Biogeosciences Discuss., 8, C5200–C5207, 2012
www.biogeosciences-discuss.net/8/C5200/2012/

Biogeosciences Discussions

Interactive comment on "The metabolic response of pteropods to ocean acidification reflects natural CO_2-exposure in oxygen minimum zones" *by* A. E. Maas et al.

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Received and published: 8 January 2012

We thank the reviewer for her/his very helpful and constructive suggestions for our paper. Below, we respond to each of the comments on a point by point basis. Reviewer remarks are in plain text and the author response is in bold. In general, we have worked to expand the methods section, to include more current OA-related literature and to provide a more contextualized discussion of the results and implications of our work.

. . . a major issue with this work is that of the five species examined four are migratory and one species is of the non-migratory kind. It is not possible to conclude on the

basis of one single non-migratory species (Diacria quadridentata) never found below the mixed layer, that all non-migratory thecosomes will not be able to withstand low pH/high CO2 conditions. . . The dataset as it is now cannot be employed to support the idea/statement that the evolutionary ecology or pre-exposure of these groups of pteropods may determine their relative vulnerability to future OA scenario: at best the author could briefly suggest this, but this study (unfortunately) cannot be considered conclusive. . .I have to suggest the authors substantially modify their manuscript focusing on the ecophysiology of warm-water pteropods and avoid inferring on the ecological significance of the evolutionary ecology. In particular, the title has to be changed (as what it states is unsupported), and equally parts of the introduction and discussion relative to the testing of the main hypothesis are changed.

Our results were never meant to be interpreted as indicating that all non-migratory thecosomes will be susceptible to conditions of low pH/hypercapnia. The more important point is that there are species of open ocean zooplankton which do experience and survive under these conditions over short time scales, and that there appear to be species-specific differences in tolerance which appear to be linked to natural exposure to environmental stress. This is particularly interesting because it involves pteropods, a group which has frequently been cited as being especially sensitive to acidification. We do not feel that the manuscript makes the claim that the reviewer attributes to it. To clarify the point the authors have changed the title and slightly modified their text:

TITLE: "The metabolic response of pteropods to acidification reflects natural CO2-exposure in oxygen minimum zones"

ABSTRACT: "This indicates that the natural chemical environment of individual species may influence their resilience to ocean acidification."

DISCUSSION: "However, these distributional patterns and physiological studies do not rule out the possibility that ocean acidification may have severe effects

on pteropods. In fact, our results indicate that some species of non-migratory species such as Diacria quadridentata could, in the absence of acclimation and adaptation, be significantly impacted by even brief periods of exposure to CO2 with unknown implications for species fitness, biogeography and survival."

Page 10298 – line 28 and Page 10299 – line 16. Incubation time varies between 6 and 18h. Why was this not standardize? Could the author provide a rational for not doing so? Finally, and most importantly did the authors included incubation time as a covariate in the analysis (beyond calculating rates by h-1) to control for variation in resting/incubation time?

Incubation time varied because we only had two size respiration chambers 10 mL and 50 mL. The volume of these chambers could not be reduced below a certain point to allow for the manipulation of the chamber during the process of withdrawing water for analysis. With these limits on the chamber volume the only factor which could be controlled was the duration of the experiment. Since the metabolic rate varied between species and there was a range of individual organismal size there was initially some guess work which went into determining how long the respiration experiments needed to run in order for there to be a noticeable change in the oxygen level in the chamber. A sentence has been added to this effect:

"Respiration experiments were run for a period of time which allowed for there to be a noticeable change in oxygen saturation based on the individual size and metabolic rate of the various species."

Statistical analysis indicates that there is no effect of incubation time on the metabolic rate over a 6-18 hour period:

"The duration of the experiment (between 6-18 hours) did not affect the metabolic rate of pteropods (one-way ANCOVA: H. striata $F(1,37) = 0.03$ $p = 0.86$, C. virgula $F(1,9) = 0.17$, $p = 0.69$, C. pyramidata $F(1,15) = 1.21$, $p = 0.29$, C. longirostris

$F(1,32) = 1.05$, $p = 0.31$, D. quadridentata $F(1,15) = 2.69$ $p = 0.12$)."

Also I suggest strongly the authors do acknowledge (briefly) in the discussion the (potential) limitations of using short term exposures to low pH (6-18h) when inferring on chronic exposure to OA conditions. The authors do actually suggest that their responses documented in migratory thecosome pteropods to short term response to high CO2 might be a 'best case scenario' (when compared to future chronic exposures). However, it is important that the authors discuss the potential for all pteropods not to have reached a new stable status when metabolic responses were measured. The risk is that the authors are potentially reporting pteropods metabolic rates during 'overshooting'.

The authors have expanded their discussion of the differences between acute and chronic exposure to hypercapnia in the context of their experiments:

"The mechanisms of compensation for changes in acid-base imbalance in marine species involve an up-regulation of active ion-transportation, the production of bicarbonate and other buffers and changes in metabolic substrate use (Walsh and Milligan, 1989; Seibel and Walsh 2001; Portner et al., 2005). Full compensation for these changes often takes up to 48-72 h (Seibel and Walsh 2003). The response measured in our experiments, being after only 6-18 h of exposure, may not be one of a final stable steady state and cannot be interpreted as indicative of a response to chronic acidification, only to the type pteropods would experience during short migrations into regions of hypercapnia."

Page 10299 – line 22. The pH levels used (8.32 and 7.96) may not be representative of future OA scenarios, but given global change (included OA) is a regional event, and I do not know the characteristics of the carbonate system of the sea water from the study area it is difficult to say. However, the authors do mention in the Introduction and Discussion about pH < 7.6 and undersaturation with respect to aragonite. At the pH the authors worked there should not be undersaturation for aragonite (or calcite).

In turns, it is difficult to talk about OA despite the pH decrease is approximately 0.3 – given OA includes not only a reduction in pH but also in [CO32-]. No details on the carbonate system are reported here. In particular, it appears the authors carried out pH measurements but did not measure TA, DIC or pCO2. How did the authors verify that the CO2 concentration in the sea water was 380/400 and 1000ppm for their control and acidified treatments, respectively? Measuring pH is not sufficient, even if the authors used pre-mixed gasses. The work for this aspect does not seem to meet the required by current standards in OA literature. Most importantly, it is not possible to discuss the data not having an idea of what DIC and pCO2 are, and even more [CO32-] Ωara and Ωcalc are.

As was mentioned in Response to reviewers 1-3, the DIC and alkalinity of the system were not properly measured. Our estimates of the carbonate system are based on the known alkalinity of the region, and upon temperature, salinity and our pH measurements. Text has been added to both the methods and discussion which better elaborate on our estimates of the carbonate chemistry of the system:

"Profiles of pH in the ETP in 2008 were measured using the standard SOP for pH analysis with m-cresol purple (Byrne and Elliott, unpublished data). Carbonate chemistry of the region was estimated using WOCE alkalinity values (P-18 1994 and 2008), pH and CTD profiles of salinity and temperature using the CO2sys developed by Lewis and Wallace (1998). The system was run using the seawater pH scale, Dickson KHSO4, and constants from Dickson and Millero, 1987. WOCE alkalinity data from 200 m was relatively consistent at nearby latitudes between 1994 (2298 $\pm$ 9.2) and 2008 (2300.5 $\pm$ 4.5), suggesting that these values are reasonable estimates of OMZ alkalinity."

"Assuming an average salinity of 34.7, a temperature of 10° C, a depth of 200 m (CTD data) and incorporating the measured pH with the known alkalinity of the region, aragonite is undersaturated in the OMZ (CO2sys: seawater pH scale,

Dickson KHSO4, and constants from Dickson and Millero, 1987; ΩAr $=$ 0.65)."

Since there was no alkalinity taken from the experimental runs, it is impossible to estimate the carbonate chemistry of the experiments, however this method has been successfully used by the authors under conditions where DIC/TA were measured suggesting that bubbling achieves the desired CO2 concentration (Seibel et al. in press).

Page 10297 – line 6 and Page 10300 – line 24. Remove references Seibel et al. 2011 and Maas et al. 2011 altogether here and elsewhere, as one is submitted and the other one only in preparation. Alternatively provide more information and write 'Seibel/Maas et al. unpublished', until these ms are eventually accepted. As a review I cannot access this information at the moment.

Seibel et al. is now in press. Maas et al. is still in prep and has been removed from the manuscript.

Page 10303 – lines 4 to 8. I strongly suggest the authors include in this section (and make use of) relevant references on the metabolic responses of mollusks (e.g. Gutowska et al. 2008; Rosa and Seibel 2008; Comeau's work; Cumming et al. 2011; Melatunan et al. 2011).

The authors have expanded their discussion of what has been seen previously in the literature:

"Organismal response to acidified conditions has increasingly been shown to be highly species specific, with a great deal of variation within the mollusk group in particular. High CO2 decreases the metabolic rate in the mussel Mytilus galloprovincialis (Michaelidis et al., 2005), the snail Littorina littorea (Melatunan et al., 2011), the thecosome pteropod Limacina helicina antarctica (Seibel et al., in press) and the Humbolt squid Dosidicus gigas (Rosa and Seibel, 2008). Other research found an increase in metabolic rate of the pteropod Limacina helicina

(Comeau et al., 2009; 2010a) and in the bivalve Laternula elliptica (Cummings et al., 2011), whereas there was no change in the metabolic rate of the cuttlefish Sepia officianlis (Gutowska et al., 2008) and the mussel Mytilus edulis (Thomsen and Melzner, 2010). The cause of these variations in response have been theorized to be a result of differences in the natural levels of organismal CO2 production, respiratory pigment type, and iono-regulatory ability (Pörtner et al., 2005; Gutowska et al., 2008; Widdecomb and Spicer, 2008; Hendriks et al. 2010). The migratory behavior of pteropods in the ETP, which regularly exposes individuals to elevated CO2, may therefore predispose them to be resilient with respect to surface acidification through the use of the same physiological mechanisms by which these zooplankton cope with brief periods of hypercapnia."

The interpolation between experimental evidence and field data should be stronger and more analitycal where possible.

The authors have worked to attain a better synthesis of the experimental and field data through an expansion of the carbonate chemistry and discussions of the implications of the distribution and the results of the physiological experiments (see above).

DETAILED COMMENTS

Page 10297 – line 7. Please expand the literature support to other studies too.

Added the references Portner et al., 2005; Miles et al., 2007; Widdecombe and Spicer, 2008

Page 10300 - line 1. Please report the model of the probe and meter you used.

The model numbers have been added to the text:

"At the end of each respiration incubation (6 –18 hours), an aliquot of water was withdrawn from both the experimental and the blank chambers using a 500 μL airtight Hamilton syringe and injected past a Clarke-type O2 electrode (1302) and

meter (782) in a water-jacketed injection port (MC100, Strathkelvin Instruments, North Lanarkshire, United Kingdom; Marsh and Manahan, 1999)."

Page 10301 – line 4 and 10302 – line 10 (and elsewhere in the text). It appears that the authors use the terms 'depression' 'suppression' and 'reduction' interchangeably. If this is the case I suggest they standardize to one terminology, if not I warmly invite the authors in providing strong (even referenced) definitions for each term and use them rigorously.

Depression and suppression have been replaced with reduction throughout the text.

Figure 3 and 4 (and text). The international unit for 'hours' is 'h' and not 'hr'. Please change this.

The formatting has been changed to follow the international units.

Interactive comment on Biogeosciences Discuss., 8, 10295, 2011.