Interactive comment on “Ecosystem metabolism in a temporary Mediterranean marsh (Doñana National Park, SW Spain)” by O. Geertz-Hansen et al.

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Response to comments by Referee #1

Reviewer #1: The marsh is influenced by a wide range of abiotic factors, including draught leading to extinction of the macrophytes. Light is also argued as an important factor, but the thresholds are quite low (down to 45 uEm-2s-1), and the question is how often light is a limiting factor?

Comment: This is a relevant question that we should consider. Light is often a limiting factor for transparency can oscillate between high values and very low, < 10 cm values. The factors that lead to periods of high turbiditd and light limitation are: the input of high
suspended particle loads during the flooding season in the winter; bioturbation due to trampling by wading birds and herbivore mammals, feeding by flamingoes, present in thousands of birds in the lagoons, which produce turbidity plumes; and resuspension of the very shallow sediments during windy days. These are reported in the paper by Duarte et al. (1990).

Action: We have now discussed this issue in the text, which now reads: “Analysis of the irradiance-dependence of community metabolism (Table 3), standardized to 20 °C, indicates a light compensation point for community metabolism ranging between 42 and 255 µE m-2 s-1 across the stations, with the communities becoming heterotrophic at lower irradiances. These findings suggest that the communities may be often light limited, as the waters in the marsh oscillate between relatively high transparency and turbid conditions. The factors that lead to periods of high turbidity and light limitation include the input of high suspended particle loads during the flooding season in the winter; bioturbation due to trampling by wading birds and herbivore mammals, feeding by flamingos, present in thousands of birds in the lagoons, which produce turbidity plumes; and resuspension of very shallow sediments during windy days (Duarte et al. 1990).”

Reviewer #1: Are data available on light conditions in the marsh, which could be extrapolated to indicate the extent of light limitation? Resuspension events possibly contribute to impoverished light conditions. Is there any data available such events over a growth period? The discussion of the results could benefit for an assessment of the influence of the abiotic factors over the growth period.

Comment: We concur that such data would be very informative. Regrettably, evaluating the frequency of light limitation would have required continuous records of underwater irradiance over the growth season, which are not available.

Reviewer #1: The paragraph (first pg 6505) on turnover rates for macrophytes is not so clear, as the text is mixing up high and low turnover rates. Macrophyte rates are low
compared the pelagic compartment, which is a key issue for this paper, but they are high compared to other studies of macrophytes, which is also an important conclusion of the paper.

Comment: We agree.

Action: We have qualified the turnover rates estimated for macrophytes. The text now reads: “The ratio of benthic gross production to macrophyte biomass was very high (>0.12 d-1) for macrophyte biomasses below 10 g C m-2 and declined to 0.05-0.10 d-1 for macrophyte biomasses above 20 g C m-2 (Fig. 6). Accounting for macrophyte respiration and some (but small) contribution of microphytobenthos at high macrophyte biomasses, the relative growth rates of macrophytes would be lower than 0.05-0.10 d-1, which are quite high for macrophyte communities.”

Reviewer #1: I do not fully understand how to read the relationship between NCP and irradiance in fig. 7. Where is it possible to see the morning and afternoon values (arrow??)?

Comment: We apologise because the figure was missing the arrows.

Action: We have revised Fig. 7 to improve clarity, and added the arrows as well as labels identifying the morning and afternoon sections of the trajectories.

Reviewer #1: It is not clear how the numbers in Table 3 have been achieved from this figure?

Comment: The results shown in Table 3 were not derived from Figure 7. The results shown in Table 3 were derived from data on oxygen evolution and irradiance measured along 24 hrs - similar to that shown in Fig. 7, which provides an example - but where the data were normalised to 20 °C to avoid the hysteresis observed in Fig. 7, which was attributable to the differences in temperature for comparable irradiances during the morning and afternoon/evening. The procedures used to derive metabolic rates are described in detail in the methods section, and the temperature corrections for
respiration rates are reported in the results section, which reads: “We found, by fitting an Arhenius equation to the field data obtained during the night, respiration rates to increase about 3-fold for a 10 oC temperature increase (Q10 = 2.9). Therefore, the irradiance needed for gross production to balance respiration was much higher in the afternoon than that in the morning.”

**Reviewer #1**: It could be interesting with a note on the status of the marshes today 20 years after this study.

Comment: We agree.

Action: We have added some comments on the status of the marshes in the Study Area section. The text now reads “The Doñana marsh experienced a dry period after the completion of this study and returned to a wet period in the 1995-1996 hydrological cycle, with dry years, when the marsh is not fully flooded and macrophyte cover in the spring is limited in 1998-1999 and 2004-2005.”.

**Reviewer #1**: Did the authorities manage the marsh according to the suggestions, and was this management successful in the conservation of the marshes and the water fowl?

Comment: No, the managers did not follow our advice, since this was not supported to-date by published scientific research. The publication of this paper should inform managers and help guide their management practices.

**Reviewer #1**: The paper is generally well written, with some clarifying needs provided below in the detailed comments. The generality of the paper can be expanded by including a table on more recent measurements of productivity in marshes and macrophyte beds (several authored by CM Duarte) and comparing the results from Donana with these.

Comment: We have not included such table, since the table would have only two additional entries relative to that already published by López-Arcilla et al. (2004). However,
we now compare our estimates to those in that compilation and include a narrative comparison of the metabolic rates obtained here with those reported from another aquatic ecosystem within the Doñana National Park as well as rates reported for macrophyte beds and seagrasses. The text now reads: “The metabolic rates obtained for the marsh here are not as high as metabolic rates derived for other aquatic ecosystems in the Doñana National park, such as the hypertrophic Santa Ollala lagoon, supporting high gross primary production (average 2.9 g C m\textsuperscript{-2} d\textsuperscript{-1}), but net heterotrophic communities (López-Arcilla et al. 2004), and were below the mean gross primary production for seagrass meadows of 3.1 g C m\textsuperscript{-2} d\textsuperscript{-1} (Duarte et al. 2010) but higher than most shallow lakes in the compilation in Table 3 by López-Arcilla et al. (2004).”

**Reviewer #1:** Minor comments:

6495 – missing 5 in front of “now at” Abstract: l 8: suggest to change to: between 42 to 255 “below which: : :” is redundant. Is already mentioned in sentence Strongly used 3 times in the same sentence! 6498, l8: not clear what you mean by temporary at

Comment: This errors have been all corrected.

**Response to comments by Referee #2**

**Reviewer #2:** The data set presented here was collected in 1991, it would certainly be of great interest to have some recent comparative data.

Comment: We regret that no further studies on metabolism in the marsh have been conducted since our study. We hope that the (delayed) publication of this research will estimulated further metabolic studies.

**Reviewer #2:** A major concern I have is the use of dissolved oxygen concentration to determinate net community production and respiration in a system where temperature changes are in the order of 10\(^\circ\) C during 24h. How did the authors deal with this fact, in both the bottle incubations and the in situ measurements? This aspect is briefly
discussed in the context of respiration being a temperature-dependent process (p. 6501 and p. 6503), but the oxygen concentration itself is temperature dependent. How did the authors dissociate these issues?

Comment: Temperature changes affect two components of our study: metabolic rates, and saturation levels. Effects on metabolic rates were explored and shown to correspond to an Arhenius-like relationship for respiration rates, which were then corrected to $20^\circ C$ for comparative purposes, and the effect of temperature on saturation levels affects air-sea exchange, which was also considered in our calculation. Another possible effect is bubble formation, which may affect the accuracy of oxygen estimates. However, we did not observe such bubbling during our sampling.

**Reviewer #2:** Material and Methods p. 6500, last paragraph: I suggest the authors explicitly state that benthic community metabolism was estimated as the difference between whole system and pelagic metabolism.

Comment: We agree.

Action: We have done so.

**Reviewer #2:** Results and Discussion p. 6503, last paragraph: It would help if the authors were more precise when using the term “community”. In this case, is the whole community considered? The same for Fig. 3: I suppose these data present whole community respiration and gross production?

Comment: We agree.

Action: We have now specified “(benthic + pelagic)” where appropriate, throughout the text and figure and table headings.

**Reviewer #2:** p. 6504, line 6-7: It would be important to confirm the “close” relationship by some correlation coefficient.

Comment: We agree.
Action: The text now reads “Though phytoplankton biomass was low (Table 1), our estimates of pelagic production (Table 2) showed a close relationship to planktonic biomass \((r = 0.80, P = 0.02)\).”. Fig. 4 has been eliminated (as requested below).

**Reviewer #2**: p. 6505, last paragraph: The results and discussion on Fig. 7 are quite difficult to follow. One reason for this might be that the arrows are missing on Fig. 7.

Comment: We apologise because the figure was missing the arrows.

Action: We have revised Fig. 7 to improve clarity, and added the arrows as well as labels identifying the morning and afternoon sections of the trajectories.

**Reviewer #2**: Table 2. Station 0 should be Station 9

Comment: This was a file translation error.

**Reviewer #2**: Fig. 3: I am not convinced that the mean value should be indicated on the graph.

Comment: We believe the mean value is informative, in that it shows that the overall metabolism is autotrophic.

**Reviewer #2**: Fig. 4: The information given in this graph can easily be described in the text. I suggest eliminating Fig. 4.

Comment: We agree, since the correlation coefficient is now provided.

Action: We have now removed Fig. 4.

**Reviewer #2**: Fig. 5: As above, I am not convinced that these results need to be shown on a graph.

Comment: We agree.

Action: We have now removed Fig. 5.

**Response to comments by Referee #3**
Reviewer #3: Anthropogenic pressure has increased the past 20 years, implying that the metabolic balance may have changed in the course of these years.

Comment: This is a protected area where anthropogenic pressure is managed to be kept low. Although metabolic rates have not been assessed again, there is no evidence that this may have changed due to anthropogenic pressure. Interannual changes in hydrological processes are, as discussed in the paper, the main source of variability in this ecosystem.

Reviewer #3: It would be interesting to have recent data as well, and maybe a short comment on that would be worthwhile.

Comment: We agree. Unfortunately, community metabolism has not been assessed since our study. We hope that the (delayed) publication of this research will stimulate further metabolic studies.

Action: We have commented on the changes that have occurred in the ecosystem since our study. The text now reads: “The Doñana marsh experienced a dry period after the completion of this study and returned to a wet period in the 1995-1996 hydrological cycle, with dry years, when the marsh is not fully flooded and macrophyte cover in the spring is limited in 1998-1999 and 2004-2005.”

Reviewer #3: Please see below minor corrections:

Indicate correlation coefficients and p-values in Fig. 3, 4, 5 and 6. Specify which relationships were significant in the text (e.g. P6504 L24-25, P6506 L 1-2).

Action: We have made the corrections requested.

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