Springs–neaps cycles in daily total seabed light: Daylength-induced changes

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ABSTRACT

In shallow, tidal seas, daily total seabed light is determined largely by the interaction of the solar elevation cycle, the tidal cycle in water depth, and any temporal variability in turbidity. Since tidal range, times of low water, and often turbidity vary in regular ways over the springs–neaps cycle, daily total seabed light exhibits cycles of the same periodicity. Corresponding cycles are likely to be induced in the daily total primary production of benthic algae and plants, particularly those light-limited specimens occupying the lower reaches of a sub-tidal population. Consequently, this effect is an important control on the growth patterns, depth distribution and survival of, for example, macroalgal forests and seagrass meadows.

Seasonal changes in daylength exert an important additional control on these cycles, as they alter the fraction of the tidal and turbidity cycles occurring within daylight hours. Bowers et al. (1997) modelled this phenomenon numerically and predicted that for a site with low water at about midday and midnight at neaps tides, 6 am and 6 pm at springs, daily total seabed light peaks at neaps in winter, but the 'sense' of the cycle 'switches' so that it peaks at springs in summer — the longer daylength permits the morning and evening low water springs to contribute substantially to the daily total. Observations for such a site in North Wales (UK), presented in this paper, show that no such 'switch' occurs, and neaps tides host the largest daily totals throughout the year. The predicted 'switch' is not observed because turbidity increases generally at spring tides, and specifically at low water springs, both of which were not accounted for in the model. Observations at a second site in Brittany (France), diametrically opposite in terms of the times of low water at neaps and at springs, indicate a peak at springs throughout the year.

Analytical tools are developed to calculate the percentage of daily total sea surface irradiance reaching the bed at a site of interest on any given day, and to determine the sense of any springs–neaps cycle thereof for a given season. The conditions required for a 'switch' are explored graphically, resulting in the identification of criteria (and a useful parameter) for predicting their occurrence. Consequences for the growth patterns, depth limits and long-term survival of benthic algae and plants are discussed.

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1. Introduction

Light is of primary importance to most biological communities as it provides the energy required for photosynthesis. Ambient light fields are rarely spatially homogenous and almost always vary in time. In marine environments, the ebb and flood of the tide, changes in water clarity, variable sea surface reflectance, and wave-lensing effects combine to increase the variability in the quantity and quality of light reaching benthic algae or plants far beyond that at Earth's surface, as experienced by terrestrial ecosystems (Dring, 1992; Kirk, 1994; Lobban and Harrison, 1997).

High temporal variability in seabed light means that benthic algae and plants experience periods of sufficient and insufficient light over a range of timescales (Anthony et al., 2004). Whilst they are able to store photosynthate, and thus survive extended (but largely unknown) periods of insufficient light (Vant et al., 1986), the growth and survival of an alga or plant ultimately depend upon its ability to maintain a positive energy balance in the longer term (Dennison, 1987; Duarte, 1991). This means that it must receive sufficient light to permit net photosynthesis frequently enough and for sufficient duration to offset periods of lesser light availability and net respiration. It follows that any regular temporal patterns in light availability, such as those imposed by the tide (Bowers et al., 1997; Dring, 1987), are highly important in regulating the growth, depth distribution and long-term survival of benthic algae and plants.

The amount of light incident upon the sea surface at a point in time is governed by the solar elevation (a function of time of day, time of year, and latitude) and the nature of any cloud cover. Some incident light is reflected at the air–sea boundary. If solar elevation is low and the water's surface is very smooth the reflected fraction can be large

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(Kirk, 1994). However, under most conditions the majority of incident light penetrates into the water column. There, it is scattered and absorbed such that it is often greatly attenuated by the time it reaches the seabed. The degree of attenuation is determined by the water depth and the clarity, or conversely the turbidity, of the water. In a shallow, tidal sea, therefore, temporal patterns in light at the seabed are largely governed by the interaction of three cycles: the solar elevation cycle; the tidal cycle in water depth; and any cyclical behaviour in turbidity.

Springs–neaps modulations are present in tidal and turbidity cycles at sites with appreciable lunar semi-diurnal (M_2) and solar semi-diurnal (S_2) tidal constituents. The tidal range grows (spring tides) and shrinks (neaps tides) with a 14.79 day periodicity, as the tide generating forces of the moon and the sun are aligned or anti-aligned. Furthermore, the times of low water advance by about 50 min each day over the springs–neaps cycle, as the period of the larger amplitude M_2 constituent is 12 h 25 min. Temporal patterns in instantaneous seabed irradiance will, therefore, evolve from day to day as the springs–neaps cycle progresses. Since daily total seabed irradiance is given by the area beneath these instantaneous irradiance curves, a corresponding springs–neaps cycle might be expected in the daily totals also. These cycles are the subject of this paper. Their importance lies in their potential ability to induce similar cycles in daily total benthic primary production, particularly of those light-limited plants and algae occupying the lower reaches of a sub-tidal population.

The exact variations in tidal range and turbidity over the springs–neaps cycle are (locally) exclusive to a particular site. Furthermore, the times of low water at different phases of the springs–neaps cycle are also site-specific; the times of low water at springs and neaps, for example, can be understood to be determined by the phase of the S_2 tide at that site (in this paper, expressed as the phase lag, in degrees, of the S_2 tidal constituent behind the corresponding constituent of the equilibrium tide at Greenwich) (Pingree and Griffiths, 1981). Thus, the form of any springs–neaps pattern in daily total seabed irradiance will be highly site-specific. It will not, however, be constant over time. Seasonal changes in daylength exert an important additional control on the patterns, as they alter the fraction of the tidal water depth (and turbidity) cycles occurring within daylight hours. This additional control is the primary focus of the current work.

The importance of the tide as a control on seabed irradiance has been noted by several authors (Anthony et al., 2004; Bowers and Brubaker, 2004, 2010; Carter and Rybicki, 1990; Gévaert et al., 2002, 2003; Koch and Beer, 1996; Pilgrim and Millward, 1989; Topliss et al., 1980). Regular changes in instantaneous and daily total seabed irradiance over the springs–neaps cycle have been explored theoretically by Dring (1987) and by Bowers et al. (1997). Observations of this phenomenon have also been reported: for winter in the Irish Sea by Topliss (1977); and for autumn and winter in the southern North Sea by Dring and Lüning (1994).

Bowers et al. (1997) modelled the springs–neaps cycle in daily total seabed irradiance for a site in North Wales (UK) with an S_2 phase of about 0°. Such a site always has low waters occurring at about 6 am and 6 pm (GMT) at spring tides; they will have advanced incrementally to about midday and midnight by neaps, seven days later. Interestingly, they predicted a 'switch' would occur in the 'sense' of the cycle; it would peak at neaps, or be *neaps-dominated*, in winter, owing to the low water of neaps tides occurring at midday. However, as the daylength increases with the arrival of summer, the morning and evening low waters of spring tides would contribute sufficiently to the daily total for it to exceed that at neaps and for the cycle to become *springs-dominated*. The turbidity was treated as constant over time in this numerical model, which is unlikely to be the case, and so it is unclear whether this switch occurs in reality.

In this paper, winter and summer observations of seabed irradiance are presented for the study site modelled in Bowers et al. (1997). The observations are used to test the aforementioned prediction of a switch. We investigate how the original prediction is affected by efforts to

model variation in turbidity appropriately. Finally, analytical equations are developed for calculating two parameters at sites of interest: the percentage of daily total sea surface irradiance reaching the bed on any given day, P; and the 'springs–neaps dominance ratio', $D_{S/N}$ — a ratio devised to indicate the 'sense' of the cycle (i.e., springs- or neaps-dominated) for a given time of year. Both tools offer practical means of probing springs–neaps cycles in P, and they can be applied in winter and summer to identify, or rule out, a switch. However, we finish the paper by offering some graphical tools and mathematical criteria for identifying the possibility of such a switch more easily.

2. Materials and methods

2.1. Site description

Two study sites feature in this paper. The focus is on Menai Strait (North Wales, UK) data throughout. Data from the Bay of Brest (Brittany, France) are included to provide an additional test of the analytical tools presented.

2.1.1. Menai Strait, North Wales

The Menai Strait (Fig. 1) is a narrow, shallow sea strait separating the Isle of Anglesey from the North Wales mainland. It occupies a composite valley, which was submerged following deglaciation (Embleton, 1964). It is orientated southwest to northeast, has a minimum width of about 300 m, a maximum width of about 2 km, and a length of 20 km.

The depth of the strait below Lowest Astronomical Tide (LAT) varies from a maximum of 22 m, just to the northeast of the mooring, to a minimum of 1–2 m, at the southwest end, where a sandy sill exists near Caernarvon (Harvey, 1968). Irregular bed topography makes the identification of a single representative depth difficult. However, a mean depth estimate in the region 10–15 m is sensible and a value of 13 m was used for modelling purposes by Bowers (2003).

The dynamics of the water flow in the strait are dominated by tidal forcing (Kratzer et al., 2003). The average tidal range is 6.5 m at spring tides and 3.5 m at neaps tides (Buchan et al., 1967; Harvey, 1968), and strong tides are characteristic; the mean tidal current is 0.7 m s^{-1}, though currents over 1 m s^{-1} occur at spring tides (Bowers, 2003). Consequently, the water column remains vertically mixed throughout the year, with little difference between surface and bottom water in terms of temperature, salinity and suspended particulate matter (SPM) (Buchan et al., 1967).

The combination of a large tidal excursion (14 km at springs) relative to the length of the strait and a tide-induced residual flow to the southwest (Harvey, 1968) ensures that the strait is well flushed with water from the Irish Sea. Freshwater discharge into the strait (predominantly by the Ogwen and Seiont Rivers) is small compared with both the tidal prism and the residual flow; the salinity is typically in the range 32–34 (Buchan et al., 1967) — much like that of the adjacent regions of the Irish Sea.

Other than at the sandy, southwest end, the bed is rocky and scoured at the narrow, turbulent sections (which typically host steep, rocky shoals) and thick mud is deposited near the inner banks of some bends and in embayments, where the tidal scour is relatively weak (Buchan et al., 1967). At the site of our mooring (53°12.52′N 4°12.18′W), the bed is of compacted mud and boulders, and is sufficiently level for the deployment of a bed frame hosting instrumentation.

The water flowing through the Menai Strait usually carries a heavy load of SPM (Buchan et al., 1967). Optically, therefore, light attenuation is strongly influenced by this suspended material, but it is also influenced by coloured dissolved organic matter (CDOM) and, intermittently, phytoplankton blooms.

The phase of the S_2 tide at the Menai Strait is approximately 0° (referenced to Greenwich) (Pingree and Griffiths, 1981). Consequently, high water spring tides occur at midday and midnight (GMT). At neaps tides, it is the low waters that occur at these times.