Tidal flat gross primary production mapping using hyperspectral remote sensing: a mesoscale approach to constrain new radiometric indices

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Abstract. Global carbon budget calculations exclude intertidal mudflats, despite the fact that their contribution is expected to be high, and may account for up to 20% of global ocean production. As such, estimation of the true contribution of intertidal mudflats to the overall carbon budget is needed, and remote sensing is a promising tool to reach this goal. The main innovation in this study is the constraint of a set of new and existing radiometric indices, achieved by coupling hyperspectral remote sensing (hundreds of spectral bands with half maximum length, FWHM <10 nm) and the gross primary production (GPP, *i.e.*, sediment-air carbon dioxide (CO_2) fluxes) of microphytobenthos (MPB), based on pigment changes caused by photophysiological responses (*i.e.*, xanthophyll cycle (XC) and Chl *a* activities) and photosynthetic efficiency (PAM-fluorometry). The ultimate goal is to develop mapping algorithms that may be implemented to estimate tidal flat GPP at various scales (from cm^2 to global). Twenty-three radiometric indices were primarily screened using the reflectance (ref), the absorption coefficient (alpha) and their respective second derivative spectra obtained from hyperspectral images of MPB biofilms and corresponding GPP, under controlled conditions at 9 levels of light intensity (~50 - 2250 µmol photons m^{-2} s^{-1}) and 3 temperatures (15°C, 25°C and 40°C), for each of the four seasons. Of the 23 indices, 11 have been selected to map GPP at the mesoscale, which is a first step in mapping MPB GPP at such a large scale, allowing for predictions to be made regarding the impact of tidal ecosystems in the context of global climate change.

Keywords : intertidal mudflat, microphytobenthos, GPP, hyperspectral remote sensing, CO_2 fluxes

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1. Introduction

Knowledge of the global carbon (C) cycle and budget is vital to develop proper mitigation and adaptation strategies such as the conservation or restoration of ecosystems, as a means of coping with current climate change [1]. However, since the first annual global C estimation, obtained using the methods of Le Quéré et al. [2], an imbalance still remains in the global budget, corresponding to the mismatch between the estimated emissions and the estimated changes in the atmosphere, land, and ocean [3–5]. Indeed, uncertainty surrounding the global C cycle and budget feeds the weakness of the strategies implemented to reach the ultimate goal of stabilizing global mean surface temperature by 2030-2050 [6]. This is partially due to imperfections in the data used for understanding the contemporary C cycle, and more specifically the under-recognition, within global and regional C budgets, of several ecosystems belonging to the coastal zone, particularly those contributing to blue carbon [7,8].

Within the coastal zone, intertidal areas consisting of soft sediment that emerge during low tide cover more than 127 000 km^2 globally [9] and deliver multiple ecosystem services, including blue carbon [10]. Due to the abundance of microphytobenthos (MPB), which consists of a biofilm of unicellular algae that develops in the top few millimeters of sediment, often dominated by Diatoms, but with significant occurrence of Euglenids and cyanobacteria [11], intertidal mudflats constitute one of the most productive marine ecosystems on the planet [12,13]. With an annual gross primary production (GPP) estimated at around 500 Mt of C [14], these ecosystems may represent 90% of the coastal shelf width and may be responsible for up to 20% of the oceans' GPP [12,15]. Nevertheless, despite the potentially high contribution of MPB to blue carbon and the global C budget, its actual contribution remains unknown, due to its substantial temporal and geographical variability, which makes long-term and extensive spatial monitoring a challenge [16,17].

As key technology, remote sensing has the unique advantage of large-scale synchronous data acquisition and real-time dynamic monitoring. For a long time now, this technology has been used to map the diversity and biomass of

terrestrial and marine vegetation, including MPB [18–22]. More recently, remote sensing techniques and data have been used to quantify C fluxes and GPP using vegetation indices, light use efficiency models, terrestrial biosphere models, machine learning approaches, solar-induced chlorophyll fluorescence (SIF), land surface temperature, and atmospheric inversions (for a detailed review see [23]). However, to this day, only two studies have achieved the mapping of intertidal MPB GPP through multispectral remote sensing, both based on the Normalized Difference Vegetation Index (NDVI) [24,25].

Despite these recent advances, remote sensing based on multispectral technology still has limitations, providing unsatisfactory results on both terrestrial and microphytobenthic GPP, with vast inconsistencies remaining between different regions, seasons and vegetation types [26]. These inconsistencies may be due to low spectral resolutions (half maximum length, FWHM >10 nm), that are insufficient for detecting and mapping changes in relation to biological and physiological processes involved in GPP, as well as the poorly adapted position of these sensor spectral bands [27]. Hyperspectral imagery (or imaging spectroscopy) is the only technology able to cope with these issues. In fact, the taxonomic composition of MPB and the physiological properties of each group induce significant pigment composition changes, via the xanthophyll cycle (XC) that serves to prevent photoinhibition, for example, a well-known ability of Diatom dominating MPB [28–32]. To this day, only hyperspectral imagery is able to detect such changes in pigment composition; Torrecilla et al. [33] used hyperspectral imagery for discriminating phytoplankton assemblages in the open ocean, while at the same period, Méléder et al. [34] and Kazemipour et al. [35] developed specific indices for discriminating macroalgae from MPB assemblages and detecting biofilms dominated by Diatoms or Euglenids. Regarding photosynthetic efficiency, Penuelas et al. [36] developed the Photochemical Reflectance Index (PRI) as an indicator of photosynthetic efficiency for terrestrial vegetation, while Méléder et al. [37] developed a specific index for benthic Diatom light use efficiency, the MPB_{LUE}. Both indices are based on the photophysiology of plants and algae regarding light, with reflectance at 531 nm for PRI or 496 and 508 for MPB_{LUE}. These wavelengths are functionally related to the de-epoxidation stage of the XC, which consists in the light-dependent conversion of the light harvesting xanthophyll, violaxanthin, to the energy quenching xanthophylls, antheraxanthin and zeaxanthin in plants [38], or the de-epoxidation of diadinoxanthin into diatoxanthin in Diatoms [39]. While the link between these indices and photosynthetic efficiency has been well demonstrated, the use of these indices to quantify GPP (*i.e.*, carbon dioxide (CO_2) fluxes) has not yet been established, and was the main objective of the present study.

With this objective, hyperspectral images in the visible-near infrared domain (400-900nm) were obtained at the meso-scale (a few square centimeters) under various light intensities, using natural MPB biofilms sampled at

different seasons, and incubated at different temperatures. These were coupled with sediment-air CO_2 flux measurements in order to develop original algorithms for the final objective of quantifying and mapping tidal GPP.

2. Material and methods

2.1. Sampling and pre-treatment of MPB biofilms

Natural biofilm was collected at low tide in Bourgneuf Bay (Figure 1), located south of the Loire estuary (1°58–2°15W; 46°53–47°06N). This bay is the site of significant aquaculture activity, mainly oyster farming (7 122 metric tons, Barillé et al. [40], which is supported by a high biomass of MPB throughout the year [18,29,41]. Sampling was carried out during spring tides, when low tides occur around noon and the exposed surfaces are most vast, in the spring (March 21st & April 10th, 2019), autumn (October 28th, 2019), winter (January 27th, 2020) and summer (July 6th, 2020). Sampling consisted in collecting ~50 L of superficial sediment, colonized with biofilm, by scraping the firsts few millimeters of mud. Back in the laboratory, the mud was sieved using a 1 mm mesh sieve to remove any fauna.

Once sieved, the mud was homogenized in a large tank using natural seawater collected at the same time as the sediment. The mixture was distributed into two tanks of 60 x 40 x 10 cm, and the surface was smoothed. After being left overnight, the overlaying water was removed, and 30 sediment cores were prepared before the formation of any new biofilm, using PVC drilled cylinders (height = 10 cm, diameter = 8 cm). This avoided damaging the biofilm and resulted in cores with a smooth biofilm surface obtained after upward migration. The PVC cylinders were drilled laterally, allowing the sediment to be in contact with the seawater, thus avoiding desiccation and helping with temperature control, while avoiding submersion of the biofilm throughout the experiment. Every morning, the 30 sediment cores were placed in a new tank with room temperature seawater and were exposed to low irradiance (PAR: photosynthetic active radiation) of 70 µmol photons m^{-2} s^{-1} (LED Lights SL 3500, PSI, Czech Republic) to help the formation of the MPB surface biofilm [42,43]. A total of 90 cores were prepared during each seasonal phase of the experiment. Every evening, the mud (except that already in use for experimentation) was homogenized once more in the large tank with fresh seawater, and was then distributed in the two tanks and new cores were prepared the following morning. At the end of each day, three 1.5mL samples of biofilm were collected by scraping the surface of the mud in the tank into Eppendorf Safe-Lock Tubes. These were stored at -20 °C for biodiversity studies through microscopic observation (electronic and photonic), as in Méléder et al. [44].

2.2. Experimental design

To begin, at T0 the cores were incubated in water, three at a time (*i.e.*, triplicates), under an irradiance of 70 µmol photons m^{-2} s^{-1}. This level of light intensity was chosen not only to avoid any downward migration, thus maintaining the biofilm at the surface of the sediment during the whole experiment, but also for accurate photosynthetic parameters, estimated by PAM-fluorometry [42,45]. Incubation lasted 2 hours, enabling the cores to reach the required temperature (15°C, 25°C or 40°C) (Figure 2). Of the 30 cores, 3 were dedicated to respiration measurements (see 'Carbon flux measurements' part for details), while the 27 others were used for light exposition assessment. After 2 hours (T1), the maximum quantum efficiency of Photosystem II (PSII), *Fv/Fm* [46], was measured from 3 spots on 3 cores after 5 minutes at very low light (~ 30 µmol photons m^{-2} s^{-1}), in order to check the status of the biofilm using a WATER-PAM-fluorometer, optic fiber version (Walz, Effeltrich, Germany). Once *Fv/Fm* checked, the 3 cores were exposed to a specific light intensity (~ 50, 150, 350, 450, 750, 1250, 1550, 1950 or 2250 µmol photons m^{-2} s^{-1}) that was adjusted using a LED panel (LED Lights SL 3500, PSI, Czech Republic) and a photometer (MSC15, Gigahertz-Optik, Germany). The biofilm was exposed for 7 minutes to allow for a light response to take place, but preventing Diatom downward migration [47]. After 7 minutes (T2), the PSII quantum efficiency, *Fq'/Fm'* [46], of the 3 exposed cores was checked by PAM-fluorometry on 3 spots per core. Following this, the LED panel was turned-off and a hyperspectral image was taken, using a HySpex VNIR 1600 camera (Norsk Elektro Optikk, Skedsmokorset, Norway), with a spectral resolution of 4.5 nm in 160 Visible-Near Infrared (VNIR) channels, and in under 5 minutes (see 'Hyperspectral image processing' part for details). During image acquisition, halogen lamps were used to provide a full, smooth and precise irradiating spectrum between 400 nm and 2500 nm and a Spectralon® reference (with 50% reflectivity) was set up to calculate reflectance (see 'Hyperspectral image processing' part for details). The halogen lamp was switched-off after image acquisition and the LED panel was switched-on again (T3) allowing the biofilm to re-adapt to the light intensity for the carbon flux measurement. Indeed, after 5 minutes of exposure (T4), sediment-air CO_2 fluxes were measured for 15 minutes (5 min per core) using a benthic mini-chamber placed on the surface of each core and an Infrared Gas Analyzer (IRGA, EGM-5, PP-Systems, Amesbury, U.S.A) to obtain the MPB's Net Primary Production (NPP) (see 'Carbon flux measurements' part for details). In the next step (T5), a biofilm sample was taken for pigment analyses by High Performance Liquid Chromatography (HPLC). This was done using a mini contact-core (Laviale et al.'s [48] 'crème brulée' technique) derived from contact-core methodology [49], that consists in freezing the top surface of sediment (250 µm in the present case) by contact with a metal surface (1.5 cm^2) previously immersed in liquid nitrogen. The obtained sediment discs were stored in liquid nitrogen during the experiment, and kept at -80°C in the laboratory

while awaiting further pigment analysis. To achieve an exact match between pigment composition and spectral features, a second hyperspectral image was taken, which included the region of interest (ROI) corresponding to the mark left by the contact core.

Finally, after the whole experimental procedure, and in order to take into account possible intra-group light gradients caused by heterogenous lighting by the LED panel, a new Spectralon® hyperspectral image was taken but under LED lights (instead of halogen lamps) for each level of light. The true PAR received by each set of biofilm surfaces was recalculated using the spectra from the Spectralon® (see 'Hyperspectral image processing' part for details).

2.3. Carbon flux measurements

To measure carbon fluxes by IRGA (EGM-5, PP-Systems, Amesbury, U.S.A), samples were enclosed in an airtight chamber (Figure 2). Sediment-air CO_2 fluxes were determined by measuring the variation of the CO_2 concentration (in ppm) over time in the atmosphere within the enclosed chamber. A transparent chamber was fixed to the surface of the sediment core for 5 minutes to measure the variation in the internal CO_2 content as a function of time (every second), this process was repeated with the subsequent cores. Results were expressed per carbon unit in Net Community Production (NCP, mg $C.m^{-2}.h^{-1}$) and Gross Primary Production (GPP, mg $C.m^{-2}.h^{-1}$), calculated following Migné et al. [50] and Méléder et al. [25] (Eq. 1 and 2):

$$NCP = \frac{(Slope \times V)}{22.4 \times A} \times 12 \qquad (1)$$

$$GPP = NCP + CR \qquad (2)$$

Where Slope was the real-time CO_2 concentration regression (in mol CO_2 .mol $Air^{-1}.h^{-1}$); V was the chamber volume (0.1 L); A, the enclosed sediment area (0.0028 m^2); 22.4, the CO_2 molar volume at standard temperature and pressure (in L $.mol^{-1}$); 12, its molar mass (in g C .mol CO_2^{-1}).

CR was the community respiration (CR, mg $C.m^{-2}.h^{-1}$) measured using a dark benthic chamber on dedicated incubated cores allowing for GPP calculations.

2.4. Pigment analysis by High Performance Liquid Chromatography (HPLC) and diversity analysis

The samples obtained from the mini-contact cores were stored at -80°C while awaiting analysis by HPLC following Mantoura and Llewellyn [51], modified by Méléder et al. [52]. The HPLC device (Alliance HPLC System, Waters Corporation) was connected to a reverse-phase C18 separating column (SunFire C18 Column, 100Å, 3.5 µm, 2.1

mm x 50 mm, Waters Corporation) preceded by a precolumn (VanGuard 3.9mm x 5mm, Waters Corporation), a photodiode array detector (2998 PDA) and a fluorometer (Ex: 425 nm, Em: 655 nm; RF-20A, SHIMADZU). Before pigment analyses, samples were freeze-dried and weighed, then added to 1.5 mL of extraction solvent (95% methanol buffered with 2% ammonium acetate, 4°C) containing an internal standard (trans-β-Apo-8′-carotenal, 10810, Sigma-Aldrich), vortexed for 30 sec and then kept at -20°C for 15 minutes. The supernatant containing pigments were recovered after centrifugation (4528 g, 1 min at 4°C) and then filtered (0.45 µm) and transferred into a brown vial for analysis. The concentration of each pigment was determined using a calibration curve diagram created with external pigment standards (DHI LAB products, Hørsholm, Denmark). Pigment content of the biofilm was determined in concentrations ($mg.m^{-2}$), and included the principle Diatom pigments: chlorophyll *a* (Chl *a*), chlorophyll *c* (Chl *c*), diadinoxanthin (DD), diatoxanthin (DT) and fucoxanthin (Fuco). The ratio of chlorophyll *a* to chlorophyll *c* (Chl *a*/Chl *c*) was then calculated to detect whether the MPB had migrated during the experiment, this ratio was expected to increase if live cells moved deeper into the sediment. Furthermore, the xanthophyll de-epoxidation state (DES) was calculated in order to observe pigment activity in response to light intensity (*i.e.*, activation of the XC) (Eq. 3).

$$DES = \frac{DT}{DD + DT} \quad (3)$$

In addition, the sampling areas visible on the second hyperspectral images provided the ROI (see 'Hyperspectral image processing' part for details) on the corresponding first hyperspectral images, from which the spectral signature was extracted for comparison with the HPLC results.

For cell observation and identification, definitive slides were made after separating the cells from the sediment using Ludox HS-40 colloidal silica (SPCI S.A., St. Denis de la Plaine, France), as described in Méléder et al. [44]. A 48-hour decantation allowed for separation of the cells (at the bottom of the tube) and mineral particles (in the Ludox). Settled material was rinsed by centrifugation in distilled water (at least five times) and observed with a photonic microscope. Definitive slides were made after cremation (2 h, 450°C) in order to observe clean Diatom cell frustules mounted in a high-resolution Diatom mountant (Naphrax; Brunel Microscopes Ltd., Chippenham, Wiltshire, United Kingdom). Species were identified based on morphology [53,54]. When photonic microscopy was inconclusive, scanning electron microscopy was used. For the species composition analysis, a total of ~300 Diatom frustules were counted to determine the abundance of each species.

2.5. *Hyperspectral image processing*

2.5.1. Noise Reduction of Reflectance

After factory calibration, the raw data from each image was converted to radiance ($W.sr^{-1}.m^{-2}$), and reflectance by dividing each column of the image by the average intensity of the Spectralon® [55,56]. Forward minimum noise fraction (MNF) and inverse MNF (IMNF) transformations were performed to remove noise and smoothen the bands [56,57].

2.5.2. Absorption coefficient (alpha) estimation using the MicroPhytoBenthos Optical Model (MPBOM)

The MPBOM considers the MPB biofilm as a layer of pigment with a certain thickness (*i.e.*, tens to hundreds of μm), that absorbs light and is deposited on a non-transparent background [35]. As such, light is considered as being passed through the cells twice as it is reflected off the background. The biofilm's transmittance (T), which is estimated by R_A (the apparent reflectance from the image, Figure S1a), and R_B (the reflectance of the background, without biofilm) is used to calculate the absorption coefficient (alpha) (Eq. 4).

$$alpha = -ln(\sqrt[3]{T}) = -ln\left(\sqrt[6]{\frac{R_A}{R_B}}\right) \qquad (4)$$

Because it was not possible to measure the actual R_B, the reflectance of the background was estimated from the regression line of R_A in the 750–920 nm range, which provides a slope and intercept that can simulate a straight-line background R_B over the full spectral range (400–1000 nm) (for details see [35,56]).

2.5.3. Second derivative spectroscopy

Derivative techniques improve minute fluctuations in reflectance spectra and separate closely related absorption features without background effects [58,59]. After the denoising and smoothing processes, smoothed spectra were obtained. A finite approximation was applied to calculate second derivatives according to different finite band resolutions on the smoothed spectra [58–60]. The associated second derivative spectra were calculated based on the ref and alpha spectra. For each pixel, the forward second derivative of the forward first derivative for reflectance (ref) was calculated following equations 5 and 6:

$$dref(i) = (ref(i+1) - ref(i-1)) / (\lambda(i+1) - \lambda(i-1)) \qquad (5)$$

$$ddref(i) = (dref(i+1) - dref(i-1)) / (\lambda(i+1) - \lambda(i-1)) \qquad (6)$$

Whereas the forward second derivative of the backward first derivative for the absorption coefficient (alpha) was calculated following equations 7 and 8. This calculation allowed us to obtain the same polarity between both second derivatives (ref and alpha), enabling a direct comparison (*i.e.,* of the upwards absorption peak, Figure S1):

$$dalpha(i) = (alpha(i-1) - alpha(i+1)) / (\lambda(i+1)-\lambda(i-1)) \quad (7)$$

$$ddalpha(i) = (dalpha(i+1) - dalpha(i-1)) / (\lambda(i+1)-\lambda(i-1)) \quad (8)$$

Where i was the position of spectral channels (from 1 to 160).

For each pixel, four spectra were obtained (Figure S1): reflectance (ref), absorption coefficient (alpha), the second derivative of the reflectance (ddref), and the second derivative of the alpha (ddalpha).

2.5.4. Photosynthetic Active Radiation estimation and subsampling of images

The LED panel generated a light gradient from the left to the right side of the observation area (Figure 3a), although this only affected the third sample on the right. As such, the true PAR used for data analysis was estimated, rather than using the 9 levels of light previously selected for the experiments. In fact, the gradient is suspected to have induced different responses from the biofilm, in terms of CO_2 uptake, pigment composition and thus, spectral signature. For a more accurate analysis of images, the true PAR was retrieved from the radiance measured under the Spectralon®, lit by the LED panel for each of the 9 levels of light intensity. This was done by converting radiance from 400 to 700 nm into PAR (here after PARsp) using a predetermined conversion factor: W m^{-2} = 4.6 µmol photons m^{-2} [61]. Then, each hyperspectral image (Figure 3b) was subsampled into ~250 columns, each with a width of 20 pixels. The reflectance, absorption coefficient, second derivatives and radiometric indices (see 'Establishment of radiometric indices' part) were then averaged for each column, as the PARsp (red dot, Figure 3a).

2.5.5. Establishment of radiometric indices

To establish radiometric indices that could be used to predict GPP, wavelengths were selected using the second derivative (ddref and ddalpha) spectral features (Figure S1c and d) known to be assigned to the pigments: 480-530 nm for xanthophyll pigments (DD+DT, DD, DT), 540 nm for Fuco, 632 nm for Chl *c* and 673 nm for Chl *a* [37,58,59], but also 670 and 680 nm for the Chl *a* double peak detected within second derivative spectra [59,62,63]. To complete this selection of wavelengths, a stepwise regression was used to identify those significantly correlated with PARsp (see 'Data analysis' part for details), but not known to be assigned to a specific pigment. Thus, those

wavelengths whose ddref and ddalpha values were significantly related to PARsp ($p \leq 0.05$) were also selected to establish the indices (Eq. 9) and to predict GPP:

$$Index = \frac{X_{\lambda 1}}{X_{\lambda 2}} \quad (9)$$

Where $X_{\lambda 1}$ and $X_{\lambda 2}$ represent the average ref, alpha, ddref or ddalpha values over each set of ~250 columns at two different wavelengths (λ1 and λ2).

Finally, existing radiometric indices MPB_{LUE} (Eq. 10) and PRI (Eq. 11) [37,64] were also tested to predict GPP, where X represents the average ref, alpha, ddref or ddalpha values over each set of ~250 columns at the corresponding wavelengths:

$$MPB_{LUE} = X_{496}/X_{508} \quad (10)$$

$$PRI = X_{531}/X_{570} \quad (11)$$

2.5.6. Region of Interest for pigment analysis

To achieve an exact match between pigment composition and spectral features, hyperspectral images acquired after the mini contact-core sampling were used to define ROIs corresponding to the mark left after sampling, to be applied to ref, alpha, ddref, ddalpha and PARsp images in order to extract corresponding values.

2.6. Data analysis

From PAM-fluorescence, the PSII quantum efficiency (*Fq'/Fm'*) was used to calculate the relative Electron Transport Rate (rETR) (µmol $e^{-}.s^{-1}$) (Eq. 12), following Consalvey et al. [46], for a given light intensity (PARsp), and assuming photons divide equally between PSI and PSII:

$$rETR = (Fq'/Fm') \times 0.5 \times PARsp \quad (12)$$

PSII quantum efficiency (*Fq'/Fm'*) light curves were fitted using nonlinear regressions, whereas photosynthetic parameters, retrieved from light curves using PAM-fluorescence (rETR) and CO_2 fluxes (GPP), were fitted by nonlinear parametric estimation according to Platt et al.'s [65] model (Eq. 13):

$$P(PARsp) = Ps \times \left(1 - exp^{-\alpha \times PARsp/Ps}\right) \times exp^{-\beta \times PARsp/Ps} \quad (13)$$

Where P(PARsp) is the specific photosynthetic rate (rETR or GPP) at a given light intensity (PARsp); α, the maximum light utilization coefficient (*i.e.,* the slope at the origin of the curve); β, the photoinhibition parameter; and Ps, the potential maximum photosynthetic rate in the absence of photoinhibition.

Thus, photosynthetic parameters P_{max} (maximum photosynthesis rate for rETR or GPP) and E_k (light saturation parameter) were calculated using equations 14 and 15:

$$P_{max} = Ps \times \left(\frac{\alpha}{\alpha+\beta}\right) \times \left(\frac{\beta}{\alpha+\beta}\right)^{\beta/\alpha} \qquad (14)$$

$$E_k = \frac{p_{max}}{\alpha} \qquad (15)$$

Following a normality test (Shapiro-Wilk), ANOVA were carried out to evaluate the differences in PSII quantum efficiency status (*Fv/Fm* and *Fq'/Fm'*), GPP and pigment content, across sample groups (9 levels of PARsp (ranging from 50 - 2250 µmol photons m^{-2} s^{-1}), 3 temperatures (15°C, 25°C and 40°C) and 4 seasons). Among them, a 3-way ANOVA for *Fq'/Fm'* and GPP was performed, and a 2-way ANOVA for *Fv/Fm* was performed given that the measurements were made before light exposure. Since PARsp varied too much between mini contact-core ROIs to be considered as factor, an additional 2-way ANOVA was carried out for the pigments, with temperature and season (*i.e.* without light levels). Therefore, the effect of light on pigments was determined separately, by regression.

Finally, to identify wavelengths that were significantly correlated with PARsp, a stepwise regression method of bidirectional elimination was used [66]. This technique involved evaluating the magnitude of the correlation coefficient for each wavelength, beginning with the highest, and successively removing those with the weakest correlation until only those with a significant correlation remained. The method proved to be a successful approach in identifying which wavelengths are the most important in providing PARsp. Simultaneously, it was necessary to refer to the spearman correlation coefficient with a high value ($r > 0.4$) to further screen the bands that showed a strong correlation. This facilitated the subsequent establishment of the radiometric indices. A linear regression between the radiometric indices based on selected wavelengths and the GPP measured from the biofilm was then performed. Only indices corresponding to high-quality and significant regression models were selected ($p \leq 0.05$; $R^2 > 0.4$) to map GPP at the sediment core scale.

The processing of hyperspectral images was carried out using ENVI Software. All statistical analyses were performed using R software. All figures were created using GraphPadPrism software.

3. Results

3.1. PSII quantum efficiency status and biofilm GPP

According to the *Fv/Fm* measured at T1, prior to any light exposure but following incubation, the maximum efficiency of the biofilm from each core was significantly impacted by both season and incubation temperature (Figure S2, Table S1). All values were above 0.6, with the lowest value of 0.67 ± 0.01 reached in the winter at a temperature of 40°C, and the highest value of 0.74 ± 0.00 reached in the summer at 15°C. Following each light exposure, the *Fq'/Fm'* measured at T2 showed a significant effect of light (PARsp), season and temperature on the efficiency (Table S1). Globally, the highest value (0.57 ± 0.07), averaged over the 3 temperatures and the 9 levels of light, was found in the autumn and the lowest (0.44 ± 0.19) in the winter. The PSII quantum efficiency of MPB biofilms decreased with increasing light intensity (Figure 4). Similarly, GPP measured after each light exposure at T4 was significantly impacted by light, season and temperature (Figure 5, Table S1). As expected, GPP increased as light intensity increased (Figure 6), until it reached a maximum value. In a few conditions, photoinhibition (*i.e.*, a decrease after reaching the maximum) was observed based on GPP: in the spring at 25°C, and in the winter at 25°C and 40°C (Figure 6), and based on the rETR: in the spring at 40°C and in the winter at 15°C and 40°C (Figure S3). Photosynthetic parameters were obtained for all conditions, bar one (the rETR for the autumn as Platt's model did not properly fit, Figure S3): α, E_k, $rETR_{max}$ and GPP_{max} varied according to season and temperature, demonstrating their impact on *Fq'/Fm'* and GPP (Tables S2 and S3).

3.2. Pigment analysis and species composition

Pigment analysis allowed the identification and quantification of 9 pigments: in addition to Chl *a*, the main pigments observed make up the pigment-based fingerprint for Diatoms: Chl *c*, DD, DT and Fuco. Minor pigments were also detected, such as β-carotene, a known minor pigment in Diatoms. Pheophorbide *a* and pheophytin *a*, by-products of Chl *a* breakdown, were also observed, likely as a result of grazing activity on biofilm or other photosynthetic organisms such as macro-algae and plants. Lutein was also detected, demonstrating the import of detritus from plants or green algae [67]. The dominance of the biofilm by Diatoms was confirmed by microscopic observation: the main species in the MPB biofilm were: *Navicula cf. phyllepta*, *Planothidium delicatulum*, *Gyrosigma limosum*, *Staurophora amphioxys*, *Cymatosira belgica* and *Thalassiosira spp*. (Figure S4). Among them, *Navicula cf. phyllepta* was one of the dominant species in all 4 seasons, and accounted for more than 50% of spring species; *Gyrosigma limosum* accounted for around 50% of winter species. In the summer and autumn, the occurrence frequency of several main Diatom species was relatively similar. Other Diatom species with an

abundance of less than 5% were observed (Figure 6). Pooled together, these species made up 15.40% of the total population in the spring and 38.30% in the autumn, demonstrating higher diversity in the latter. It can be noted that *Euglena* were not detected by pigment analysis (*i.e.*, Chl *b*), but were observed by microscope in spring and summer samples, and accounted for 2% and 5.7% of the total population respectively (Figure 6).

The MPB biomass, expressed as Chl *a* concentration, varied with season and temperature (Table S1), but not with light (PARsp, see Figure S4). MPB biomass reached a maximum of 68.46 ± 13.12 $mg.m^{-2}$ in the winter when incubated at 15°C and a minimum of 22.95 ± 7.41 $mg.m^{-2}$ in the autumn at 15°C. To ensure that the biomass was always dominated by live Diatoms, the Chl *a*/Chl *c* ratio was verified, and was expected not to change significantly according to the level of light during experimentation. Indeed, although this ratio changed with season, and temperature (Table S1), it was not affected by light (Figure S5). Migration was also checked by comparing hyperspectral images after light exposure (at T3) and after CO_2 measurement and sampling (at T5, results not shown here). Therefore, after excluding migration effects, the relationship between pigment concentration and light intensity can be regarded as the response of Diatoms themselves to changes in light, such as activation of the XC, for example. In fact, the XC's de-epoxidation state (DES) increased with increasing light intensity (Figure 7). According to the results of the 2-way ANOVA, the season had a significant effect on the DES, whereas the effect of temperature was non-significant (Table S1). The DES was highest in the summer for high light exposure, reaching 0.42. The lowest DES was measured in the winter, under low light conditions, with a value below 0.10. The greatest amplitudes of DES were detected in the summer (min = 0.19 and max = 0.42) and in the winter (min = 0.07 and max = 0.33). DES varied less in the spring and the autumn, ranging from 0.14 to 0.33 and 0.11 to 0.29, respectively.

3.3. Radiometric indices

Throughout the experiment, a total of 108 hyperspectral images (4 seasons, 3 temperatures, 9 levels of light) were obtained. After processing, each original image was converted into four corresponding parameters: ref, alpha, ddref and ddalpha, which were used to establish radiometric indices. The second derivative spectra much aided the selection of wavelengths for establishing the indices, as they showed significant peak fluctuations at the relevant pigment absorption bands, *i.e.,* the domain of absorption of DD+DT (from 480 to 530 nm), Fuco (540 nm), Chl *c* (632 nm) and Chl *a* (673 nm) (Figure S1c and d).

First, to select wavelengths, those with the highest ($r > 0.4$) and most significant ($p < 0.05$) correlations between ddref and PARsp were selected using the stepwise regression method of bidirectional elimination. These wavelengths were: 490, 494, 496, 501, 505, 508, 515, 520, 523, 526, 530, 541, 588, 628, 632, 636, 665, 670, 673,

676, 680, 683 and 687nm (Table S4). Second, in the aim of predicting GPP, radiometric ratio indices (Eq. 5) were calculated using the 23 aforementioned wavelengths, as well as the existing indices, MPB_{LUE} and PRI. Optimal GPP-radiometric ratio index models were those with the highest ($R^2 > 0.4$) and most significant ($p < 0.05$) regressions between indices using ddref or ddalpha values, as well as GPP. As expected, these ratios were those established using wavelengths known to be assigned to the XC (DD+DT at 494nm, DT at 520 nm, see Méléder et al. 2018 for details), Chl *a* (670, 673 or 680 nm) and Chl *c* (632 nm) (Table 1). The XC-related indices fitted with GPP, except at 15°C and 25°C in the spring, and at 15°C in the summer, where $ddref_{520/632}$, $ddref_{494/632}$, $ddalpha_{520/632}$ and $ddalpha_{494/632}$ showed the most frequent significant regressions with the GPP under several conditions. PRI fitted with GPP at 15°C and 25°C in the autumn, and at 40°C in the summer, whereas MPB_{LUE} fitted at 25°C in the spring and at 15°C in the summer; $ddref_{680/670}$ and $ddalpha_{680/670}$ fitted at 15°C and 25°C in the autumn.

3.4. GPP mapping at the sediment core scale

According to the above findings, GPP mapping using radiometric indices for each core surface is possible. By comparing the models established for each radiometric index under specific conditions (season and temperature), the corresponding indices with the best model quality were selected (Table 1) and applied to sediment-core-scale GPP mapping. GPP varied from 50 mg $C.m^{-2}.h^{-1}$ in the spring at 25°C, to 350 mg $C.m^{-2}.h^{-1}$ in the summer at all three temperatures (Figure 8).

4. Discussion

4.1. Photosynthetic parameter changes detected by PAM-fluorometry and CO_2 flux measurements

It has been demonstrated, using PAM-fluorometry, that the maximum light utilization coefficient, α, globally increases with increasing temperature, however, the light saturation parameter, E_k, and the maximum relative Electron Transfer Rate, $rETR_{max}$, decrease, demonstrating a negative effect of temperature on the short-term photosynthetic efficiency of MPB, in accordance with Blanchard et al. [68,69]. Indeed, a rise in temperature increases the rate of molecular movement, and thus, the rate of physiological and biochemical reactions (chemical kinetics principle). This may benefit photosynthesis efficiency, but only up to an optimum temperature of around 20-25°C, beyond which photosynthetic efficiency decreases. In our study, the higher the temperature, the sooner the light reaches saturation point, where the rate of photosynthesis is at its maximum. Indeed, under high temperatures, the MPB needs to transfer more light energy for thermal dispersion and protection, leaving less

energy for photosynthesis, in terms of electron transport [70]. The maximum potential photosynthetic capacity is therefore reduced, with the $rETR_{max}$ showing a decrease of 60-65% between 15°C and 40°C, that may be explained as an exacerbation of the temperature effect under high levels of light, *i.e.*, increased photoinactivation or decreased repair of PSII [71].

In contrast, the changes of E_k and P_{max} with temperature under the GPP-light model do not present the same trend, with maximum values reached at 25°C and even 40°C, illustrating a positive effect. This may be explained, in part, by the fact that these photosynthetic parameters, obtained though the GPP-light model, cannot be directly compared with those from the PAM fluorometry-light model [72]. Use of PAM-fluorometry allows the detection of very fast processes, in particular the oxidation/reduction of Q_A, that occurs on thylakoids during the first stage of photosynthesis (photochemical reaction stage), and lasts a matter of seconds [46,73]. The rETR corresponds to the speed (µmol $e^-.s^{-1}$) of the electron within this chain reaction. Conversely, benthic chambers and IRGA are used to measure the photosynthetic C metabolism pathway (Benson-Basham-Calvin cycle) that corresponds to the speed of CO_2 uptake [74]. Because the fixation of CO_2 and the synthesis of organic C molecules require enzymes as acceptors, this phase, occurring in the stroma, is slower than the previous phase. Photosynthetic parameters are thus integrated over a longer period of time, a matter of minutes [75].

Although some authors agree that there is a link between rETR and GPP, in that C fixation is a linear function of rETR [76,77], a discrepancy between these two parameters, as observed in the current study, has also been described in the literature. Perkins et al. [78] demonstrated that primary production, estimate using ^{14}C, did not correlate with rETR, due in part to the light-induced migration of the cells away from the sediment surface. Indeed, GPP integrates layers at greater depth in the sediment than does rETR, and is thus impacted by the reduced efficiency of cells which migrate down from the surface. Although in our study no migration was observed, as demonstrated by a stable Chl *a*/Chl *c* ratio, and by comparing hyperspectral images before and after CO_2 measurements, a vertical turnover of cells between the surface and deeper within the sediment is possible, and would have been detected by neither the hyperspectral images, nor by PAM-fluorometry. However, although the hyperspectral data seem more closely linked to the rapid-scale changes occurring at the subsurface of the sediment, such as photosynthetic parameters measured by PAM-fluorometry [37] than they did to CO_2 flux, we investigated the possibility of mapping GPP using hyperspectral imagery nonetheless, since in the current context of global warming, C is an important entity and understanding its fate at the ecosystem scale is crucial.

4.2. Relationship between hyperspectral data and GPP

Eleven candidate indices can be used to map GPP under specific conditions, mainly based on wavelengths within the absorption region of the XC. This ecophysiological mechanism allows Diatoms to dispel excess light-energy via thermal dissipation (*i.e.,* non-photochemical quenching) [39,79]. The XC is activated under conditions of excess light through the buildup of a transthylakoid, ΔpH, that promotes the enzymatic epoxidation of DT into DD, leading to an increasing DES. Conversely, when light decreases, the conversion of DT into DD is facilitated, and the DES decreases. In terrestrial plants, a comparable process exists involving different pigments but a very similar mechanism in which vioxanthin is converted into zeaxanthin [80], supporting the hyperspectral radiometric index, the PRI, used to predict CO_2 uptake [64]. In the same way, given that the XC allows MPB to maintain high productivity rates over a wide range of light levels and under rather unpredictable light environments [81], and that it may be detectable using a hyperspectral signature [58] or index such as the MPB_{LUE} [37], it was expected that a link between CO_2 uptake and hyperspectral data be observed. However, within MPB communities, all species do not have the same ability or efficiency to activate the XC, and this may be dependent on the growth form [31,32,37]. For instance, growth-forms of epipsammic Diatoms, with limited ability for migration, use mainly the XC to cope with light changes, other growth-forms, such as that of epipelic Diatoms, that have a high ability for migration, use this behavioral response to flee high light intensities by positioning themselves deeper within the sediment according to the light gradient, thus avoiding prolonged exposure to excess light at the sediment surface [82,83]. Nevertheless, the response to light is far more complex: the balance, for a given species, between the XC or other mechanisms (e.g., photoinactivation or fast repair of PSII) and a behavioral response, also depends on acclimation (to light, temperature, and other parameters such as salinity or nutrients) [84–86]. This complexity is further increased when the response comes from a community, as is the case in the present study, due to mixed specific responses. For example, in the autumn, when communities are largely dominated by growth-form species expected to have limited migration ability (*i.e*., epipsammic Diatoms such as *Planothidium delicatulum* and thycopelagic Diatoms such as *Talassiosira* sp. and *Cymatosira belgica*), a high DES was expected, but this was not observed. On the one hand, this season corresponded to the most productive, with the highest GPP_{max} (and no saturation reached for rETR), and was the season for which the hyperspectral indices were the most efficient for mapping GPP, even though the DES varied little. On the other hand, in the spring, when the DES varied in much the same way as in the autumn, which was expected due to the MPB dominated by species with the ability to migrate (*i.e*., epipelic Diatoms such as *Navicula* cf. *phyllepta* and *Gyrosigma limosum*), the GPP was the lowest, and was poorly predicted by hyperspectral indices. In contrast, in the winter and summer, the DES was highly variable, even though

MPB was largely dominated by the epipelic Diatom *Gyrosigma limosum*, in the winter, and by epipsammic Diatoms in the summer. It might be hypothesized that in both these seasons, migration is not as prevalent as photoprotection by the XC, no matter what the growth-form, and radiometric detection of the GPP is thus possible.

In our experiments, the Chl *a*-related index, $dd_{670/680}$, was also investigated. The second derivative spectra displayed a clear shift feature between 670 and 680 nm, under different light conditions. Previous studies have already described this feature, interpreted as an interaction between pigments and proteins within PSII, that results in the change within the spectrum [37,59,62]. This change in the absorption region of Chl *a* reveals activities of this major photosynthetic pigment that may be related to photosystem stoichiometry changes [37], or to fluorescence emissions [62], namely the solar-induced chlorophyll fluorescence (SIF, [87]). However, photosystem stoichiometric adjustments take hours and even days to redirect the imbalance of excitation energy by changing the relative amounts of the two photosystems, which is a long-term acclimation process [88]. This leads the hypothesis in favor of the SIF, however, this index performed well only in the autumn, and requires further investigation.

4.3. Perspectives and upscaling

The GPP values obtained from these experiments (*i.e.,* 50 to 350 mg C m^{-2} h^{-1}) are comparable to those found for more than 30 forest ecosystems across gradients of both stand and environmental conditions: ~160 to 1 400 mg C m^{-2} h^{-1} (calculated from [89]: 700 gC m^{-2} y^{-1} to 6 000 gC m^{-2} y^{-1}, taking into account the production that occurs over 12 hours in a given day). These values support the significant potential contribution of tidal mudflats to the global C budget, and the importance of estimating MPB primary production on both a regional and a global scale. However, to reach this goal, there are challenges that have yet to be addressed. The main one being the temporal diversity of photosynthetic capacity that explains the present results, and shows not one unique radiometric index, but several, that are dependent on the season, temperature, and species diversity. While investigation at the species level, involving the controlled mixture of species under controlled conditions, has already been performed [*e.g* 31,37,85,86], such investigations have never been conducted in relation to the ability for CO_2 capture, and are therefore still needed.

The second challenge is to take into account the spatial patchiness of the biomass distribution, that results in nonlinear reflection mixing at the pixel scale [90]. Indeed, Combe et al. (2005) demonstrated that a given signature could correspond to several combinations of end-members. This effect is reduced when the absorption coefficient (alpha) is used [56], but again, no investigation into the ability for CO_2 capture has been performed. This challenge should be addressed along with the third, which is the up-scaling process. Currently, very few hyperspectral satellites such as EnMap [91] or PRISMA [92] are available, but more are planned for the upcoming decade, such

as SBG, which is planned for 2028 [93] or CHIME, planned for 2029 [94]. These sensors have spatial and spectral resolutions that are expected to capture spectral changes caused by biodiversity composition and the physiological processes that drive GPP of photosynthetic communities (from the oceans to terrestrial canopies). However, these sensors, consider MPB and it is the GPP that needs to be tested. In order to verify how GPP measured *in situ* and via hyperspectral satellite images match, and to minimalize the uncertainty, we suggest the use of a step by step up-scaling process using intermediate altitudes (from a few meters to hundreds and thousands of meters) for hyperspectral image acquisition (*i.e.*, by drone, ULM and/or airborne) [95].

5. Conclusion

In this study, we highlight the link between pigment changes (XC and/or Chl *a* activities), CO_2 uptake, and hyperspectral data. Although MPB's photophysiological response is highly complex, and the consequences of the growth forms on its ability to capture CO_2 are not yet fully understood, this study demonstrates the possibility of using hyperspectral data to predict the GPP of intertidal mudflats using a selection of 11 candidate indices. To reach our goal of mapping accurate mudflat intertidal GPP, to be integrated into the global carbon budget, two major challenges have to be addressed over the next decade: (1) gaining a better understanding of specific and mixed photophysiological responses and the ability for CO_2 capture; (2) taking into account the spatial patchiness of the biofilm through the up-scaling approach, from *in situ* to the satellite level.

6. Author contribution

VM and BJ designed the experiments. VM, BJ, MZ, PL and MG carried them out. MZ, PL and MG analyzed hyperspectral images. MZ analyzed pigment and diversity. MZ and VM performed all statistical analyses. MZ prepared the manuscript with contributions from all co-authors. VM, BJ, PL, JL and PP read and corrected intermediate and final versions of the manuscript.

7. Disclosure of interest

The authors declare that they have no conflict of interest.

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Legends of Figures

Figure 1. Study zone: Bourgneuf Bay, on France's Atlantic coast. Dark gray: continent; light gray: intertidal mudflat; blue: subtidal area; black: rocky-shore; red diamond: sampling site.

Figure 2. Experimental design. a/ incubation of sediment cores under 70 µmol photons. $m^{-2}.s^{-1}$ for 2 hours at a given temperature (15°C, 25°C or 40 °C; here 40 °C); b/ Hyperspectral image acquisition for 3 sediment cores after 7 min of exposition at a given PAR (50, 150, 350, 450, 750, 1250, 1550, 1950 or 2250 $\mu mol.m^{-2}.s^{-1}$) and at a given temperature (15°C, 25°C or 40 °C); c/ CO_2 flux measurements at the sediment/air interface using benthic mini-chambers and an Infrared Gas Analyzer (IRGA, EGM-5, PP-Systems, Amesbury, U.S.A) at a given PAR and a given temperature; d/ Work-flow. 1: LED panel (LED Lights SL 3500, PSI, Czech Republic); 2: temperature-controlled water bath; 3: HySpex VNIR 1600 camera Norsk Elektro Optikk, Skedsmokorset, Norway; 4: halogen lamp; 5: benthic mini-chambers; 6: IRGA (EGM-5, EGM-5, PP-Systems, Amesbury, U.S.A).

Figure 3. Subsampling of the images. a/ Radiance estimated from images acquired on the Spectralon®, lit by the LED panel at a given light intensity and showing a light gradient from the left to the right side of the observation area; b/ Image of the absorption coefficient (alpha) for 3 natural biofilm-covered sediment cores at a given light intensity; each core was subsampled into columns with a width of 20 pixels each (example in red), corresponding to a specific averaged PARsp (red dot).

Figure 4. Relationship between *Fq'/Fm'* (except the first dot that corresponds to the *Fv/Fm*) measured by PAM-fluorometry, and light intensity (PARsp, expressed in µmol photons m^{-2} s^{-1}) at 3 temperatures (Solid line and black dots: 15°C; dashed line and dark gray dots: 25°C; dash-dotted line and light gray dots: 40°C) for the 4 seasons: a/ spring, b/ summer, c/ autumn, d/ winter. Points and error bars represent mean and standard deviation of 3 replicates at a given light intensity (PARsp). All nonlinear regressions are significant with an R^2 value > 0.90.

Figure 5. Relationship between GPP (mg C m^{-2} h^{-1}), measured using benthic mini-chambers, and light intensity (PARsp, expressed in µmol photons m^{-2} s^{-1}) at 3 temperatures (Solid line and black dots: 15°C; dashed line and dark gray dots: 25°C; dash-dotted lines and light gray dots: 40°C) for the 4 seasons: a/ spring, b/ summer, c/ autumn, d/ winter. Points and error bars represent mean and standard deviation of 3 replicates at a given light intensity (PARsp). All nonlinear regressions are significant (Platt model) with an R^2 value > 0.80, with the exception of 15°C in the summer (R^2 = 0.64) and 15°C in the winter (R^2 = 0.72).

Figure 6. MPB biodiversity: a/ spring, b/ summer, c/ autumn, d/ winter. Other Diatoms: include multiple identified or unidentified species (less than 5% each).

Figure 7. Relationship between the de-epoxidation index (DES), calculated from pigment composition, and light intensity (PARsp, expressed in µmol photons m^{-2} s^{-1}) at 3 temperatures (Solid line and black dots: 15°C; dashed line and dark gray dots: 25°C; dash-dotted line and light gray dots: 40°C) for the 4 seasons: a/ spring, b/ summer, c/ autumn, d/ winter. All linear regressions are significant ($p \leq 0.05$).

Figure 8. Visualization of sediment-core-scale GPP mapping from different radiometric indices. Spring at 15°C is missing, due to the non-significant corresponding model. Indices used are reported in Table 1 (*).

Legends of Tables

Table 1. Radiometric indices calculated using second derivative values (ddref: second derivative of reflectance; ddalpha: second derivative of alpha) showing the most significant linear regressions ($p<0.1$) with GPP; dark green: $R^2 \geq 0.4$; light green: $R^2 < 0.4$; red: non-significant. *: most significant indices, used to map GPP (Figure 8).