, they become more beneficial, in photosynthesis amplification
 492 terms, than spring tides, where a single, large pulse of seabed light around
 493 the midday low water saturates or inhibits P_{BT} (at this depth and time of
 494 year).

495 At the community scale, the springs-neaps cycle in Ψ does not ‘switch
 496 sense’ to peak at neap tides during the summer months. Instead, Ψ
 497 ‘flatlines’ at a value of approximately 1 throughout the summer (Fig. 9(d)).
 498 The mechanism responsible is the same as that invoked above to explain

the ‘switch’. The effects are less dramatic for the case of macroalgal communities (i.e., a reduction, to nothing, of the amplitude of the springs-neaps cycle in Ψ , rather than a switch of sense) because communities do not become truly light-saturated or photoinhibited (Middelboe et al., 2006). Convergence of springs and neaps Ψ values upon a value of 1 during the summer months suggests that the tide has neither an amplifying or a reducing effect on community photosynthesis at these longer daylengths, and at this depth, in the Bay of Brest.

Fig. 10 shows F_{SN} , Ψ_{SN} (at the thallus scale), and Ψ_{SN} (at the community scale) modelled over a year at 1 m below the level of LWST in the Bay of Brest. At the thallus scale, F_{SN} and Ψ_{SN} do not correspond very closely; values of $\Psi_{SN}(thallus)$ are suppressed by the increased prevalence of light-saturation and photoinhibition in this scenario. In the summer, tidal (i.e., springs-neaps) reduction of thallus photosynthesis occurs (i.e., $\Psi_{SN}(thallus) < 1$), despite tidal amplification of irradiance (i.e., $F_{SN} > 1$).

At the community scale, the magnitudes and temporal behaviour of Ψ_{SN} more closely approach those of F_{SN} . No appreciable tidal reduction of photosynthesis is sustained through summer. This can again be explained by the absence of true light-saturation in the community-scale $P-I$ curve parameterisation. Even the largest maxima in tidally-modulated seabed irradiance, occurring at (the midday) LWST during summer, do not present a macroalgal community with such a ‘photosynthetic disadvantage’ (i.e., prolonged saturation or photoinhibition) as they do an individual/isolated kelp thallus in shallow water.

523 The annual tidal irradiance amplification factor, F_{ANN} , output by the
 524 model for a depth of 1 m below the level of LWST in the Bay of Brest was
 525 2.33. The annual photosynthesis amplification factors at the thallus and
 526 community scales, $\Psi_{ANN}(thallus)$ and $\Psi_{ANN}(community)$, for the same
 527 depth were 1.06 and 1.42, respectively.

Discussion

Observations in the Bay of Brest

528 The key physical parameters controlling the magnitude of the tidal
 529 irradiance amplification effect (on a given day) were identified by Bowers
 530 and Brubaker (2010) to be the diffuse attenuation coefficient, k_{PAR} , the
 531 tidal range, R (or amplitude, b), the times of low water relative to noon, t_{lw} ,
 532 and the daylength, L . In a qualitative sense, our observations in the Bay of
 533 Brest support this. In winter, the amplification is large at springs when R
 534 is large, k_{PAR} is elevated generally, and low water occurs at midday.
 535 Reduction occurs at neaps when R and k_{PAR} are smaller, and high water
 536 occurs at midday. This springs-neaps pattern appears to be modulated also
 537 by the seasonal cycle in daylength: it is pronounced in winter, when short
 538 days exaggerate the consequences of having either low water or high water
 539 at midday (i.e., springs and neaps respectively); it is not present in summer,
 540 when longer days permit the irradiance ‘gains’ of the midday LWST, or
 541 ‘losses’ of the midday HWNT (high water neap tide), to be offset somewhat

542 by the morning and evening high waters, or low waters, respectively.

543 Agreement between existing theory and observation has, in this paper,
 544 been demonstrated quantitatively also. Comparison of observed daily tidal
 545 irradiance amplification factors, F_{Obs} , with those predicted for the
 546 conditions on each day, F_{Pred} , using the analytical solution of Bowers and
 547 Brubaker (2010) (a function of the 4 key parameters outlined above) shows
 548 reasonable agreement. Much of the key physics underlying tidal
 549 amplification is included in the analytical solution and, based on the fact
 550 that it has performed well for two sites with contrasting tidal regimes (i.e.,
 551 the Menai Strait in the earlier work (Bowers and Brubaker, 2010) and the
 552 Bay of Brest in the current work), it can be expected to perform at least
 553 reasonably well for many more, perhaps most, coastal sites with a
 554 semi-diurnal tide.

555 As a caveat to the above, we note that a tidal cycle in k_{PAR} is present at
 556 the Bay of Brest (not shown in this paper). As for the Menai Strait
 557 (Roberts et al., 2014) and the Tamar Estuary (Pilgrim and Millward, 1989,
 558 and references therein), the cycle is out of phase with the tidal curve,
 559 reaching a maximum at low water and a minimum at high water. The
 560 Bowers and Brubaker (2010) solution assumes constant k_{PAR} over the day,
 561 and employs the daily mean value in predicting F . This was necessary in
 562 order to make the analytical solution possible. The consequence is that the
 563 solution tends to overpredict F on days where the k_{PAR} tidal cycle is
 564 particularly distinct (e.g., on 27th December $F_{Obs} = 31.5$, whereas
 565 $F_{Pred} = 43.4$ (see Fig. 6 and 7)).

Whilst we have insufficient data to say anything conclusive about the
 nature of the mechanism driving the tidal cycle in k_{PAR} , we speculate, as
 did Pilgrim and Millward (1989), that it involves the local resuspension of
 sediment by increased turbulence at low water. It could, therefore, be
 common to many shallow, coastal sites. At other sites, k_{PAR} behaviour may
 exhibit clear cycles with quarter-diurnal or semi-diurnal frequency, owing to
 tidal resuspension or tidal advection of suspended particulate matter
 (SPM) respectively (e.g., Weeks et al. (1993) and Williams et al. (1998)).
 In any case, an analytical solution of comparable simplicity to that of
 Bowers and Brubaker (2010), which incorporates such regular patterns in
 k_{PAR} , is difficult to achieve. Use of the Bowers and Brubaker (2010)
 solution to make predictions for sites with appreciable and inherent k_{PAR}
 cycles will incur some error, and the interested investigator is advised to
 model the tidal irradiance amplification effect (including the k_{PAR}
 variability) numerically in these cases.

An irradiance sensor in a simple bed frame provided the ‘tidal’
 irradiance data in the present work, whereas a novel mooring was designed
 and employed to allow irradiance in the hypothetically equivalent
 ‘non-tidal’ condition to be measured directly, rather than inferred from
 surface irradiance records. This new mooring performed encouragingly well:
 it provided high quality, continuous time series data for each campaign; it
 did not become entangled, despite tidal currents and, occasionally, strong
 wind forcing; and, most importantly, it successfully held the irradiance
 sensor at a relatively constant water depth over time.

Two limitations are associated with the use of this mooring. Firstly, whilst the irradiance data is rendered independent of tidal variations in water depth by the mooring, it is not independent of the tidal variations in k_{PAR} discussed above. Thus, it is not comprehensively ‘non-tidal’ data but, given that the tidal range in the Bay of Brest is typically much greater than the range in k_{PAR} , it is sufficiently so for our purposes. Secondly, the ‘non-tidal’ mooring was deployed further offshore than the ‘tidal’ bed frame. This allowed the requirement of equal mean depths to be satisfied, whilst preventing the ‘non-tidal’ sensor from becoming grounded at low water. As a consequence, the daily mean k_{PAR} (i.e., \bar{k}_{PAR}), as experienced by the ‘non-tidal’ sensor, was consistently lower than at the shallower ‘tidal’ bed frame site. This is not desirable (\bar{k}_{PAR} should be approximately equal in both conditions) and necessitated the application of a Lambert-Beer-based correction (see ‘Materials and methods’) to the ‘non-tidal’ data.

A workaround exists for the second limitation: deploy the bed frame further offshore also, elevating its sensor considerably to maintain the same mean depth. This is logistically much less practical, however, both in terms of the deployability of the adapted (larger) frame and of the increased danger to shipping in these relatively busy, shallow waters.

Numerical modelling predictions

The following key predictions emerged out of the modelling study, and apply to the shallow sub-tidal (i.e., 1 m below the level of LWST) in the

611 Bay of Brest:

- 612 • Annual total seabed irradiance is amplified by the tide (by a factor of
613 2.33 relative to a ‘non-tidal’ but otherwise equivalent scenario).
614 Annual total photosynthesis at the seabed is hardly amplified at all
615 by the tidal irradiance amplification (i.e., by a factor of just 1.06) at
616 the isolated, individual thallus scale, but is more substantially
617 amplified at the established macroalgal community scale (i.e., by a
618 factor of 1.42).

- 619 • When considered at springs-neaps resolution, tidal modulation of
620 seabed irradiance is of greatest significance, in terms of its influence
621 on the photosynthesis of benthic algae, during winter (when it results
622 in amplification of photosynthesis at both community and thallus
623 scales). It is of less significance during summer, when it has a
624 negligible effect at the community scale and results in a modest,
625 sustained reduction in photosynthesis at the thallus scale.

- 626 • At finer temporal resolution, a springs-neaps cycle is present in the
627 daily tidal irradiance amplification factor. Peaks are at spring tides,
628 troughs are at neap tides, and the amplitude of the cycle is large in
629 winter and considerably smaller in summer (in agreement with our
630 observations). The daily tidal photosynthesis amplification factor
631 exhibits a similar pattern during winter at both the thallus and
632 community scales. During summer, however, this pattern ‘switches

sense' (such that the peaks are at neap tides) at the thallus scale, and
 'flatlines' (at a value of approximately 1) at the community scale.

As noted previously, the springs-neaps cycle in daily tidal irradiance
 amplification factor peaks at spring tides because a low water occurs at
 about midday during springs at the Bay of Brest. Conversely, troughs are
 at neap tides because a high water occurs at midday at these times. The
 amplitude of the cycle is larger in winter because shorter daylengths
 exaggerate the difference between these two situations. The
 irradiance-amplifying potential of spring tides in winter also accounts for
 amplification predicted over longer timescales (i.e., the amplification
 occurring during winter at the springs-neaps timescale, and the overall
 annual amplification).

Whether tidal amplification of seabed light produces a similar
 amplification of seabed photosynthesis depends on how light levels compare
 with the saturation onset irradiance of a given species or community. Below
 this threshold, rates of photosynthesis respond approximately linearly to
 the time course of instantaneous irradiance, and photosynthesis
 amplification corresponds with the prevailing irradiance amplification.
 Should irradiances exceed this threshold (as occurs more frequently in
 summer), the relationship between irradiance amplification and
 photosynthesis amplification becomes more complex, and (as we have
 shown) their respective factors may differ. The response of the isolated,
 individual thallus and that of the established macroalgal community will

656 differ in this respect because their photosynthesis-irradiance characteristics
 657 are different (Gévaert et al., 2003; Middelboe et al., 2006): a kelp thallus
 658 may become light-saturated and even photoinhibited, but an established
 659 macroalgal community is unlikely to become truly light-saturated.
 660 Generally, the consequence is that, at the thallus scale, photosynthesis
 661 amplification factors readily depart from their corresponding irradiance
 662 amplification factors (including the case whereby photosynthesis is reduced
 663 despite irradiance being amplified by the tide), whilst at the community
 664 scale, there is likely to be a more consistently positive correlation between
 665 tidal irradiance amplification and photosynthesis amplification.

666 The numerical model was constructed using widely accepted
 667 parameterisations of key physical and biological processes. For example,
 668 surface irradiance was modelled using well-known equations found in Gates
 669 (1980), Kirk (1994), and others, the attenuation of irradiance with water
 670 depth was modelled using the Lambert-Beer Law, tidally-varying water
 671 depth was modelled as the sum of two sinusoidal tidal constituents (M_2 and
 672 S_2), and P - I curves were modelled with the Peeters and Eilers (1978)
 673 Equation (appropriate at the thallus scale) and the Lederman and Tett
 674 (1981) Equation (appropriate at the community scale). The main
 675 limitations of the work are associated with the use of photosynthesis
 676 parameters, controlling the precise shape of the P - I curves, that are
 677 unchanging over time.

678 In fact, the shape of a P - I curve exhibits a dependence on water
 679 temperature and substrate (i.e., CO_2) availability, both of which are liable

to change, to varying degrees, over the timescales considered here (Dring, 1992; Hurd et al., 2014). Furthermore, a P - I curve can be temporally dynamic owing to mechanisms endogenous to the alga, particularly those which permit it to maximise its performance in any situation (Delebecq et al., 2013). Notably, algae are known to acclimate to changes in the intensity and spectral quality of the ambient light, on timescales ranging from minutes to months, by adjustments to their photosynthetic apparatus (Dring, 1992; Kirk, 1994; Falkowski and Raven, 1997; Hurd et al., 2014). Short-term adjustments (e.g., minutes to days) include changes to the Photosystem II absorption cross-section, changes to the position and orientation of chromatophores, and photoprotective mechanisms, such as non-photochemical quenching (i.e., the harmless dissipation of excess light energy as heat) (Nultsch and Pfau, 1979; Müller et al., 2001; Duarte et al., 2013). Longer-term adjustments (e.g., days to months) include changes to pigment content and composition (Kirk, 1994).

Duarte et al. (2013) noted that P - I curve parameters should be considered as variables rather than constants. As discussed, these variables are functions of many environmental parameters (e.g., temperature, CO_2 concentration, ambient light intensity and quality) and have, as yet, not been parameterised satisfactorily. We chose to employ a ‘static’, or fixed, P - I curve taken from the literature when modelling photosynthesis over time from modelled irradiance (as did Zimmerman et al. (1994)). Whilst this is likely to be a reasonable first order approximation (see Middelboe et al., 2006), the accuracy of model estimates / predictions will undoubtedly

704 be improved if studies like those of Gévaert et al. (2003) and Duarte et al.
 705 (2013) can be built upon to provide generalisable parameterisations of a
 706 P - I curve's 'dynamic' nature.

707 The are a number of broad implications of the modelling study that can
 708 be extended to sites other than they Bay of Brest. Demonstrated for the
 709 first time in this work, the effect of the tide in amplifying or reducing
 710 time-integrated seabed light is likely to induce a similar effect on
 711 time-integrated benthic photosynthesis. These effects are likely to be more
 712 strongly coupled at the macroalgal community scale (which is arguably
 713 more ecologically relevant than that of the isolated thallus). To extend
 714 comments made by Bowers and Brubaker (2010), just as error will be
 715 introduced to modelled estimates of seabed light if tidal effects are
 716 neglected, for example by employing a mean water depth and clarity over
 717 time, the same is likely to be true of modelled estimates of seabed
 718 photosynthesis. At many sites, neglecting the tidal effects will lead to
 719 underestimates of time-integrated irradiance and photosynthesis in the
 720 subtidal zone.

721 We have shown that the time course of benthic photosynthesis and
 722 time-integrated benthic photosynthesis in the shallow subtidal appear to be
 723 controlled, at least in part, by the tidal characteristics of the site in
 724 question, through their modulation of seabed irradiance (i.e., the times of
 725 low water, t_{lw} , and their advance through the springs-neaps cycle, and the
 726 tidal range, R , and its variability). Observed differences in these aspects of
 727 benthic photosynthesis from site to site may be attributable to differences

728 in t_{lw} , R , k_{PAR} and L behaviour between the sites, rather than (or in
729 addition to) abiotic and biotic factors identified in the literature to date.

730 We speculate that there may be a second important spatial (i.e., depth)
731 component to the effect of tidal modulation of seabed light on benthic
732 photosynthesis and ecology. Since subtidal benthic algae are readily
733 light-limited, and different species possess different light
734 requirements/tolerances, it is natural to hypothesise that such an effect
735 might influence the depth distribution of these species differentially, in turn
736 influencing characteristics of the prevailing benthic community such as
737 depth gradients in species composition, vertical zonation patterns, and
738 overall areal extent and algal cover. A modelling approach such as the one
739 adopted here cannot be employed to investigate this until the effects of
740 photoacclimation on photosynthesis parameters (in the depth dimension)
741 have been adequately quantified and parameterised for key species. This is
742 a problem of considerable importance to the field of modelling
743 shallow-water benthic productivity, and is our primary recommendation as
744 a direction for future research.

745 In terms of the practical relevance of this work, habitat managers and
746 policy makers should be aware that projects which alter the tidal
747 characteristics of a particular coastline, such as the construction of barrages
748 or lagoons for tidal energy extraction, and the changes to tides that are
749 predicted to occur with sea-level variability (e.g., Neill et al., 2010) are
750 likely to affect the time course of photosynthesis in, and the overall
751 productivity of, benthic plants and algae, through the tide's influence on

752 the available seabed light.

References

- 753 Ackleson, S.G., 2003. Light in shallow waters : A brief research review.
754 *Limnology and Oceanography* 48, 323–328.
- 755 Bowers, D.G., Brubaker, J.M., 2004. Underwater sunlight maxima in the
756 Menai Strait. *Journal of Optics A: Pure and Applied Optics* 6, 684–689.
- 757 Bowers, D.G., Brubaker, J.M., 2010. Tidal amplification of seabed light.
758 *Journal of Geophysical Research* 115, C09008.
- 759 Bowers, D.G., Tett, P., Walne, A.W., 1997. A note on seabed irradiance in
760 shallow tidal seas. *Journal of the Marine Biological Association of the*
761 *United Kingdom* 77, 921–928.
- 762 Brock, T.D., 1981. Calculating solar radiation for ecological studies.
763 *Ecological Modelling* 14, 1–19.
- 764 Cooper, P.I., 1969. The absorption of solar radiation in solar stills. *Solar*
765 *Energy* 12, 333–346.
- 766 Delebecq, G., Davoult, D., Menu, D., Janquin, M.A., Dauvin, J.C.,
767 Gévaert, F., 2013. Influence of local environmental conditions on the
768 seasonal acclimation process and the daily integrated production rates of
769 *Laminaria digitata* (Phaeophyta) in the English Channel. *Marine Biology*
770 160, 503–517.

- 771 Delmas, R., 1981. Étude de l'évolution saisonnière des sels nutritifs dans
772 la rade de Brest en fonction des apports fluviaux et des échanges avec
773 l'Iroise. Ph.d. thesis. Université de Bretagne Occidentale, Brest.
- 774 Delmas, R., Tréguer, P., 1983. Évolution saisonnière des nutriments dans
775 un écosystème eutrophe d'Europe Occidentale (la rade de Brest).
776 Interactions marines et terrestres. *Oceanologica Acta* 6, 345–355.
- 777 Dring, M.J., 1992. The biology of marine plants. Cambridge University
778 Press, Cambridge.
- 779 Duarte, P., Ramos, M., Calado, G., Jesus, B., 2013. Laminaria hyperborea
780 photosynthesis-irradiance relationship measured by oxygen production and
781 pulse-amplitude-modulated chlorophyll fluorometry. *Aquatic Biology* 19,
782 29–44.
- 783 Duffie, J.A., Beckman, W.A., 2013. Solar engineering of thermal
784 processes. John Wiley and Sons, Hoboken. Fourth edition.
- 785 Falkowski, P.G., Raven, J.A., 1997. Aquatic photosynthesis. Blackwell,
786 Oxford.
- 787 Gates, D.M., 1980. Biophysical Ecology. Springer-Verlag, New York.
- 788 Gévaert, F., Créach, A., Davoult, D., Holl, A.C., Seuront, L., Lemoine, Y.,
789 2002. Photo-inhibition and seasonal photosynthetic performance of the
790 seaweed *Laminaria saccharina* during a simulated tidal cycle: chlorophyll

- 791 fluorescence measurements and pigment analysis. *Plant, Cell and*
792 *Environment* 25, 859–872.
- 793 Gévaert, F., Créach, A., Davoult, D., Migné, A., Levavasseur, G., Arzel,
794 P., Holl, A.C., Lemoine, Y., 2003. *Laminaria saccharina* photosynthesis
795 measured in situ: photoinhibition and xanthophyll cycle during a tidal
796 cycle. *Marine Ecology Progress Series* 247, 43–50.
- 797 Heck, K.L., Hays, G., Orth, R.J., 2003. Critical evaluation of the nursery
798 role hypothesis for seagrass meadows. *Marine Ecology Progress Series* 253,
799 123–136.
- 800 Hily, C., Potin, P., Flocl'h, J.Y., 1992. Structure of subtidal algal
801 assemblages on soft-bottom sediments: fauna/flora interactions and role of
802 disturbances in the Bay of Brest, France. *Marine Ecology Progress Series*
803 85, 115–130.
- 804 Hurd, C.L., Harrison, P.J., Bischof, K., Lobban, C.S., 2014. *Seaweed*
805 *ecology and physiology*. Cambridge University Press, Cambridge.
- 806 Kirk, J.T.O., 1994. *Light and photosynthesis in aquatic ecosystems*.
807 Cambridge University Press, Cambridge. Second edition.
- 808 Kreith, F., Kreider, J.F., 1978. *Principles of solar engineering*.
809 McGraw-Hill, New York.

- 810 Kumar, L., Skidmore, A.K., Knowles, E., 1997. Modelling topographic
811 variation in solar radiation in a GIS environment. *International Journal of*
812 *Geographical Information Science* 11, 475–497.
- 813 Lederman, T.C., Tett, P., 1981. Problems in modelling the
814 photosynthesis-light relationship for phytoplankton. *Botanica Marina* 43,
815 305–314.
- 816 Mann, K.H., 1972. Ecological energetics of the sea-weed zone in a marine
817 bay on the Atlantic coast of Canada. II. Productivity of the seaweeds.
818 *Marine Biology* 14, 199–209.
- 819 Middelboe, A.L., Sand-Jensen, K., Binzer, T., 2006. Highly predictable
820 photosynthetic production in natural macroalgal communities from
821 incoming and absorbed light. *Oecologia* 150, 464–476.
- 822 Milankovitch, M., 1930. Mathematische klimalehre und astronomische
823 theorie der klimaschwankungen. *Handbuch der Klimatologie*, Band I, Teil
824 A. Gebruder Borntraeger, Berlin.
- 825 Monbet, Y., Bassoullet, P., 1989. Bilan des connaissances
826 océanographiques en rade de Brest. Rapport CEA/IPSN, code DERO/EL
827 89-23, IFREMER-DEL-BP 70-29280. Technical Report. IFREMER.
828 Plouzané.
- 829 Müller, P., Li, X.P., Niyogi, K.K., 2001. Non-Photochemical Quenching. A
830 Response to Excess Light Energy. *Plant Physiology* 125, 1558–1566.

- 831 Naylor, E., 2010. Chronobiology of marine organisms. Cambridge
832 University Press, Cambridge.
- 833 Neill, S.P., Scourse, J.D., Uehara, K., 2010. Evolution of bed shear stress
834 distribution over the northwest European shelf seas during the last 12,000
835 years. *Ocean Dynamics* 60, 1139–1156.
- 836 Nultsch, W., Pfau, J., 1979. Occurrence and biological role of light-induced
837 chromatophore displacements in seaweeds. *Marine Biology* 51, 77–82.
- 838 Peeters, J.C.H., Eilers, P., 1978. The relationship between light intensity
839 and photosynthesis - a simple mathematical model. *Hydrobiological*
840 *Bulletin* 12, 134–136.
- 841 Pilgrim, D.A., Millward, G.E., 1989. Variation in the diffuse optical depth
842 of the bed of a tidal estuary, in: McManus, J., Elliott, M. (Eds.),
843 *Developments in Estuarine and Coastal Study Techniques*. Olsen and
844 Olsen, Fredensborg, pp. 101–107.
- 845 Pingree, R.D., Griffiths, D.K., 1981. S2 tidal simulations on the
846 north-west European shelf. *Journal of the Marine Biological Association of*
847 *the United Kingdom* 61, 609–616.
- 848 Ricker, W.E., 1973. Linear regressions in fishery research. *Journal of the*
849 *Fisheries Research Board of Canada* 30, 409–434.
- 850 Roberts, E.M., 2015. Tidal modulation of seabed light and its implications
851 for benthic algae. Ph.D. thesis. Bangor University.

- 852 Roberts, E.M., Bowers, D.G., Davies, A.J., 2014. Springs-neaps cycles in
853 daily total seabed light: Daylength-induced changes. *Journal of Marine*
854 *Systems* 132, 116–129.
- 855 Salomon, J.C., Breton, M., 1991. Numerical study of the dispersive
856 capacity of the Bay of Brest, France, towards dissolved substances., in:
857 Lee, J.H.W., Cheung, Y.K. (Eds.), *Environmental Hydraulics*, Balkema,
858 Rotterdam. pp. 459–464.
- 859 Steneck, R.S., Graham, M.H., Bourque, B.J., Corbett, D., Erlandson,
860 J.M., Estes, J.A., Tegner, M.J., 2002. Kelp forest ecosystems: biodiversity,
861 stability, resilience and future. *Environmental Conservation* 29, 436–459.
- 862 Thouzeau, G., Chauvaud, L., Grall, J., Guérin, L., 2000. Rôle des
863 interactions biotiques sur le devenir du pré-recrutement et la croissance de
864 *Pecten maximus* (L.) en rade de Brest. *Comptes Rendus de l'Académie*
865 *des Sciences - Series III - Sciences de la Vie* 323, 815–825.
- 866 Topliss, B.J., Hunter, J.R., Simpson, J.H., 1980. Simultaneous
867 measurements of transparency and irradiance in the coastal waters of
868 North Wales. *Marine Environmental Research* 4, 65–79.
- 869 Weeks, A.R., Simpson, J.H., Bowers, D.G., 1993. The relationship
870 between concentrations of suspended particulate material and tidal
871 processes in the Irish Sea. *Continental Shelf Research* 13, 1325–1334.

- 872 Williams, J.J., Humphery, J.D., Hardcastle, P.J., Wilson, D.J., 1998. Field
873 observations of hydrodynamic conditions and suspended particulate matter
874 in the southern North Sea. *Continental Shelf Research* 18, 1215–1233.
- 875 Zimmerman, R.C., Cabello-Pasini, A., Alberte, R.S., 1994. Modeling daily
876 production of aquatic macrophytes from irradiance measurements: a
877 comparative analysis. *Marine Ecology Progress Series* 114, 185–196.

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Figure legends

- 889 1 Schematic demonstrating how the exponential attenuation of
 890 irradiance, I , with depth, z , can lead to tidal amplification
 891 (after Bowers and Brubaker (2010)). The disproportionately
 892 large ‘gain’ in tidally-modulated seabed irradiance, I_{BT} , at
 893 low tide (compared to that at mid tide) is not matched by
 894 the similarly defined ‘loss’ at high tide. The magnitude of the
 895 amplification will depend upon the diffuse attenuation coeffi-
 896 cient, k_{PAR} (which controls the rate of exponential attenuation
 897 with depth), and the tidal range, R . Sea surface irradiance,
 898 I_0 , varies throughout the day (not illustrated), meaning that
 899 the timing of low waters, t_{lw} , and the daylength, L , are also
 900 important.
- 901 2 Photosynthesis-irradiance ($P-I$) curves generated using the
 902 two equations employed in this study. The Peeters and Eilers
 903 (1978) Model (Eq. 7) is appropriate for thallus-scale pho-
 904 tosynthesis, and input values used to produce the curve are
 905 representative of *Saccharina latissima* (values from Gévaert
 906 et al., 2003). The Lederman and Tett (1981) Model (Eq. 8)
 907 is appropriate for macroalgal community-scale photosynthesis,
 908 and input values used were from Middelboe et al. (2006). See
 909 Table 1 for input values.

- 910 3 The Bay of Brest study site at the western extremity of the
 911 Brittany Peninsula (inset). Deployed instrumentation is in-
 912 dicated with black squares and a bold typeface (see text for
 913 details).
- 914 4 Schematic of the moorings deployed to observe tidal irradiance
 915 amplification.
- 916 5 Summer campaign time series data. Panel (a) shows sea sur-
 917 face irradiance, I_0 ; (b) shows tidally-modulated seabed irra-
 918 diance, I_{BT} , and water depth, z_T , from the bed frame; and
 919 (c) shows ‘non-tidal’ sub-surface irradiance, I_{BNT} , and wa-
 920 ter depth, z_{NT} , from the surface-moored frame. Panel (d)
 921 displays daily tidal irradiance amplification factors, F , deter-
 922 mined in accordance with Eq. 2 (daily irradiance totals es-
 923 timated by numerical integration using the trapezium rule).
 924 Note the \log_{10} scale used on the vertical axis. Grey-shaded
 925 areas represent night-time.

- 926 6 Winter campaign time series data. Panel (a) shows sea sur-
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 934 Note the \log_{10} scale used on the vertical axis. Grey-shaded
 935 areas represent night-time.
- 936 7 Predicted daily tidal irradiance amplification factors, F_{Pred} ,
 937 generated using the Bowers and Brubaker (2010) analytical
 938 solution (Eq. 4), plotted against the observed values, F_{Obs} .
 939 Logarithmically-scaled axes provide improved clarity at small
 940 F values, where all of the summer points and about half of
 941 the winter points are clustered. The dashed line represents
 942 the hypothetical case whereby theory and observation agree
 943 perfectly.

- 8 Conditions under which photosynthesis amplification factors,
 944 Ψ , and irradiance amplification factors, F , may converge (left
 945 hand panels) or differ (right hand panels). See text for expla-
 946 nation. Irradiances are observed values (30 minute averages).
 947 Rates of photosynthesis are inferred using the relevant $P-I$
 948 equations (see Theory). Times of low and high waters are de-
 949 noted by LW and HW respectively in the uppermost panels.
- 9 Numerical model output over a year at 1 m below the level
 951 of LWST. Panel (a) shows daily mean tidal range, \bar{R} , and
 952 its springs-neaps variation, for reference. (b) shows the daily
 953 tidal irradiance amplification factor, F . (c) and (d) show the
 954 analogously defined daily tidal photosynthesis amplification
 955 factor, Ψ , determined at the thallus and community scales,
 956 respectively. Peaks in F and Ψ are labelled S (springs) or
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 958 year. The sense ‘switching’ behaviour of cycles in Ψ at the
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 960 discussed in the text. Input values were representative of the
 961 Bay of Brest, and of a thallus of *Saccharina latissima* (in the
 962 case of (c)) or an established macroalgal community (in the
 963 case of (d)).
 964

965 10 Springs-neaps irradiance amplification factors, F_{SN} , and springs-
 966 neaps photosynthesis amplification factors, Ψ_{SN} , output by
 967 the numerical model for a depth of 1 m below LWST in the
 968 Bay of Brest. Two Ψ_{SN} curves are shown, representing model
 969 runs with $P-I$ parameterisations appropriate at the thallus
 970 scale and at the community scale. The dash-dotted line indi-
 971 cates the threshold above which amplification is said to have
 972 occurred and below which reduction has occurred.

Tables

Table 1: Input parameters and their values for the numerical model. Surface irradiance and tidal parameters were selected to be representative of the Bay of Brest. Photosynthesis parameters were selected to be representative of a thallus of *Saccharina latissima* or an established macroalgal community (see text).

Parameter	Symbol(s)	Value
Sea surface irradiance parameters		
Latitude of Bay of Brest	γ	48.3°
Solar constant (PAR component)*	I_{SC}	2400 $\mu\text{mol quanta m}^{-2} \text{s}^{-1}$
Atmospheric attenuation coeff.	k_{Atmos}	0.01
Tidal cycle parameters		
M_2 period	-	12.421 h
S_2 period	-	12 h
M_2 amplitude	-	2.1 m
S_2 amplitude	-	1.0 m
M_2 phase	-	0°
S_2 phase	-	180°
\bar{k}_{PAR} variation parameters (dependence on \bar{R})		
Max. (winter) gradient	m	0.1 m^{-2}
Intercept	c	0.4 m^{-1}
Photosynthesis parameters		
Max. rate of photosyn.	$P_{m,t}$, $P_{m,c}$	1 (arbitrary units)
Optimum irradiance**	$I_{m,t}$	300 $\mu\text{mol quanta m}^{-2} \text{s}^{-1}$
Saturation onset irradi.**	$I_{k,t}$	100 $\mu\text{mol quanta m}^{-2} \text{s}^{-1}$
Saturation onset irradi.***	$I_{k,c}$	291 $\mu\text{mol quanta m}^{-2} \text{s}^{-1}$

* A solar constant of 1373 W m^{-2} (total solar irradiance) is assumed, of which approximately 38% (521.74 W m^{-2}) is PAR (Kirk, 1994). This is multiplied by the approximate conversion factor $4.6 \mu\text{mol quanta J}^{-1}$, which arises from assuming PAR has a mean wavelength of 550 nm, to provide the PAR component in the appropriate units for this study. ** Approximated from Gévaert et al. (2003), and applied to the thallus-scale P - I equation (Eq. 7). *** Value from Middelboe et al. (2006), and applied to the community-scale P - I equation (Eq. 8).

Figures

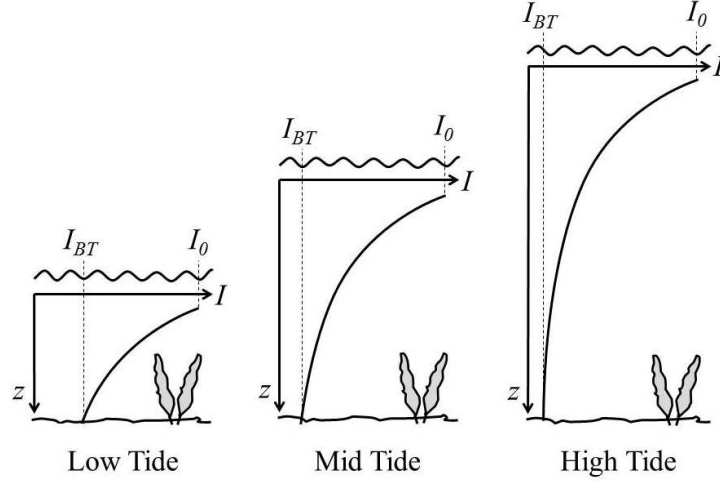


Figure 1: Schematic demonstrating how the exponential attenuation of irradiance, I , with depth, z , can lead to tidal amplification (after Bowers and Brubaker (2010)). The disproportionately large ‘gain’ in tidally-modulated seabed irradiance, I_{BT} , at low tide (compared to that at mid tide) is not matched by the similarly defined ‘loss’ at high tide. The magnitude of the amplification will depend upon the diffuse attenuation coefficient, k_{PAR} (which controls the rate of exponential attenuation with depth), and the tidal range, R . Sea surface irradiance, I_0 , varies throughout the day (not illustrated), meaning that the timing of low waters, t_{lw} , and the daylength, L , are also important.

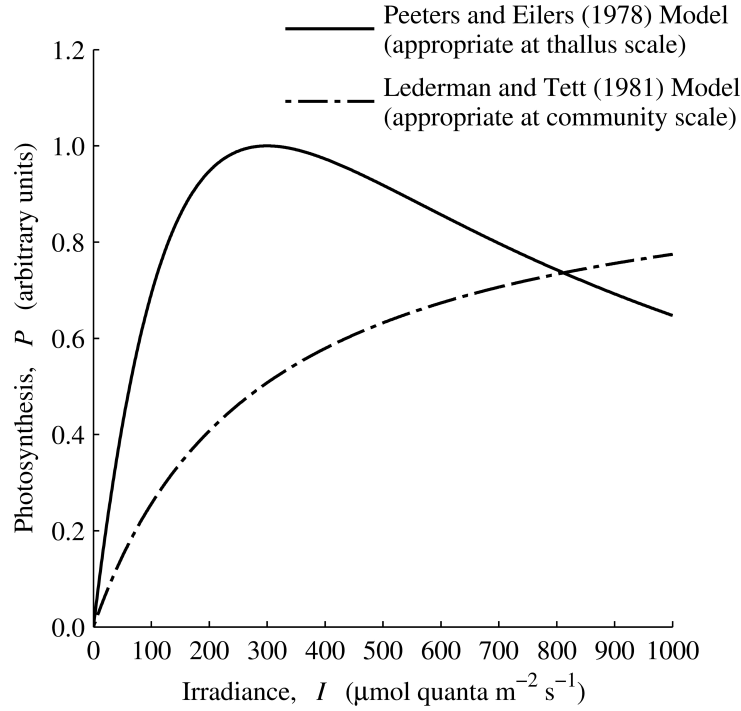


Figure 2: Photosynthesis-irradiance ($P-I$) curves generated using the two equations employed in this study. The Peeters and Eilers (1978) Model (Eq. 7) is appropriate for thallus-scale photosynthesis, and input values used to produce the curve are representative of *Saccharina latissima* (values from Gévaert et al., 2003). The Lederman and Tett (1981) Model (Eq. 8) is appropriate for macroalgal community-scale photosynthesis, and input values used were from Middelboe et al. (2006). See Table 1 for input values.

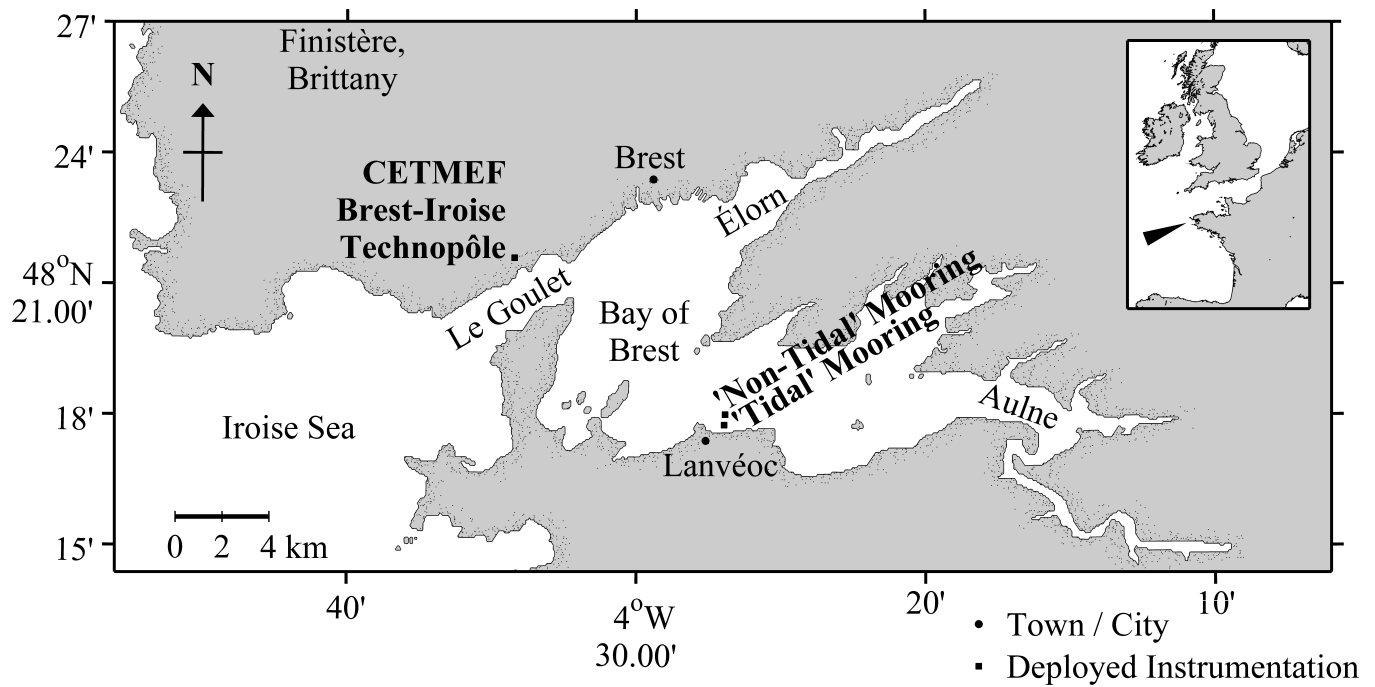


Figure 3: The Bay of Brest study site at the western extremity of the Brittany Peninsula (inset). Deployed instrumentation is indicated with black squares and a bold typeface (see text for details).

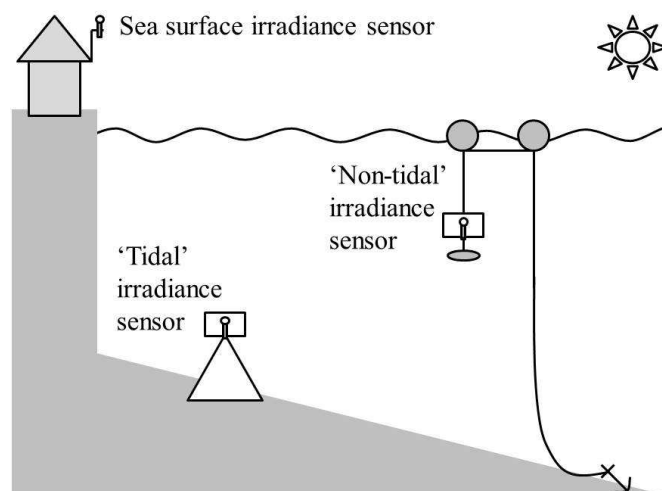


Figure 4: Schematic of the moorings deployed to observe tidal irradiance amplification.

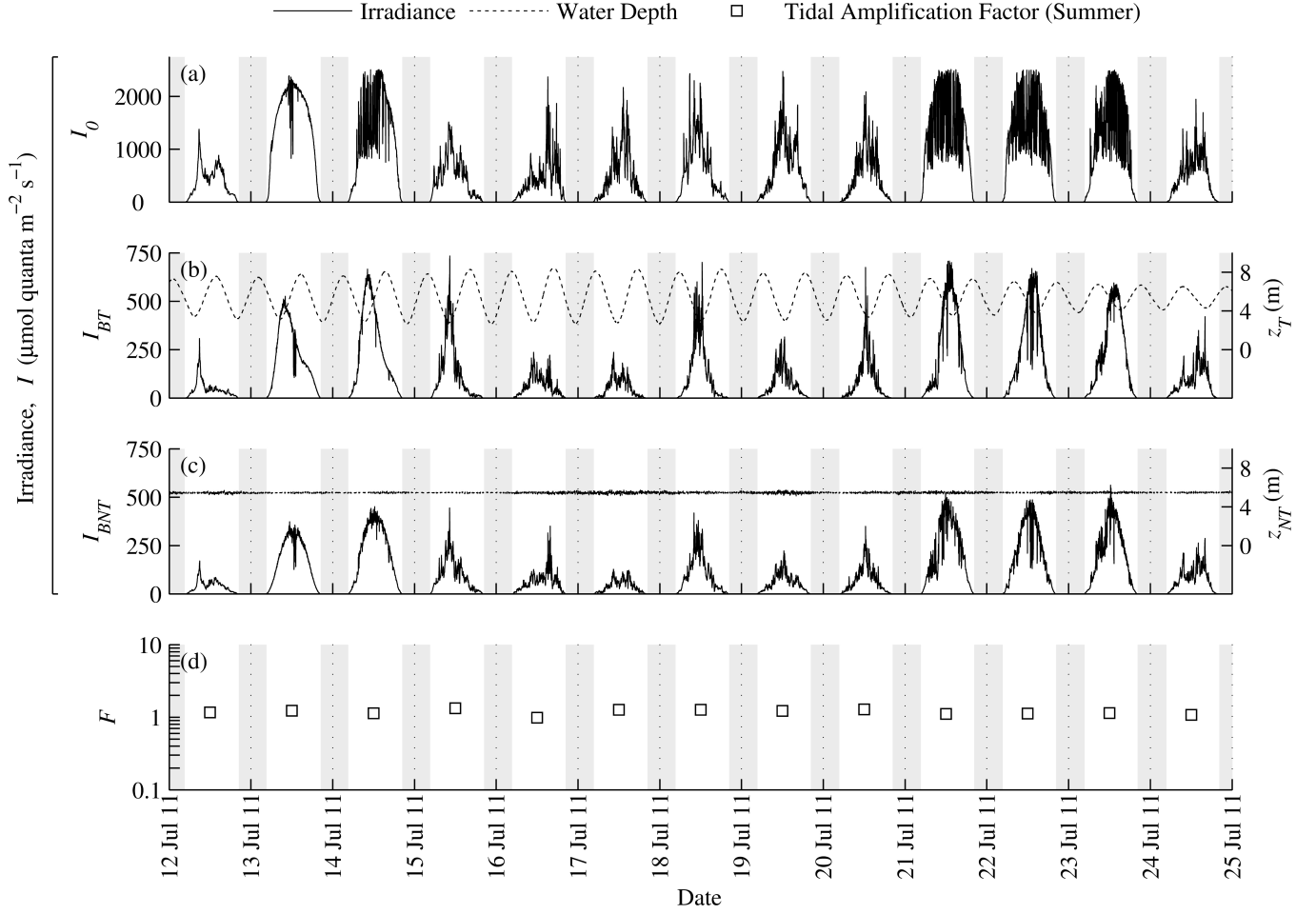


Figure 5: Summer campaign time series data. Panel (a) shows sea surface irradiance, I_0 ; (b) shows tidally-modulated seabed irradiance, I_{BT} , and water depth, z_T , from the bed frame; and (c) shows ‘non-tidal’ sub-surface irradiance, I_{BNT} , and water depth, z_{NT} , from the surface-moored frame. Panel (d) displays daily tidal irradiance amplification factors, F , determined in accordance with Eq. 2 (daily irradiance totals estimated by numerical integration using the trapezium rule). Note the \log_{10} scale used on the vertical axis. Grey-shaded areas represent night-time.

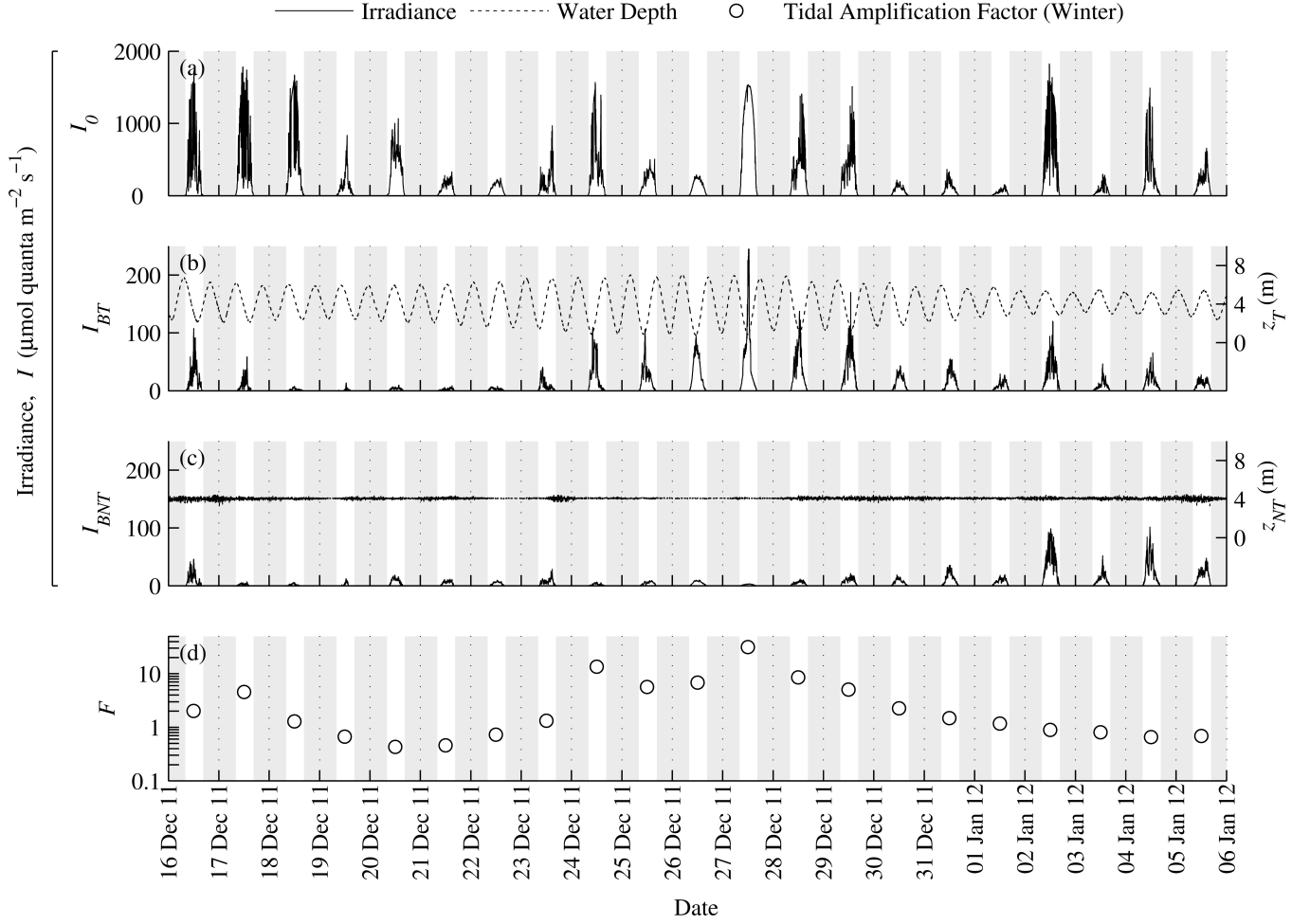


Figure 6: Winter campaign time series data. Panel (a) shows sea surface irradiance, I_0 ; (b) shows tidally-modulated seabed irradiance, I_{BT} , and water depth, z_T , from the bed frame; and (c) shows ‘non-tidal’ sub-surface irradiance, I_{BNT} , and water depth, z_{NT} , from the surface-moored frame. Panel (d) displays daily tidal irradiance amplification factors, F , determined in accordance with Eq. 2 (daily irradiance totals estimated by numerical integration using the trapezium rule). Note the \log_{10} scale used on the vertical axis. Grey-shaded areas represent night-time.

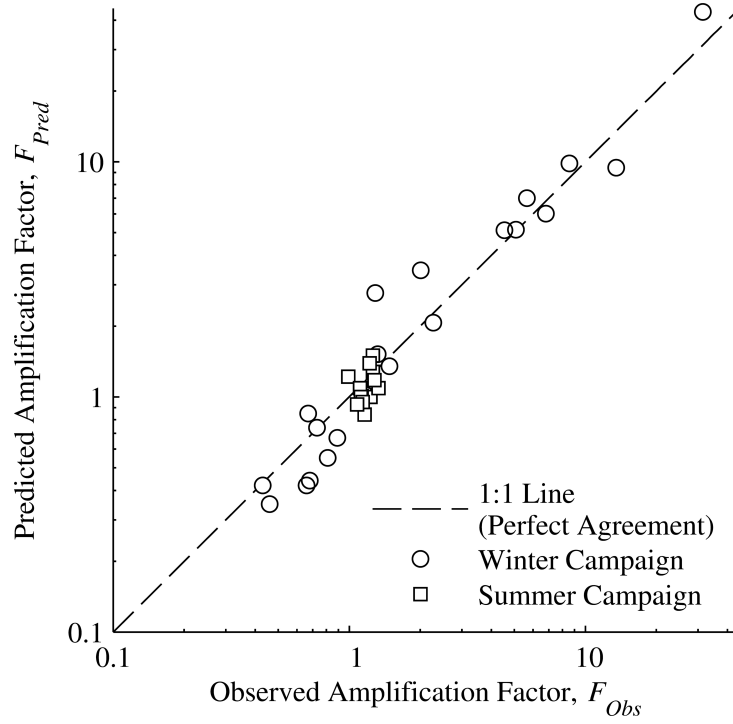


Figure 7: Predicted daily tidal irradiance amplification factors, F_{Pred} , generated using the Bowers and Brubaker (2010) analytical solution (Eq. 4), plotted against the observed values, F_{Obs} . Logarithmically-scaled axes provide improved clarity at small F values, where all of the summer points and about half of the winter points are clustered. The dashed line represents the hypothetical case whereby theory and observation agree perfectly.

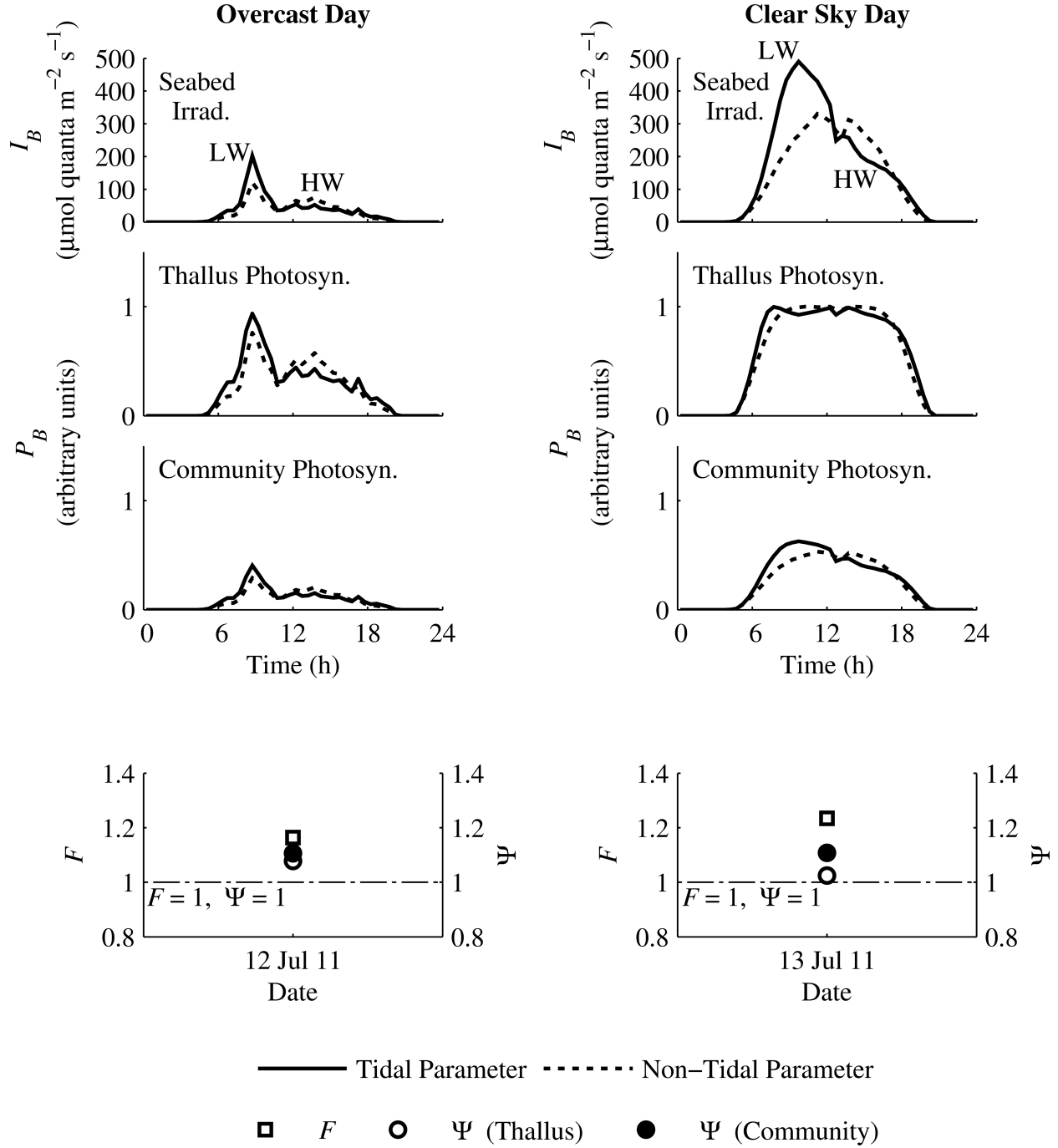


Figure 8: Conditions under which photosynthesis amplification factors, Ψ , and irradiance amplification factors, F , may converge (left hand panels) or differ (right hand panels). See text for explanation. Irradiances are observed values (30 minute averages). Rates of photosynthesis are inferred using the relevant P - I equations (see Theory). Times of low and high waters are denoted by LW and HW respectively in the uppermost panels.

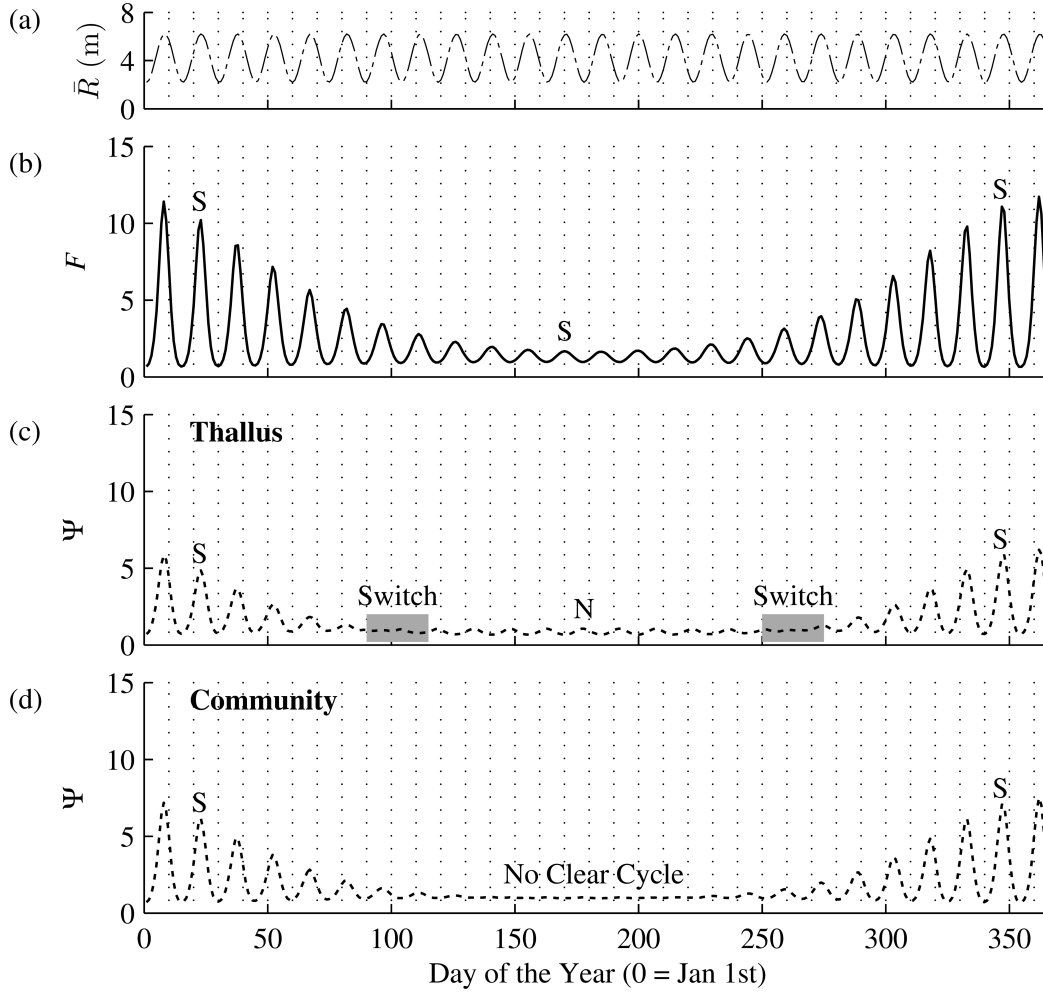


Figure 9: Numerical model output over a year at 1 m below the level of LWST. Panel (a) shows daily mean tidal range, \bar{R} , and its springs-neaps variation, for reference. (b) shows the daily tidal irradiance amplification factor, F . (c) and (d) show the analogously defined daily tidal photosynthesis amplification factor, Ψ , determined at the thallus and community scales, respectively. Peaks in F and Ψ are labelled S (springs) or N (neaps) to denote the sense of cycles at various times of year. The sense ‘switching’ behaviour of cycles in Ψ at the thallus scale, and the lack thereof at the community scale, is discussed in the text. Input values were representative of the Bay of Brest, and of a thallus of *Saccharina latissima* (in the case of (c)) or an established macroalgal community (in the case of (d)).

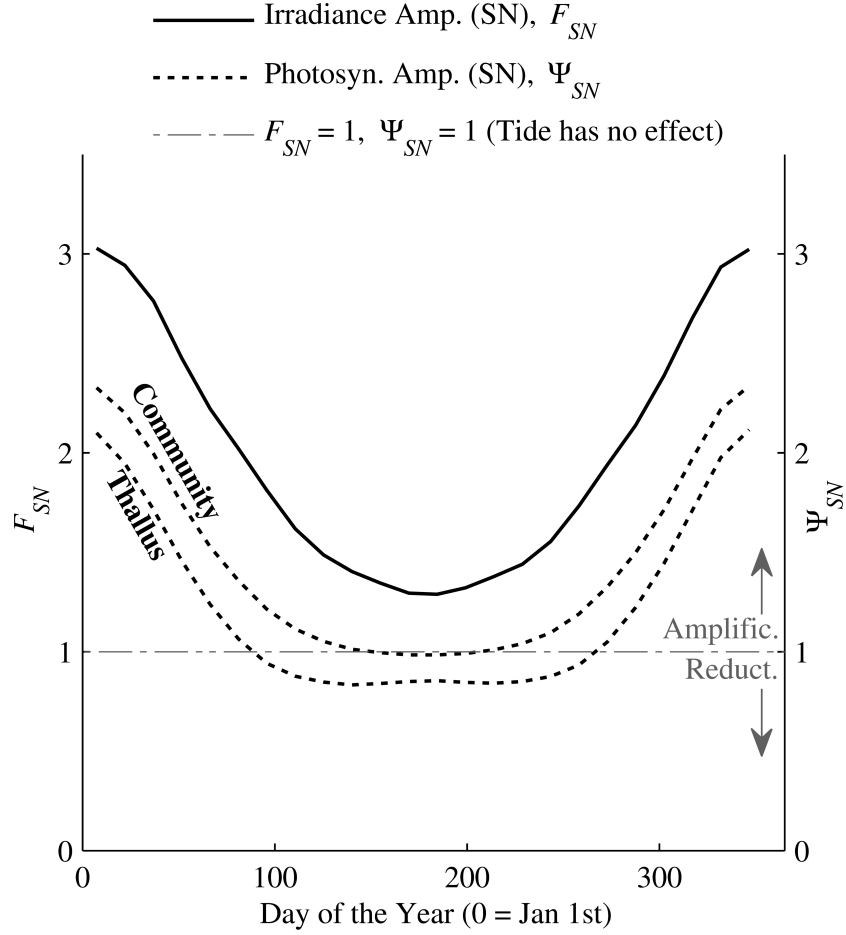


Figure 10: Springs-neaps irradiance amplification factors, F_{SN} , and springs-neaps photosynthesis amplification factors, Ψ_{SN} , output by the numerical model for a depth of 1 m below LWST in the Bay of Brest. Two Ψ_{SN} curves are shown, representing model runs with P - I parameterisations appropriate at the thallus scale and at the community scale. The dash-dotted line indicates the threshold above which amplification is said to have occurred and below which reduction has occurred.