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Interactive comment on “Spatial and temporal CO₂ exchanges measured by Eddy Correlation over a temperate intertidal flat and their relationships to net ecosystem production” by P. Polensaere et al.

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General comments:

"CO₂ fluxes data obtained with the micrometeorological Eddy Correlation (EC) technique carried out at different seasons over an intertidal lagoon are presented and discussed. In particular, net ecosystem exchanges at low tide are linked to the cover of *Zostera noltii* meadow. Such studies are needed to better understand the CO₂ flux variability in coastal areas and the role of these systems in the global carbon cycle. The EC technique provides integrated measurements and is especially relevant."

We thank Referee#2 for this positive comment. The results shown in the present study

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indeed demonstrate the interest and great potential of the Eddy Covariance technique for CO₂ flux measurements over tidal environments, although logistics is difficult in muddy tidal flats.

"However, it should be supplemented by complementary approaches providing for example data on benthic and pelagic respiration and production to understand and untangle processes that determine fluxes. Most of the interpretations given here suffer from not being supported by such data. Furthermore, some arguments of the discussion are not very convincing, if not invalid, and some references are not properly used. A serious revision is then recommended."

Indeed, our Eddy Covariance measurements are not supported by benthic and pelagic respiration/production data obtained by different methods such as short incubations (¹⁴C, benthic chambers) or biomass measurements. In the revised manuscript, we will discuss more deeply our Eddy Covariance data with some other data available from previous studies in the Arcachon lagoon (see table below). Note however that comparisons with other methods are sometime difficult, as they are made at spatial and temporal scales not always comparable to the changes occurring in situ with tide and light. For instance, what a ¹⁴C incorporation means in a system where water disappears twice a day? Also, in the case of intertidal area, methods might be affected by bias such as in situ vegetation patchiness (benthic chambers CO₂ NPP and CR), light availability (¹⁴C planktonic GPP), etc. . . , which would be integrated by the Eddy Covariance. Imprecisions and also inappropriate references used in the manuscript will be carefully checked and corrected in the next version.

Specific comments:

1. "In the introduction, the release of CO₂ due to carbonate precipitation in aquatic system is not clearly presented (p.6, l.5-12). Carbonate precipitation and dissolution affect DIC concentration. The precipitation of calcium carbonate results in the sequestering of carbon and decreases DIC but is accompanied by a shift of pH that induces

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the release of CO₂ (see Ware et al, 1991. Coral Reefs 11: 127-130)."

We are aware of CO₂ release by CaCO₃ precipitation in coastal systems (e.g. Abril et al., 2003) In the revised manuscript, the part of the present introduction dealing with precipitation/dissolution processes (p.6 l.5,6 and 7) will be described with more detail citing the suggested reference.

2. "The third focus (p.8, l.13) being not attainable (as explained in the discussion) should not be announced in the introduction."

True. The third focus will be removed from the introduction in the revised manuscript.

3. "A detailed description of the data processing is given in Polsenaere et al (2011), which is just submitted and then not available. Reference to this paper should be avoided."

Our attempts with these two papers were to detail the Eddy Correlation methodology in the other paper and the CO₂ fluxes in relation to ecology of tidal flats in the present manuscript. This reference will be removed from the bibliography list and only cited inside the manuscript text.

4. "In the results section, when the lagoon is presented as a source or sink of CO₂ to the atmosphere according to fluxes measured at each season, it would be more relevant to refer to daily fluxes rather than to average fluxes, provided that daily fluxes given in Table 1 do correspond to the mean daily budget. (The meaning of daily fluxes should be specified.) For example, daily fluxes ranged from 0.1 to 1.0 $\mu\text{mol.m}^{-2}\text{s}^{-1}$ (i.e. source of CO₂) in autumn 2007 at station 2 while average fluxes ranged from -10.0 to 18.6 $\mu\text{mol.m}^{-2}\text{s}^{-1}$ (i.e. either sink or source of CO₂)."

In the revised manuscript, daily fluxes will be also given in g C m⁻² day⁻¹ in the tables.

5. "The result section 3.5 is very confusing and comprises some part of discussion with references to published work. This paragraph should be rewritten. I suggest to present here only the evolution of the *Zostera noltii* cover (Table 2 should give results of the 5

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satellite images analyse) and to relate spatial and temporal CO₂ fluxes variations to it only in the discussion."

The section 3.5 can be simplified. As suggested by the anonymous Referee#1, the parts (with references to published work) dealing with the gross of the seagrass in the mudflat will be displaced in the Material and Method. The relationships between the seagrass covers and the CO₂ flux variations will be handled in the discussion (section 4.1.1) as rightly suggested by the Referee#2.

6. "The discussion section should be reorganized. It would make more sense to discuss first the diurnal and tidal changes in NEE and then to relate them to NEP. This would also permit the reader to understand the note in the Tables 2 and 3 and Figure 8 legend concerning discarded data."

We will completely reorganize the discussion section in the revised manuscript, according to Reviewers 1 and 2 suggestions.

7. "The authors assumed that benthic CR was equivalent to NEE at night and benthic NEP was equivalent to NEE averaged over the daytime (p. 5471, l. 1-3), but the results they obtained in April 2009 refute this assumption. Indeed, other processes must be taken into account as negative NEE at night could not be ascribed to benthic CR. This should be discussed before interpreting as NEP NEE measured at the other dates."

The part dealing with negative or close to zero CO₂ fluxes measured in April 2009 at low tide night (p.22, l.4-17) was placed after the NEP/NEE interpretations at the other dates because it represents a particular season where only such flux directions were observed. As shown in this discussion part, different processes such carbonate dissolution, microphytobenthic cell migrations through the sediment, are involved but remain minor during the three other deployments. Indeed, they are very few significant negative NEE data at night in April 2009 and most low tide/night data give a zero flux. We recognize these few negative values are indeed difficult to explain. We will take in consideration this comment according to the reorganization of the discussion in the

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next version of the manuscript.

8. "The authors ascribed the highest positive CO₂ fluxes at night at station 2 to benthic CR enhanced by the intense grazing of meiofauna and macrofauna on microphytobenthos (p. 5471, l. 24-28) and argued that this could confirm the more significant contribution of microphytobenthos at station 2 than at station 1. However, in intertidal sediments the major part of the benthic community respiration is generally ascribed to heterotrophic bacteria (see for example Hubas et al., 2006. MEPS 316: 53-68. And references therein). Furthermore, bacterial activity should be greater in *Z. noltii* bed sediments than in unvegetated sediments as demonstrated by Isaksen and Finster (1996. MEPS, 137: 187-194) in the Arcachon Bay."

The explanation for high benthic respiration rates measured at Station 2 in September/October 2007 could be indeed specified. Intense grazing of meiofauna and macrofauna on microphytobenthos is able to occur on unvegetated sediments (Middelburg et al., 2000; Spilmont et al., 2006). Also, heterotrophic bacteria largely contribute to the benthic community respiration as measured by Hubas et al. (2006) for instance. Goto et al. (2001, J. Exp. Mar. Biol. Ecol. 257:73–86) have precisely shown benthic bacteria can utilize exudates from microphytobenthos. Consistent with results of Isaksen and Finster (1996), higher respiration rates were measured using benthic chambers in the lagoon in September/October 2007 over a seagrass station (0.72 g C m⁻² day⁻¹) than an unvegetated station (0.27 g C m⁻² day⁻¹) (Davoult et al., unpublished data). The results obtained by the Eddy Covariance technique at the ecosystem scale seem to show the contrary. This will be definitely discussed in the revised manuscript and this also shows the interest to add a new part in the discussion dealing with comparisons between different methodologies and their possible bias (i.e. spatial heterogeneity by benthic chambers) as suggest here.

9. "The assumption that GPP and CR would be lower and characterized by a slower time scale variation in seagrass meadow than in microphytobenthic community is not valid. GPP and CR of *Z. noltii* beds have been shown to be as high as, or even higher

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than, in tidal microphytobenthic communities (see for example Ouisse et al., 2010. *Hydrobiologia*, 649: 3-11) and rapid response of both GCP and CR to environmental change (i.e. at tide scale) has been demonstrated (see Clavier et al., 2011. *Aquat. Bot.* 95: 24-30 or Ouisse et al., in press. doi: 10.3354/meps09274)."

Here again, the interest of CO₂ flux methodology inter-comparison is needed and will be discussed in the revised manuscript. The main issue is that for the present time, few studies deal with Eddy Covariance CO₂ flux measurements over intertidal area. The results presented here can suffer from weakness in the length of data sets (especially at Station 2 which last only four days compared to the other deployments). However, it is not appropriate to qualify these results as not valid; differences between CO₂ flux measurements by Eddy Covariance and benthic chambers obviously exist mainly due to temporal and spatial integration divergence. Benthic chambers suffer from variability of intertidal sediment habitat resulting from spatial patchiness in particular. Also, surface heating during low tide can interfere with metabolic processes in tidal flats. Results can be discussed according to the methodology but the Eddy Covariance technique shows at sufficient temporal and spatial resolutions a difference between seagrass and microphytobenthic metabolic cycles in the lagoon in terms of intensity and duration.

10. "The reference to Spilmont et al. (2006) to explain processes leading to negative CO₂ fluxes at LT/Night (p. 5472, l. 11) is inappropriate and the given hypothesis are not convincing. First, as already pointed out (see point 8), the major part of the benthic community respiration in soft sediment is ascribed to heterotrophic bacteria and Spilmont et al. (2006) do measure release of CO₂ to the atmosphere under dark incubations in spite of the microphytobenthos migration. Second, has the *Z. noltii* meadow of the Arcachon Bay been reported to be a site of high CaCO₃ dynamics and does CaCO₃ dissolution significantly occur under emersion? What are the assumptions of Zemmeling et al. (2009) who also reported negative CO₂ fluxes at LT/Night?"

Zemmeling et al. (2009) did not propose any explication for their negative CO₂ fluxes

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at low tide during the night. The reference to Spilmont et al. (2006) is not appropriate here in the submitted manuscript (p.22, l.11) and will be displaced. However, Spilmont et al. (2006) do measure CO₂ release to the atmosphere under dark incubations when seagrass or microphytobenthic communities are suddenly exposed to dark conditions during the day. Due to the fast carbon recycling in tidal environments, these respirations could largely differ from those measuring during the real night conditions as it is done with the Eddy Covariance technique. Also microphytobenthos migrations could not occur and be measured during these experimental conditions. Several hypotheses are presented in this part to explain the negative CO₂ fluxes measured in April 2009 at Station 1 at LT/Night. CaCO₃ dissolution is one of them and is able to happen at low tide in presence of small amount of water. CaCO₃ dissolution could occur in the wet mud sediment or in the small channels patchy distributed over the intertidal flat. The CO₂ fluxes coming from those channels are necessarily measured by the Eddy Covariance technique despite their small influence generally observed over the three other deployments. Further researches need to be obtained to know if CaCO₃ dissolution rates generally prevail in spring in the lagoon compared to the other seasons.

11. "There is no biological meaning in a linear relationship between light and production. Models classically used to relate production to light (i.e. light response curves) take into account a saturation (or even an inhibition) at high light."

Indeed, for light response curves, models classically take into account a saturation at high light (Ik, Migné et al., 2004). We are all aware of that. The scope here is not to establish real P-I curves, with a "biological meaning". The data we are presenting here are not biological data either, they are physical data that is CO₂ turbulent measured several meters above the surface where biology is active. What we are doing here is searching for any existing correlation between NEE and light. Because NEE cannot be explained by biology alone (although biology is one of the main driver), no ideal NEE-I curve is expected. As we observed a statistically significant trend we think interesting (positive or negative, apparently depending on the habitat), and important to discuss it.

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12. "The hypothesis of a reduced community metabolism at high tide compared to low tide (p. 5478, l. 11) is refuted by recent publications showing that carbon fluxes are far greater under water than in air on *Z. noltii* beds (Clavier et al., 2011. *Aquat. Bot.* 95: 24-30 and Ouisse et al., in press. doi: 10.3354/meps09274)."

We did not know this paper at the time of submitting. We will incorporate it and evoke the potential impact of the *Zostera noltii* primary production during the immersion in the revised version. Larger GPP of *Zostera notlii* at high tide is not contradictory with our data, to the contrary. It is important to note that during high tide, our Eddy Covariance (water-air CO₂ fluxes) does not measure the same as Clavier's benthic chamber (DIC uptake). The quantity of DIC available in water during high tide (buffer capacity) and the short residence time of water over the tidal flat each tide would make our high tide data perfectly consistent with both *Zostera noltii* and phytoplankton uptake. We precisely observed uptake at high tide during the day during the productive periods of the seagrass in the flat. This will be discussed in the revised manuscript with the cited references.

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g C m ⁻² day ⁻¹ (Mt C yr ⁻¹)	Primary producers	NCP	NPP	GPP	CR	Methods	References	
LOW TIDE - BENTHIC METABOLISM	<i>Zostera noltii</i>		0.34-0.49 (8.88-12.71)			Biomasses (Dry Weight)	Auby, 1991	
		0.5		1.22	0.72	Benthic chambers CO ₂ fluxes	Davoult et al. (unpublished data) from 2005 to 2007 (March, May and September)	
		1.25		1.86	0.61	Eddy Correlation CO ₂ fluxes	this study (Station 1, LT in July and September 2008)	
	Microphytobenthos			0.09-0.22 (4.93-12.27) 0.29-0.32 (16.13-17.62)			Chlorophyll <i>a</i> concentrations	Auby, 1991 Auby (unpublished data)
		1.31		1.58	0.27	Benthic chambers CO ₂ fluxes	Davoult et al. (unpublished data) from 2005 to 2007 (in March, May and September)	
		1.72		4.55	2.83	Eddy Correlation CO ₂ fluxes	this study (Station 2, in September- October 2007)	
HIGH TIDE - BENTHIC & PELAGIC METABOLISM	Phytoplankton		0.25 (16.07)			¹⁴ C short incubations at incident light	Glé et al., 2008 (year 2003)	
		0.21		0.98	0.78	Eddy Correlation CO ₂ fluxes	this study (Station 1, HT in July 2008)	

Fig. 1.

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