

Net community metabolism of a *Posidonia oceanica* meadow

Willy Champenois , Alberto V. Borges *

University of Liège, Chemical Oceanography Unit, Liège, Belgium

Abstract

We report a 12-yr data set (August 2006–October 2018) of nearly continuous estimates ($n = 3275$) of gross primary production (GPP), community respiration (CR), and net community production (NCP) in a *Posidonia oceanica* seagrass meadow, computed from O_2 measurements on a mooring at 10 m bottom depth in the Bay of Revellata (Corsica). Both NCP and CR were correlated to GPP and followed the leaf biomass seasonal cycle. The meadow was net autotrophic (NCP of $23 \pm 8 \text{ mol } O_2 \text{ m}^{-2} \text{ yr}^{-1}$, GPP [$83 \pm 16 \text{ mol } O_2 \text{ m}^{-2} \text{ yr}^{-1}$] > -CR [$-60 \pm 9 \text{ mol } O_2 \text{ m}^{-2} \text{ yr}^{-1}$]), in agreement with oxygen oversaturation (104% at annual scale, 101% in winter, and 109% in summer). Calcification (CAL) and $CaCO_3$ dissolution (DIS) rates were evaluated from dissolved inorganic carbon measurements in benthic chamber incubations (August 2006–2009). The meadow was found to be a net sink of $CaCO_3$ (DIS > CAL) at an annual rate of $7 \text{ mol } CaCO_3 \text{ m}^{-2} \text{ yr}^{-1}$ that matched estimates of $CaCO_3$ deposition on the meadow by sedimentation from the water column. CAL from epiphyte coralline algae was correlated to GPP, but CAL : GPP ratio (0.1) was lower than reported for coralline algae in cultures (0.6) due to the additional contribution of *Posidonia* to GPP. Both NCP and net DIS contributed to an annual CO_2 sink of $-30 \text{ mol } CO_2 \text{ m}^{-2} \text{ yr}^{-1}$ distinctly stronger than the estimated net air-sea CO_2 flux ($-1 \text{ mol } CO_2 \text{ m}^{-2} \text{ yr}^{-1}$). This suggests that CO_2 input by vertical mixing and/or transport by horizontal advection also strongly contribute to the net atmospheric CO_2 exchange.

The balance at community scale between gross primary production (GPP) and community respiration (CR, negative flux) is net community production (NCP = GPP + CR) and reflects whether a community is net autotrophic (NCP > 0, GPP > CR) or net heterotrophic (NCP < 0, GPP < CR) (Supporting Information Fig. S1). This is an important metric to describe organic matter flows in marine communities, because a net autotrophic community is a net producer of organic matter and either stores or exports organic matter to adjacent communities, while a net heterotrophic community is a net consumer of organic matter that is sustained by inputs of organic matter from adjacent communities. In theory, a net autotrophic community should act as a sink of atmospheric CO_2 , and a net heterotrophic community should act as a source of CO_2 to the atmosphere, although, in practice, this is rarely the case because CO_2 in seawater will also depend on other biological processes such as calcification (CAL), as well on a variety of other processes such as horizontal (advection) and vertical (mixing) transport of CO_2 (Borges et al. 2006). Among coastal systems, estuaries are in majority net heterotrophic, while mangroves, salt-marshes, coral reefs, macrophyte-

dominated communities, and the rest of continental shelves are in majority net autotrophic (Gattuso et al. 1998).

Marine phanerogams are macrophytes of terrestrial origin that spend their entire life cycle submerged in the ocean and form extensive meadows. In seagrass meadows, there are two main primary producer compartments: the seagrass itself and epiphytic algae, and a smaller compartment related to microphytobenthos on the sediment and on the seagrass shoots. Epiphytic algae contribute between 20% and 60% of total seagrass meadow primary production (Marbà et al. 2006). Regarding the fate of seagrass biomass, only 10% is lost through direct grazing (Cebrián and Duarte 1998) and the majority of the biomass loss is through shedding of leaves that contribute to other detritus (organic particles from the water column plus animal feces) collectively called “litter.” Seagrass litter is the main transfer pathway to secondary production through detritivory and to adjacent communities through physical transport (Cebrián and Duarte 1998).

Posidonia oceanica is a seagrass endemic of the Mediterranean Sea that grows in mono-specific meadows that occasionally extend down to 40 m deep. These meadows cover a surface estimated between 12,000 and 50,000 km^2 corresponding to 0.5% to 2.0% of the total surface of the Mediterranean Sea and 2.5% to 10.0% of its continental shelf (Telesca et al. 2015). The extent and density of *P. oceanica* meadows is declining in the Mediterranean Sea due to degradation of water quality, although the

*Correspondence: alberto.borges@uliege.be

Additional Supporting Information may be found in the online version of this article.

rate of decline is very uncertain (Telesca et al. 2015; de los Santos et al. 2019). *P. oceanica* meadows function as a spawning ground, a nursery and habitat for about 400 plant species and thousands of animal species, in total representing approximately 20% of the species in the Mediterranean Sea (Boudouresque 2006).

Primary production in seagrass meadows can be measured using different techniques. The oldest techniques were based on measuring the change of leaf biomass either at the level of a single leaf with a marking technique (Zieman 1974), of a shoot based on a lepidochronological analysis (Pergent and Pergent-Martini 1991), or of a meadow patch based on a harvesting technique (Bay 1984). These techniques only provide the leaf net biomass accumulation or growth and do not account for other components of NCP such as biomass burial in sediments or export to adjacent systems, and are destructive. Incubations with radioactive (^{14}C) or stable (^{13}C) carbon isotope tracers allow to measure primary production (Mateo et al. 2001) but CR needs to be measured by additional parallel incubations. Such an approach is usually made with *ex situ* incubations and does not allow accounting for the production of dissolved organic carbon (DOC) that could represent a significant portion of NCP (Barrón and Duarte 2009). DOC exudation from seagrass occurs mostly during the day (Penhale and Smith 1977) and fuels microbial respiration in the rhizosphere and water column (Moriarty et al. 1986). To derive whole community metabolism and measure individually GPP and CR several techniques are based on mass balancing O_2 or CO_2 fluxes that can be categorized into discrete and near-continuous. The incubation with a benthic chamber is a discrete method based on measuring the change during 24 h of O_2 or CO_2 in a very small isolated portion of the community ($\sim 0.01 \text{ m}^2$) (Barrón et al. 2006; Champenois and Borges 2012). This method is intrusive, time-consuming, and can lead to several artifacts linked to physical disturbance of sediments and damage of plant roots and rhizomes or to abnormally high accumulation of O_2 within the chamber (Champenois and Borges 2012). Near-continuous methods are based on the direct measurement of O_2 or CO_2 in the water column and allow to integrate CR and GPP over larger surfaces ($> 100 \text{ m}^2$) in a nonintrusive way. These techniques are routinely used by mass balancing changes of O_2 concentration (Odum 1956) measured by optodes on a mooring (Champenois and Borges 2012, 2019) or by directly determining the O_2 fluxes by eddy-covariance (Long et al. 2015; Koopmans et al. 2020). With available technology and sensors, eddy-covariance measurements are limited to short deployments (< 1 week) while optodes can be maintained on a mooring for years with minimal maintenance. Both techniques might underestimate GPP because they do not account for O_2 in the form of small bubbles either accumulated in aerenchyma or released from the surface of leaves. The presence of bubbles can be continuously detected with acoustic techniques although not quantitatively (Felisberto

et al. 2015), and bubble release can be discretely quantified with funnel traps (Long et al. 2020). However, small bubble formation on the surface of leaves only occurs in extremely well illuminated conditions, typically at water depths around $\sim 0.5 \text{ m}$ (Long et al. 2020).

The present study is in continuity of two previous analysis of community metabolism based on the O_2 mass balance (Odum 1956) using a mooring equipped by three optodes at 10 m depth in a *P. oceanica* seagrass meadow in the Bay of Revellata in Corsica (Champenois and Borges 2012, 2019). The first study reported GPP, CR, and NCP during 3 years (2006–2009) and focused on the comparison of metabolic measurements derived from the mooring measurements and parallel benthic incubations, as well as, on the effect of the mild winter of 2006–2007 on NCP (Champenois and Borges 2012). The second study focused only on GPP and showed there were marked inter-annual variations of GPP for the 2006–2016 period that were attributed to year-to-year differences in winter-time storms, light availability, and water temperature (Champenois and Borges 2019). The present study allows to extend the period of analysis to 12 years (2006–2018) and focuses on determining the full budget of carbon in the seagrass meadow both related to the “organic metabolism” (GPP, CR, NCP) and the “inorganic metabolism” related to CaCO_3 precipitation (CAL) and dissolution (DIS), that is compared to the air–sea exchange of CO_2 derived from measurements on a mooring of the partial pressure of CO_2 ($p\text{CO}_2$).

Material and methods

Site description

The Bay of Revellata is located in North-Western Corsica (France), and is open North-Eastwards, hence, is protected from the dominant local wind (Libeccio). The deepest part of the bay is 100 m and the average slope of the seafloor is 2%. The *P. oceanica* meadow is present continuously between 5 and 38 m depth (small isolated patches can be found up to 2 m depth). Maps of the coverage of *P. oceanica* meadows as well as other benthic communities in the Bay of Revellata are given in Champenois and Borges (2012) and Velimirov et al. (2016). Moorings (42.5800°N 8.7251°E) were deployed at 10 m depth at proximity of the STARESO research station, and benthic incubations (10 m depth), pore-water sampling (8 m depth) and CH_4 sampling in surface waters were carried out close to the moorings.

Moorings

In August 2006 we deployed two moorings at 10 m bottom depth at a distance of 5 m from each other. One mooring was equipped with three optodes for dissolved O_2 measurements and water temperature (Aanderra 3835) at three depths (4.5, 7.0, and 9.5 m). This mooring was maintained until October 2018. The measurements were interrupted for a few days every 3 months for maintenance and calibration of the optodes, as explained in detail by Champenois and Borges (2012).

A second mooring was deployed for measurements of the pCO₂ in seawater with a Pro-Oceanus CO₂-Pro from Pro-Oceanus Systems Inc. that was powered with an external battery pack. The instrument and battery pack were placed on the seafloor at 10 m depth at 5 m distance from the optode mooring, and water was pumped into the instrument with a Seabird SBE 5T Pump from a depth of 2 m with a tube attached to a floater. This mooring was deployed in August 2006 and acquired data until August 2007, when it was retrieved.

Benthic incubations

From August 2006 to August 2009, we carried out 15 benthic incubations at 10 m depth within a radius of approximately 20 m of the optode mooring (Supporting Information Table S1). The benthic chambers consisted of a polyvinyl chloride (PVC) cylindrical base (9 cm internal diameter, 25 cm internal length) and a Plexiglas cylinder (9 cm internal diameter, 61 cm internal length). We used three benthic chambers as replicates. The day before the start of the incubation, the PVC bases were inserted about 15 cm deep into the vegetated sediment, in three random spots, by underwater divers. At dawn of the next day, the Plexiglas chambers were fixed on the PVC bases. On average, six *P. oceanica* shoots were enclosed in each chamber. A water pump plugged to the chamber was used during 7 min to homogenize the water within the chamber prior to sampling, and remained stopped until the next sampling. Three samplings were made at dawn (T0), at dusk (T1), and at dawn 24 h later (T2), and each time eight polypropylene syringes of 60 mL were sampled from inside the chamber as well as outside water to compute the dilution of chamber water by outside water at each sampling (given the chamber volume is fixed because the chamber is rigid). Immediately after the end of the dive, the content of the syringes was transferred to a biological oxygen demand (BOD) bottle of 60 mL to which the two Winkler reagents were added. Then, pH was measured and 100 mL of water were filtered with 0.2- μ m porosity polyethersulfone syringe filters and stored in polyethylene bottles for the determination of total alkalinity (TA). At the end of the incubation, the *P. oceanica* shoots were harvested for the determination of leaf biomass. The shoots were rinsed with freshwater, the length and width measured, the epiphytes scrapped with a razor blade and dry weight determined after drying in an oven during 48 h at 60°C. The shoot density was computed from the count of *P. oceanica* shoots within a frame (25 cm \times 40 cm) thrown randomly (10–15 times) within a 20 m radius of incubation site.

Pore-water sampling

Pore water was sampled for the determination of H₂S and O₂ requiring relatively large amounts of water, so the sampling depths in the sediment were very coarse (within the top 0.5, 10, and 20 cm). We used home-made needles in stainless

steel with a 2 mm internal diameter (3 mm external diameter). The tip that was inserted in the sediment was stoppered but had two lateral slits of 3 mm length to allow pore water to enter and the other end was plugged to a polypropylene syringe of 60 mL. Sampling was done by underwater divers in vegetated sediment and bare sediment at 8 m bottom depth close to the mooring site. The stainless steel needles plugged to the syringes were pushed into the sediment to desired depth and spaced 50 cm from each other. The needle and syringe were first rinsed and flushed with 5 mL of pore water. Then the syringes were filled sequentially by 10 mL increments separated by 2-min intervals. After the dive, for each depth, the content of the syringe was transferred to two 60-mL BOD bottles, and fixed with a Zn acetate solution for H₂S and Winkler reagents for O₂.

Methane sampling

Samples for the determination of dissolved CH₄ concentration were collected in surface waters (~ 1 m) with polypropylene syringes of 60 mL by scuba divers along a bathymetric transect from 10 to 30 m depth. After the dive, the content of the syringes was transferred to two 60-mL borosilicate serum bottles, poisoned with an HgCl₂ saturated solution (100 μ L), sealed with butyl stoppers and crimped with an aluminum caps. Samples were stored in the dark at room temperature until analysis.

Laboratory analysis

Oxygen was measured by Winkler titration with a potentiometric end-point determination using the protocol, reagents, and calibrations given by Knap et al. (1996), with a precision of $\pm 1 \mu\text{mol kg}^{-1}$ and an estimated accuracy of $\pm 5 \mu\text{mol kg}^{-1}$.

pH was measured with a glass electrode (Metrohm 6.0232.100) calibrated on the Total Hydrogen Ion Concentration Scale with 2-amino-2-hydroxymethyl-1,3-propanediol and 2-aminopyridine buffers prepared in artificial seawater with a salinity of 38 (Dickson 1993), with an accuracy of ± 0.004 pH units.

TA was measured by titration with HCl 0.1 M, and data were quality checked with Certified Reference Material acquired from Andrew Dickson (Scripps Institution of Oceanography, University of California, San Diego), with a precision of $\pm 2 \mu\text{mol kg}^{-1}$ and an estimated accuracy of $\pm 4 \mu\text{mol kg}^{-1}$.

H₂S was measured with the Cline (1969) colorimetric method based on spectrophotometric absorption measurements at 670 nm after addition of a solution of sulfate *N,N*-dimethyl-*p*-phenylenediamine in presence of FeCl₃ in a 6 M HCl solution. The calibration was made with a solution of Na₂S (9H₂O) standardized with KH(IO₃)₂.

CH₄ was measured by headspace technique (20 mL N₂ headspace in 60-mL serum bottles) with a gas chromatograph (SRI 8610C) with flame ionization detection calibrated with CH₄ : CO₂ : N₂O : N₂ mixtures (Air Liquide Belgium) of 1, 10,

and 30 ppm CH₄, with a precision of ± 3.9%, and an accuracy better than ± 10% (Wilson et al. 2018).

Metabolic calculations and statistical analysis

Optodes measure and log the oxygen saturation level (% O₂), and the O₂ dissolved concentrations were computed from the saturation level given by Benson and Krause (1984) from temperature and a constant salinity of 38. The computation of metabolic rates (GPP, CR, NCP) by open water mass balance of O₂ is based on the Odum (1956) method: the hourly change of O₂ in the mixed layer corrected for the exchange of O₂ with the atmosphere during nighttime corresponds to hourly rate of CR; the hourly change of O₂ in the mixed layer corrected for the exchange of O₂ with the atmosphere during daytime corresponds to hourly rate of NCP; assuming that the hourly rate of CR is constant through the daily cycle, hourly rate of GPP is computed as NCP + CR (where CR is a negative flux) (Supporting Information Fig. S1). GPP is integrated at daily scale by multiplying the hourly rate by the photoperiod (Hd). CR is integrated at daily scale by multiplying the hourly rate by 24. Daily integrated NCP is computed as the sum of daily integrated GPP and daily integrated CR.

Since the water column at the mooring site was always vertically isothermal (mixed from surface to seafloor, Champenois and Borges 2012) computations were made using the integrated O₂ content in the whole water column (10 m) based on the measurements at the 3 depths (4.5, 7.0, and 9.5 m). The data are integrated to provide the vertical integrated content of O₂ (Q_{O₂} in mmol m⁻²) on an hourly basis. Computations were made by considering a 24-h cycle starting at sunrise of a given day. Daily integrated CR (mmol O₂ m⁻² d⁻¹) was computed according to:

$$CR = 24 \times \left(\sum ((Q_{O_{2n}})_{t+1} - (Q_{O_{2n}})_t) + \sum FO_{2n} \right) / Hn,$$

where (Q_{O_{2n}})_{t+1} - (Q_{O_{2n}})_t is the change in Q_{O₂} during nighttime (Q_{O_{2n}}) between two hourly intervals (*t*), FO_{2n} is the air-sea O₂ exchange at each *t* during nighttime computed using the Ho et al. (2006) gas transfer parameterization as function of wind speed (where the efflux of O₂ from water to atmosphere corresponds to positive FO_{2n}), and Hn is the nighttime duration given by:

$$Hn = 24 - Hd.$$

Daily integrated GPP (mmol O₂ m⁻² d⁻¹) is computed according to:

$$GPP = \sum ((Q_{O_{2d}})_{t+1} - (Q_{O_{2d}})_t) + \sum FO_{2d} - CR,$$

where (Q_{O_{2d}})_{t+1} - (Q_{O_{2d}})_t is the change in Q_{O₂} during daytime (Q_{O_{2d}}) between two *t*, FO_{2d} is the air-sea O₂ exchange at each *t* during daytime.

∑FO_{2n} corresponded on average to 6% ± 27% of ∑((Q_{O_{2n}})_{t+1} - (Q_{O_{2n}})_t) and ∑FO_{2d} corresponded on average to 8% ± 20% of ∑((Q_{O_{2d}})_{t+1} - (Q_{O_{2d}})_t) showing that, at our particular productive and shallow site, the contribution of the air-sea O₂ exchange to the overall O₂ budget and on the calculation of metabolic rates was marginal.

For the benthic chamber incubations, GPP, NCP, and CR were computed as above for the data from the optodes, except that Q_{O₂} (mmol m⁻²) was computed from the O₂ concentration (mmol m⁻³), the volume of the chamber (m³) divided by the surface of the chamber (m²), and the FO₂ term was ignored. The scaling to the surface of the meadow was done by normalizing the metabolic fluxes by the number of shoots within each benthic chamber, and then using the shoot density using the average value from all measurements (425 ± 92 shoots m⁻²).

Dissolved inorganic carbon (DIC) and the calcite and aragonite saturation levels were computed from pH and TA measurements using carbonic acid constants of Mehrbach et al. (1973) with Microsoft Excel version of CO2SYS. This allowed pH to be recomputed from temperature of measurement to in-situ temperature.

The air-sea flux of CO₂ (and CH₄) was computed from air-sea concentration gradient of CO₂ (and CH₄) and the gas transfer velocity of Ho et al. (2006) computed from wind speed. The atmospheric pCO₂ was obtained at Lampedusa island from GLOBALVIEW-CO₂ (Carbon Cycle Greenhouse Gases Group of the National Oceanic and Atmospheric Administration, Earth System Research Laboratory), and converted into wet air using the water vapor algorithm of Weiss and Price (1980). The atmospheric CH₄ was assumed equal to 1.8 ppm.

Statistical tests and type II linear regressions (Deming) were made with Graphpad Prism (version 7.04). Annual fluxes were derived from the average of spline cubic curves on the benthic incubation values or the monthly means of metabolic fluxes derived from optode mooring.

Results and discussion

Seasonal and interannual variability of GPP, CR, and NCP

We obtained 3275 measurements of community metabolism fluxes during a period of 12 yr over a *P. oceanica* meadow at 10 m depth (Fig. 1a). GPP ranged between 0.4 and 1818 mmol O₂ m⁻² d⁻¹ and averaged 229 ± 180 mmol O₂ m⁻² d⁻¹; CR ranged between -1370 and -0.5 mmol O₂ m⁻² d⁻¹ and averaged -163 ± 140 mmol O₂ m⁻² d⁻¹; NCP ranged between -166 and 539 mmol O₂ m⁻² d⁻¹ and averaged 63 ± 64 mmol O₂ m⁻² d⁻¹.

The variations of the daily values of the three community metabolic fluxes were dominated by strong day-to-day variability (Fig. 1a), while the monthly averaged values showed more regular seasonal variations but also interannual variations (Fig. 1b). The seasonal cycle of GPP followed the one leaf

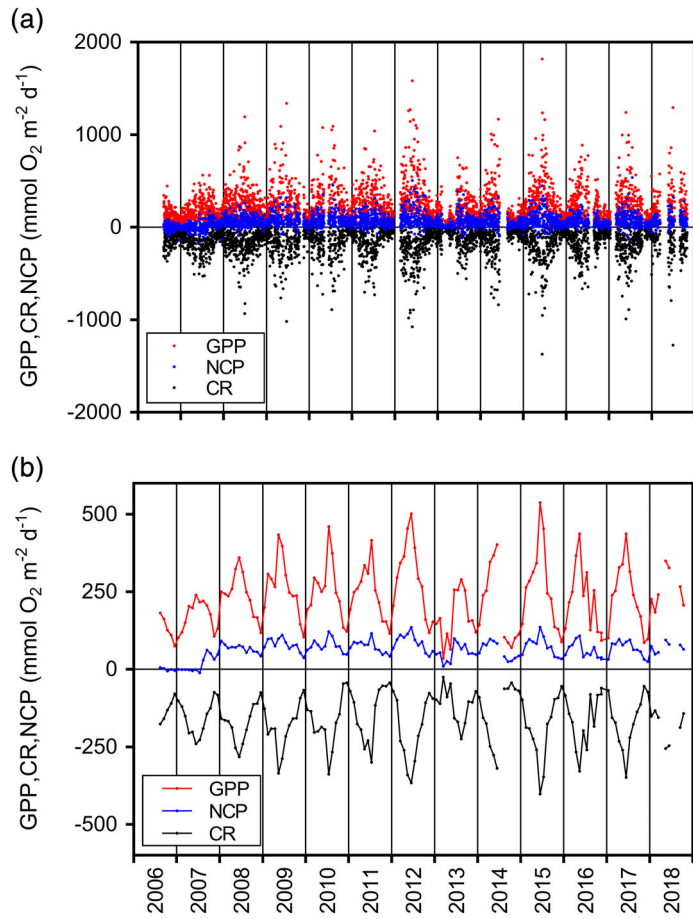


Fig. 1. Gross primary production (GPP), community respiration (CR), net community production (NCP) in mmol O₂ m⁻² d⁻¹ over a *Posidonia oceanica* meadow in the Bay of Revellata at 10 m bottom depth from 7 August 2006 to 29 October 2018, given as (a) daily values ($n = 3275$) and as (b) monthly averages. Data gaps correspond to periods of maintenance of optodes or data loss due to instrument malfunction.

biomass with a yearly minimum in November–December and a maximum in June–July (Bay 1984). Interannual variations of GPP were driven by variable light regime (due to changes in incoming light and shading from phytoplankton) as well as water temperature, and fall- and wintertime storms (Champenois and Borges 2019). The years with the lowest GPP were 2007 and 2015, due to low fall–winter storms that did not trigger the export of litter and consequently inhibited the development of benthic sciaphile macroalgae (Champenois and Borges 2012, 2019). For other years, GPP was repeatable for the period from September to February, so interannual variations of GPP were mostly observed during the period from March to August. During this period, interannual variations of GPP were mostly due to interannual variations of incoming solar radiation and slightly modulated to other factors such as nutrient inputs and water temperature (Champenois and Borges 2019). We validated the statistical model of GPP developed from the 2006 to 2016 data-set (Champenois and Borges 2019) with the independent data point in 2017 (Supporting Information Fig. S2).

The seasonal variations of CR mirror closely the seasonal variations of GPP (Fig. 1b), as previously shown in other individual macrophyte communities (Barrón et al. 2006; Koopmans et al. 2020), as well as across various individual systems of a given community (Gattuso et al. 1998). The close coupling of GPP and CR occurred at seasonal scale (Fig. 1b) but also at daily scale, whatever the season, as shown by two time series of 10 d in winter and summer (Fig. 2). The CR measurements correspond to the sum of autotrophic respiration (AR) and heterotrophic respiration (HR) (Supporting Information Fig. S1). It is notoriously difficult to separate the individual contribution of AR and HR to CR (Del Giorgio and Williams 2005). AR is linked to GPP at scale of minutes to hours, while HR is linked to GPP at the scale of hours to days for bacteria and days to weeks for metazoans (Del Giorgio and

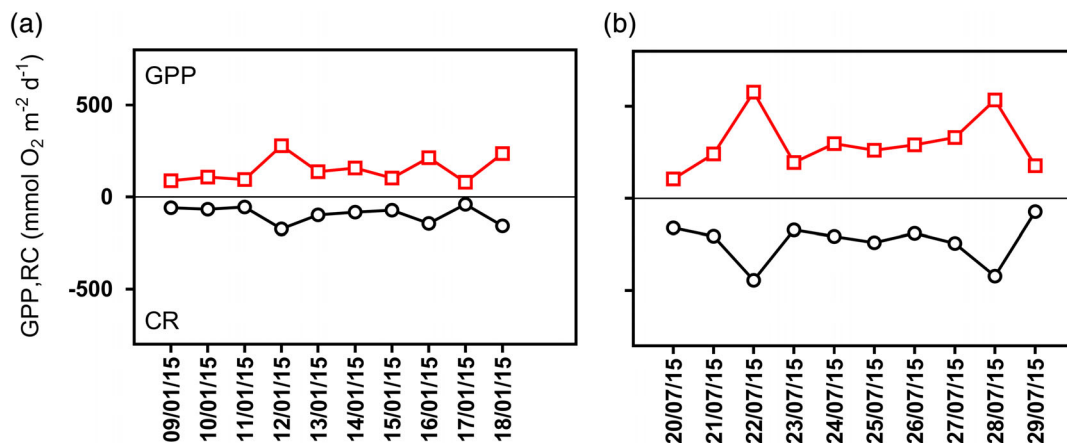


Fig. 2. Two examples of 10 d time series of gross primary production (GPP) and community respiration (CR) in mmol O₂ m⁻² d⁻¹ over a *Posidonia oceanica* meadow in the Bay of Revellata at 10 m bottom depth during winter (a) and summer (b). Note the different scales of Y-axis.

Williams 2005). In seagrasses, AR corresponds on average to 57% of GPP according to Duarte and Cebrián (1996). It is then likely that the tight symmetry between CR and GPP is mainly due to a close coupling between AR and GPP. There is a tight coupling between mitochondrial respiration and photosynthesis in microalgae (Bailleul et al. 2015) and higher terrestrial plants (Noguchi and Yoshida 2008). However, Rasmussen and Björk (2014) showed for *Zostera marina* that mitochondrial respiration was downregulated by light. Yet, this does not necessarily exclude that AR might be enhanced during nighttime, following higher GPP linked to better light conditions.

In addition, *P. oceanica* could release substantial amounts of DOC according to Barrón and Duarte (2009). Heterotrophic bacteria can rapidly assimilate freshly produced phytoplanktonic DOC (Marañón et al. 2004; Morana et al. 2014), and if this also occurs in *P. oceanica* meadows, enhanced HR in response to DOC release associated to high GPP might also contribute to the close coupling of GPP and CR. Adams et al. (2016) investigated the mechanism responsible for the hysteresis in diurnal pattern of oxygen flux in *Zostera muelleri* and tested whether this was caused by HR stimulated by DOC exudation or changes in AR. They concluded that the rate of DOC exudation by seagrass was not sufficient to support a diurnal variation in HR. So, whether the observed coupling of GPP and CR is related to a specific coupling of AR or HR to GPP remains an open question.

NCP also showed distinct seasonal and inter-annual variations (Fig. 1 and Supporting Information Fig. S3). NCP was in general minimal in November–December, on average $\sim 40 \pm 15 \text{ mmol O}_2 \text{ m}^{-2} \text{ d}^{-1}$ (Fig. 3b) corresponding to the period of minimal canopy biomass (Fig. 3a). This was followed by an increase of NCP due to the growth and elongation of *P. oceanica* leaves that peaked in biomass in June with NCP averaging $\sim 83 \pm 39 \text{ mmol O}_2 \text{ m}^{-2} \text{ d}^{-1}$ (Fig. 3a,b). In September, there was a slight increase of NCP averaged for the 12 yr (Fig. 3a) due to the export of litter with fall storms allowing light penetration to the sediment and *P. oceanica* rhizomes and the development of benthic sciaphile macroalgae. For individual years (Supporting Information Fig. S3), the increase of NCP in September was distinctly observed in 2008, 2009, 2012, 2013, 2015, and 2016, but less marked in 2010, 2011, and 2017. The absence of storms in fall–winter 2007 and 2014 did not flush the meadow of litter, blocking the development of benthic sciaphile macroalgae, consequently, no increase of NCP was observed in September of these 2 years.

NCP was significantly positively correlated to GPP (Fig. 4a), in agreement with the general pattern in several marine ecosystem from a meta-analysis by Duarte and Agustí (1998). During periods of high production of organic matter (high GPP) there is a tendency for accumulation of organic matter that can be exported or stored (positive NCP), while during periods of low GPP there is a tendency to consume exhaustively the lower available resources driving systems toward low or

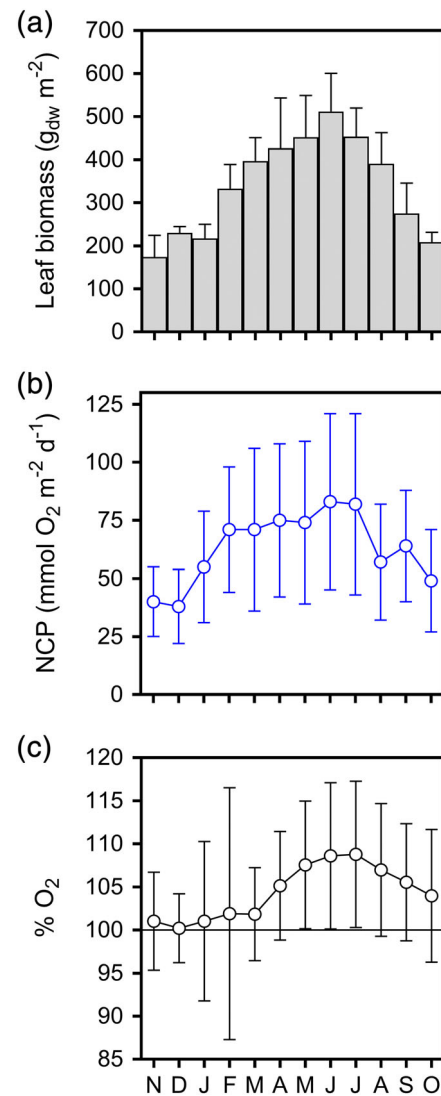


Fig. 3. Climatological monthly average over a *Posidonia oceanica* meadow in the Bay of Revellata at 10 m bottom depth of leaf biomass (1976–1977) (Bay 1984) (a), of net community production (NCP) in $\text{mmol O}_2 \text{ m}^{-2} \text{ d}^{-1}$ (b) and oxygen saturation level (%O₂) (equilibrium with the atmosphere = 100%) at 9.5 m depth (just above the top of the seagrass canopy) (c) (7 August 2006–29 October 2018). Error bars correspond to the standard deviation on the mean.

negative NCP. NCP was also significantly correlated with CR (Fig. 4b) although with more scatter (lower r^2). The NCP-CR correlation was probably indirect and spurious, reflecting the strong correlation between GPP and CR (Fig. 4c).

Net community metabolic status

Community metabolic data and %O₂ data show the studied *P. oceanica* meadow at 10 m was net autotrophic at yearly scale (Fig. 4a). The overall average of NCP during the whole 12-yr period was positive ($23 \pm 8 \text{ mol O}_2 \text{ m}^{-2} \text{ yr}^{-1}$), and GPP ($83 \pm 15 \text{ mol O}_2 \text{ m}^{-2} \text{ yr}^{-1}$) > -CR ($-60 \pm 9 \text{ mol O}_2 \text{ m}^{-2} \text{ yr}^{-1}$).

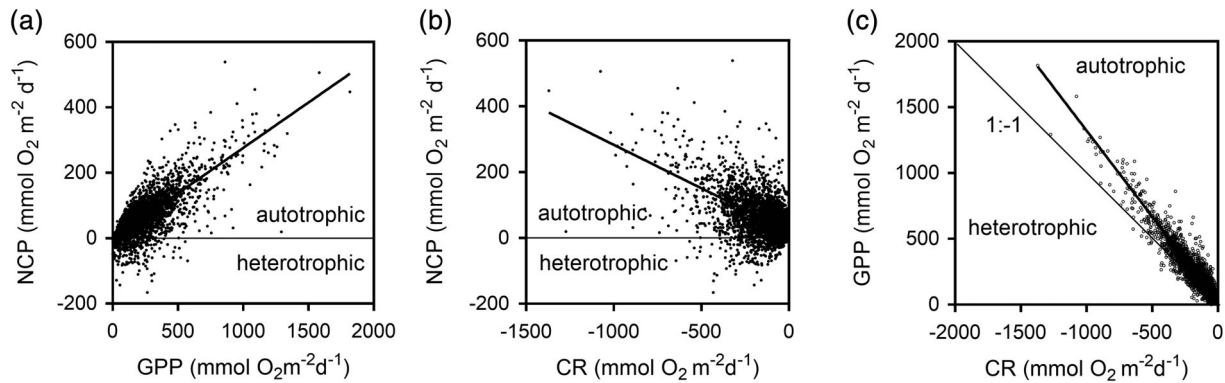


Fig. 4. Net community production (NCP) vs. gross primary production (GPP) (a), NCP vs. community respiration (CR) (b), and GPP vs. CR in $\text{mmol O}_2 \text{m}^{-2} \text{d}^{-1}$ (c) over a *Posidonia oceanica* meadow in the Bay of Revellata at 10 m bottom depth from 7 August 2006 to 29 October 2018. Solid thick lines indicate linear regression: $\text{NCP} = 0.28 (\pm 0.01) \text{GPP} - 1.3 (\pm 1.5)$ ($r^2 = 0.55$, $p < 0.0001$, $n = 3275$), $\text{NCP} = -0.26 (\pm 0.01) \text{CR} + 19.1 (\pm 2.0)$ ($r^2 = 0.24$, $p < 0.0001$, $n = 3275$), $\text{GPP} = -1.31 (\pm 0.01) \text{CR} + 15.5 (\pm 1.9)$ ($r^2 = 0.89$, $p < 0.0001$, $n = 3275$).

This was also reflected on comparison of individual GPP and CR measurements (Fig. 4c). The slope of the regression (-1.31) was statistically lower than -1 (at 95% confidence intervals -1.33 to -1.28) (corresponding to a balanced metabolism, $\text{GPP} = \text{CR}$), and for 90% of individual measurements $\text{GPP} > -\text{CR}$ ($n = 2944$ vs. $n = 3275$). If data from year 2007 are excluded, because it was abnormal due the absence of fall-winter storms that off-set the normal patterns of community metabolism (Champenois and Borges 2012), then 94% of individual measurements $\text{GPP} > -\text{CR}$ ($n = 2722$ vs. $n = 2895$). In addition, % O_2 generally followed the patterns of NCP (Fig. 4c) with higher values in June–July ($108.6\% \pm 8.5\%$) and lowest values in November–December ($100.6\% \pm 5.0\%$), and an overall average of $104.3\% \pm 8.4\%$. An overall oversaturation of O_2 with respect to atmospheric equilibrium is only possible in a system where there is a production of O_2 by GPP in excess of CR, corresponding by definition to a net autotrophic system.

In the same site (Bay of Revellata), Velimirov et al. (2016) arrived at the opposite conclusion that the *P. oceanica* meadow was net heterotrophic based on bacterial carbon demand (BCD) derived from incubations of ^3H -thymidine and ^{14}C -leucine in both the water column and sediment, which were found to be in excess of primary production. There are several possible explanations for the opposing conclusions on net community metabolism of the present study and the one of Velimirov et al. (2016). First, the BCD was compared to *P. oceanica* primary production estimated from change of leaf biomass from Bay (1984) (combination of marking technique and harvesting technique). However, the majority of the BCD in the water column should be fueled by DOC exudation that could be substantial in *P. oceanica* meadows (Barrón and Duarte 2009), but cannot be accounted by the estimation of primary production based on change of leaf biomass. Second, the BCD data of Velimirov et al. (2016) were acquired in 1992 and 1993 and were compared to *P. oceanica* primary production estimates from different years (1978, 1981, 1984, 1995,

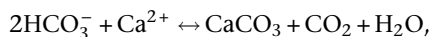
2002, 2003), when our own measurements show that GPP and CR can be extremely variable from day-to-day, seasonally, and year to year (Fig. 1a,b). Third, the benthic BCD reported by Velimirov et al. (2016) is mostly likely overestimated due to an overestimation of the oxic sediment layer, over which the benthic BCD was vertically integrated. Velimirov et al. (2016) integrated the BCD over an oxygenated layer of 10 cm (the method to determine the depth of this layer was not specified by the authors). This is an extremely deep sediment oxygenated layer, usually only encountered in abyssal oceanic sediments (> 4000 m bottom depth), while sediment oxygenated layer has a thickness of only a few mm in coastal sediments (Glud et al. 1994). Measurements of O_2 profiles in sediments at two sites in *P. oceanica* meadows in Mallorca show an oxic layer of 0.2–0.4 cm (Holmer et al. 2003). These values of oxygen penetration depth are consistent with those reported in other seagrass sediments of 0.1–0.2 cm (Trevathan-Tackett 2017; Brodersen et al. 2019). To our best knowledge, data of highly resolved sediment O_2 microprofiles are unavailable in the *P. oceanica* meadow of the Bay of Revellata. But, we obtained, with a coarse sampling method, H_2S pore-water concentrations (Supporting Information Table S2) show that H_2S was always present at 10 cm depth, and in the top 1 cm H_2S was nearly always present. In addition, O_2 was always below detection at all sampled depths, suggesting the oxic layer should have been shallower than 1 cm in both bare and vegetated sediments. For an oxic layer of 10 cm, Velimirov et al. (2016) computed a benthic BCD of $33.2 \text{ mol C m}^{-2} \text{ yr}^{-1}$ at 10 m bottom depth that added to the pelagic BCD ($14.5 \text{ mol C m}^{-2} \text{ yr}^{-1}$), gave a total BCD of $47.7 \text{ mol C m}^{-2} \text{ yr}^{-1}$. This value of BCD was well in excess of *P. oceanica* primary production at 10 m bottom depth of $20 \pm 4 \text{ mol C m}^{-2} \text{ yr}^{-1}$ reported by Velimirov et al. (2016). Reintegrating benthic BCD with a shallower but still probably overestimated value of sediment oxic layer of 0.5 cm, would yield a total (water column and sediment) BCD of 16.2 mol C

$\text{m}^{-2} \text{yr}^{-1}$. Such reevaluated estimate of BCD would be lower than the estimate of *P. oceanica* primary production given by Velimirov et al. (2016) ($20 \pm 4 \text{ mol C m}^{-2} \text{yr}^{-1}$ at 10 m bottom depth), and also than our own estimate of net primary production (NPP) of $37 \pm 6 \text{ mol C m}^{-2} \text{yr}^{-1}$ (also at 10 m bottom depth), implying a net autotrophic status. Our own estimate of NPP was computed as $\text{NPP} = \text{GPP} - \text{AR}$, assuming AR corresponds to 57% of GPP (Duarte and Cebrián 1996), and using a photosynthetic quotient (PQ) of 1 (see below). Note that anaerobic benthic organic matter degradation (dominated by sulfate reduction) was $\sim 1 \text{ mol C m}^{-2} \text{yr}^{-1}$ in a pristine meadow site in Mallorca (Holmer et al. 2003).

The metabolic balance of *P. oceanica* meadows in the Bay of Revellata was also found to be positive (net autotrophic) based on O_2 benthic incubations in the 1980s (Frankignoulle and Bouqueneau 1987), as well as in two other *P. oceanica* meadows in the Mediterranean (Magalluf Bay and Sounion) (Barrón et al. 2006; Apostolaki et al. 2010). Net autotrophy is also in agreement with the fact these communities store (Mateo et al. 1997) and export to adjacent communities very large amounts of organic matter (Cebrián and Duarte 1998), and are net producers of O_2 in excess of atmospheric equilibrium (see above).

Comparison of community metabolic rates based on oxygen and inorganic carbon changes

The overall carbon budget in seagrass meadows depends on the balance of processes of production, destruction, storage, and export of organic matter and of CaCO_3 , respectively, the “organic carbon metabolism” and the “inorganic carbon metabolism” (Barrón et al. 2006; Yates and Halley 2006; Howard et al. 2018; Van Dam et al. 2019). We carried out measurements of DIC and TA in benthic chambers that allow computing the net daily fluxes of these two quantities (F_{DIC} and F_{TA} , respectively). The regression of F_{DIC} as function of F_{TA} (Supporting Information Fig. S4) gave a slope of 0.48 ± 0.17 which is consistent with the one expected if the relative variation of TA with regards to DIC is driven by CaCO_3 precipitation or DIS (Smith and Key 1975), according to equation:



whereby for each mole of CaCO_3 precipitated (or dissolved), the decrease (or increase) of DIC is two times lower than the decrease (or increase) of TA.

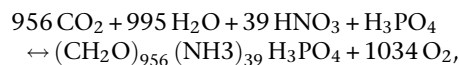
The flux of DIC can then be corrected to only give the flux of DIC related to organic carbon metabolism (DIC*) by removing the term related to CAL/DIS (Smith and Key 1975), according to:

$$\text{DIC}^* = \text{DIC} - \text{TA}/2.$$

The consistency of this approach can be tested by comparing NCP derived from O_2 incubations (abbreviated as previously—

NCP) with NCP derived from uncorrected DIC (NCP_{DIC}) and DIC* ($\text{NCP}_{\text{DIC}^*}$). The slope of the regression of NCP vs. NCP_{DIC} of -0.51 ± 0.18 (at 95% confidence intervals -0.96 to -0.12) was lower than the slope of the regression of NCP vs. $\text{NCP}_{\text{DIC}^*}$ of -0.71 ± 0.17 (at 95% confidence intervals -1.08 to -0.34) (Supporting Information Fig. S5). This confirms that DIC dynamics were affected by CAL/DIS and that DIC* gives a better estimate of the changes of DIC related to organic production/destruction processes.

Yet, the direct comparison community metabolic rates derived from O_2 changes and DIC* changes requires the conversion of rates measured by O_2 changes in rates expressed in carbon. The PQ corresponds to the molar ratio of the release of O_2 to the consumption of DIC during photosynthesis while the respiratory quotient (RQ) corresponds to the molar ratio of the release of DIC to the consumption of O_2 during organic matter mineralization. The values of PQ and RQ depend on the relative abundance of carbon, nitrogen and phosphorous of the average composition of organic matter that for *P. oceanica* leaves is given, according to Atkinson and Smith (1983), by the following equation:



which allows to compute a theoretical value of 1.08 for PQ and of 0.92 for RQ for production and respiration of *P. oceanica* organic matter.

Nighttime CR from DIC* change ($\text{CR}_{\text{DIC}^*(\text{night})}$) was computed from F_{DIC} during nighttime ($F_{\text{DIC}(\text{night})}$) and F_{TA} during nighttime ($F_{\text{TA}(\text{night})}$) according to:

$$\text{CR}_{\text{DIC}^*(\text{night})} = F_{\text{DIC}(\text{night})} - 0.5 \times F_{\text{TA}(\text{night})}.$$

$\text{CR}_{\text{DIC}^*(\text{night})}$ was well correlated to CR derived from O_2 incubations (abbreviated as previously—CR) and the resulting slope was -0.97 ± 0.18 not statistically different from -1 (at 95% confidence intervals -1.35 to -0.59) and close to the theoretical RQ of 0.92. (Supporting Information Fig. S6). Assuming that $\text{CR}_{\text{DIC}^*(\text{night})}$ is the same during the night and during the day, it is used to derive the GPP based on changes of DIC* ($\text{GPP}_{\text{DIC}^*}$) according to:

$$\text{GPP}_{\text{DIC}^*} = \text{NCP}_{\text{DIC}^*} - \text{CR}_{\text{DIC}^*}.$$

$\text{GPP}_{\text{DIC}^*}$ was well correlated to GPP derived from O_2 incubations (abbreviated as previously—GPP) and the resulting slope was -1.03 ± 0.21 not statistically different from -1 (at 95% confidence intervals -1.48 to -0.58), was identical to the experimentally determined RQ, and close to the theoretical PQ of 1.08. (Supporting Information Fig. S6). Hereafter, we will consider $\text{PQ} = \text{RQ} = 1$.

The net daily F_{TA} (hereafter F_{TA}) was almost always positive (from the sediment to the water column) (Fig. 5a). This

implies there was a net DIS in the sediments that needs to be compensated by an input of allochthonous CaCO_3 particles (from outside of the meadow). For the August 2006–2009 sampling period, the net DIS averaged $6.8 \pm 4.9 \text{ mol CaCO}_3 \text{ m}^{-2} \text{ yr}^{-1}$ which is close to the CaCO_3 sedimentation from the

water column to the meadow of $7.2 \text{ mol CaCO}_3 \text{ m}^{-2} \text{ yr}^{-1}$ reported by Dauby et al. (1995) from sediment trap deployments over the *P. oceanica* meadow in the Bay of Revellata.

The F_{TA} was always positive during nighttime ($F_{\text{TA}(\text{night})}$) and generally close to 0 (or sometimes negative) during daytime ($F_{\text{TA}(\text{day})}$) (Fig. 5b). DIS could not have occurred in the water column because the calcite and aragonite saturation levels were above 5.5 and 3.5, respectively. We assume DIS only occurred in sediments and was independent from night and day cycles (constant whatever the period of the day). We also assume that CAL was only related to epiphytic or benthic algae, mostly related to coralline algae (Mazzella et al. 1989; Jacquemart and Demoulin 2006). We further assumed that CAL is linked to coralline algae photosynthesis (Borowitzka and Larkum 1981), and only occurred during daytime. Based on the above assumptions, we conclude that, during daytime, CAL compensated DIS, leading to $F_{\text{TA}} \leq 0$ (Fig. 5b), allowing to compute daily integrated rates of DIS and CAL, according to:

$$\text{DIS} = (F_{\text{TA}(\text{night})}/\text{Hn}) \times 24,$$

where Hn is the number of hours during the night.

$$\text{CAL} = -0.5 \times (F_{\text{TA}(\text{day})} - (F_{\text{TA}(\text{night})}/\text{Hn}) \times \text{Hd}),$$

where Hd is the photoperiod in h.

CAL followed a seasonal cycle and was highest in summer 2006, 2008, and 2009, but not 2007, possibly due the fact this was an exceptional year, as explained above (Fig. 5c). CAL was positively related to GPP (Supporting Information Fig. S7). This confirms our above assumption that CAL is linked to

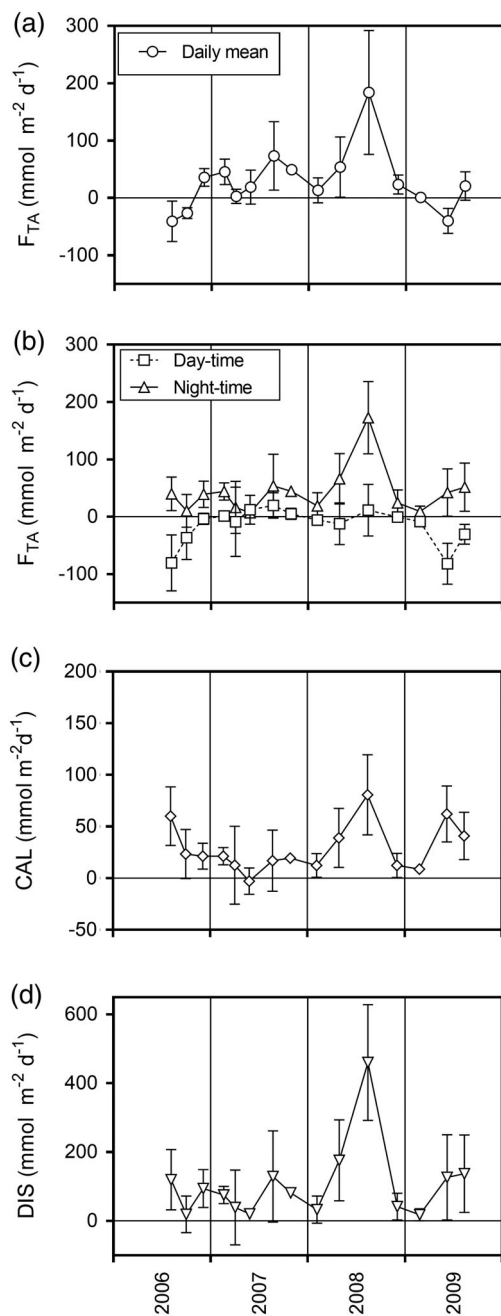


Fig. 5. Total alkalinity (TA) fluxes (F_{TA}) from benthic chamber incubations during 24 h, net daily (a), and during daytime (dawn to dusk) or nighttime (dusk to dawn) (b), and calcification (CAL) (c) and CaCO_3 dissolution (DIS) in $\text{mmol m}^{-2} \text{ d}^{-1}$ (d) over a *Posidonia oceanica* meadow in the Bay of Revellata at 10 m bottom depth from 6 August 2006 to 12 August 2009 ($n = 15$). Error bars correspond to standard deviation of fluxes computed from triplicate benthic chamber incubations.

Table 1. Net annual gross primary production (GPP), community respiration (CR), net community production (NCP), calcification (CAL), CaCO_3 dissolution (DIS) and resulting CO_2 fluxes in a *Posidonia oceanica* meadow in the Bay of Revellata at 10 m bottom depth. Net DIS was computed from CAL-DIS, and compared well with a different estimate based on the daily net change of total alkalinity during the incubations of $6.8 \pm 4.9 \text{ mol CaCO}_3 \text{ m}^{-2} \text{ yr}^{-1}$.

Organic metabolism ($\text{mol O}_2 \text{ m}^{-2} \text{ yr}^{-1}$)	
GPP	83.3 ± 16.0
CR	-60.1 ± 9.0
NCP	23.2 ± 8.2
Inorganic metabolism ($\text{mol CaCO}_3 \text{ m}^{-2} \text{ yr}^{-1}$)	
CAL	10.8 ± 4.0
DIS	-21.4 ± 8.0
Net DIS	-10.6 ± 8.9
CO_2 fluxes ($\text{mol CO}_2 \text{ m}^{-2} \text{ yr}^{-1}$)	
CO_2 uptake from NCP	-23
CO_2 uptake from net DIS	-6
Net CO_2 uptake	-30

photosynthesis due to coralline algae (Borowitzka and Larkum 1981). While GPP represents the whole community, epiphyte and *P. oceanica* leaf GPP can be assumed to covary as the extension of *P. oceanica* leaves will provide extra surface for the development of epiphytes. The average CAL for the August 2006–2009 sampling period was $10.8 \pm 3.8 \text{ mol CaCO}_3 \text{ m}^{-2} \text{ yr}^{-1}$.

DIS also followed a seasonal cycle and was highest in summer (Fig. 5d). DIS in *P. oceanica* meadows is probably coupled (at least partly) to the acidification due to CO_2 from benthic aerobic respiration and to oxidation by O_2 of H_2S , as discussed in Barrón et al. (2006) and in agreement with the ratio of DIC to TA in pore water in the Bay of Revellata (Moulin et al. 1985). Benthic respiration most probably increases in summer due to temperature increase, to translocation of oxygen to sediments (Borum et al. 2006), and to supply of labile

organic matter to the sediments that should track leaf GPP. Indeed, DIS was found to be related to both CR and water temperature (T in $^\circ\text{C}$), according to:

$$\text{DIS} = -133.3 + 7.89T - 0.612 \text{ CR} \quad (F = 6.169 > Q_{F(0.95,2,12)} 3.89, r^2 = 0.71)$$

with DIS in $\text{mmol m}^{-2} \text{ d}^{-1}$ and CR in $\text{mmol m}^{-2} \text{ d}^{-1}$.

Although CR combines both sediment and water column respiration, it is plausible that benthic respiration tracks CR, at least at seasonal scale.

Organic and inorganic carbon mass balance

Organic metabolism was greater than inorganic metabolism in the studied *P. oceanica* meadow at 10 m bottom depth

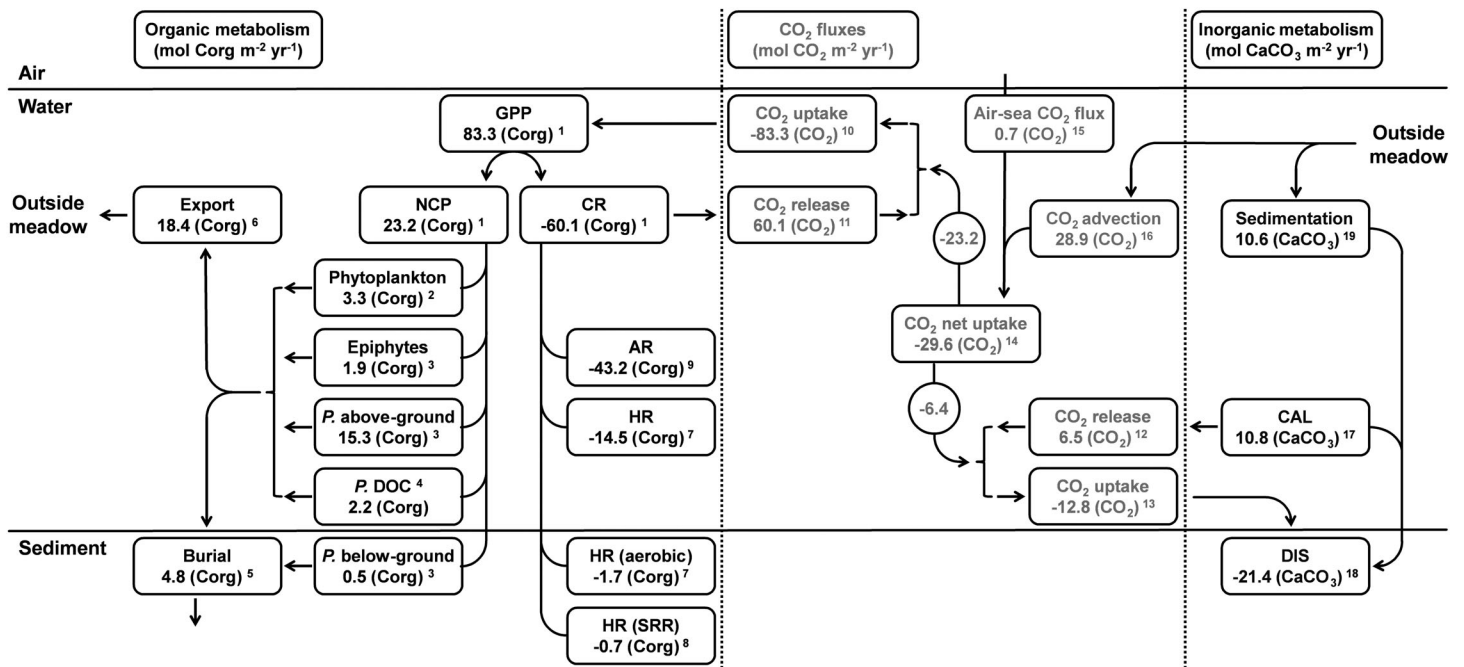


Fig. 6. Budget of fluxes of organic carbon (Corg) ($\text{mol Corg m}^{-2} \text{ yr}^{-1}$), particulate inorganic carbon ($\text{mol CaCO}_3 \text{ m}^{-2} \text{ yr}^{-1}$), and CO_2 ($\text{mol CO}_2 \text{ m}^{-2} \text{ yr}^{-1}$) in a *Posidonia oceanica* seagrass meadow at 10 m depth, based on measurements from this study in the Bay of Revellata and literature data at the same site or from other *P. oceanica* meadows. ¹Gross primary production (GPP), community respiration (CR), net community production (NCP) based mass balance of O_2 measured with optodes on a mooring (12-yr average, this study); ²Phytoplankton primary production (phytoplankton) based on ¹⁴C incubations reported by Dauby (1985) in the Bay of Revellata; ³Primary production based on biomass change of *P. oceanica* leaves (*P.* above-ground), of *P. oceanica* rhizomes and roots (*P.* below-ground), and epiphytes reported by Bay (1984) in the Bay of Revellata; ⁴Dissolved organic carbon (DOC) exudation by *P. oceanica* leaves (*P.* DOC) computed as $\text{NCP} - \text{phytoplankton} - \text{epiphytes} - \text{P. above-ground} - \text{P. below-ground}$; ⁵Sedimentary organic carbon burial rates (burial) based on radiocarbon dating and carbon content from sediment cores in seven *P. oceanica* meadows (Spain and Italy) by Mateo et al. (1997); ⁶Export of organic carbon to adjacent systems (Export) computed as $\text{NCP} - \text{burial}$; ⁷Bacterial heterotrophic respiration (HR) based on ³H-thymidine et ¹⁴C-leucine incubations from Velimirov et al. (2016) in the Bay of Revellata, but the benthic HR (aerobic) was reintegrated vertically over 0.5 cm; ⁸Sulfate reduction rate (SRR) based on ³⁵S-sulfate core incubations reported in two pristine *P. oceanica* meadows in Spain by Holmer et al. (2003) and Gacia et al. (2012); ⁹Autotrophic respiration (AR) computed as $-\text{CR} + \text{AR} + \text{HR} + \text{HR (aerobic)} + \text{HR (SRR)}$; ¹⁰ uptake of CO_2 by GPP computed as $-\text{GPP}$; ¹¹Release of CO_2 by CR computed as $-\text{CR}$; ¹²Release of CO_2 by calcification (CAL) computed as $0.6 \times \text{CAL}$ (Frankignoulle et al. 1994); ¹³Uptake of CO_2 by benthic CaCO_3 dissolution (DIS) computed as $0.6 \times \text{DIS}$ (Frankignoulle et al. 1994); ¹⁴Net community CO_2 uptake (CO_2 net uptake) computed as $-\text{GPP} - \text{CR} + 0.6 \times \text{CAL} - 0.6 \times \text{DIS}$; ¹⁵Air-sea CO_2 flux estimated from the measurements of the partial pressure of CO_2 in the Bay of Revellata (this study); ¹⁶Inputs of CO_2 by water masses circulating over the *P. oceanica* meadow computed as $-\text{CO}_2$ net uptake - air-sea CO_2 flux; ¹⁷CAL derived from total alkalinity (TA) changes during benthic incubations over vegetated sediments in the Bay of Revellata (this study); ¹⁸DIS derived from TA changes during benthic incubations over vegetated sediments in the Bay of Revellata (this study); ¹⁹Sedimentation of CaCO_3 from the water column to the *P. oceanica* meadow (Sedimentation) computed as $-\text{DIS} - \text{CAL}$.

(Table 1). The CAL : GPP ratio was 0.12 on average in the studied *P. oceanica* meadow which is lower than the CAL : GPP ratio reported for coralline algae of ~ 0.7 (El Haïkali et al. 2004) and ~ 0.5 (Martin et al. 2013). The CAL : NPP ratio in the studied *P. oceanica* meadow was on average 0.29 which was also lower than global average estimated by van der Heijden and Kamenos (2015) for coralline algae of 1.6. The CAL : GPP and CAL : NPP were both about five times lower in the studied *P. oceanica* meadow than for the same ratios reported in the literature for coralline algae. This is in agreement with the fact that primary production is sustained by both *P. oceanica* itself and epiphyte algae, while CAL is only sustained by coralline algae. Nevertheless, the CAL : GPP of 0.12 in the studied *P. oceanica* meadow at 10 m depth is quite high, and only 2–3 times lower to the one reported in coral reefs of 0.2–0.3 (Langdon et al. 2000).

We separated carbon fluxes into different components using our own measurements and values from other studies in the Bay of Revellata or in other *P. oceanica* meadows (Fig. 6). AR represented 72% of CR which indicates that the close coupling of CR and GPP (Fig. 1b) seemed to be mainly related to a coupling of AR and GPP (see above). AR represented 52% of GPP, in agreement with the value $57\% \pm 6\%$ reported for seagrasses by Duarte and Cebrián (1996). Sulfate-reduction rates represented about 29% of total sedimentary HR, within the range (23–43%) typical for seagrass sediments (Holmer et al. 1999). Phytoplankton only contributed to 14% of total NCP, showing the overwhelming dominance of the contribution to NCP from the benthic compartment, itself largely dominated by *P. oceanica*, as epiphytes only contributed to 8% of total NCP. The DOC exudation rate we computed ($2.2 \text{ mol m}^{-2} \text{ yr}^{-1}$) was comparable to the value based on direct DOC measurements reported by Barrón and Duarte (2009) of $4.4 \pm 0.9 \text{ mol m}^{-2} \text{ yr}^{-1}$. Barrón and Duarte (2009) concluded that DOC exudation corresponded to 72% of NCP, although their NCP value of $6.1 \text{ mol m}^{-2} \text{ yr}^{-1}$ was particularly low, almost four times lower than our own NCP estimate. Our own estimate of DOC exudation corresponded to $\sim 10\%$ of NCP. The DOC exudation we estimated and that was measured by Barrón and Duarte (2009) corresponds to the net flux of DOC (that escapes microbial consumption of DOC). Assuming that the majority of pelagic HR is fueled by DOC exudation, than gross DOC exudation ($16.7 \text{ mol m}^{-2} \text{ yr}^{-1}$) corresponds to 20% of GPP, a value typical of marine phytoplankton (Baines and Pace 1991). The majority of NCP was exported out of the meadow ($\sim 79\%$) and a small fraction buried in sediments ($\sim 21\%$). Note that exported organic matter can be further buried in adjacent coastal sediments, and even in deep-sea sediments (Duarte and Krause-Jensen 2017). The positive NCP and the net DIS both drove a sink of CO_2 . For each mole of CaCO_3 dissolved, CO_2 decreases by about 0.6 mol because CO_2 is in equilibrium with HCO_3^- in seawater (Frankignoulle et al. 1994). The net balance of CO_2 in the *P. oceanica* meadow was $-29.6 \text{ mol m}^{-2} \text{ yr}^{-1}$ with DIS

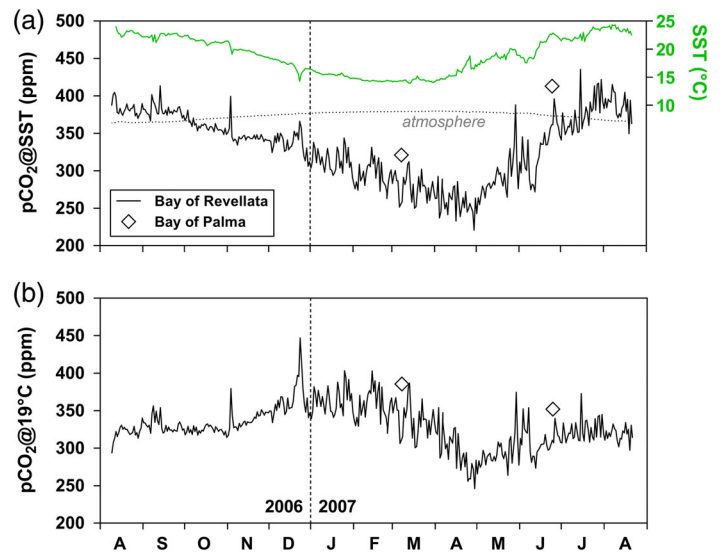


Fig. 7. Seawater partial pressure of CO_2 (pCO_2 , ppm) at sea surface temperature (SST in $^{\circ}\text{C}$) ($\text{pCO}_2@SST$) (a) and normalized to constant temperature of 19°C ($\text{pCO}_2@19^{\circ}\text{C}$, Takahashi et al. 2002) (b) in surface water (2 m depth) over a *Posidonia oceanica* meadow in the Bay of Revellata at 10 m bottom depth from 9 August 2006 to 20 August 2007. Diamonds indicate pCO_2 in surface water data obtained in March 2002 and June 2002 over a *P. oceanica* meadow in the Bay of Palma (Gazeau et al. 2005). Dotted line indicates the atmospheric pCO_2 .

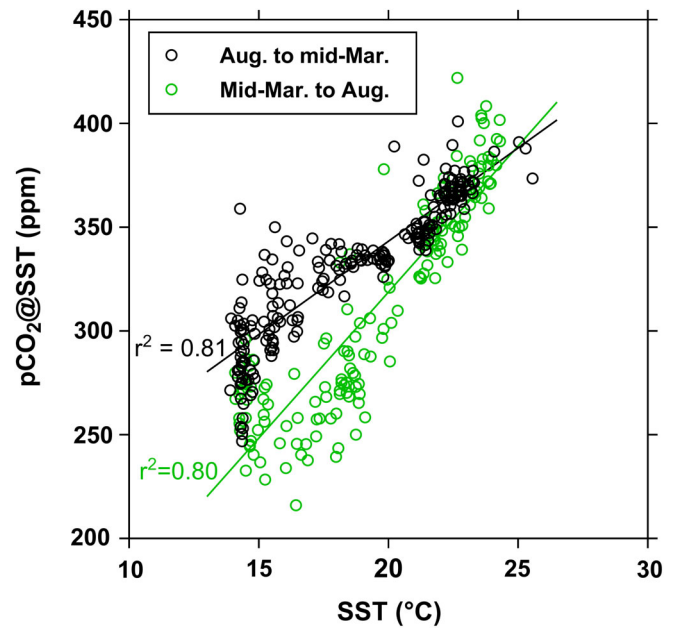


Fig. 8. Seawater partial pressure of CO_2 (pCO_2 , ppm) at sea surface temperature (SST in $^{\circ}\text{C}$) ($\text{pCO}_2@SST$) vs. SST in surface water (2 m depth) over a *Posidonia oceanica* meadow in the Bay of Revellata at 10 m bottom depth from 9 August 2006 to 20 August 2007. Data were separated in two groups before and after the annual SST minimum, from August 2006 mid-March 2007 and from mid-March 2007 to August 2007. Solid lines indicate the linear regressions.

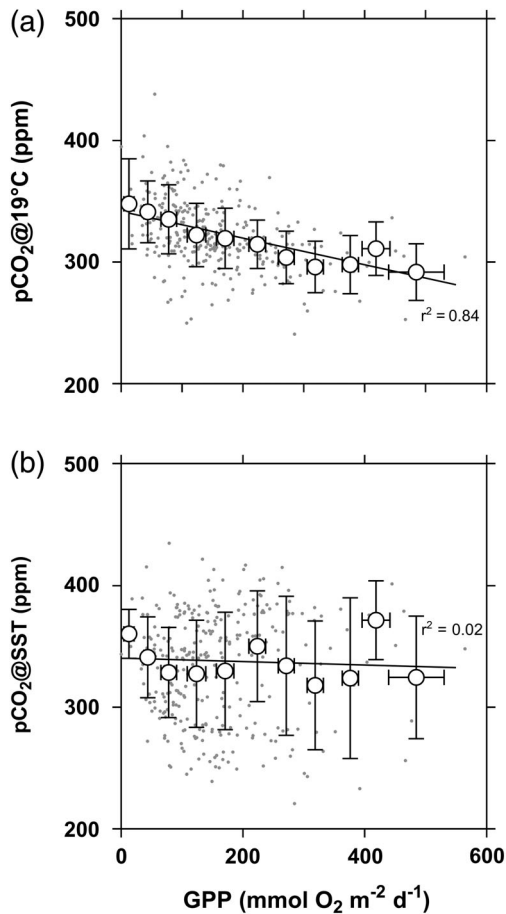


Fig. 9. Seawater partial pressure of CO₂ (pCO₂, ppm) normalized to constant temperature of 19°C (pCO₂@19°C, Takahashi et al. 2002) **(a)** and at sea surface temperature (SST in°C) (pCO₂@SST) **(b)** in surface water (2 m depth) vs. gross primary production (GPP, mmol O₂ m⁻² d⁻¹) over a *Posidonia oceanica* meadow in the Bay of Revellata at 10 m bottom depth from 9 August 2006 to 20 August 2007. Solid line indicates the linear regression. Gray dots show raw data, the open circles show the averages by bins. Error bars correspond to standard deviation on the averages by bins.

only contributing to 22%, the rest was contributed by NCP (Fig. 6; Table 1).

The pCO₂ data (Fig. 7) allow to compute an atmospheric CO₂ sink of $-0.7 \text{ mol m}^{-2} \text{ yr}^{-1}$ (Supporting Information Fig. S8, Fig. 6). The *P. oceanica* meadow was also a small source of CH₄ to the atmosphere at rate of $0.006 \text{ mol CH}_4 \text{ m}^{-2} \text{ yr}^{-1}$ (Supporting Information Table S3), about 100 times lower than the CO₂ sink. Nevertheless, values of CH₄ in surface waters were generally much higher than values in surface waters of the open Mediterranean Sea (de la Paz et al. 2015), and seasonal variations seem related to sediment resuspension during winter (Supporting Information Table S3) in relation to storms (Dauby et al. 1995). The comparison of metabolic balance of CO₂ and the air–sea CO₂ flux is misleading, as these processes are usually uncoupled (Borges et al. 2006). Indeed, the lowest values of pCO₂ at in situ sea surface temperature (SST) (pCO₂@SST) were observed in April,

while the highest pCO₂@SST values were observed in August. The pCO₂ values decreased regularly from August 2006 to late April 2007, then increased from April to August 2007, following the SST seasonal cycle. This can be explained by temperature effect on Henry's constant (Takahashi et al. 2002). Indeed, pCO₂@SST correlated well to SST but with different slopes for period of summer–fall–winter transition and the period of winter–spring–summer transition (Fig. 8). The period of winter–spring–summer transition was characterized by *P. oceanica* leaf growth, biomass accumulation and increasing trend in NCP (Fig. 3b) and was characterized by lower pCO₂@SST values at a given temperature than for period of summer–fall–winter transition (Fig. 8) that was characterized by *P. oceanica* leaf senescence and decreasing trend in NCP (Fig. 3a). This was consistent with the trends of pCO₂ normalized to a constant temperature of 19°C (pCO₂@19°C). This normalization removes the effect of temperature on CO₂ solubility, consequently, the variations of pCO₂@19°C reflect the effect of the other biogeochemical processes (biological activity and/or physical mixing) (Takahashi et al. 2002). Indeed, pCO₂@19°C increased during the summer–fall–winter transition period (August to late February) and decreased during the winter–spring–summer transition period (early March to late May) (Fig. 7b). Furthermore, pCO₂@19°C was significantly negatively correlated to GPP, while pCO₂@SST was uncorrelated to GPP, confirming the confounding effect of temperature on pCO₂ over biological processes (Fig. 9). Data of pCO₂ have also been reported in a *P. oceanica* meadow in the Bay of Palma, and both the pCO₂@SST and pCO₂@19°C followed the same seasonal pattern as in the Bay of Revellata with lower pCO₂ values in spring than summer (Fig. 7a,b). The pCO₂@SST and pCO₂@19°C in the Bay of Palma were higher than in the Bay of Revellata of about 25 ppm and this might reflect the fact that the data in the Bay of Palma were obtained over the full depth range of the meadow (down to about 50 m bottom depth) while the data in Bay of Revellata were only from 10 m bottom depth, so the difference might represent spatial variability of surface pCO₂ due to seafloor depth. The spatial distribution reported by Gazeau et al. (2005) in the Bay of Palma shows that the pCO₂ values over the meadow were 40 ppm lower than the pCO₂ values from offshore waters. In addition, the difference might simply be due to different pCO₂ value of the offshore water incoming into the bay that sets a “background” pCO₂ value that decreases as the water mass travels over the meadow (Gazeau et al. 2005).

In conclusion, the direct comparison of CO₂ uptake from community metabolism to air–sea CO₂ fluxes is difficult due to additional processes that affect CO₂ dynamics, namely, physical processes (water temperature changes, vertical mixing, and water mass horizontal transport). In the case of communities with a low spatial extent and short residence time such as seagrass meadows, community metabolism will only marginally modify the CO₂ content of incoming offshore water. The CO₂ content of incoming offshore water is probably the most important factor setting the direction and

intensity of air–sea CO₂ fluxes in such marine communities (Gazeau et al. 2005; Borges et al. 2006). In our particular case, air–sea CO₂ flux could only balance 2% of total community net CO₂ uptake, and we assume that the majority of total community net CO₂ uptake (98%) was sustained by CO₂ from external water masses advected on the meadow (Fig. 6).

Data availability statement

Data sets are publically available and can be downloaded from zenodo.org (Borges and Champenois 2021).

References

- Adams, M. P., A. J. P. Ferguson, P. S. Maxwell, B. A. J. Lawson, J. Samper-Villarreal, and K. R. O'Brien. 2016. Light history-dependent respiration explains the hysteresis in the daily ecosystem metabolism of seagrass. *Hydrobiologia* **766**: 75–88. doi:10.1007/s10750-015-2444-5
- Apostolaki, E. T., M. Holmer, N. Marbà, and I. Karakassis. 2010. Metabolic imbalance in coastal vegetated (*Posidonia oceanica*) and unvegetated benthic ecosystems. *Ecosystems* **13**: 459–471. doi:10.1007/s10021-010-9330-9
- Atkinson, M. S., and S. V. Smith. 1983. C:N:P: Ratios of benthic marine plants. *Limnol. Oceanogr.* **28**: 568–574. doi:10.4319/lo.1983.28.3.0568
- Bailleul, B., and others. 2015. Energetic coupling between plastids and mitochondria drives CO₂ assimilation in diatoms. *Nature* **524**: 366–369. doi:10.1038/nature14599
- Baines, S. B., and M. L. Pace. 1991. The production of dissolved organic matter by phytoplankton and its importance to bacteria: Patterns across marine and freshwater systems. *Limnol. Oceanogr.* **36**: 1078–1090. doi:10.4319/lo.1991.36.6.1078
- Barrón, C., C. M. Duarte, M. Frankignoulle, and A. V. Borges. 2006. Organic carbon metabolism and carbonate dynamics in a Mediterranean seagrass (*Posidonia oceanica*) meadow. *Estuar. Coasts* **29**: 417–426. doi:10.1007/BF02784990
- Barrón, C., and C. M. Duarte. 2009. Dissolved organic matter release in a *Posidonia oceanica* meadow. *Mar. Ecol. Prog. Ser.* **374**: 75–84. doi:10.3354/meps07715
- Bay, D. 1984. A field study of the growth dynamics and productivity of *Posidonia oceanica* (L.) Delile in Calvi Bay, Corsica. *Aquat. Bot.* **20**: 43–64. doi:10.1016/0304-3770(84)90026-3
- Benson, B. B., and D. Krause Jr. 1984. The concentration and isotopic fractionation of oxygen dissolved in freshwater and seawater in equilibrium with the atmosphere. *Limnol. Oceanogr.* **29**: 620–632. doi:10.4319/lo.1984.29.3.0620B
- Borges, A. V., L.-S. Schiettecatte, G. Abril, B. Delille, and F. Gazeau. 2006. Carbon dioxide in European coastal waters. *Estuar. Coast. Shelf Sci.* **70**: 375–387. doi:10.1016/j.ecss.2006.05.046
- Borum, J., K. Sand-Jensen, T. Binzer, O. Pedersen, and T. M. Greve. 2006. Oxygen movement in seagrasses, p. 255–270. *In* A. W. D. Larkum, R. J. Orth, and C. M. Duarte [eds.], *Seagrasses: Biology, ecology and conservation*. Dordrecht, The Netherlands: Springer.
- Borowitzka, M. A., and A. W. D. Larkum. 1981. Calcification in algae: Mechanisms and the role of metabolism. *Crit. Rev. Plant Sci.* **6**: 1–45. doi:10.1080/07352688709382246
- Boudouresque, C. F., and others. 2006. *Préservation et conservation des herbiers à Posidonia oceanica*. Monaco: Ramoge Publisher, p. 202.
- Borges, A. V., and W. Champenois. 2021. Oxygen saturation, water temperature, gross primary production, community respiration, net community production, partial pressure of CO₂ over a *Posidonia oceanica* meadow in the Bay of Revellata (2006–2018). *Limnol. Oceanogr.* doi:10.5281/zenodo.4421348
- Brodersen, K. E., S. M. Trevathan-Tackett, D. A. Nielsen, R. M. Connolly, C. E. Lovelock, T. B. Atwood, and P. I. Macreadie. 2019. Oxygen consumption and sulfate reduction in vegetated coastal habitats: Effects of physical disturbance. *Front. Mar. Sci.* **6**: 14. doi:10.3389/fmars.2019.00014
- Cebrián, J., and C. M. Duarte. 1998. Patterns in leaf herbivory on seagrass. *Aquat. Bot.* **60**: 67–82. doi:10.1016/S0304-3770(97)00070-3
- Cline, J. D. 1969. Spectrophotometric determination of hydrogen sulphide in natural water. *Limnol. Oceanogr.* **14**: 454–458. doi:10.4319/lo.1969.14.3.0454
- Champenois, W., and A. V. Borges. 2012. Seasonal and inter-annual variations of community metabolism rates of a *Posidonia oceanica* seagrass meadow. *Limnol. Oceanogr.* **57**: 347–361. doi:10.4319/lo.2012.57.1.0347
- Champenois, W., and A. V. Borges. 2019. Inter-annual variations over a decade of primary production of the seagrass *Posidonia oceanica*. *Limnol. Oceanogr.* **64**: 32–45. doi:10.1002/lno.11017
- Dauby, P. 1985. Plankton productivity in gulf of Calvi (Corsica), p. 442–450. *In* R. Van Grieken and R. Wollast [eds.], *Progress in Belgian oceanographic research*. Antwerp, Belgium: Antwerp Univ. Press.
- Dauby, P., and others. 1995. Particle fluxes over a Mediterranean seagrass bed: A one year case study. *Mar. Ecol. Prog. Ser.* **126**: 233–246. doi:10.3354/meps126233
- de la Paz, M., I. E. Huertas, S. Flecha, A. F. Ríos, and F. F. Pérez. 2015. Nitrous oxide and methane in Atlantic and Mediterranean waters in the Strait of Gibraltar: Air-sea fluxes and inter-basin exchange. *Prog. Oceanogr.* **138**: 18–31. doi:10.1016/j.pocean.2015.09.009
- Del Giorgio, P. A., and P. J. L. B. Williams. 2005. *Respiration in aquatic ecosystems*. New York, Oxford Univ. Press, p. 315. doi:10.1093/acprof:oso/9780198527084.001.0001
- de los Santos, C. B., and others. 2019. Recent trend reversal for declining European seagrass meadows. *Nat. Commun.* **10**: 3356. doi:10.1038/s41467-019-11340-4
- Dickson, A. G. 1993. pH buffers for sea water media based on the total hydrogen ion concentration scale. *Deep-Sea Res.* **40**: 107–118. doi:10.1016/0967-0637(93)90055-8

- Duarte, C. A., and J. Cebrián. 1996. The fate of marine autotrophic production. *Limnol. Oceanogr.* **41**: 1758–1766. doi:10.4319/lo.1996.41.8.1758
- Duarte, C. M., and S. Agustí. 1998. The CO₂ balance of unproductive aquatic ecosystems. *Science* **281**: 234–236. doi:10.1126/science.281.5374.234
- Duarte, C. M., and D. Krause-Jensen. 2017. Export from seagrass meadows contributes to marine carbon sequestration. *Front. Mar. Sci.* **4**: 1–13. doi:10.3389/fmars.2017.00013
- El Haikali, B., N. Bensoussan, J.-C. Romano, and V. Bousquet. 2004. Estimation of photosynthesis and calcification rates of *Corallina elongata* Ellis and Solander, 1786, by measurements of dissolved oxygen, pH and total alkalinity. *Sci. Mar.* **68**: 45–56. doi:10.3989/scimar.2004.68n145
- Felisberto, P., and others. 2015. Acoustic monitoring of O₂ production of a seagrass meadow. *J. Exp. Mar. Biol. Ecol.* **464**: 75–87. doi:10.1016/j.jembe.2014.12.013
- Frankignoulle, M., and J.-M. Bouquigneau. 1987. Seasonal variations of the diel carbon budget of a marine macrophytes ecosystem. *Mar. Ecol. Prog. Ser.* **38**: 197–199. doi:10.3354/meps038197
- Frankignoulle, M., C. Canon, and J.-P. Gattuso. 1994. Marine calcification as a source of carbon dioxide: Positive feedback of increasing atmospheric CO₂. *Limnol. Oceanogr.* **39**: 458–462. doi:10.4319/lo.1994.39.2.0458
- Gacia, E., N. Marbà, J. Cebrián, R. Vaquer-Sunyer, N. Garcias-Bonet, and C. M. Duarte. 2012. Thresholds of irradiance for seagrass *Posidonia oceanica* meadow metabolism. *Mar. Ecol. Prog. Ser.* **466**: 69–79. doi:10.3354/meps09928
- Gattuso, J.-P., M. Frankignoulle, and R. Wollast. 1998. Carbon and carbonate metabolism in coastal aquatic ecosystems. *Annu. Rev. Ecol. Syst.* **29**: 405–434. doi:10.1146/annurev.ecolsys.29.1.405
- Gazeau, F., and others. 2005. Whole system metabolism and CO₂ fluxes in a Mediterranean Bay dominated by seagrass beds (Palma Bay, NW Mediterranean). *Biogeosci.* **2**: 43–60. doi:10.5194/bg-2-43-2005
- Glud, R. N., J. K. Gundersen, B. B. Jørgensen, N. P. Revsbech, and H. D. Schulz. 1994. Diffusive and total oxygen uptake of deep-sea sediments in the eastern South Atlantic Ocean: In situ and laboratory measurements. *Deep Sea Res I* **41**: 1767–1788. doi:10.1016/0967-0637(94)90072-8
- Ho, D. T., C. S. Law, M. J. Smith, P. Schlosser, M. Harvey, and P. Hill. 2006. Measurements of air-sea gas exchange at high wind speeds in the Southern Ocean: Implications for global parameterizations. *Geophys. Res. Lett.* **33**: L16611. doi:10.1029/2006GL026817
- Holmer, M., F. Ø. Andersen, N. Holmboe, E. Kristensen, and N. Thongtham. 1999. Transformation and exchange processes in the Bangrong mangrove forest-seagrass bed system, Thailand. Seasonal and spatial variations in benthic metabolism and sulfur biogeochemistry. *Aquat. Microb. Ecol.* **20**: 203–212. doi:10.3354/ame020203
- Holmer, M., C. M. Duarte, and N. Marbà. 2003. Sulfur cycling and seagrass (*Posidonia oceanica*) status in carbonate sediments. *Biogeochemistry* **66**: 223–239. doi:10.1023/B: BIOG.0000005326.35071.51
- Howard, J. L., J. C. Creed, M. V. P. Aguiar, and J. W. Fouquerean. 2018. CO₂ released by carbonate sediment production in some coastal areas may offset the benefits of seagrass “Blue Carbon” storage. *Limnol. Oceanogr.* **63**: 160–172. doi:10.1002/lno.10621
- Jacquemart, J., and V. Demoulin. 2006. Inventaire des macroalgues éphiphytes des feuilles de *Posidonia oceanica* (L.) Delile dans la baie de la Revellata (Calvi, Corse). *Lejeunia* **181**: 70.
- Knap, A. H., A. E. Michaels, A. Close, E. H.W. Ducklow and A. G. Dickson, 1996. Protocols for the Joint Global Ocean Flux Study (JGOFS) core measurements. Bergen, Norway, UNESCO. JGOFS Report no. 19. Available from http://ijgofs.whoi.edu/Publications/Report_Series/JGOFS_19.pdf
- Koopmans, D., M. Holtappels, A. Chennu, M. Weber, and D. de Beer. 2020. High net primary production of Mediterranean Seagrass (*Posidonia oceanica*) meadows determined with aquatic Eddy covariance. *Front. Mar. Sci.* **7**: 1–13. doi:10.3389/fmars.2020.00118
- Langdon, C., and others. 2000. Effect of calcium carbonate saturation state on the calcification rate of an experimental coral reef. *Global Biogeochem. Cycles* **14**: 639–654. doi:10.1029/1999GB001195
- Long, M. H., K. Sutherland, S. D. Wankel, D. J. Burdige, and R. C. Zimmerman. 2020. Ebullition of oxygen from seagrasses under supersaturated conditions. *Limnol. Oceanogr.* **65**: 314–324. doi:10.1002/lno.11299
- Long, M. H., P. Berg, and J. F. Falter. 2015. Seagrass metabolism across a productivity gradient using the eddy covariance, Eulerian control volume, and biomass addition techniques. *J. Geophys. Res.* **120**: 3624–3639. doi:10.1002/2014JC010352
- Marañón, E., P. Cermenó, E. Fernández, J. Rodríguez, and L. Zabala. 2004. Significance and mechanisms of photosynthetic production of dissolved organic carbon in a coastal eutrophic ecosystem. *Limnol. Oceanogr.* **49**: 1652–1666. doi:10.4319/lo.2004.49.5.1652
- Marbà, N., M. Holmer, E. Gacia, and C. Barron. 2006. Seagrass beds and coastal biogeochemistry, p. 135–157. *In* A. W. D. Larkum, R. J. Orth, and C. M. Duarte [eds.], *Seagrasses: Biology, ecology and conservation*. Dordrecht, The Netherlands, Springer. doi:10.1007/978-1-4020-2983-7_6
- Martin, S., A. Charnoz, and J.-P. Gattuso. 2013. Photosynthesis, respiration and calcification in the Mediterranean crustose coralline alga *Lithophyllum cabiochae* (Corallinales, Rhodophyta). *Eur. J. Phycol.* **48**: 163–172. doi:10.1080/09670262.2013.786790
- Mateo, M. A., J. Romero, M. Pérez, M. M. Littler, and D. S. Littler. 1997. Dynamics of millenary organic deposits resulting from the growth of the Mediterranean seagrass *Posidonia oceanica*. *Estuar. Coast. Shelf Sci.* **44**: 103–110. doi:10.1006/ecss.1996.0116

- Mateo, M. A., P. Renom, M. A. Hemminga, and J. Peene. 2001. Measurement of seagrass production using the ^{13}C stable isotope compared with classical O_2 and ^{14}C methods. *Mar. Ecol. Prog. Ser.* **223**: 157–165. doi:10.3354/meps223157
- Mazzella, L., M. B. Scipione, and M. C. Buia. 1989. Spatio-temporal distribution of algal and animal communities in a *Posidonia oceanica* meadow. *Mar. Ecol.* **10**: 107–129. doi:10.1111/j.1439-0485.1989.tb00069.x
- Mehrbach, C., C. H. Culbertson, J. E. Hawley, and R. M. Pytkowicz. 1973. Measurements of the apparent dissociation constants of carbonic acid in seawater at atmospheric pressure. *Limnol. Oceanogr.* **18**: 897–907. doi:10.4319/lo.1973.18.6.0897
- Morana, C., H. Sarmiento, J.-P. Descy, J.-M. Gasol, A. V. Borges, S. Bouillon, and F. Darchambeau. 2014. Production of dissolved organic matter by phytoplankton and its uptake by heterotrophic prokaryotes in large tropical lakes. *Limnol. Oceanogr.* **59**: 1364–1375. doi:10.4319/lo.2014.59.4.1364
- Moriarty, D. J. W., R. L. Iverson, and P. C. Pollard. 1986. Exudation of organic carbon by the seagrass *Halodule wrightii* Aschers and its effect on bacterial growth in the sediment. *J. Exp. Mar. Biol. Ecol.* **96**: 115–126. doi:10.1016/0022-0981(86)90237-6
- Moulin, E., A. Jordens, and R. Wollast. 1985. Influence of the aerobic bacterial respiration on the early dissolution of carbonates in coastal sediments, p. 196–208. *In* R. Van Grieken and R. Wollast [eds.], *Progress in Belgian Oceanographic Research: Proceedings of a symposium held at the Palace of Academies Brussels. 3–5 March 1985.* Antwerp Univ. Press. Antwerp, Belgium.
- Noguchi, I., and K. Yoshida. 2008. Interaction between photosynthesis and respiration in illuminated leaves. *Mitochondrion* **8**: 87–99. doi:10.1016/j.mito.2007.09.003
- Odum, H. T. 1956. Primary production in flowing waters. *Limnol. Oceanogr.* **1**: 102–117. doi:10.4319/lo.1956.1.2.0102
- Penhale, P. A., and W. O. Smith. 1977. Excretion of dissolved organic carbon by eelgrass (*Zostera marina*) and its epiphytes. *Limnol. Oceanogr.* **22**: 400–407. doi:10.4319/lo.1977.22.3.0400
- Pergent, G., and C. Pergent-Martini. 1991. Leaf renewal cycle and primary production of *Posidonia oceanica* in the bay of Lacco Ameno (Ischia, Italy) using lepidochronological analysis. *Aquat. Bot.* **42**: 49–66. doi:10.1016/0304-3770(91)90105-E
- Rasmusson, L. M., and M. Björk. 2014. Determining light suppression of mitochondrial respiration for three temperate marine macrophytes using the Kok method. *Bot. Mar.* **57**: 483–486. doi:10.1515/bot-2014-0046
- Smith, S. V., and G. S. Key. 1975. Carbon dioxide and metabolism in marine environments. *Limnol. Oceanogr.* **20**: 493–495. doi:10.4319/lo.1975.20.3.0493
- Takahashi, T., and others. 2002. Global sea–air CO_2 flux based on climatological surface ocean pCO_2 , and seasonal biological and temperature effects. *Deep-Sea Res. II* **49**: 1601–1622. doi:10.1016/S0967-0645(02)00003-6
- Telesca, L., and others. 2015. Seagrass meadows (*Posidonia oceanica*) distribution and trajectories of change. *Sci. Rep.* **5**: 12505. doi:10.1038/srep12505
- Trevathan-Tackett, S. M. 2017. Sediment anoxia limits microbial-driven seagrass carbon remineralization under warming conditions. *FEMS Microbiol. Ecol.* **93**: others. doi:10.1093/femsec/fix033
- Van Dam, B. R., C. Lopes, C. L. Osburn, and J. W. Fourqurean. 2019. Net heterotrophy and carbonate dissolution in two subtropical seagrass meadows. *Biogeosciences* **16**: 4411–4428. doi:10.5194/bg-16-4411-2019
- van der Heijden, L. H., and N. A. Kamenos. 2015. Reviews and syntheses: Calculating the global contribution of coralline algae to total carbon burial. *Biogeosciences* **12**: 6429–6441. doi:10.5194/bg-12-6429-2015
- Velimirov, B., and others. 2016. Estimating carbon fluxes in a *Posidonia oceanica* system: Paradox of the bacterial carbon demand. *Estuar. Coast. Shelf Sci.* **171**: 23–34. doi:10.1016/j.ecss.2016.01.008
- Weiss, R. F., and B. A. Price. 1980. Nitrous oxide solubility in water and seawater. *Mar. Chem.* **8**: 347–359. doi:10.1016/0304-4203(80)90024-9
- Wilson, S. T., and others. 2018. An intercomparison of oceanic methane and nitrous oxide measurements. *Biogeosciences* **15**: 5891–5907. doi:10.5194/bg-15-5891-2018
- Yates, K. K., and R. B. Halley. 2006. Diurnal variation in rates of calcification and carbonate sediment dissolution in Florida Bay. *Estuar. Coasts* **29**: 24–39. doi:10.1007/BF02784696
- Zieman, J. C. 1974. Methods for the study of the growth and production of turtle grass, *Thalassia testudinum* König. *Aquaculture* **4**: 139–143. doi:10.1016/0044-8486(74)90029-5

Acknowledgments

We thank P. Lejeune and the STARESO team for logistical support, L.-S. Schiettecatte for help in sampling during the first year of the time series, B. Delille for help in setting up the Pro-oceanus, C. Champenois and M.-V. Commarieu for support during the underwater dives, the Oceanology Laboratory (ULiège) for lending the incubation chambers and water pumps, an anonymous reviewer and associate editor for suggestions that helped to improve the previous version of the manuscript. This work was funded by the Fonds National de la Recherche Scientifique (FNRS) (contracts F.4513.06, 2.4.511.09 and 2.4.637.10) and the Territorial Collectivity of Corsica and the Rhone-Mediterranean and Corsica Water Agency (STARE-CAPMED—Station of reference and research on change of local and global anthropogenic pressures on Mediterranean ecosystem drifts). A.V.B. is a research director at the FNRS and co-first author.

Conflict of Interest

None declared.

Submitted 06 July 2020

Revised 08 January 2021

Accepted 18 January 2021

Associate editor: Robinson Fulweiler