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Interactive comment on “Physiological basis for high CO₂ tolerance in marine ectothermic animals: pre-adaptation through lifestyle and ontogeny?” by F. Melzner et al.

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Reply to reviewer 3, J.-C. Massabuau

Dear Jean-Charles,

thanks for the constructive and interesting review. We appreciate several of your very insightful comments and especially liked the comments on freshwater systems, which are very important. You are right in suggesting that it is a difficult task to balance this paper between not overly challenging the non-physiologist and sounding too trivial for the specialist. We kept the manuscript simple and stream-lined in order to convey some central messages that are not typically in the mind set of biologists / geochemists

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from other disciplines in the field (e.g. extracellular carbonate system speciation, the concept of the relative changes in the $p\text{CO}_2$ a cell encounters). Because of this we also believe that we should not incorporate too much additional information on specialized problems in respiratory physiology. We will discuss in detail some of the points raised in your review:

(R3 1) It is probably true that in the present ocean acidification context, possibly nobody stressed, by writing it, that extracellular CO_2 partial pressures are living with much higher CO_2 values than in the open ocean. But besides that, I am surprised by the absence of a statement recalling that in freshwaters, most partial pressures of CO_2 are significantly higher than in the present, and possibly the future, ocean. In freshwaters, the average excess is 8 times above air values (0.3 kPa, 3200 μatm , Rebsdorf et al. 1991), with a maximum well above 30 (12 000 μatm . Massabuau and Fritz, 1984). Yet everybody knows that numerous aquatic animals and aquatic plants are living there quite well. To discuss that point is evidently an open question. What is the difference between respiratory physiology in freshwater and seawater species if there is one? An interesting recent paper about the CO_2 range found in freshwaters, and the limiting putative role of CO_2 excess for aquatic plants, can be found in Demars and Trémolières (2009).

Reply: Freshwater systems are indeed less well buffered and display a higher variability in $p\text{CO}_2$. In terms of acid-base physiology, the crucial differences are the ion gradients that are orders of magnitude different between both habitats. As many acid-base regulatory processes in seawater are dependent on the utilization of gradients in $[\text{Na}^+]$ and $[\text{HCO}_3^-]$ (e.g. Perry & Gilmour, 2006), this feature clearly distinguishes both habitats. In addition, a greater sensitivity of marine habitats probably is tightly related to the fact, that calcification in many taxa is very dependent on the carbonate system speciation, which is strongly affected by elevated $p\text{CO}_2$ (e.g. Fabry et al. 2008). Still, it would definitely be nice to see a review that summarizes the potential effects of elevated atmospheric $p\text{CO}_2$ on freshwater habitats (especially when thinking

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about calcifying invertebrates, such as the bivalve Anodonta). However, this is clearly outside the expertise of the authors of this paper.

(R3 2) Another point is that blood, as well as intracellular, CO₂ partial pressure and pH are not fixed values. They are variable set points used by the cells to manipulate and regulate their metabolic needs at different rates (Busa and Nuccitelli, 1983; Malan, 1999). Aquatic animals are also known for their ability to adjust their blood pH at different set points before and after a meal (Legeay and Massabuau, 1999) as well as following a circadian rhythm (Sakakibara et al., 1987), dependently or independently of the water oxygenation status.

Reply: This is true, acid-base equilibria can be shifted; however, the major trends are taxon specific and thus we find them relatively constant within a certain range (e.g. see fig 2 in the ms). The classic examples of p_{Hi} as a regulator of metabolic state in Artemia or sea urchin sperm (Busa & Nuccitelli 1983, 1984, Johnson et al. 1983) certainly are extreme examples of p_{Hi} regulation. We thought that going into too much detail here would rather confuse than enlighten the reader, so we would like to point the attention to the excellent reviews of Guppy (1994), Guppy & Withers (1999), Hochachka and Lutz (2001) as well as Hochachka & Somero (2002) that discuss the regulatory role of p_{Hi} in much detail. As for ocean acidification, all studies so far could show that p_{Hi} was rapidly regulated in response to hypercapnia (e.g. Larsen et al. 1997, Michaelidis et al. 2005, 2006), thus we did not place a focus on p_{Hi} regulation in our paper.

(R3 3) Finally, the existence of ventilatory responses to CO₂ changes (hyperventilation in response to CO₂ induced acidosis) has been demonstrated in water breathing animals (Massabuau and Burtin, 1985) and it can be an efficient way to regulate blood pH (Burtin and Massabuau, 1988). It has often been a missed point in numerous previous reviews where the emphasis was on relatively large water CO₂ changes. Based on what is expected today, these ventilatory adjustments could be efficient. However, an increase in ventilatory activity should be associated with changes in internal O₂ partial pressures as most water breathers aim at maintaining their ventilatory activity at

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minimal values (Massabuau, 2001).

Reply: Typically, hyperventilation does not seem to be utilized by marine animals to a large degree in order to compensate extracellular pH. A CO₂/pH dependent ventilatory drive is present in some marine groups (e.g. crustacea: Massabuau & Burtin 1985, fish: Gilmour 2001). However, the principle mechanism of pH compensation is via the accumulation of bicarbonate / extrusion of protons (e.g. fish: Larsen et al. 1997, crustacean: Spicer et al. 2007, Pane & Barry 2007, cephalopoda: Gutowska et al. 2009 J Comp Phys B in press). In the cephalopod study (Gutowska et al. 2009 in press, please feel free to contact us for a copy) we found a minor increase in ventilation rate in response to 0.6 kPa of hypercapnia (increase in ca. 10% in ventilation rate). However, the partial pHe compensation was achieved by means of net bicarbonate accumulation. Even in the crayfish study mentioned (Burtin & Massabuau 1988) it seems that ventilatory control of pHe only occurs in the virtual absence of Na⁺ in the experimental water and not under control conditions. This very nice study rather could point at the necessity for high water Na⁺ during hypercapnia for efficient proton extrusion via sodium coupled transporters in the gill epithelia in this species.

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