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Discussions

Interactive comment on "Physiological basis for high CO_2 tolerance in marine ectothermic animals: pre-adaptation through lifestyle and ontogeny?" *by* F. Melzner et al.

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Reply to reviewer 1

Reviewer 1 is essentially making one central statement, claiming that the novelty value of our manuscript is not very high. He / she argues that there have been several reviews in the recent past that proposed similar ideas. However, the reviewer does not mention or discuss the novel concepts that we present here. We strongly disagree with the reviewer's line of argumentation and will in detail point out (i) what novel concepts we developed for this review and (ii) why there is a sustained need for synthesis papers that reach out to the wider scientific community interested in ocean acidification research.

(i) Novel concepts

In order to predict the vulnerability of marine organisms to future ocean acidification, it is imperative to know what pCO2 values cells experience in today's ocean. Previous reviews have not considered this aspect. We specifically focus on extracellular pCO2 variations in different taxa and give the physiological background that makes this data accessible. We also present the idea that hypercapnia may be an integral part of the ontogeny of many marine metazoans. In our view, such an 'inventory' approach is absolutely essential for the generation of meaningful hypotheses for future studies.

1. Relative changes in extracellular pCO2 may define vulnerability to future acidification

The main novel concept that we present is best illustrated with Figure 3: The extracellular pCO2 of cells of marine organisms varies by an order of magnitude. While unicellular organisms are surrounded by an extracellular medium with a pCO2 of $\sim$400μatm (the ocean), metazoan cells are exposed to an extracellular fluid (blood, hemolymph, coelomic fluid) with much higher pCO2 values, typically between $\sim$1000-4000 μatm. This may render unicellular organisms more sensitive to changes in pCO2. Future changes in seawater pCO2 will result in less dramatic changes in extracellular pCO2 for metazoan cells (see Fig 3 and text for an extended discussion). The reasons for high extracellular pCO2 values in marine metazoans are related to diffusion processes, which we explain in detail in the text.

In order to convey this message, we went through the literature of the past 30 or so years and carefully reviewed the extracellular acid-base status of representative taxa, analyzing a large number of papers. We used the available information to calculate pCO2 under control and exercise conditions, and also compiled routine and active metabolic rates (Fig 2). A careful scan of the literature will reveal that such a (time-consuming, but rewarding) effort has previously not been undertaken. This analysis also demonstrates that certain taxa (more than others) have the capacity to actively modify their extracellular carbonate system speciation, a feature that is closely related to a high ion regulatory capacity.

2. Active metazoan cells experience high fluctuations in extracellular pCO2 during rest / exercise, this requires an efficient ion exchange apparatus, a feature that may be beneficial under acidified conditions

Reviewer 1 is correct in stating that the hypothesis of the ‘acidification tolerant, high metabolic physiotype’ has been brought up before, especially by the very good synthesis work of Seibel & Walsh (2001, 2003) in the context of deep vs. shallow water marine species’ sensitivity to elevated pCO2. We give credit to the important contributions of these authors on pages 4710 and 4716. However, the main objective of this review is to explore in more detail, what causal chain of physiological adaptations leads to such a more tolerant physiotype (‘pre-adaptive physiological traits’). We specifically hypothesize that the ion regulatory machinery necessary to balance the dramatic acid-base disturbances during exercise / recovery from exercise (see Fig 2) forms the basis for the efficient pH regulatory reaction observed in more tolerant taxa under acidified conditions. We give examples of net-proton excretion rates of various high-metabolic organisms during exercise / recovery from exercise and also explain, how gill ion transport processes are responsible for these (Fig 4). Finally, we also discuss recent studies that have looked into gill ion exchanger activities / gene expression patterns of metazoans subjected to hypercapnic conditions (Fig 5). Such a systematic analysis is necessary, and has not been undertaken to this degree in previous synthesis efforts.

3. Hypercapnia may be an integral component of the life cycle of many marine metazoan species

The recent discovery that the pCO2 in marine animal egg fluids can reach very high values (1000-4000 μatm, Gutowska & Melzner 2009, Fig 6) during embryonic development is important (see Fig 3, 6). Egg fluids of other marine animals are also likely to be characterized by very high pCO2 values (see text). Embryonic hypercapnia may thus be one important reason, why the molecular inventory to cope with acid-base disturbances is present in many species. These ideas are also novel and are important for the field. They can lead to systematic, hypothesis driven research on the sensitivity of lecitothrophic vs. oligotrophic embryos and larvae to high CO2 conditions.

In summary, we present several important new aspects & ideas in this review to shed more light on the underlying physiological traits leading to the (previously) mentioned tolerant high-power physiotypes. These concepts are important for future research efforts. We do not understand why reviewer 1 did not acknowledge or provide feedback on these ideas.

(ii) Why is there a need for yet another synthesis paper?

The audience for this paper is the ocean acidification community in general (biologists, chemists, physicists, geologists), not the physiological community. During several seminars in the recent past that one of us (Melzner) gave in front of mixed audiences, the need to present basic physiological concepts in an understandable fashion was perceived (it would, in fact, be interesting to receive feedback from the community on this forum). Thus, this paper is written in a way to explain basic aspects of acid-base physiology, buffering, ion transport and respiratory physiology (see Fig 1, 4) in order to (i) be able to develop a logical chain of argument that leads to the conclusion that high metabolic animals may be pre-adapted to future ocean acidification and (ii) that explains the significance of the novel concepts that have been outlined above. This has not been done in such a manner in previous review papers. In the course, we refer to a number of excellent review papers that will lead the reader into more detail on specific aspects of key physiological processes (e.g. Schipp 1979, Cameron 1986, Heisler 1987, Wheatly & Henry 1992, Tufts & Perry 1998, Evans et al. 2005, Perry & Gilmour 2006 and several others). We believe that this review is written in the spirit of the Monaco conference as it tries to form a bridge between different disciplines and provides an integrated framework for future research.

Minor comment:

Regarding the high sensitivity of squid proposed by Pörtner et al. (2004): The model calculations in Pörtner et al. (2004) are based on the assumption of a rapid change in pCO2 and extracellular pH following the non-bicarbonate buffering line. Recent research on the cephalopod Sepia officinalis (Gutowska et al. submitted to J Comp Phys B) indicates that this species can accumulate extracellular bicarbonate significantly above the non-bicarbonate buffer line, protecting pHe and blood oxygen transport. It is likely (but needs to be established) that squid species will also regulate pHe efficiently under similar conditions (e.g. Pörtner et al. 1991).

Interactive comment on Biogeosciences Discuss., 6, 4693, 2009.