Technical Note: Estimating light-use efficiency of benthic habitats using underwater O₂ eddy covariance

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0. Abstract

Light-use efficiency defines the ability of primary producers to convert sunlight energy to primary production and is computed as the ratio between the gross primary production and the intercepted photosynthetic active radiation. While this measure has been applied broadly within the atmospheric sciences to investigate resource-use efficiency in terrestrial habitats, it remains underused within the aquatic realm. This report provides a conceptual framework to compute hourly and daily light-use efficiency using underwater O₂ eddy covariance, a recent technological development that produces habitat-scale rates of primary production under unaltered in situ conditions. The analysis, tested on two flux datasets, documents that hourly light-use efficiency may approach the maximum theoretical limit of 0.125 O₂ photon⁻¹ under low light conditions but it decreases rapidly towards the middle of the day and is typically an order of magnitude lower on a 24 h basis. Overall, light-use efficiency provides a useful measure of habitat functioning and facilitates site comparison in time and space.

1. Introduction

1.1 Eddy covariance estimates of benthic primary production

Underwater eddy covariance (EC) is a recent technological development that has emerged as an important tool in benthic primary production studies. One of its key attributes is that it generates benthic O₂ fluxes at a high temporal resolution (typically ~15 min) over several days, and it does so for large seafloor areas (10s of m², i.e. on a habitat-scale) and under unaltered in situ conditions (Berg et al.,
Eddy covariance thus overcomes many of the limitations of traditional methods (e.g. chamber incubations) and enables primary production rates to be measured within a wide range of benthic habitats (Chipman et al., 2016; Hume et al., 2011; Long et al., 2013; Volaric et al., 2018; Attard et al., 2019b). Additionally, the EC method can resolve very small benthic fluxes down to ~1 mmol O$_2$ m$^{-2}$ d$^{-1}$ or less (Berg et al., 2009; Donis et al., 2016), which allows reliable measurements of primary production to be made in low-activity benthic settings, such as in high-latitude environments in winter and in deep phototrophic communities (Attard et al., 2014; Attard et al., 2016).

### 1.2 Constraining hourly and daily GPP

Sources of variability within EC O$_2$ fluxes can be broadly grouped into two categories, namely (1) sources that bias the measured EC flux away from the ‘true’ benthic flux (i.e. when EC O$_2$ flux ≠ benthic O$_2$ flux) due to e.g. non-steady state conditions within the benthic boundary layer and (2) ‘true’ temporal variability in the benthic O$_2$ exchange rate (i.e. when EC O$_2$ flux = benthic O$_2$ flux) due to e.g. flow-induced advective pore water exchange in highly permeable sediments (Table 1). Despite there being numerous sources of variability, high-quality EC fluxes often show a tight coupling to sunlight (photosynthetic active radiation, PAR) availability on the hourly timescale, indicating a dominant primary production signal in many aquatic systems (Berg et al., 2013; Chipman et al., 2016; Attard et al., 2014; Attard et al., 2015; Rheuban et al., 2014; Long et al., 2013; Long et al., 2015; Koopmans et al., 2020; Rovelli et al., 2017).

Under ideal conditions, the measured EC fluxes represent the balance between habitat GPP and $R$. Hourly and daily GPP may therefore be computed from the EC fluxes by offsetting daytime fluxes by the dark $R$ rate, as $GPP = FLUX_{day} + |FLUX_{night}|$. It is well known that this approach provides
conservative estimates of GPP, since R typically is higher during daytime in the presence of photosynthesis (Fenchel and Glud, 2000; Hotchkiss and Hall, 2014). Indeed, several EC studies have documented lower O₂ effluxes in the evening than in the morning under similar light intensities (a so-called ‘hysteresis’), and high R rates at the onset of darkness (Rovelli et al., 2017; Rheuban et al., 2014; Koopmans et al., 2020). It is generally understood that R is stimulated by GPP; it increases progressively throughout the day as labile photosynthates accumulate (Epping and Jørgensen, 1996; de Winder et al., 1999), and the magnitude of the hysteresis is related to the light history (Adams et al., 2016). While it is highly relevant to quantify daytime R, direct measurements are usually not available.

1.3 Light-use efficiency

Gross primary production can be formulated as the product of incident PAR, the fraction of absorbed PAR (fAPAR), and the light-use efficiency (LUE), that is \( GPP = PAR \times fAPAR \times LUE \) (Monteith et al., 1977). The LUE indicates the efficiency with which absorbed PAR is converted to GPP. This approach has been applied broadly within the atmospheric sciences to investigate crop yield, productivity and resource-use efficiency among terrestrial biomes using eddy covariance flux tower data (Stocker et al., 2018; Hemes et al., 2020). In aquatic environments, the LUE has been applied primarily on the microscale to investigate energy budgets of photosynthetic microbial mats and symbiont-bearing corals (Al-Najjar et al., 2010; Al-Najjar et al., 2012; Brodersen et al., 2014). These detailed measurements have revealed that most (> 80 %) of the incident solar energy is dissipated as heat, and conservation by photosynthesis typically is < 5 %. Despite low energy utilization, some benthic ecosystems such as coral reef symbionts seem particularly efficient at converting PAR to GPP, with LUE approaching the theoretical limit of 8 mol photons of PAR required to produce 1 mol of O₂ through GPP (0.125 O₂
photon$^{-1}$) (Brodersen et al., 2014). To our knowledge there is one study using chamber incubations that employs the \textit{LUE} approach to investigate benthic primary production in lakes (Godwin et al., 2014), and this remains unexplored within underwater EC studies. Since the \textit{EC} method can produce hourly and daily \textit{GPP} measurements across many different habitat types (Attard et al., 2019b), applying the \textit{LUE} approach could provide a useful measure of the efficiency with which solar energy is converted to \textit{GPP} on the spatial scale of whole habitats. A key requirement for computing the \textit{LUE} is to have reliable estimates of \textit{GPP}. In this report we will therefore aim to provide a conceptual framework for computing hourly \textit{GPP} from EC fluxes, and from this, compute the \textit{LUE}. We then test this approach on measured EC flux data.

2. Materials and methods

2.1 Eddy covariance data

This study uses a four day long EC data from Attard et al. (2014) and a three day long dataset from Attard et al. (in review). Attard et al. (2014) performed seasonal measurements at subtidal (3-22 m depth) light-exposed benthic habitats in a sub-Arctic fjord in Greenland, whereas Attard et al. (in review) conducted their seasonal study on a 5 m deep mussel reef in the Baltic Sea. Two flux datasets were selected from these two studies to represent datasets with and without flux hysteresis. Instrument setup and data processing is described in detail in these papers. In short, the EC instrumentation consisted of a single-point acoustic velocimeter (Vector, Nortek), a fast-response O$_2$ microsensor setup (McGinnis et al., 2011), and a downwelling cosine \textit{PAR} sensor (QCP-2000, Biospherical Instruments or LI-192, Li-Cor) mounted onto the frame. The instrument was deployed from a small research vessel and was left to collect data over several days. Benthic O$_2$ fluxes were extracted for consecutive 10- or 15-
min periods using the software package SOHFEA (McGinnis et al., 2014), and the fluxes were bin-
averaged to 1 h for interpretation.

2.2 Computing hourly GPP

2.2.1 Defining a daytime $R$ rate

Time series of EC fluxes were split into individual 24 h sections representing periods from midnight to midnight. Each 24 h time series was aligned with corresponding seabed $PAR$ data. Daytime periods were defined as periods when $PAR > 2.0 \ \mu$mol m$^{-2}$ s$^{-1}$. Each 24 h section therefore had two night-time periods- the first from midnight to sunrise ($N_1$), and the second from sunset to midnight ($N_2$). Four options for computing the daytime $R$ rate were explored. The first two approaches assumed a static $R$ rate during the day whereas the third and fourth approaches assumed dynamic (time-variable) daytime $R$. In the first approach, daytime fluxes were offset by $|N_1|$ and in the second approach, daytime $R$ was defined as an average of $N_1$ and $N_2$ fluxes ($|N_1 + N_2|$). These two approaches are expected to work best when $O_2$ fluxes do not show a hysteresis. However, for other datasets that do show substantial hysteresis, this approach might underestimate $R$ (and therefore $GPP$) in the second half of the day. The third and fourth approach attempted to correct for this by assuming a dynamic hourly daytime $R$ rate that increases progressively throughout the day. The third approach assumed a linear increase in hourly daytime $R$ with time from $|N_1|$ to $|N_2|$, whereas the fourth approach assumed a sigmoidal increase with time from $|N_1|$ to $|N_2|$ in concert with changes in seabed $PAR$. To calculate the shape of the sigmoidal curve for this fourth approach, the $PAR$ time series was integrated over time and the resultant data were fitted with a sigmoidal (Boltzmann) function as:
\[ \int_{0}^{24} PAR(t) = A_2 + (A_1 - A_2)/(1 + \exp \left(\frac{PAR - x_0}{dx}\right)) \]

where \( A_1 \) and \( A_2 \) were the initial and final \( PAR \) values, \( x_0 \) is the centre of the curve, and \( dx \) is a time constant. This function gave very tight fits to the integrated \( PAR \) data \((R^2 > 0.99)\). The fitting parameters \( x_0 \) and \( dx \) were then used to define the sigmoidal increase in daytime respiration from \( A_1 \) to \( A_2 \) (\(|N_1| \) to \(|N_2|\)). Hourly daytime \( R \) rates were computed using this approach, and then summed with their corresponding measured daytime flux to compute the \( GPP \).

### 2.2.2 Light-saturation curves

The ability of the four approaches to produce reliable estimates of hourly \( GPP \) was evaluated using light-saturation curves. Several mathematical formulations are available to investigate photosynthetic performance (Jassby and Platt, 1976), but benthic studies typically use linear regression or the tangential hyperbolic function by Platt et al. (1980):

\[ GPP = P_m \times \tanh \left( \frac{\alpha I}{P_m} \right) \]

where \( P_m \) is the maximum rate of benthic gross primary production (in mmol O\(_2\) m\(^{-2}\) h\(^{-1}\)), \( I \) is the near-bed irradiance (PAR; in \( \mu \)mol photons m\(^{-2}\) s\(^{-1}\)), and \( \alpha \) is the quasi-linear initial slope of the curve (mmol O\(_2\) m\(^{-2}\) h\(^{-1}\) \([\mu \text{mol PAR m}^{-2} \text{s}^{-1}]\)). From these curves it is possible to derive the photoadaptation parameter \( I_k \) (\( \mu \)mol PAR m\(^{-2}\) s\(^{-1}\)) as \( I_k = P_m/\alpha \). If we assume that hourly benthic \( GPP \) is predominantly driven by \( PAR \), then high-quality light saturation curves for \( GPP \) should (a) show a high correlation with \( PAR \) (high \( R^2 \) value), and (b) have a low standard error for the fitting parameters \( P_m, \alpha, \) and \( I_k \). High-quality hourly \( GPP \) values should also be non-negative. Non-linear curve fitting was performed in OriginPro.
2020 using a Levenberg-Marquardt iteration algorithm, and the standard error of the fitting parameters was scaled with the square root of reduced chi-squared statistic.

2.3 Estimating light-use efficiency

2.3.1 Constraining the fraction of absorbed PAR (fAPAR)

Direct measurements of fAPAR can be made using two PAR sensors to resolve both incident and reflected PAR. In benthic environments, PAR absorbance typically is above 80% of incident near-bed irradiance in sedimentary habitats and approaches 100% in habitats with greater structural complexity (higher light scattering) such as in seagrass beds (Al-Najjar et al., 2012; Zimmerman, 2003). Therefore, while it is advisable (and feasible) to quantify both incident and reflected PAR throughout the EC deployment for LUE estimates, assuming fAPAR = 1.0 is expected to only induce a slight bias (underestimate) to the LUE. Since fAPAR was not measured in the studies by Attard et al. (2014) and Attard et al (in review), this study assumes fAPAR = 1.0. To test the validity of this assumption, direct measurements of fAPAR were made on a separate occasion at a site with bare sediments in Oslofjord in Norway in July 2019. Here, two cross-calibrated high-quality cosine PAR sensors (a Biospherical QCP-2000 and a Li-cor LI-192) were affixed to a frame and placed on the seafloor at a water depth of 8 m, with the sensors located 0.5 m above the seabed. The sensors logged incident and reflected PAR (µmol photons m⁻² s⁻¹) every minute over 3 days.

2.3.2 Computing hourly and daily light-use efficiency (LUE)

Once the best method for computing GPP was identified, hourly GPP was converted from units of mmol O₂ m⁻² h⁻¹ to µmol O₂ m⁻² s⁻¹ and the hourly LUE was computed as \( LUE_{\text{hourly}} = \frac{GPP_{\text{hourly}}}{PAR_{\text{hourly}} \times fAPAR} \), with units of O₂ photon⁻¹. Similarly, daily GPP (mmol O₂ m⁻² d⁻¹), computed as
\[ GPP = F_{\text{LUX}_{\text{day}}} + |F_{\text{LUX}_{\text{night}}}|, \] and daily integrated \( PAR \) (mmol photon m\(^{-2}\) d\(^{-1}\)) were used to compute daily \( LUE \) (O\(_2\) photon\(^{-1}\)) as \( LUE_{\text{daily}} = \frac{GPP_{\text{daily}}}{PAR_{\text{daily}} \times fAPAR} \).

3. Results and Discussion

3.1 Hourly \( GPP \) and light-saturation curves

In the four-day dataset from Greenland (Attard et al., 2014), hourly \( GPP \) ranged from 0 to 8 mmol O\(_2\) m\(^{-2}\) h\(^{-1}\) under maximum daytime irradiance of up to 400 \( \mu \)mol photons m\(^{-2}\) s\(^{-1}\). Hourly \( GPP \) measured in the first half of the day were very similar to rates resolved in the second half of the day under similar \( PAR \) intensities, indicating no substantial flux hysteresis (Fig. 1). Hourly \( GPP \) showed a tight correlation with seabed \( PAR \), with \( R^2 \) values for the light-saturation curves ranging from 0.83 to 0.93 (Fig. 1). Overall, the highest \( R^2 \) values for the light-saturation curves for this dataset were achieved using a static daytime \( R \) rate which was defined as an average of all night-time fluxes (\(|N_1 + N_2|\)). This approach achieved \( R^2 \) values in the light-saturation curves that were up to 10 % higher than when \( R \) was defined using the first night-time period alone (\(|N_1|\)).

In the EC dataset from the Baltic Sea, a clear hysteresis was observed in the O\(_2\) fluxes. Hourly O\(_2\) fluxes in the second half of the day were up to 4-fold lower than within the first half of the day under similar irradiance levels. Light-saturation curve \( R^2 \) values varied depending on the method used to define the daytime \( R \) rate (Fig. 2). In all three days from this dataset, the highest \( R^2 \) values were obtained using dynamic daytime \( R \) rates defined as either a linear or sigmoidal increase with time. These two approaches produced \( GPP \) estimates with the best quality: all hourly \( GPP \) values were positive, and the fitting parameters \( P_m, I_k \) and \( \alpha \) had the lowest standard errors (Fig. 2). While \( P_m \) and \( \alpha \) showed good...
agreement between the four methods, static $R$ approaches tended to overestimate the $I_k$ since hysteretic fluxes tend to bias light-saturation curves towards linearity.

Hourly $GPP$ computed using sigmoidal increases in daytime $R$ for the Baltic Sea dataset ranged from 0 to 7 mmol O$_2$ m$^{-2}$ h$^{-1}$ under $PAR$ levels of up to 350 µmol photons m$^{-2}$ s$^{-1}$ (Fig. 3). Light-saturation curves provided high $R^2$ values for day 1 and day 3 of 0.83 and 0.81. The light-saturation curve for day 2 converged to a linear fit with an $R^2$ of 0.94 (Fig. 3).

### 3.2 Light-use efficiency

Hourly $LUE$ estimates for the two datasets indicated high $LUE$ of up to 0.09 O$_2$ photon$^{-1}$ under light-limiting conditions of < 20 µmol $PAR$ m$^{-2}$ s$^{-1}$ (Fig. 4). Light-use efficiency declined quasi-exponentially with time (and $PAR$) to around one-tenth of the value by the middle of the day, and then it increased again towards sunset to $LUE$ values comparable to the morning. This observation is consistent with the microsensor and benthic chamber studies by Al-Najjar et al. (2012), Brodersen et al. (2014) and Godwin et al. (2014) who document maximum $LUE$ under light-limiting conditions and a decline in $LUE$ under high irradiance levels typical of the middle of the day. Daily $LUE$ estimated as the ratio between $GPP_{daily}$ and $PAR_{daily}$ (both in mmol mm$^{-2}$ d$^{-1}$) ranged from 0.008 to 0.013 O$_2$ photon$^{-1}$ in Greenland and was 0.006 to 0.007 O$_2$ photon$^{-1}$ in the mussel bed dataset from the Baltic Sea (Fig. 5). This indicates that the soft sediment habitat in Greenland had higher photosynthetic efficiency than the rocky mussel bed in the Baltic Sea on a daily timescale for the investigated data. However, in all cases daily $LUE$ is $\sim$ an order of magnitude or lower than the theoretical maximum of 0.125 O$_2$ photon$^{-1}$.

The $LUE$ values presented in this study are expected to be underestimated due to the assumption of $fAPAR = 1.0$ (i.e. by assuming that all incident $PAR$ is absorbed by the seabed). A fraction of the
incoming irradiance is reflected and thus is not available for photosynthesis. Reflected \( \text{PAR} \) ranged from 17.5 % to 1.9 % in the study on microbial mats by Al-Najjar et al. (2012) and was up to 12 % in the coral symbiont study by Brodersen et al. (2014). Direct measurements of \( f_{\text{APAR}} \) were not available for the datasets used in this study, but measurements from a bare sediments site in Oslofjord indicated reflected \( \text{PAR} \) on the order of 8-10 % (Fig. 6). It is therefore likely that the \( LUE \) estimates presented in this study are underestimated by \( \sim 10 \% \).

4. Conclusion

A key requirement of the \( LUE \) approach is high-quality \( GPP \) data. Despite there being numerous potential obstacles to obtaining this data (Table 1), a growing number of eddy covariance studies document tight relationships between hourly fluxes and sunlight availability in a wide array of aquatic habitats such as in sediment deposits, seagrass canopies, coralline algal beds and coral reefs (Berg et al., 2013; Chipman et al., 2016; Attard et al., 2014; Attard et al., 2015; Rheuban et al., 2014; Long et al., 2013; Long et al., 2015; Koopmans et al., 2020; Rovelli et al., 2017). In this study, \( R^2 \) values for light-saturation curves ranged from 0.83 to 0.94 indicating a predominant primary production signal, and this gives credence to applying the \( LUE \) approach.

Constraining the daytime \( R \) rate on an hourly timescale is clearly a challenge, especially on the spatial scales included within eddy covariance measurements. Assuming a linear or sigmoidal increase in \( R \) with time is consistent with observations of accumulating leached photosynthates such as carbohydrates that stimulate daytime \( R \) (de Winder et al., 1999; Epping and Jørgensen, 1996); however, more experimental data are required to investigate these assumptions in detail. The theoretical maximum \( LUE \) of 0.125 \( \text{O}_2 \) photon\(^{-1} \) provides an upper constraint on the \( GPP \) that is possible for given \( \text{PAR} \) level.
Hourly LUE at the start and at the end of the day often approached the theoretical maximum (Fig. 4), so it is unlikely that the GPP rates in these datasets were substantially underestimated.

Light-saturation curves are a useful tool to evaluate flux hysteresis and ways to correct for this. There are several considerations when computing hourly GPP that will influence both the $R^2$ value as well as the fitting parameters $P_m$, $\alpha$ and $I_k$. Since these parameters hold real-world significance (i.e. they are not just operators within the mathematical expression; Jassby and Platt (1976)) it is important to consider factors that may introduce bias.

Overall, the LUE approach provides a useful means to compare photosynthetic performance of submerged habitats on hourly and daily timescales. This provides opportunities to generate hypotheses about the importance of habitat structure (e.g. organization of photosynthetic elements) and energy flow. In terrestrial environments, this approach has been used to investigate the effects of biodiversity and biodiversity loss on habitat productivity. Similar analyses ported to the aquatic realm would constitute timely studies.
5. Data availability
The hourly PAR and eddy covariance fluxes required to generate these datasets will be made openly available in a FAIR-aligned data repository upon acceptance of the manuscript.

6. Author contribution
KMA conceived the idea, collected the data and processed the data. KMA wrote the manuscript with input from RNG.

7. Acknowledgements
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8. References


Table 1: Sources of EC flux variability can be broadly grouped into two categories: (1) sources that bias the measured EC flux away from the ‘true’ benthic flux (i.e. when EC O₂ flux ≠ benthic O₂ flux) and (2) ‘true’ temporal variability in the benthic O₂ exchange rate (i.e. when EC O₂ flux = benthic O₂ flux)

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<th>EC O₂ flux = benthic O₂ flux</th>
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<td>Non steady-state conditions within the benthic boundary layer</td>
<td>(Holtappels et al., 2013; Brand et al., 2008)</td>
<td>Changes in diffusive boundary layer thickness in cohesive sediments</td>
<td>(Kuhl et al., 1996)</td>
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<td>Sensor stirring sensitivity</td>
<td>(Holtappels et al., 2015)</td>
<td>Pore-water advection in permeable sediments</td>
<td>(Cook et al., 2007; McGinnis et al., 2014)</td>
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<td>Surface wave influence</td>
<td>(Berg et al., 2015; Reimers et al., 2016)</td>
<td>Diel fauna activity</td>
<td>(Wenzhofer and Glud, 2004)</td>
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<td>Sensor response time</td>
<td>(McGinnis et al., 2008; Berg et al., 2015)</td>
<td>Sediment resuspension</td>
<td>(Toussaint et al., 2014), Camillini et al. In review</td>
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<td>Internal plant O₂ storage, canopy storage, or bubbling</td>
<td>(Attard et al., 2019a; Rheuban et al., 2014; Long et al., 2020)</td>
<td>Oxidation of anaerobic metabolites in sediments</td>
<td>(Fenchel and Glud, 2000)</td>
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<td>Photosynthesis-coupled respiration</td>
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Fig. 1: Eddy covariance data measured over four consecutive days in Greenland showing seabed PAR (top panels), hourly GPP (middle panels) and corresponding light-saturation curves (bottom panels). Symbols in the middle and bottom panels are colour-mapped by h of day. Light-saturation curves are fitted to the data showing the maximum rate of GPP ($P_m$, mmol $O_2$ m$^{-2}$ h$^{-1}$), the photoadaptation parameter $I_k$ (µmol PAR m$^{-2}$ s$^{-1}$), the initial slope of the curve $\alpha$, and the coefficient of determination ($R^2$). Data modified from Attard et al. (2014).
Fig. 2: Different approaches for defining the $R$ rate during the day (and therefore the hourly $GPP$) from eddy covariance fluxes showing hysteresis: (a) $R = \overline{N_1}$, (b) $R = \overline{N_1} + \overline{N_2}$, (c) $R$ increases linearly from $N_1$ to $N_2$, and (d) $R$ increases from $N_1$ to $N_2$ following a sigmoidal curve. Bottom panels show corresponding light-saturation curves and fitting parameters for the maximum rate of $GPP$ ($P_m$, mmol $O_2$ m$^{-2}$ h$^{-1}$), the photoadaptation parameter $I_k$ (µmol PAR m$^{-2}$ s$^{-1}$), the initial slope of the curve $\alpha$, and the coefficient of determination ($R^2$). Symbols in bottom panels are colour-mapped by h of day. Data modified from Attard et al. (in review).
Fig. 3: Eddy covariance data measured over three consecutive days in the Baltic Sea showing seabed PAR (top panels), hourly GPP (middle panels) and corresponding light-saturation curves (bottom panels). Symbols in the middle and bottom panels are colour-mapped by h of day. Light-saturation curves are fitted to the data showing the maximum rate of GPP ($P_m$, mmol O$_2$ m$^{-2}$ h$^{-1}$), the photoadaptation parameter $I_k$ (µmol PAR m$^{-2}$ s$^{-1}$), the initial slope of the curve $\alpha$, and the coefficient of determination ($R^2$). Data modified from Attard et al. (in review).
Fig. 4: Hourly light-use efficiency (LUE, log-axis) plotted against incoming irradiance (seabed PAR) for the two eddy flux datasets collected in Greenland and the Baltic Sea. The broken line indicates the theoretical maximum of 0.125 O₂ photon⁻¹.
Fig. 5: (a) Daily seabed PAR, (b) daily benthic GPP, and (c) daily LUE. The broken line in (c) indicates the theoretical maximum of 0.125 O$_2$ photon$^{-1}$. 
Fig. 6: Measurements of incident and reflected seabed PAR made using two cosine PAR sensors over a habitat with bare sediments at 8 m depth in Oslofjord in July 2019. Reflected PAR was typically 8-10% of incident PAR, indicating that ~90% of incident PAR was absorbed by the benthos.