Interactive comment on "Species interactions can shift the response of a maerl bed community to ocean acidification and warming" by Erwann Legrand et al.

We thank the referee and appreciate the thoughtful and constructive comments. We have fully considered the referee's comments and improved the manuscript accordingly. Answers to referee's comments are in red color.

The study by Legrand et al. assessed the metabolic responses of a range of species associated to maerl beds (incl coralline algae, grazers and epiphytic fleshy algae), as well as the metabolic responses of the maerl assemblage to changes in seawater carbonate chemistry and temperature across two climatic seasons. The authors found complex interactions among experimental factors and seasons on the species and community metabolism. The coralline algae exhibited responses which were expected under CO_2 perturbation experiments, but importantly, the study documented significant changes to grazers' metabolism and enhanced epiphytic algal biomass under CO_2 enrichment. Although ecological interactions were not directly assessed, changes in the metabolic responses of the experimental species are assumed to influence species interactions. Based on these results the authors were able to propose that ocean acidification and warming will have considerable impacts on the functioning of maerl beds.

I read this manuscript with great interest and believe the authors have done a comprehensive and thorough study. Most studies in the field of impacts of climate change on marine systems focus on responses of one or two species, generally within the same taxonomic group, and it is refreshing to see that this study took a step forward and assessed the impacts at the community level during two climatic seasons. Individual responses focussed on a range of response variables, incl chlorophyll (for the algae), net production, respiration, net calcification (light and dark), and excretion for the grazers. In combination with the assemblage's responses, this allowed the authors to discuss some potential ecological implication such as shifts in species composition, competition, carbon storage, etc. The Methods are generally well described and provide enough detail so that other researchers can repeat the experiments. Methods are appropriate for ocean acidification research.

Main comments

I have two main comments to the paper. First, seasonal effects on both the individual and assemblage responses were not fully explored or discussed in the m/s. One of the strengths of

this m/s is that it was conducted in two different climatic seasons, but how the strength of the responses varied between seasons was not clear. I would suggest that the authors include a section where this comment can be fully addressed.

Answer: We agree with this comment. A new paragraph has been added in the discussion to explore the seasonal effects on species and community metabolism. In the result section, the influence of season has been detailed for each species and the community. Further information was also added throughout the m/s to understand how the strength of the response varied between the two seasons tested.

(L. 262-267): "Assemblage exhibited a strong seasonal pattern for all metabolic parameters, which is consistent with the higher metabolism in the summer for most of the species incubated at the specific scale. This higher metabolism in the summer has already been evidenced in urchins (Brockington and Peck, 2001), gastropods (Davies, 1966; Innes and Houlihan, 1985; Martin et al., 2006b) and living maerl (Potin et al., 1990; Martin et al., 2006a) and is strongly related to changes in numerous environmental and biological variables, such as light intensity and photoperiod, temperature and nutrient or food availability (Godbold and Solan, 2013; Thomsen et al., 2013)."

The statistical analyses seem to be well executed, however, I would argue that because there were significant interactions between treatments (OA, temp, and season), there is a need to conduct further statistical analyses within treatment combinations, as in several instances, the main factor was significant, but in fact it was only significant for one or the other season, or under a particular treatment combination. For example, in line 213, "R was significantly reduced by the high temperature condition in the winter, whereas an increase in R was observed in the summer." This statement is fine, but is not actually supported by a statistical analysis as Table 3 only provides p values for the main effects. This issue is also evident 216-219. Underwood (1997; Experiments in Ecology: Their Logical Design and Interpretation Using Analysis of Variance, Cambridge University Press) provides information on this topic. These new analyses could be included as supplementary material.

A: According to the comments of Referee #1, we have modified statistical analyses. The seasonal effect has now been tested separately (using t-tests) in order to keep a balanced statistical design. The effect of temperature and pCO_2 was analyzed through 2-way ANOVA for each season separately. When an interactive effect of temperature and pCO_2 was observed, interaction plots were performed and provided in the supplementary material. (L. 197-198)

"When 2-way AVNOVAs showed significant results, post hoc tests (Tukey honest significant difference, HSD) were performed to compare the four treatments." (according to suggestions of Referee #2). Results have been shown in corresponding graphs.

There are some statements that are not supported by the experiments. Although the authors demonstrated changes in algal and grazer metabolisms, species interactions among those organisms were not examined experimentally. E.g. Line 251. "Our study demonstrates that the response of maerl bed communities to increased temperature and pCO2 conditions is a complex function of direct effects of climate variables on species physiology and shifts in species interactions". Reword this statement.

A: We agree with this comment and, as suggested by the reviewer, this sentence has been reworded: (L. 253-254) "The response of communities to increased temperature and pCO2 conditions is likely to be a complex function of direct effects of climate variables on species physiology and shifts in species interactions (Lord *et al.*, 2017)."

Lord, J. P., Barry, J. P., and Graves, D.: Impact of climate change on direct and indirect species interactions, Marine Ecology Progress Series, 571, 1-11, 2017.

Minor comments

Unclear why chla was measured on dead Lithothamnion. Provide a brief justification in section 3.3.

A: A sentence has been added in the "Material and Methods" section to justify chlorophyll a measurements: (L. 185-186) "In dead maerl, chlorophyll *a* content was measured in order to check for the presence of associated microflora and potential subsequent metabolism."

Line 90: In general avoid single-sentence paragraphs.

A: The sentence was grouped with the following paragraph

Line 237: ".. having positive effect". Was this effect significant?

A: More details have been provided due to the change in statistics recommended by referees: (L. 241-243) "Epiphyte biomass was not affected by increased temperature or pCO_2 in the winter (2-way ANOVA, p=0.95 and 0.67 respectively), while an interactive effect of temperature and pCO_2 was observed in the summer (p=0.013, supplementary material e)."

L260-280: This is a very long paragraph, try breaking it into two.

A: This paragraph has now been divided in 2 paragraphs in the revised manuscript.

L285-305: ´ This is also a very long paragraph.

A: This paragraph has now been divided in 2 paragraphs in the revised manuscript.

L291: Ordonez et al. (Ordonez Alvarez et al. ´ 2014 Effects of ocean acidification on population dynamics and community structure of crustose coralline algae. Biological Bulletin 226, 255-268.) also found a failure in recruitment of tropical CCA and importantly documented shifts in species composition.

A: The reference has now been added in the revised manuscript. (L. 304)

Line 303: "However, the present findings do not support this idea, because a decline in Gl was observed under high pCO2 despite high". Short et al (2014) paper dealt with minute algal turfs which may have altered the thickness of the diffusive boundary layer on the coralline algae. The macroalgae investigated in the present study were much bigger and may interact in many different ways. It is perhaps very difficult to generalise the impacts of epiphytic algae on coralline algae given the diversity of algae in marine systems. Perhaps a line or two addressing this would be useful.

A: We agree with this comment. We have completed with the following sentences: (L. 314-325) "Conversely, other studies evidenced that the overgrowth of epiphytic fleshy algae may shade underlying coralline algae and reduce coralline net calcification rates (Garrabou and Ballesteros, 2000; Martin and Gattuso, 2009). The present findings support this idea, because a decline in assemblage G_l was observed under high pCO_2 and high epiphyte biomass. […] Thus, overgrown maerl would be negatively affected by the direct effect of ocean acidification on calcification rates and indirect effects due to shifts in competition dynamics with fleshy epiphytic algae (Kuffner et al., 2008). However, the response of epiphytic algae is likely to be specie-specific and it appears difficult to generalize the impacts of epiphytic algae on coralline algae."

Pages 14-15: Grazing responses may also be altered by changes in seaweed allelopathic compounds, brought about by changes in composition, quantity, or in the magnitude/potency of the allelopathic interactions. A recent study showed that the potency of allelopathic interactions towards a tropical coral was intensified under ocean acidification conditions (Del

Monaco et al. 2017 Effects of ocean acidification on the potency of macroalgal allelopathy to a common coral. Scientific Reports 7, 41053). May be worth adding this potential mechanism as drivers of changes in species interactions in response to acidification and warming.

A: As suggested by the reviewer, we have now added this information: (L. 377-378) “Algal palatability to grazers may also be affected by predicted changes through shifts in the composition and the quantity of allelopathic compounds, as suggested by Del Monaco et al. (2017).”