



# High Net Primary Production of Mediterranean Seagrass (*Posidonia oceanica*) Meadows Determined With Aquatic Eddy Covariance

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We report primary production and respiration of *Posidonia oceanica* meadows determined with the non-invasive aquatic eddy covariance technique. Oxygen fluxes were measured in late spring at an open-water meadow (300 m from shore), at a nearshore meadow (60 m from shore), and at an adjacent sand bed. Despite the oligotrophic environment, the meadows were highly productive and highly autotrophic. Net ecosystem production (54 to 119 mmol m<sup>-2</sup> d<sup>-1</sup>) was about one-half of gross primary production. In adjacent sands, net primary production was a tenth- to a twentieth smaller (4.6 mmol m<sup>-2</sup> d<sup>-1</sup>). Thus, *P. oceanica* meadows are an oasis of productivity in unproductive surroundings. During the night, dissolved oxygen was depleted in the open-water meadow. This caused a hysteresis where oxygen production in the late afternoon was greater than in the morning at the same irradiance. Therefore, for accurate measurements of diel primary production and respiration in this system, oxygen must be measured within the canopy. Generally, these measurements demonstrate that *P. oceanica* meadows fix substantially more organic carbon than they respire. This supports the high rate of organic carbon accumulation and export for which the ecosystem is known.

**Keywords:** seagrass, *Posidonia oceanica*, Mediterranean, respiration, primary production, eddy covariance, oxygen flux, photosynthesis

## INTRODUCTION

Seagrass meadows are highly productive coastal habitats (Bay, 1984; Frankignoulle and Bouqueneau, 1987) that can be a net sink for atmospheric CO<sub>2</sub> (Duarte et al., 2010). Net production commonly exceeds 1 kg C dry weight m<sup>-2</sup> year<sup>-1</sup> (Duarte and Chiscano, 1999). Seagrass meadows worldwide are threatened by eutrophication, turbidity, climate change, and other

factors (Orth et al., 2006). Seagrass productivity for a given meadow is determined by the balance of photosynthesis and respiration. This balance is determined by the response to environmental factors such as nutrient availability (Short, 1987; Powell et al., 1989; Udy and Dennison, 1997), temperature (Bulthuis, 1987; Alcoverro et al., 1995; Collier and Waycott, 2014), water velocity (Fonseca and Kenworthy, 1987; Thomas et al., 2000; Peralta et al., 2006), CO<sub>2</sub> availability (Zimmerman and Kremer, 1986; Koch, 1994), and irradiance (Dennison and Alberte, 1985; Peralta et al., 2002; Ralph et al., 2007). Among these factors, the photosynthetic response of seagrasses to irradiance is fundamental. However, the response of a complete meadow is not documented by *in situ* studies. Our understanding of the photosynthetic response of seagrass to irradiance is generally based on incubations of individual leaves or leaf fragments. High levels of irradiance saturate photosynthesis in these tissues (e.g., Pirc, 1986). In natural seagrass meadows, however, self-shading may allow seagrasses to utilize light up to peak midday summertime irradiance, without saturation of photosynthesis (Sand-Jensen et al., 2007). The interaction of steep solute and velocity gradients around seagrass leaves may also alter nutrient availability (Thomas et al., 2000) and photosynthetic rates (Koch, 1994). Additionally, because of temporal and spatial variability in metabolism, scaling up from incubations of leaves and leaf tissues is problematic. Therefore, *in situ* techniques are needed to improve our understanding of the response of seagrass meadows to changes in the drivers of metabolism.

The two primary techniques that have been used to quantify seagrass productivity *in situ* are benthic chambers and the diel-change technique (Odum, 1956; Howarth and Michaels, 2000). The diel-change technique makes measurements under true, *in situ* conditions, but it has substantial uncertainties. The upstream contributing area can be hundreds to thousands of meters in length (Reichert et al., 2009), diminishing the precision of measurement of metabolism in a discrete habitat of interest. Diel-change measurements of metabolism can also be biased by changes in circulation, by differing habitat types in the contributing area, by stratification, and by calculation of gas exchange at the air-water interface (Staehr et al., 2010; Long et al., 2015a). Conversely, benthic chambers allow measurements of community respiration and primary production over a discrete area with no gas-transfer correction. However, chambers are invasive. They are inserted into sediments, cutting through below-ground tissues and sediment layers. They also alter the light environment, prohibit hydrodynamic exchange, and accumulate the products of metabolism, potentially altering fluxes (Campbell and Fourqurean, 2011; Olivé et al., 2016). The effect of chambers on benthic metabolism has been studied in detail in permeable sediment. Organic matter mineralization in sands is enhanced by pore water advection (Huettel and Gust, 1992; Boudreau et al., 2001) with the result that oxygen uptake can be a function of the chamber stirring speed (Forster et al., 1996). Therefore, metabolism of sands determined with benthic chambers may differ from metabolism determined under dynamic *in situ* conditions (e.g., Berg et al., 2013).

An alternate *in situ* metabolism approach is the eddy covariance technique (Berg et al., 2003). Oxygen fluxes are quantified as the mean product of the fluctuating components of vertical velocity and oxygen concentration in turbulent flow over the habitat of interest. The resulting fluxes have a contributing area of tens of meters square (Berg et al., 2007). Fluxes are measured at high frequency (e.g., 5 Hz), allowing the user to quantify the diel photosynthetic response to light, among other variables. The technique has been used to quantify metabolism of *Zostera marina*, *Thalassia testudinum*, and *Zostera noltii* (Rheuban et al., 2014a,b; Long et al., 2015b; Lee et al., 2017; Attard et al., 2019; Berg et al., 2019). Among the discoveries is that over an annual cycle, *Zostera marina* meadows are heterotrophic or negligibly autotrophic (Rheuban et al., 2014a; Attard et al., 2019) although by particle-trapping they may still act as a net carbon sink (Greiner et al., 2013).

In contrast to many other seagrass species, *P. oceanica* meadows can be highly autotrophic, with a median ratio of community gross primary production to respiration of 1.65 (Duarte et al., 2010). On a mass-specific basis, the primary productivity of *P. oceanica* relative to other seagrasses is low. However, *P. oceanica* maintains a high meadow productivity due to its high biomass (Ott, 1980; Bay, 1984). *Posidonia oceanica* has greater above-ground biomass than many other seagrass species (Duarte and Chiscano, 1999). Self-shading, caused by horizontal fronds at the top of their canopies, reduces light penetration into their canopies by 50% (Dalla Via et al., 1998). Below-ground biomass for the species is commonly five to ten times greater than other species (Duarte and Chiscano, 1999) leading to the formation of a dense, fibrous “matte” of intertwined roots, rhizomes, and leaf sheaths resulting from the production and accretion of this material within the meadow over time (Mateo et al., 1997). Organic matter may remain in mattes for thousands of years (Mateo et al., 1997; Serrano et al., 2012) contributing to the formation of significant carbon deposits (37 kg m<sup>-2</sup> within the first meter; Fourqurean et al., 2012). Because our understanding of *P. oceanica* community metabolism is based primarily on benthic chamber work, the measured rates of production and respiration of the ecosystem may differ from those occurring under *in situ* conditions. The lack of true, *in situ* measurements also leaves us without a quantitative understanding of the photosynthetic response of the ecosystem to light, among other drivers.

The objective of this study was to quantify the primary production and respiration of *Posidonia oceanica* meadows. The resulting measurements were used to quantify net ecosystem metabolism (NEM) and investigate photosynthesis as a function of irradiance. We used the eddy covariance technique (Berg et al., 2003) to make these measurements under *in situ* illumination and hydrodynamic conditions. Measurements were made near the seasonal peak of carbon acquisition to quantify how the potential for NEM in this ecosystem compares to other seagrasses. To capture some diversity in the potential differences in primary production and respiration between meadows, we selected two meadows located at the same water depths but at different distances from shore. We studied one meadow in 2016, and the second meadow in 2017. In both years, the study was conducted

in the month of May under similar environmental conditions. Additional measurements of primary production and respiration were made over nearby sands in 2017.

## MATERIALS AND METHODS

### Study Sites

The study was conducted in the NW Mediterranean Sea, at the island of Elba, Italy in the Tuscan Archipelago. The island is surrounded by *P. oceanica* beds from depths of 5 to 40 m. The meadow examined in the first year of the study (open-water) was located 300 m from the southwest corner of the island (42.7421 N, 10.1183 E). The meadow examined in the second year of the study (nearshore) was located 60 m from the north shore (42.8087 N, 10.1472 E). Both meadows were located at 13 m depth. At each meadow, eddy covariance oxygen fluxes were measured for 2 days. At the open-water seagrass meadow the 2 days were continuous from 15 to 18 May 2016. At the nearshore meadow, the measurement days (13 and 25 May 2017) were not continuous. Both seagrass meadows were visually dense (e.g., **Figure 1**), with 60-cm-tall canopies, and were exposed to low water velocities during the study period ( $<3 \text{ cm s}^{-1}$ , **Table 1**). Surficial sediments beneath the meadows were typical of *P. oceanica*; they were composed of fibrous mats of intertwined rhizomes and roots in excess of 20 cm thick. In addition to seagrass meadows, eddy covariance oxygen fluxes were also measured over a broad area of bare sands (100 m  $\times$  50 m) adjacent to the nearshore meadow over two nights and one day on 23 May 2017. Eddy covariance instruments were positioned approximately 50 m from the seagrass edge in the predominant, along-shore current direction.

### Eddy Covariance and Environmental Measurements

Water velocity for eddy covariance measurements was determined at 16 Hz with an acoustic Doppler velocimeter (ADV; Vector, Nortek AS). Oxygen concentration was determined at 5 Hz with high speed ( $t_{90} = 0.25 \text{ s}$ ) optode minisensors of 50 or 430  $\mu\text{m}$  in diameter (PyroScience GmbH). Dissolved oxygen measurements were made by the manufacturer's oxygen meter, which was placed in a submersible housing with an optical port for the fiber-optic cable of the minisensor. Optodes have been successfully used for eddy covariance measurements previously (Chipman et al., 2012; Berg et al., 2016) and they lack stirring sensitivity (Holtappels et al., 2015). Optodes were calibrated in air-saturated and anoxic water before and after each deployment. The instruments were mounted to a tripod frame with 4 cm-wide legs spaced 1.2 m apart. The sensors were aligned at a 40-degree angle to the velocimeter, and the tip located 2 cm from the edge of the velocimeter measuring volume. This distance was sufficient to minimize acoustic interference of velocity measurement in this low-backscatter environment. The legs of the frame were adjusted to allow for measurements at a height of about 0.3 m above the top of seagrass canopies (**Figure 1**) and 0.25 m over sands.



**FIGURE 1** | Eddy covariance instruments at the open-water seagrass meadow at Elba, Italy in May of 2016. The velocimeter is upright, in titanium, with three receivers aligned toward the measurement volume. Aligned beside the measurement volume are a prototype sensor (results not included in this study), and the pencil-sized eddy covariance oxygen minisensor.

**TABLE 1** | Environmental conditions during oxygen flux measurements including integrated photosynthetically active radiation (PAR) and day/night water velocities ( $\pm$  s.d.) measured above the habitat of interest.

Site	Date	PAR (mol photons $\text{m}^{-2} \text{d}^{-1}$ )	Water velocity ( $\text{cm s}^{-1}$ )	
			day	night
Nearshore day 1	13 May 2017	5.15	$2.1 \pm 1.4$	$0.7 \pm 0.6$
Nearshore day 2	25 May 2017	6.24	$2.8 \pm 1.3$	$2.5 \pm 1.4$
Open-water day 1	16 May 2016	5.76	$1.2 \pm 0.4$	$0.6 \pm 0.2$
Open-water day 2	17 May 2016	6.49	$1.6 \pm 0.7$	$1.0 \pm 0.7$
Bare sand	23 May 2017	8.66	$2.4 \pm 1.1$	$2.0 \pm 1.0$

Sites include two seagrass meadows and bare sand at the island of Elba, Italy.

Multi-parameter probes that measured  $\text{O}_2$  concentration (RBR Ltd.) were mounted at heights of 0.2 m and 1.0 m above the seafloor at the open-water meadow. By an oversight, the lower probe was positioned 0.6 m above the seafloor for the deployments in year two at the nearshore meadow. This precluded within-canopy dissolved oxygen measurements at the nearshore meadow. A single eddy covariance instrument frame was used to collect all of the measurements made in this study. Irradiance was quantified with HOBO Pendant luminescence sensors (Onset Computer Corp.), cross-calibrated for photosynthetically active radiation (PAR, 400–700 nm) by a LI-192 (LI-COR, Inc.) sensor as demonstrated by Long et al. (2012). The instrument frame was deployed by divers at the research sites and was aligned to minimize tilt. The time series of mean  $\text{O}_2$  concentration variation recorded by the fast optodes reproduced those recorded by the  $\text{O}_2$  logger positioned above the canopy. Thus, fluctuations recorded by the fast optode were accurate.

Supporting measurements were made of nutrient concentrations at the open-water meadow in 2016. Water samples, collected 1 m above the bed by divers, were filtered over

0.2  $\mu\text{M}$  and then frozen until analysis. Nutrient concentrations ( $\text{NH}_4^+$ ,  $\text{NO}_3^-$ ,  $\text{PO}_4^{3-}$ ) were determined with a segmented flow nutrient analyzer (QuAAtro, Seal Analytical GmbH). The detection limits of phosphate, nitrate, and ammonium were 0.010, 0.016, and 0.07  $\mu\text{mol L}^{-1}$ . Shoot density at each of the meadows was determined by divers using a negatively buoyant ring to define an area of 0.25  $\text{m}^2$ . Ten replicate measurements were made at random locations at each of the sites.

## Eddy Covariance Calculations

The velocity and oxygen time series, recorded at 16 Hz by the ADV, were downsampled to the optode sampling frequency of 5 Hz and were processed similarly to the procedure described by Holtappels et al. (2013). The tilt of the ADV was corrected using the planar fit method by Wilczak et al. (2001). A running average with a window of 300 s was subtracted from the time series to calculate the fluctuating vertical velocity ( $w'$ ) and  $\text{O}_2$  concentration ( $C'$ ). At slow water velocities, a temporal offset of up to a few seconds can occur between the recording of an event's velocity and its oxygen concentration (McGinnis et al., 2008). To account for this, the cross-correlation of  $w'$  and  $C'$  were calculated in hour-long intervals using stepwise time shifts to a maximum 4 s. The median time shift was 0.8 s. The time shift with the highest cross correlation coefficient was used to calculate the flux. The eddy covariance  $\text{O}_2$  flux ( $J_{EC}$ ) in the vertical direction was calculated as

$$J_{EC} = \overline{w'C'}$$

where the overbar indicates averaging. Instantaneous fluxes ( $w'C'$ ) were added over time to calculate cumulative fluxes in hour-long intervals. Particle collision with the tip of  $\text{O}_2$  minisensors can cause erratic fluxes (e.g., Lorrai et al., 2010). We examined the dataset for spikes in the  $\text{O}_2$  data that co-occurred with abrupt changes in calculated fluxes. Few hour-long averaging intervals (4%) were affected and they were excluded from further analyses.

In a further step, we accounted for oxygen storage in the water layer between the measurement volume of the eddy covariance system and the sediment surface. In a first approximation, we assumed that the  $\text{O}_2$  concentration at the measurement volume represented the  $\text{O}_2$  concentration in the entire bottom layer. This assumes that there was no vertical oxygen gradient in the bottom layer. We made this correction according to Rheuban et al. (2014b).

$$J_{biotic} = J_{EC} + h \frac{\Delta C}{\Delta t}$$

where  $J_{EC}$  is the eddy covariance flux,  $h$  is the height of the velocity measurement volume above the bed, and  $\frac{\Delta C}{\Delta t}$  is the change in the  $\text{O}_2$  concentration at the measurement volume over time for each 1h interval. From these corrected fluxes, we infer hourly benthic biological  $\text{O}_2$  flux ( $J_{biotic}$ ). Where  $\text{O}_2$  production is negative there is benthic  $\text{O}_2$  consumption. Hourly fluxes are reported in diel units ( $\text{mmol m}^{-2} \text{d}^{-1}$ ) for calculation of diel metabolism.

The storage-corrected, hourly  $\text{O}_2$  fluxes were grouped by irradiance. Dark intervals were designated those that received

<1% maximum diel irradiance. These were used to calculate respiration ( $R$ ), gross primary production ( $GPP$ ), and  $NEM$  in an approach similar to Hume et al. (2011). To accommodate datasets with observations in excess of 24 h, metabolic fluxes were calculated as

$$R = \overline{|J_{biotic\ dark}|}$$

$$GPP = (\overline{J_{biotic\ light}} + R) \frac{h_{light}}{h_{diel}}$$

$$NEM = (GPP - R)$$

where  $J_{biotic\ dark}$  is a nighttime flux of 1 h duration,  $J_{biotic\ light}$  is a daytime flux of 1 h duration, and  $h_{light}$  and  $h_{diel}$  are the hours of daytime (14 during experimental measurements) and hours in a complete diel cycle (24). To examine the photosynthetic response of seagrass meadows to their changing light environment, photosynthesis-irradiance relationships were fit with a hyperbolic tangent function (Jassby and Platt, 1976) which was modified to account for respiration according to Rheuban et al. (2014a). The fit was calculated as

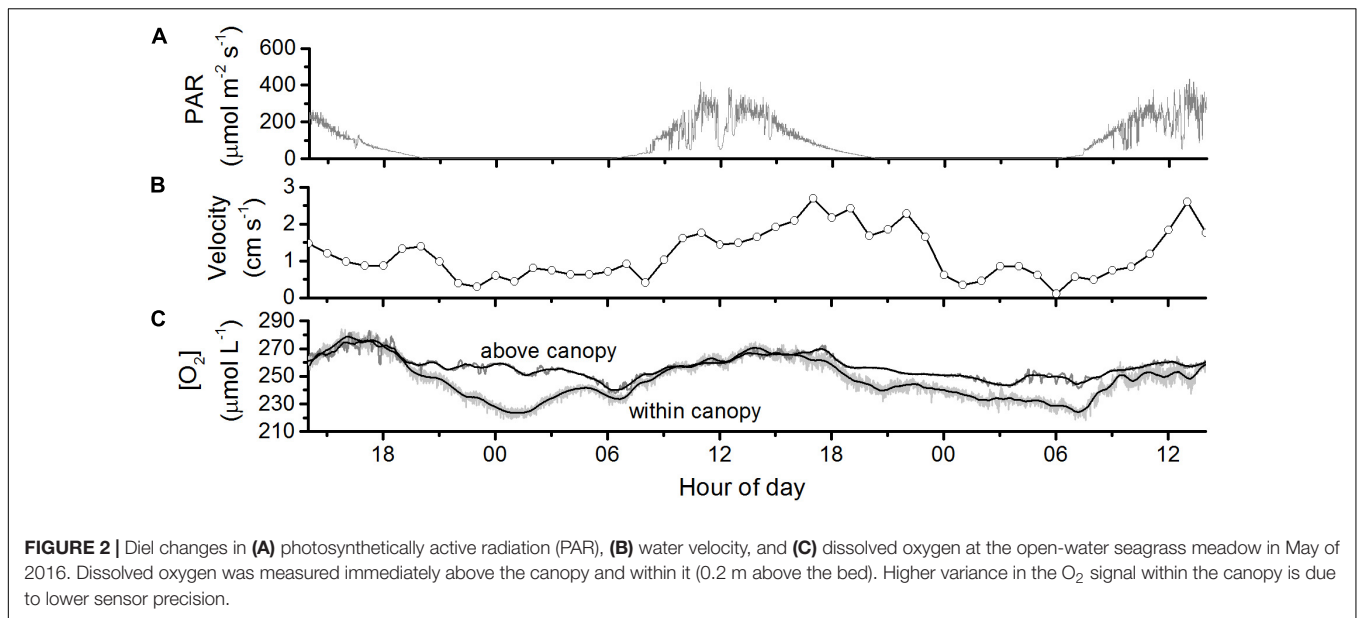
$$Flux = P_{max} \tanh \frac{I}{I_k} - R_I$$

where  $P_{max}$  is the maximum photosynthetic rate,  $I_k$  is the saturation irradiance, and  $R_I$  is respiration. The irradiance at which net oxygen production equals zero is the irradiance compensation point ( $I_C$ ; Falkowski and Raven, 2013). To examine the effect of the open-water versus nearshore meadow on  $NEM$  we used a Student's  $t$ -test at a significance level of  $p = 0.05$ . A separate Student's  $t$ -test was performed to test if the mean seagrass meadow productivity was greater than that of nearshore sands.

## RESULTS

### Environmental Conditions

During May of 2016 and May of 2017 a total of 139 h of eddy covariance fluxes were measured for the study. Percent areal coverage of *P. oceanica* in the meadows, estimated from plan-view underwater images, was high (95–99%) at both meadows. Shoot densities at the nearshore meadow ( $379 \pm 56$ ; uncertainty represents standard error,  $n = 10$ ) were similar to the open-water meadow ( $434 \pm 28$ ,  $n = 10$ ). Measurements were made on mostly sunny or completely sunny days. Photosynthetically active irradiance was similar above the seagrass meadows on measurement days (Table 1). Water velocities were lower at the open water meadow, and peaked during the day at both meadows. Water temperatures throughout the study periods across years were similar (17.4 to 18.8°C). Water column nutrients were determined in the water column above the open water meadow in 2016. N-nutrients were very depleted (the sum of  $\text{NO}_3^-$ ,  $\text{NO}_2^-$  and  $\text{NH}_4^+$  was  $0.73 \pm 1.0 \mu\text{mol L}^{-1}$ ,  $n = 7$ ) and phosphates were below detection ( $0.01 \mu\text{mol L}^{-1}$ ).



## Oxygen Storage in Seagrass Meadows

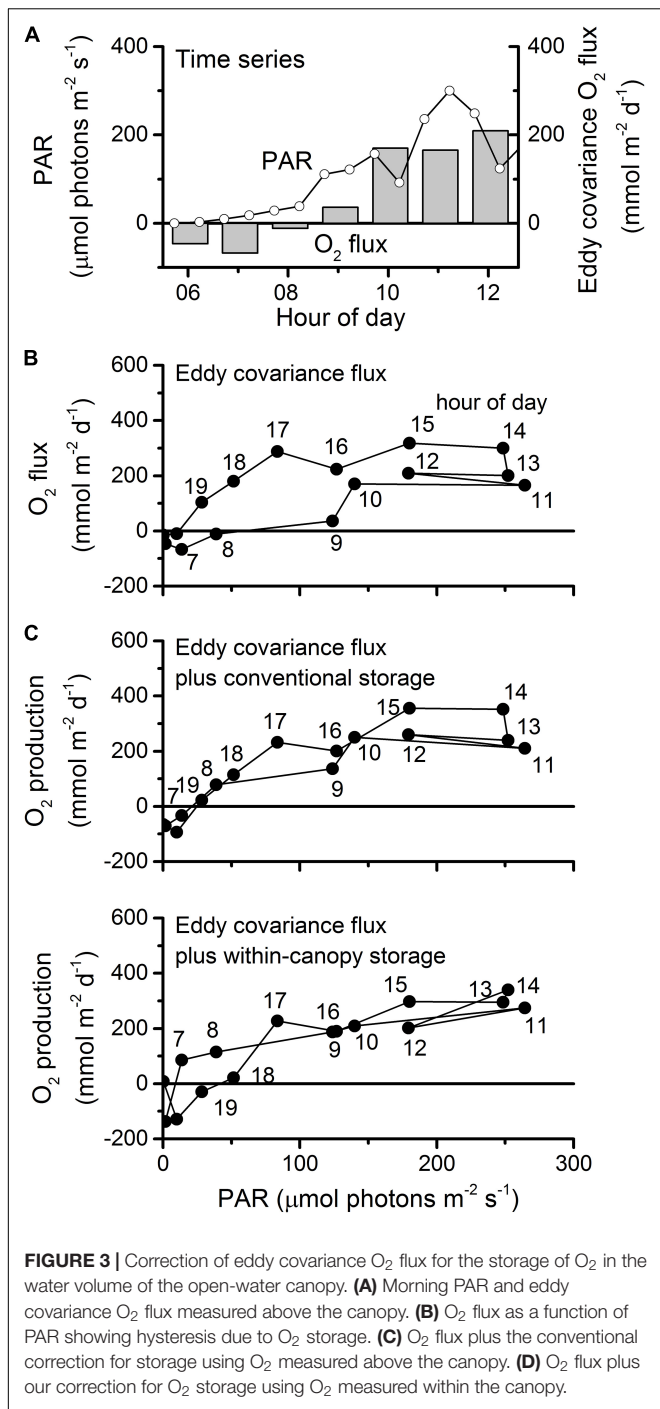
At the open-water meadow, nighttime dissolved oxygen within the canopy fell by 20–30  $\mu\text{M}$  relative to overlying water (Figure 2). During the day, the dissolved oxygen levels within the canopy were equal to those in overlying water. The efflux of oxygen due to photosynthesis increased suddenly in the late morning (Figure 3A). When plotting eddy covariance fluxes versus light intensities we observed a hysteresis, namely oxygen fluxes were lower in the early morning than in the afternoon at the same light intensities (Figure 3B). For example, O<sub>2</sub> flux at 17:00 h was 275  $\text{mmol m}^{-2} \text{d}^{-1}$  while at greater light intensity in the morning (09:00) it was close to zero. The conventional correction for O<sub>2</sub> storage below the eddy measurement volume, using the change in dissolved O<sub>2</sub> at the measurement volume (Rheuban et al., 2014b), was insufficient to resolve the hysteresis (Figure 3C). This conventional correction relies on the assumption that turbulence mixes dissolved oxygen thoroughly through the seagrass canopy and down to the seafloor. This assumption may be valid where the seagrass canopy is small, biomass is low, or water velocities are high, one or more of which attributes are true in each of the prior studies of eddy covariance oxygen fluxes over seagrasses (their results are summarized in Supplementary Table S1). However, it was not valid for this *P. oceanica* meadow. Instead, we needed to account for the depletion and replenishment of dissolved O<sub>2</sub> within the canopy to resolve the hysteresis (Figure 3D).

In a novel approach, to account for depletion and replenishment of O<sub>2</sub> within the meadow, we assumed a linear O<sub>2</sub> concentration profile between the eddy measurement volume and an O<sub>2</sub> logger placed 0.2 m above the bed. We chose a linear concentration profile to allow for turbulent mixing of overlying water into the canopy and its attenuation with depth (as described by Ikeda and Kanazawa, 1996). Storage was calculated from the change over time in the estimated mean O<sub>2</sub> concentration below the eddy covariance measurement volume. Diel respiration and

GPP, calculated from the thus-corrected O<sub>2</sub> fluxes were 1.5 and 1.2 times the measured above-meadow fluxes, respectively. The above-canopy versus within-canopy storage correction was a small part (3–12%) of this correction, but it had a large effect on hourly productivity in the early morning and evening (the difference between Figures 3C,D). At the nearshore meadow, O<sub>2</sub> production was also lower in the early morning than in the late afternoon at the same light levels (Supplementary Figure S1). The conventional storage correction was also insufficient to completely resolve the hysteresis at this meadow. Therefore, similar to the open-water meadow, the nearshore meadow may also have had reduced hydrodynamic exchange. However, the lack of oxygen measurements within the canopy of the nearshore meadow prevented further correction, so fluxes at that meadow are presented with the conventional storage correction only.

## Primary Production and Respiration

O<sub>2</sub> production and consumption, calculated from storage-corrected fluxes, followed similar diurnal patterns at both meadows (Figure 4). Daytime O<sub>2</sub> production exceeded nighttime O<sub>2</sub> consumption on both days. Intermittent cloud cover reduced available light during the morning at each of the meadows. This resulted in temporary decreases in observed PAR of up to 80% (Figure 4) and lower overall PAR exposure on the first day at each of the meadows (Table 1). Plotted as a function of irradiance, diel oxygen flux resembled a saturation curve (Figure 5). The maximum photosynthetic response ( $P_{max}$ ) was not met in either meadow. However, the saturation irradiance ( $I_K$ ) was less than one-half of peak irradiance at both meadows. This indicates that at high irradiance, the photosynthetic response of both meadows was approaching light saturation, where greater irradiance yielded little gain in photosynthetic production. The light compensation point ( $I_C$ ) varied between 6 and 17% of the peak irradiance.



Respiration, gross primary production, and net ecosystem metabolism varied across sites, but all meadows were highly autotrophic (Figure 6 and Table 2). NEM at the nearshore meadow was somewhat elevated relative to the open-water meadow but the differences were not significant (Student's  $t$ -test,  $p \geq 0.05$ ). Metabolic fluxes over bare sands were very small and net autotrophic. Bare sand GPP exceeded R by 50%. However, GPP was 10- to 16-fold smaller than meadow GPP. As a

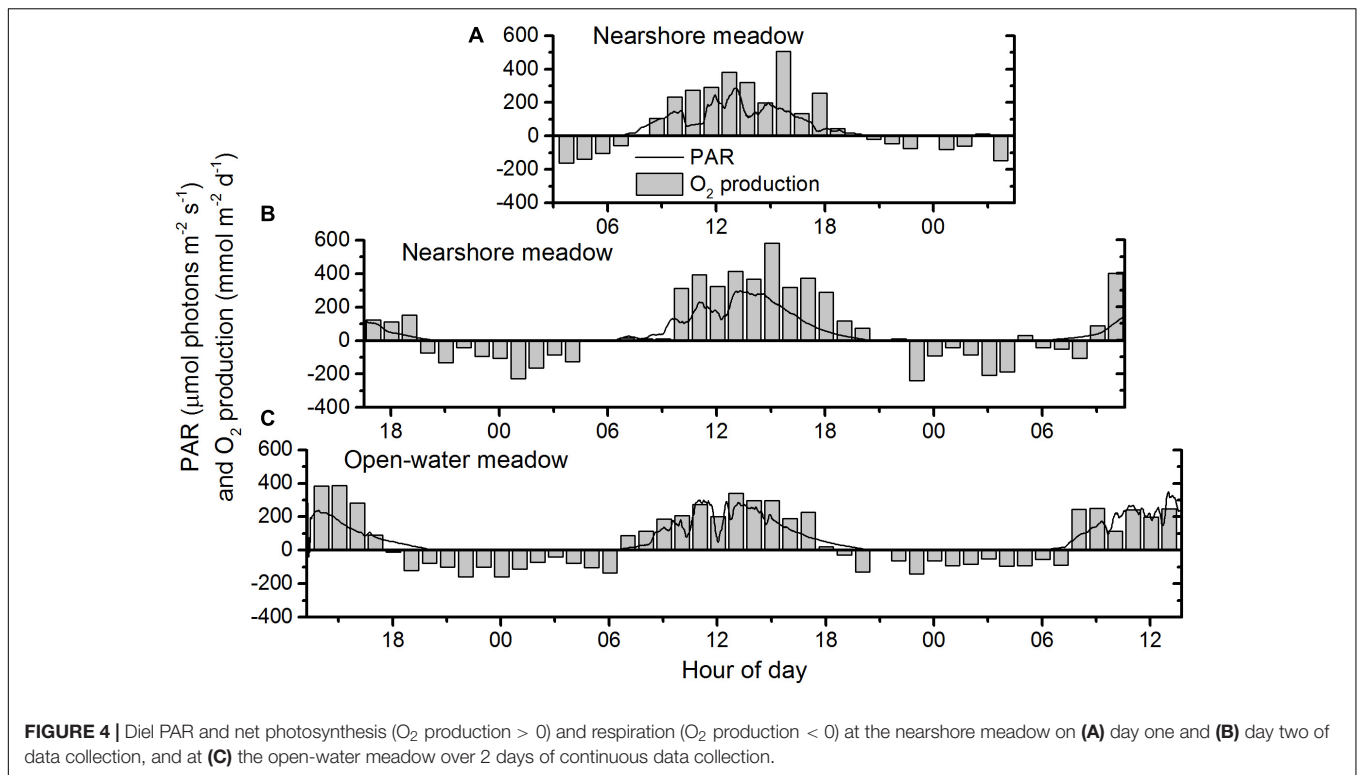
result, the NEM of sand was about 20-fold smaller than that of seagrass meadows.

## DISCUSSION

### Photosynthetic Response to Irradiance

After the within-canopy storage correction,  $O_2$  production in the early morning was greater than  $O_2$  production in the evening at the same light levels (Figure 3D). This is consistent with enhanced respiration at the end of the day as observed in a *Zostera marina* meadow (Rheuban et al., 2014b). The resulting photosynthetic response of *P. oceanica* meadows to irradiance was surprisingly similar to the photosynthetic response of *P. oceanica* leaf segments to irradiance (Pirc, 1986; Ruiz and Romero, 2001). Self-shading within dense meadows is thought to allow seagrass to utilize all available irradiance, up to midday peaks in summer (Binzer et al., 2006; Sand-Jensen et al., 2007). This would result in a productive state of light limitation, where photosynthesis increases linearly with irradiance. In support of this possibility, *P. oceanica* meadows rely on carbohydrate reserves to fuel growth during the winter. This allows the canopies to be highly developed for light capture by late spring (Alcoverro et al., 2001b). However, *P. oceanica* meadows did not produce oxygen in proportion to irradiance up to peak irradiance at midday. In comparison of our results with other studies, it is important to note that the photosynthetic response to irradiance of *P. oceanica* leaves collected at different water depths is generally similar (Olesen et al., 2002), even where acclimation to depth occurs (Dattolo et al., 2014). Light saturation at the nearshore meadow ( $77 \pm 15 \mu\text{mol photons m}^{-2} \text{s}^{-1}$ ) and at the open-water meadow ( $113 \pm 21 \mu\text{mol photons m}^{-2} \text{s}^{-1}$ ) occurred at less than half of peak irradiance. These saturating irradiances substantially exceed those determined in other studies using rapid light curves to determine electron transport rates on *P. oceanica* leaves (Dattolo et al., 2014; Cox et al., 2016). However, our results match saturation irradiances of *P. oceanica* leaf segments in some laboratory incubations (Pirc, 1986; Ruiz and Romero, 2003), and are well within the range reported in the literature (Drew, 1979; Alcoverro et al., 1998, 2001b; Ruiz et al., 2001). The similarity of our results with laboratory incubations indicates that photosynthetic production of *P. oceanica* meadows, similar to individual leaves, is limited by the photosynthetic capacity of leaf tissues.

This response contrasts with the linear increase in photosynthesis of mature *Z. marina* and *T. testudinum* meadows *in situ* as irradiance increases up to the midday peak in irradiance during summer (Rheuban et al., 2014a; Long et al., 2015b). In those more eutrophic environments light attenuates at shallower depths due to greater suspended particulate material including phytoplankton. Therefore, light limitation of primary production in those environments is more likely. In *P. oceanica* meadows, the lack of light limitation suggests that a factor other than light may limit primary production. Nutrient limitation may contribute. Chlorophyll content and the maximum photosynthetic rate of seagrasses increase with nutrient availability (Agawin et al., 1996; Alcoverro et al., 1998; Lee and Dunton, 1999). Limited



**FIGURE 4 |** Diel PAR and net photosynthesis ( $O_2$  production  $> 0$ ) and respiration ( $O_2$  production  $< 0$ ) at the nearshore meadow on **(A)** day one and **(B)** day two of data collection, and at **(C)** the open-water meadow over 2 days of continuous data collection.

availability of N and P nutrients may limit their ability to make use of the abundant light. Further measurements would improve our understanding of this response.

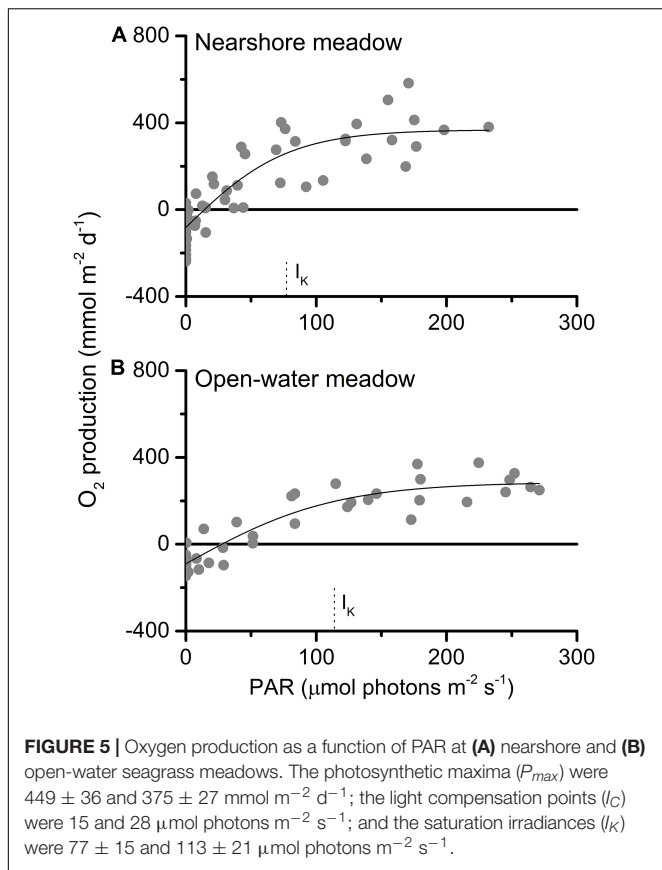
The irradiance compensation points ( $I_C$ ) of *P. oceanica* meadows in our study, in contrast, were generally greater than those of *P. oceanica* leaf segments documented in the literature. Nearshore and open-water meadow  $I_C$  were 15 and 28  $\mu\text{mol photons m}^{-2} \text{s}^{-1}$ , or 6 and 11% of peak irradiance (Figure 5). Literature values of leaf segment  $I_C$  are between 4 and 14  $\mu\text{mol photons m}^{-2} \text{s}^{-1}$  (Drew, 1979; Pirc, 1986; Ruiz and Romero, 2001, 2003; Ruiz et al., 2001; Olesen et al., 2002), with the exception of more eutrophic meadows in NE Spain with higher values (Alcoverro et al., 1998, 2001a,b). The elevated  $I_C$  in *P. oceanica* meadows in our study indicates, unsurprisingly, that respiration of the meadow is greater than that of leaf tissues alone. Compared with the  $I_C$  of other seagrass species determined using eddy covariance, *P. oceanica* has lower light requirements. It was less than that of *Z. marina* meadows in Virginia coastal bays (21% of peak irradiance, Rheuban et al., 2014a) and less than that of *T. testudinum* meadows in Florida Bay (24% of peak irradiance, Long et al., 2015b). Therefore, *P. oceanica* meadows require less light to generate a positive carbon balance. It is worth noting that the time-averaged  $I_C$  for a light-stressed *P. oceanica* meadow can be far greater (Gacia et al., 2012).

## Highly Autotrophic Production of *Posidonia oceanica* Meadows

The mean ratio of GPP to R of *P. oceanica* meadows in this study was 1.90 (Supplementary Table S1), indicating that almost

one-half of the gross carbon fixed during photosynthesis either accumulates or is exported. This rate is higher than the median reported benthic chamber ratio of *P. oceanica* GPP to R (1.64,  $n = 18$ ; Duarte et al., 2010). The high rate of net production of *P. oceanica* that we observe is sufficient to support the high storage and export of fixed carbon for which this ecosystem is known. The mean net oxygen production was  $77.1 \pm 17.9 \text{ mmol m}^{-2} \text{d}^{-1}$  (Table 2). Assuming a photosynthetic quotient of 1.0, this results in a net carbon fixation of  $0.93 \text{ g C m}^{-2} \text{d}^{-1}$ . Net organic carbon storage in *P. oceanica* sediments is estimated at  $21 \text{ g m}^{-2} \text{y}^{-1}$  (Serrano et al., 2012). This is equivalent to  $4.8 \text{ mmol C m}^{-2} \text{d}^{-1}$ , or 6.2% of our measurements of NEM. The primary loss of fixed carbon in *P. oceanica* meadows (70%) is the annual export of sloughed leaves (Mateo et al., 2003). An additional pathway is dissolved organic carbon exudation. A median rate is  $10.7 \pm 2.9 \text{ mmol C m}^{-2} \text{d}^{-1}$  in spring and summer ( $n = 18$ ; Barrón and Duarte, 2009), equivalent to 14% of NEM. Combined, these loss estimates account for 90% of fixed carbon, indicating that the meadows can sustain them. Seasonal measurements of metabolism would be highly valuable for constraining the carbon budget further.

The installation and use of benthic chambers may affect seagrass metabolic fluxes. To investigate, we looked for systematic differences between our measurements and measurements of *P. oceanica* metabolism determined using benthic chambers (compiled by Duarte et al., 2010), including a more recent study (Gacia et al., 2012). We compared only measurements made at the seasonal peak of *P. oceanica* primary production in May and June (Frankignoulle and Bouqueneau, 1987), for a total of 11 benthic chamber measurements made at water

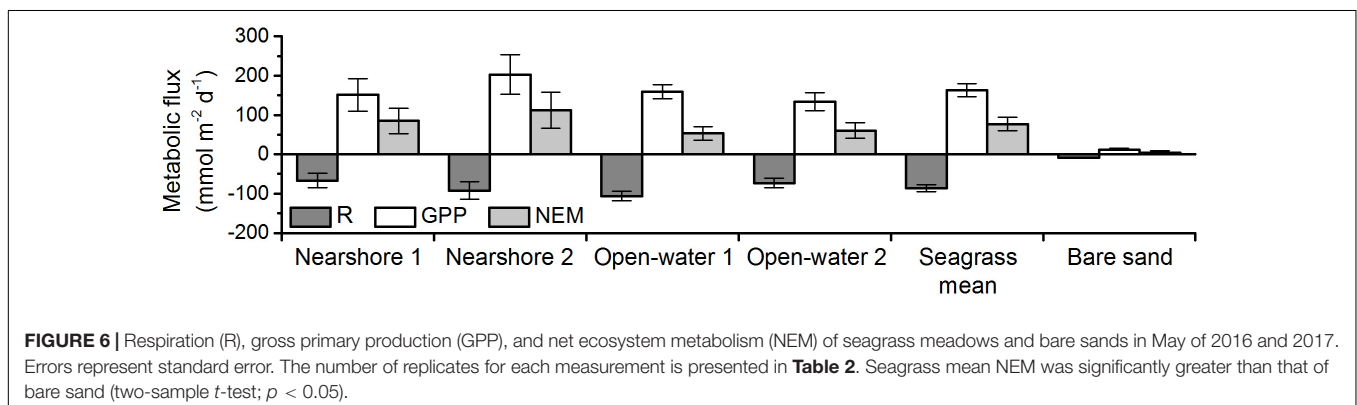


depths of 4 to 22 m. We found that the median NEM of *P. oceanica* meadows determined with benthic chambers was half of our measurements ( $36 \text{ mmol m}^{-2} \text{d}^{-1}$ , with a range of  $-15$  to  $137 \text{ mmol m}^{-2} \text{d}^{-1}$ ). This suggests that benthic chambers may underestimate the net production of seagrass meadows. An additional comparison can also be made to diel-change measurements of *P. oceanica* metabolism. May and June NEM of a *P. oceanica* meadow in Corsica determined with the diel-change technique ( $70 \text{ mmol m}^{-2} \text{d}^{-1}$ ,  $n = 6$ ; Champenois and Borges, 2012) matched the median NEM of our measurements. However, median R and GPP determined with the diel-change

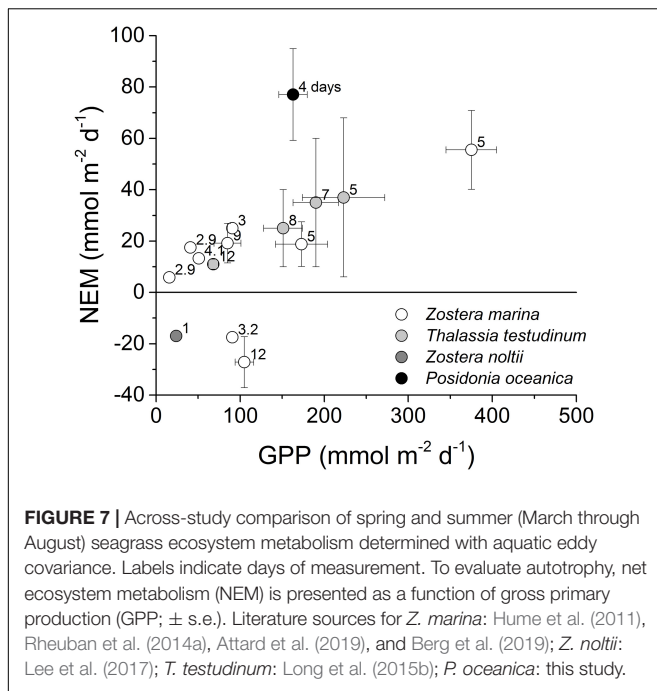
technique was 2- and 3-fold greater than our measurements, respectively. The shoot density in the Corsican meadow matched shoot density at Elba meadows. The differences between these measurements may be due to differences among the meadows, but biases in techniques may also contribute. Long residence times and stratification introduced high variance for diel change measurements of metabolism in *T. testudinum*, in comparison to eddy covariance measurements (Long et al., 2015a). Similar issues could contribute to the differences documented here.

Prior studies utilizing the eddy covariance technique in spring and summer identified a lower rate of NEM as a fraction of GPP in *Zostera marina* meadows in Virginia coastal bays (Rheuban et al., 2014a), and in *Thalassia testudinum* meadows in Florida Bay, United States (Long et al., 2015b), than we observed in *P. oceanica* meadows (Figure 7). Gross primary production in *P. oceanica* meadows was less than that of these other meadows, but due to the low respiration of *P. oceanica*, their NEM was greater. More recent studies include summer eddy covariance measurements of *Z. marina* metabolism in the Baltic Sea (Attard et al., 2019), and *Z. noltii* in the Black Sea (Lee et al., 2017). The proportion of GPP to R was higher for *Z. marina* in the Baltic Sea than in Virginia coastal bays, but overall NEM was small, one-fourth or less that of *P. oceanica* (Figure 7). Net losses of biomass were observed for *Z. noltii* (Lee et al., 2017). For a complete evaluation of the metabolism of *P. oceanica* meadows, seasonal measurements are needed. *Posidonia oceanica* grows at the expense of carbon reserves for most of the year, only replenishing those reserves in the late spring and summer (Alcoverro et al., 2000). Therefore, spring and summer will be a period of maximum net organic carbon storage. The ecosystem may be net heterotrophic in other seasons. However, looking at metabolism in this season only, our measurements suggest that *P. oceanica* meadows store a greater proportion of organic production in the highly oligotrophic Mediterranean than *Zostera* and *Thalassia* meadows in more eutrophic seas. Our results suggest that diel organic carbon storage in *P. oceanica* in late spring is distinctly greater than that of *Z. marina* and *T. testudinum*. This distinct behavior can be examined in distinct aspects of its physiology and its environment.

Among the aspects of physiology that may contribute to high net production in *P. oceanica* meadows in late spring is the long







turnover time of above- and below-ground biomass. *Posidonia oceanica* below-ground biomass is the highest among seagrasses, and above-ground biomass is among the highest (Duarte and Chiscano, 1999; Lavery et al., 2013). The energy spent on biomass production, however, is average (Duarte and Chiscano, 1999). To explain this discrepancy, *P. oceanica* roots and rhizomes have turnover times that exceed those of other seagrasses. *Posidonia oceanica* roots and rhizomes have a turnover time on the order of centuries (Romero et al., 1994), and leaves have a turnover time of nearly a year (Hemminga et al., 1999). As a result, *P. oceanica* maintains higher above- and below-ground biomass at a lower metabolic cost than other seagrasses (Olesen et al., 2002). This would allow for greater production as a fraction of GPP. Among these attributes, the maintenance of very high below ground biomass is surprising for a highly autotrophic species. Below-ground biomass confers an advantage in the acquisition of nutrients, but it is also a metabolic burden (Hemminga, 1998). Without oxygenation of roots, hydrogen sulfide intrusion can kill *P. oceanica* (Calleja et al., 2007). In one defense against this problem, *P. oceanica* roots and rhizomes have a high fiber and phenolic content (Harrison, 1989). This, in combination with low nutrient availability, would minimize their heterotrophic organic matter mineralization (Mateo et al., 1997; Serrano et al., 2012). As a result, sulfide production due to the anaerobic mineralization of this material by heterotrophic bacteria would also be minimized. Many other physiological factors would contribute to the net production of *P. oceanica*, including the low compensating irradiance of *P. oceanica* leaves (Alcoverro et al., 1998), and the export of sloughed leaves from the ecosystem.

Among the aspects of the environment that may contribute to the high net production in *P. oceanica* meadows in late spring are light availability, and the scarcity of nutrients

and labile organic matter. Light availability in relation to *Z. marina* and *T. testudinum* was discussed briefly above. Nutrient addition enhances benthic respiration, reducing the organic carbon stored in *P. oceanica* sediments (Lopez et al., 1998). Persistent addition can drive a metabolic change from *P. oceanica* meadow autotrophy to net heterotrophy (Apostolaki et al., 2010). Allochthonous organic matter fuels net respiration in *Z. marina* meadows (Rheuban et al., 2014a), but it is almost absent from the oligotrophic Mediterranean in summer (Copin-Montégut and Avril, 1993). There are photosynthetic diatoms, foraminifera, and dinoflagellates in these sands that are capable of producing  $14 \text{ mmol O}_2 \text{ m}^{-2} \text{ d}^{-1}$  (Sevilgen, 2008). The small nighttime oxygen uptake, and small net autotrophy over a diel cycle (Table 2) is evidence that there is little labile organic matter available for heterotrophs. Looking beyond seagrass meadows, when energy is abundant, carbohydrate storage can be stimulated by nutrient limitation in fungi, algae, plants, and bacteria (Lillie and Pringle, 1980; Zimmerman and Kremer, 1986; Wang and Tillberg, 1996; Børsheim et al., 2005). The high storage of organic carbon in *P. oceanica* meadows in late spring and summer may be similar. Additional ecological factors that could contribute to the high net production of *P. oceanica* meadows include the lower algal cover (McGlathery, 2001) and lower invertebrate densities (Boström and Bonsdorff, 1997).

## Posidonia oceanica, an Oasis in the Desert

The high productivity of *P. oceanica* seagrass meadows is consistent with the high productivity of *P. oceanica* plants determined by laboratory-irradiance, benthic chambers, leaf-tagging, and biomass measurements (Drew, 1979; Ott, 1980; Libes, 1986; Pergent et al., 1994), thus emphasizing the importance of seagrass in the local organic carbon budget (Duarte et al., 2010). Implicit in these prior observations is the high productivity of *P. oceanica* relative to surrounding sands, but direct comparisons have rarely been made. In contrast to the high productivity of meadows, we also found that Mediterranean sands are unusually unproductive. Specifically, the respiration that we measured in Elba sands (Table 2) was among the lowest reported for coastal permeable sediments (reviewed by Huettel et al., 2014). Benthic fluxes determined with chambers can

**TABLE 2** | Community metabolic fluxes including respiration (R), gross primary production (GPP), and net ecosystem metabolism (NEM;  $\pm$  standard error).

Site	R ( $\text{mmol m}^{-2} \text{ d}^{-1}$ )	n (h)	GPP ( $\text{mmol m}^{-2} \text{ d}^{-1}$ )	n (h)	NEM ( $\text{mmol m}^{-2} \text{ d}^{-1}$ )
Nearshore day 1	$66.4 \pm 18.3$	10	$151.4 \pm 41.8$	14	$85.0 \pm 32.5$
Nearshore day 2	$91.8 \pm 22.6$	20	$203.7 \pm 50.6$	14	$119.1 \pm 46.1$
Open-water day 1	$106.2 \pm 11.7$	10	$159.8 \pm 17.6$	14	$53.6 \pm 17.2$
Open-water day 2	$73.0 \pm 12.4$	10	$133.3 \pm 22.0$	14	$60.3 \pm 19.7$
Seagrass mean	$85.9 \pm 8.9$	50	$162.9 \pm 16.9$	56	$77.1 \pm 17.9$
Bare sand	$8.0 \pm 1.5$	19	$12.6 \pm 2.4$	14	$4.6 \pm 4.3$

Because daytime oxygen production responds to light intensity, the measurement uncertainty of GPP was determined from the measurement uncertainty of R, determined over one night, normalized to GPP.

depend on the stirring speed (Janssen et al., 2005). Nevertheless, prior measurements of metabolic flux using benthic chambers in oligotrophic Mediterranean sands gave similar results to our study. The median benthic respiration in May and June in Mallorca sands was  $8.6 \text{ mmol C m}^{-2} \text{ d}^{-1}$  (range of 6.9 to 9.1,  $n = 4$ ; Barrón et al., 2006a). The median NEM elsewhere in the Spanish Mediterranean in May and June was  $-2.1 \text{ mmol m}^{-2} \text{ d}^{-1}$  (range of  $-4$  to 11,  $n = 12$ ; Holmer et al., 2004; Gazeau et al., 2005; Barrón et al., 2006a). Taken together, the results agree that there is little organic carbon production or mineralization in these sands. Consistent with this observation, organic matter concentrations in the epilimnion of the Mediterranean are so low in the summer that many benthic suspension feeders undergo dormancy to avoid starvation (Coma and Ribes, 2003).

The capacity of *P. oceanica* to flourish and produce abundant biomass in oligotrophic water can be explained in terms of the acquisition and retention of nutrients. *Posidonia oceanica* take up nutrients through roots and leaves primarily in winter and early spring, when nutrients are more abundant (Lepoint et al., 2002). Nutrients are reallocated before leaves are shed (Alcoverro et al., 2000). Seagrasses collect particles passively, through flow-attenuation and particle deposition (Gacia et al., 1999, 2002). Seagrasses also collect particles actively. Macro- and epifaunal suspension feeders enhance particle filtering by orders of magnitude over surrounding sands (Lemmens et al., 1996). The mineralization of these particles supplies nutrients for seagrass growth (Evrard et al., 2005; Barrón et al., 2006b).

## Potential for Nutrient Recycling Within the Canopy

Our results suggest that the resistance to mass transfer of *P. oceanica* meadows may be useful for nutrient retention. Generally, hydrodynamic exchange is expected to enhance seagrass photosynthetic production by increasing the exposure of seagrass to nutrients in the surrounding environment (Thomas et al., 2000). It is surprising, then, that a resistance to mass transfer may be common in *P. oceanica* meadows (e.g., Hendriks et al., 2014). One explanation is that the reduction in dissolved oxygen within the meadow at night (Figure 2) is consistent with the retention of the products of ecosystem respiration. This would include remineralized nutrients. *Posidonia oceanica* take up phosphorus and nitrogen through roots and leaves (Fresi and Saggiomo, 1981; Lepoint et al., 2002). Nutrient uptake by roots, while supplemented by nitrogen-fixation (Garcias-Bonet et al., 2016), is diffusion-limited, and thus may be insufficient to meet nutrient requirements (Lepoint et al., 2002). Material deposited in seagrass meadows is typically low in nitrogen and phosphorus, but nevertheless over annual cycles can meet the demand of *P. oceanica* (Gacia et al., 2002). We estimated the potential benefit of nutrient retention by assuming Redfield ratios of nutrients in mineralized organic matter (C:N:P of 106:16:1, mineralized by 138 moles of  $\text{O}_2$ ; Redfield, 1958). Under the assumption that nitrogen is mineralized to nitrate, a  $20 \text{ } \mu\text{mol L}^{-1}$   $\text{O}_2$ -deficit between the meadow and overlying waters corresponds to a  $2.3 \text{ } \mu\text{mol L}^{-1}$  (i.e.,  $2.3 \text{ mmol m}^{-3}$ ) increase in  $\text{NO}_3^-$ . For a 0.6 m-high canopy this amounts to  $1.4 \text{ mmol m}^{-2}$  of extra  $\text{NO}_3^-$ , or

$12 \text{ mmol m}^{-2} \text{ d}^{-1}$  of GPP by the Redfield ratio. This is between 7 and 9% of GPP of the meadow. The same increase in GPP also applies to phosphorus. Given the high C:N:P of *P. oceanica* leaves (median of 534:21:1, Duarte, 1990), and that half of *P. oceanica* nutrients are translocated from old to new leaves for growth (Alcoverro et al., 2000), the importance of this source of new nutrients may be far greater. Due to hydrodynamic retention, nutrient concentrations at the base of *P. oceanica* meadows in summer are elevated to, e.g.,  $1 \text{ } \mu\text{mol L}^{-1} \text{NO}_3^-$ ,  $1 \text{ } \mu\text{mol L}^{-1} \text{NH}_4^+$ , and  $0.1 \text{ } \mu\text{mol L}^{-1} \text{PO}_4^{3-}$  (Gobert et al., 2002). Without retention, these remineralized nutrients may be lost to overlying and surrounding waters.

Based on these observations, we propose that diel oscillations in water velocity caused by the diurnal sea breeze may benefit seagrasses growing in the Mediterranean. For a seagrass meadow to recycle nutrients that were mineralized during the night into daytime photosynthetic production, hydrodynamic exchange would need to be reduced during the night and into the morning. Late in the morning, after nutrients had been depleted, it may be an advantage for hydrodynamic exchange to be enhanced, to prevent accumulation of  $\text{O}_2$  which can cause photorespiration (Falkowski and Raven, 2013). Interestingly, as a result of the diurnal sea breeze, this is the diel pattern in water velocities at Elba (Table 1). This diel pattern is dominant on Mediterranean coasts from May into September (Furberg et al., 2002), and thus may be exploited by *P. oceanica* when nutrient limitation is at a maximum.

## DATA AVAILABILITY STATEMENT

Hourly aquatic eddy covariance fluxes and environmental data for this study will be made available through the PANGAEA data repository (<https://www.pangaea.de/>; Koopmans et al., 2020).

## AUTHOR CONTRIBUTIONS

DB conceived the study. All authors contributed to field work. MW coordinated field work. DK and MH analyzed the eddy covariance data. All authors discussed the results and contributed to the interpretation. DK wrote the manuscript. All authors contributed to it.

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## SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fmars.2020.00118/full#supplementary-material>

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**Conflict of Interest:** MW was employed at HYDRA Marine Sciences GmbH.

The remaining authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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