

Interactive comment on “The response of seagrass (*Posidonia oceanica*) meadow metabolism to CO₂ levels and hydrodynamic exchange determined with aquatic eddy covariance” by Dirk Koopmans et al.

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We thank the referee for his careful reading of our manuscript and his thoughtful suggestions for its improvement. He raised points that we had not considered and identified mistakes in a few of our assumptions. His recommendations are listed below in italic. Our responses follow in regular type.

Title is clear and reflects the approach taken in the paper. I would suggest adding ‘light

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availability’ to the title, e.g. “. . .response of seagrass meadow metabolism to CO₂ levels, light availability, and hydrodynamic exchange. . .”

We agree that diurnal light availability is a significant portion of the results of the manuscript. We will change the title to “The response of seagrass (*Posidonia oceanica*) meadow metabolism to CO₂ levels, light availability, and hydrodynamic exchange determined with aquatic eddy covariance.”

Abstract

L13-15: It would be useful to give some indication of actual rates.

We will alter the abstract to state “Seagrass net ecosystem metabolism was 53 to 112 mmol m⁻² d⁻¹.”

*L14: This sentence seems to contradict itself. Perhaps, simply: “Thus, *P. oceanica* meadows are oases of productivity.”*

We understand the contradiction but would like to include a mention of the low productivity of the surrounding area. We would change the statement to “*P. oceanica* meadows are oases of productivity in unproductive surroundings.”

L17: “Oxygen depletion and replenishment within the meadow does not contribute to turbulent O₂ flux” This needs to be clarified. Clearly, this process affects the turbulent O₂ flux as resolved using the AEC, mostly by ‘dampening’ the flux signal (Fig. S1). Perhaps: is not captured by turbulent fluxes measured above the canopy?

We understand your point. We would alter the abstract to state “Oxygen depletion and replenishment within the meadow are not included in turbulent fluxes above the meadow.” We respond in more detail at your suggestion to lines 132-133, below.

Methods

L86-87: Study site descriptions. For future studies I would recommend considering

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biodiversity aspects more carefully. Meadow height and coverage are of interest, but quantifying shoot densities, animal and plant biomass, and presence of ephemeral algae, for instance, would go a long way with helping to better interpret the resolved rates of metabolism.

We agree. We also would have liked to include these measurements in our characterizations of the sites and we regret that we did not address these shortcomings in our manuscript. We will include discussions of the advantages of shoot density and biomass measurements. Additionally, macroalgae in particular can enhance primary production and respiration in seagrass meadows (McGlathery 2001). No macroalgae were observed within seagrass meadows at our study sites. Benthic macroalgae was present near the meadows at Panarea, however. We will state this in the study site descriptions.

L87: Please add daily integrated PAR, or daily average PAR to Table 1 or 2. Otherwise it is very difficult to interpret GPP values at the different sites.

We agree that adding daily average PAR to one of the tables will help the manuscript. We will include it in Table 2 to show variation from day-to-day. We will also include nutrient concentrations.

L99: Should read "10s of m²".

This is an important mistake. Thank you for catching it. The footprint is 10s of meters squared and not 10 m². We will update this in our copy of the manuscript.

L132-133: ". . .do not contribute to fluxes above the meadow". They do, otherwise you wouldn't measure a dampened flux. It is essentially a "missed flux"; a flux that is not captured by AEC measurements above the canopy.

To be more precise we will state that "The diurnal variations in mean O₂ concentration within this layer are driven by photosynthesis and respiration, but do not lead immediately to dynamics in fluxes above the meadow. Due to the reservoir in the canopy,

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fluxes above the meadows are not instantly (or directly) coupled to the processes in the canopy."

L140: Is there another way to phrase this, instead of 'negative production'? Consumption reflects (secondary) production.

We will state that "The net benthic uptake of oxygen represents O₂ consumption."

Results

L174-176: How were these incubations performed? Presumably only on parts of the leaves?

This was an oversight on my part. We will include the following in the methods. "An oxygen microsensor was prepared and calibrated as described previously (Revsbech 1989). The sensor was mounted on a motorized micromanipulator. Motor control and data acquisition was performed with custom made software (e.g., de Beer and Schramm 1999). Whole seagrass plants, rooted in sediment, were placed in an aquarium. Leaves were attached with rubber bands to a sponge and the microsensor tip was positioned at the leaf surface. While the whole plant was exposed to light-dark dynamics at 370 $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$, oxygen dynamics were recorded."

L180: Should read ". . .overlying seawater".

We agree and will make the change.

L186-187: Is this referring to photosynthetic production or to net O₂ flux? That is, is this difference due to actual decreased photosynthetic production, or is it due to higher photosynthesis-coupled respiration in the afternoon?

This is an error on my part. I had stated "photosynthetic production" but you are correct that we cannot distinguish photosynthetic production from photosynthesis-coupled respiration. We will change the text from "photosynthetic production" to "O₂ production". Specifically, we will state "After the correction, O₂ production in the early morning was

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greater than O₂ production in the evening at the same light levels...”

L195: GPP values in Table 2. What explains the difference in GPP from one day to the next at the open-water and nearshore seagrass meadows? Light availability, perhaps? It would be informative to have daily integrated PAR values (e.g. in mol photons m⁻² d⁻¹) for day 1 and day 2.

We will include mean daily PAR in Table 2 for readers to evaluate for themselves, but briefly, irradiance can explain day-to-day differences in primary production at the nearshore meadow, but it cannot explain differences in primary production at the open-water meadow.

A factor in day-to-day variability that we have not addressed in this manuscript is spatial heterogeneity in the meadows. As flow direction changes, the footprint of the eddy covariance technique will follow. Differences in the abundance of seagrass in different directions from the eddy covariance instruments might explain this variability at the open-water meadow. We will also include this description in the discussion.

L213-214: “In none of the meadows P_{max} was reached” needs to be rephrased.

We will change the text to “The maximum photosynthetic rate, P_{max}, calculated according to Eq. 6, was not reached in any of the meadows”

L215: “I_k varied was one-third. . .” rephrase.

We will change the manuscript so that it states “(I_k) was one-third of peak irradiance”

Discussion

L230: Typo- should read “greater”.

Thank you for catching it. We will correct the typo.

L234: I suppose that differences in above- vs below-ground biomass, i.e. the ratio between photosynthetic and non-photosynthetic tissue can be different for different

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species of seagrass (e.g. Duarte and Chiscano 1999 Aquatic Botany). Furthermore, it is important to keep in mind that eddy fluxes represent habitat-scale fluxes, and not just seagrass respiration. Animals, for instance, will contribute through respiration and bioturbation.

We agree that differences in above- vs. below-ground biomass could contribute to differences in metabolism between species. *P. oceanica* has the greatest below-ground biomass of the three species, but surprisingly it has the lowest below-ground productivity (Duarte and Chiscano 1989). Ten percent of fixed carbon is allocated to root growth in *P. oceanica*. Thirty percent of fixed carbon is allocated to root growth in the other species. The low proportion of primary production dedicated to root growth in *P. oceanica* may help keep respiration low. We will add this point to the discussion.

We also agree that other flora and fauna within the meadows may contribute differences in meadow metabolism. Animals, as you suggest, are a good example. There can be up to 50,000 benthic invertebrates in a square meter of *Z. marina* meadow (Bostrom and Bonsdorff 1997). It is also relevant that *P. oceanica* peat can be millenia old (Mateo et al., 1997), therefore few consumers are making a living off of it. We regret that we did not include biological surveys of the study sites. We will include a discussion of these points.

L252: “Epifauna biomass. . .” Presumably autotrophic epiphytes would contribute to the eddy flux signal also?

This is another aspect of the habitat which is of general interest but was beyond the scope of our experimental design. We discuss the contribution of autotrophic epiphytes to primary production in the Introduction (lines 57 and 58). They can enhance photosynthetic O₂ production of seagrass leaves by up to 50% (Libes 1986). We will also include a description that epiphytes were present in all meadows.

L258-259: This conclusion is based upon a ‘snapshot’ dataset. Without investigating this in more detail (e.g. a seasonal study), it may come across as a little premature. It

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should be stated clearly that these results are specific for the period of investigation.

We will include the duration of measurements. We will write that “Fluxes were determined over only one day and two nights at the CO₂ vent, but despite similarities in the drivers of primary production (Table 2), NEM at the CO₂ vent was one-sixth to one-twelfth that of the other meadows (Table 2).”

L265: “. . .but the negligible NEM suggests that this meadow was not storing organic carbon.” It really depends on how production and respiration are partitioned within that habitat. This statement suggests that all of the new production by the seagrass is consumed, but seagrass C:N typically is high, so what is consuming all of that biomass? Presumably these plants are growing and are shedding leaves on an annual basis. There exist other sources of organic matter than the seagrass themselves. One alternative theory could be that seagrass GPP > R, but R is stimulated by sediment entrapment, resulting in a GPP similar to R.

This is a good question. We will adapt our discussion to address it. To begin, we will clarify in the manuscript that net ecosystem metabolism at the CO₂ vent meadow was small. ‘Negligible’ is less accurate. For context, we will compare seagrass meadow primary production and respiration across species using other eddy covariance studies. Interestingly, the proportion of GPP to R at the CO₂ vent is similar to the proportion in *Z. marina* and *T. testudinum* meadows in the Mid-Atlantic Bight and in Florida Bay, respectively. Therefore, the high respiration compared to gross primary production at the CO₂ vent may be common in other seagrass species. The respiration of imported organic matter is a possible explanation, as you suggest.

L287: “. . .hydrodynamic exchange with surrounding waters is limited.” Again, this is based on a small dataset, and was not observed at the other sites. ‘Can be limited’, perhaps?

We will change the text to state “hydrodynamic exchange with surrounding waters can be limited.”

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L325: “These meadows had high productivity. . .” Is this referring to NEM? If so, this needs to be specified.

We will change the text to read “These meadows had a high net ecosystem productivity”

L329-332: As I understand it, the point being made here is based upon a single flux dataset (the one that required O₂ storage correction). The other datasets did not require this correction, and thus (presumably), this functional adaptation applies only to this one site. However, GPP and NEM rates at the nearshore seagrass sites (no storage) were comparable or higher than the rates observed at the offshore site, which seems contradictory.

P. oceanica meadows are distributed broadly in coastal areas of the Mediterranean up to 40 m depth. Thus, the open-water meadow, where the correction due to storage was needed, may be more representative than the nearshore meadow. Indeed, a resistance to mass transfer in *P. oceanica* meadows may be common. It causes the elevation of nutrients and diel oscillations in pH within *P. oceanica* meadows (Gobert et al., 2002; Hendriks et al., 2014). We thank you for pointing out this gap in our manuscript. We will include these points in the discussion.

We will also alter the text of section 4.3, starting at line 287, to address the effects of hydrodynamic exchange at each of the sites. The text will state that “Generally, hydrodynamic exchange enhances seagrass photosynthetic production by increasing the delivery of CO₂ and nutrients and increasing the removal of excess O₂ (Koch 1994; Thomas and Cornelisen 2003; Mass et al., 2010). The nearshore meadow was exposed to greater water velocities than the open-water meadow. Consistent with this, the nearshore meadow was also the site of greater primary production. Given the advantages of hydrodynamic exchange for enhancing primary production, it is surprising that the open-water meadow would tolerate a resistance to mass transfer. As an explanation we suggest that reduced hydrodynamic exchange would benefit

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seagrass if limiting nutrients that were produced during mineralization at night were retained for primary production during the day.”

Figures

Figure 3: Typo in units for PAR (should be $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$) Figure 5: Typo in units for PAR (should be $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$)

We will correct the typos in the figures to $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$.

We wish to thank the referee again for his thoughtful contributions to our manuscript.

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