

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

General Comments

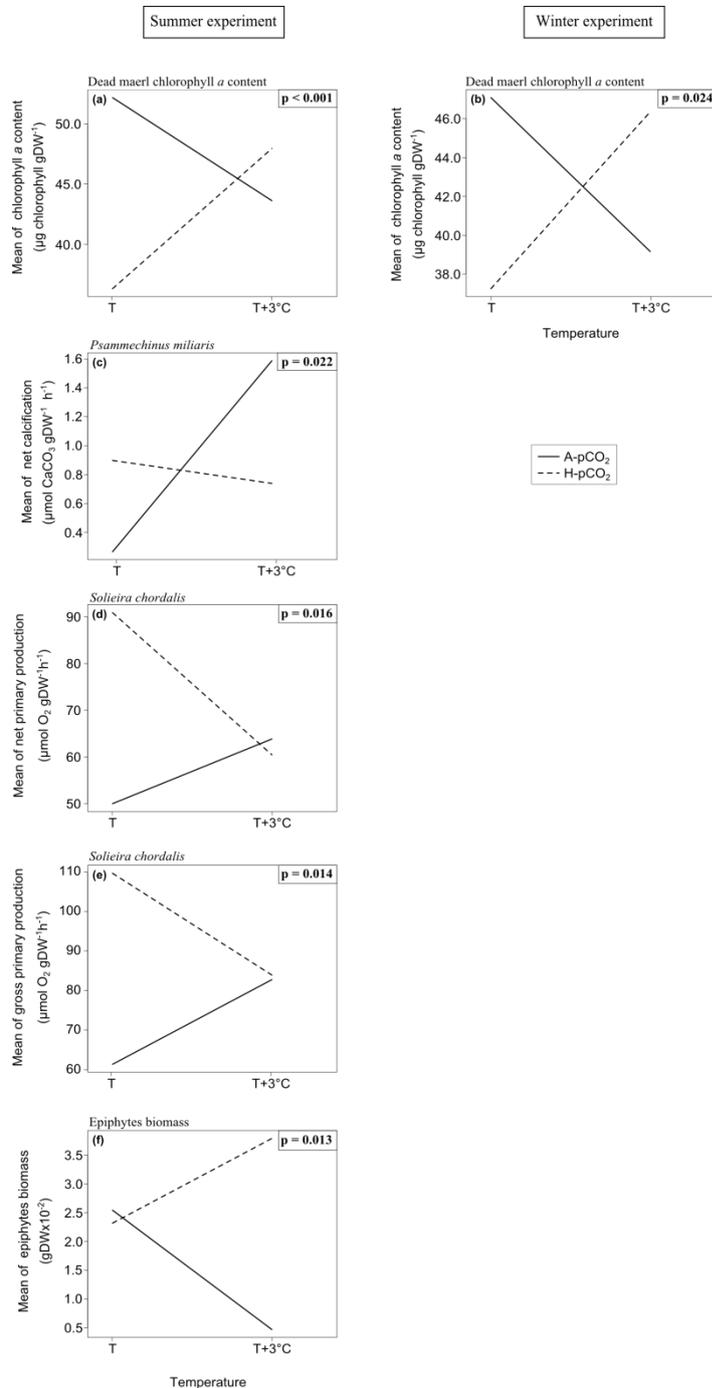
We thank the referee for the thoughtful and constructive comments that helped to improve the manuscript. We considered all the suggestions and improved the manuscript accordingly. Answers to referee’s comments are in red color.

The manuscript "Species interactions can shift the response of a maerl bed community to ocean acidification and warming" describes a novel experiment with an interesting approach on community interactions under predicted global climate change that are generally lacking in the literature. Considering ocean acidification and warming are occurring simultaneously and interdependently, experiments that investigate the effects of both factors on marine organisms are important for understanding future changes in physiology and ecology. The authors were able to do this in their study, and not only did they investigate effects of ocean warming and acidification on the physiology of single organisms, but also of communities. Through their experimental design, they are able to describe changes in species interactions under future climate change conditions, which is currently rare in the literature. The experimental design is good and the manuscript is well written thorough.

My main criticism is that the results could be described more clearly and thoroughly. The interactions between the independent variables should be described more clearly. Interaction plots could help with the interpretation of the statistical analysis of the effect of season, temperature and CO₂ on the independent variables. The authors tested the effect of season on the dependent variables, but they often fail to describe this effect in the results section, and focus only on the CO₂ and temperature effect. They also fail to mention in some cases that temperature ameliorates the negative effect of pCO₂ on some variables, which is important considering both warming and acidification are occurring interdependently. I have made specific comments below.

A: The statistics have been changed according to the comment of Reviewer #1. The seasonal effect has been analyzed separately using t-tests. The effect of increased pCO₂ and temperature on the metabolism of species and assemblage was examined in the winter and the summer using 2-way ANOVA. When an interactive effect of pCO₂ and temperature was evidenced, interaction plots were performed and provided in supplementary material to this

paper. As suggested by the reviewer, the seasonal effect on metabolic parameters has now been discussed in the discussion section of the revised manuscript (L. 263-267). We also considered more closely the importance of season in the response of organisms and assemblages to acidification and warming.



Supplementary material. Interaction plots for the effects of temperature and pCO₂ on dead maerl chlorophyll *a* content in (a) the summer and (f) winter seasons, (b) *P. miliaris* net calcification in the summer, *S. chordalis* (c) net and (f) gross primary production in the

summer, and (e) epiphytes biomass in the summer. Plots were done only when an interactive effect of temperature and pCO₂ was detected using 2-way ANOVA (p-value in bold).

Specific Comments

Materials and Methods

Line 141-142 "Before incubation, epiphytic algae that spontaneously grew on *L. corallioides* during the experiments were carefully removed and incubated separately." I assume this was done after the assemblage measurements were made? The authors could clarify this here.

A: Assemblage incubation was performed first. After this, epiphytic algae were removed from maerl. The sentence has been modified: (L. 137-138) "After assemblage incubations, epiphytic algae that spontaneously grew on *L. corallioides* during the experiments were carefully removed and incubated separately."

Line 156 What buffer solutions were used to calibrate the reactive spots?

A: (L. 152-154) "The 0% buffer solution was prepared by dissolving 1 g of sodium sulfite (Na₂SO₃) in 100 mL of seawater. The 100% buffer solution was prepared by bubbling air into 100 mL of seawater using an air-pump for 20 min to obtain air-saturated seawater." This information has been added in the revised m/s.

Results

In the results headings, the authors mention acidification and warming, but ignore the factor season

A: The factor season has now been taken into account for grazers (L. 203-205), living maerl (L. 214), dead maerl (L. 225-226), epiphyte biomass (L. 240-241) and assemblages (L. 245-246).

Lines 205-208 I think the results can be described more thoroughly here. There actually was not a negative effect of CO₂ and temperature on GI compared to the control. Temperature increased calcification rates in the summer. CO₂ alone did not seem to have an effect in either season. The combination of high CO₂ and temperature in summer negated the positive effect of temperature.

A: The main effect of season on *P. miliaris* has been mentioned (L. 203-204). The sentence on the effect of temperature and pCO₂ on *P. miliaris* G₁ has been reworded: (L. 206-207) “*P. miliaris* G₁ was significantly affected by the interaction between temperature and pCO₂ in the summer (Fig. 1b, supplementary material b), which negated the positive effect of increased temperature and pCO₂ alone.”. We also used interaction plots (in supplementary material) to illustrate pCO₂ and temperature combined effect.

The authors should mention there was a main effect of season on *P. miliaris* E. Excretion was highest under control conditions in the summer. High temperature, CO₂ and the combination of both decreased excretion rates in the summer.

A: We have added the effect of season on *P. miliaris* E. We have reworded this section: (L. 208-209) “*P. miliaris* E was higher under control conditions in the summer and increased temperature significantly reduced *P. miliaris* E (Table 4; Fig. 1c).”

Lines 209-210 It is confusing to say R was positively or negatively affected - please rather describe if it increased or decreased. Also, although there was no temperature or CO₂ affect on R, G₁, or E, there was a strong effect of season.

A: We agree with the Reviewer and changed the sentence accordingly: (L. 210-211) “In *J. exasperatus*, R increased under elevated temperature but in winter conditions only (Table 4; Fig. 1g).” The effect of season has now been added.

Line 213 Please add the effect of season, e.g. "Living maerl GPP did not differ among temperature and pCO₂ conditions, but there was a strong effect of season, with higher rates in the summer than in the winter."

A: The effect of season has now been added: (L. 214) “The metabolism of living *L. corallioides* was higher in the summer than in the winter, except for NPP (Table 3).”

Line 215 Add the effect of season on chlorophyll a

A: We have added: (L. 217-218) “No effect of season was observed on chlorophyll *a* content (Tables 3; 6).”

Line 216 "Temperature had a positive effect on the G₁ of living maerl. Conversely, G₁ was significantly reduced under high pCO₂..." The authors fail to mention that in the combined

treatment, temperature alleviated the negative effect of pCO₂. This is very important to the story.

A: The sentence has been revised due to the change in statistical design. (L. 218-219) “The G₁ of living maerl was not significantly influenced by increased temperature and pCO₂, regardless of the season”

Line 220 "Net dissolution, because G_d was negative, was recorded in the winter under high pCO₂ conditions" But dissolution was less in the combined temperature + CO₂ treatment in the winter, so temperature alleviated some of the negative effect of CO₂ in the winter, although net dissolution still occurred.

A: A sentence has been added: (L. 222-223) “This negative effect of increased pCO₂ was alleviated under elevated temperature.”

Line 222 Again, mention the main effect of season

A: The effect of season has now been added (L. 225-226).

Line 223 I did not see an interaction between season and pCO₂ for GPP in Table 3 Line 225 Mention the effect of season on dead maerl

A: We apologize for this mistake, this has been withdrawn. The sentence has been modified to consider the effect of season (L. 225-226).

Line 233 "R was enhanced by the high temperature and pCO₂ conditions..." alone, and their combination resulted in the greatest R rates.

A: We have added this information: (L. 238-239) “R was enhanced by the high temperature and pCO₂ conditions and their combination resulted in a greater R”

Line 238 Add that temperature alone decreased epiphyte biomass in the summer.

A: We have added “Epiphyte biomass was not affected by increased temperature or pCO₂ in the winter (2-way ANOVA, p=0.95 and 0.67 respectively), while an interactive effect of temperature and pCO₂ was observed in the summer (p=0.013, supplementary material e).”

Line 240 "No temperature effect was observed..." But all response variables were higher in the summer than in the winter.

A: The effect of season has now been added (L. 246-247).

Line 248 "In the summer, the interactive effect of temperature and pCO₂ increase was more complex, with a (change to) increase in G_d detected under high temperature conditions only."

A: The sentence has been changed: (L. 250-251) "In the winter, high pCO₂ increased net dissolutions rates, while in the summer G_d increased under elevated temperature."

Discussion

The authors state that "ocean acidification and warming will strongly destabilize communities through both direct effects on species physiology and changes in the interaction strengths between coralline algae, fleshy algae, and grazers." Based on the assemblage data, I do not think that the effect is so negative, at least in the summer. There is a strong difference in the effect of the combination of CO₂ and temperature in winter and summer. In summer, assemblages exposed to high temperature and pCO₂ combined actually had similar to or even slightly higher light calcification rates than the ambient treatment. In winter, there was a decrease in light calcification compared to the ambient treatment, but the positive effect of temperature and the negative effect of pCO₂ were weakened when the two were combined. I think it is important for the authors to point out that the combination of pCO₂ and temperature often subdued the effects of each single factor, because it illustrates the point that experiments investigating only the effect of pCO₂ or temperature may present more dramatic responses than when the two are combined, which represents a more realistic scenario.

A: The conclusion section has been reworded to consider this comment and those of Referee #1 and #3: "In conclusion, the community response to climate change does not appear to be only the result of individual species' metabolic responses, but also strongly depends on shifts in species interactions. In contrast with other studies, which evidenced larger impacts of the combination of increased pCO₂ and temperature than that of these factors alone (Reynaud et al., 2003; Anthony et al., 2008; Martin and Gattuso, 2009; Rodolfo-Metalpa et al., 2010), we showed here that the effects of pCO₂ and temperature on maerl bed communities were weakened when these factors were combined. Under the predicted business-as-usual conditions, epiphyte overgrowth may exacerbate the negative impact of climate change on underlying coralline algae. Here, we also demonstrated that climate change may affect grazer physiology, with major consequences on their ability to regulate epiphyte biomass. Climate change may also affect other components that we did not assess in the present study, such as

algal palatability and potential changes in grazer trophic behavior (Campbell et al., 2014; Duarte et al., 2015; Poore et al., 2013; Poore et al., 2016). 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). In order to better understand the consequences of climate change on ecosystem functioning, further work should focus on the response of marine communities and consider more specifically shifts in species interactions, including changes in trophic interactions between algae and grazers.”

Technical Comments

Line 129: insert "the" before CO2SYS

A: Done (L. 125)

It would be helpful to be able to identify statistically significant differences in the figures

A: (L. 197-198) “When 2-way ANOVAs showed significant results, post hoc tests (Tukey honest significant difference, HSD) were performed to compare the four treatments.” Results have been added on corresponding graphs. We have also added the direction of changes (2-way ANOVA) in tables 4, 5, 7 and 8 and interaction plots (in supplementary material) when a significant interaction between pCO₂ and temperature was detected.