

Interactive comment on “Kinetic bottlenecks to chemical exchange rates for deep-sea animals – Part 1: Oxygen” by A. F. Hofmann et al.

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The paper by Hofmann et al is an attempt to combine physical characteristics of seawater into mechanistic equations to “better visualize, map, comprehend and predict the impact of ocean deoxygenation on aerobic life”. While I applaud the attempt, and its probably worth pointing out that temperature and pressure play a role in oxygen supply, I just don’t see that this paper was successful in the stated goal of providing information on aerobic limits to marine life.

Moreover, while the information provided may be new to oceanographers, its not new in general. The role of temperature and pressure on oxygen supply was recently reported (Verberk et al., 2011). The oxygen supply to marine eggs has been reviewed many times (Strathmann, R. R. and colleagues; Melzner et al., 2011). The role of oxygen

C4870

gradients for animals without known circulatory systems has also been considered extensively (e.g. Thuesen, E. V. and colleagues). The kinetic mechanisms controlling oxygen demand of crustaceans, cephalopods and fishes have been studied extensively for over a century. August Krogh discussed the kinetics of oxygen provision to animal tissues nearly a century ago. From the last century of work, including several decades of work on oxygen minimum zone animals (Childress and colleagues), it has become apparent that oxygen demand is not limited by existing environmental oxygen down to a critically low level (~0.5 kPa) because animals are adapted to the oxygen levels in which they live.

This literature is not considered in this manuscript.

Hofmann et al state that “The problem of setting limits for aerobic respiration has been traditionally defined as a series of simple oxygen concentration limits” (Page 13819: Line 16) and that such an approach is insufficient because it does not include essential temperature, pressure, diffusivity and related factors. I agree that oxygen concentration is an insufficient parameter. However, the use of oxygen as an index of marine aerobic performance cannot be improved by inclusion of additional physical parameters. In fact, I disagree that limits for aerobic respiration are traditionally defined by oxygen concentration. ...it has only been defined this way by oceanographers.

The problem of setting limits is typically approached by measuring critical oxygen partial pressures on live animals, a measure that integrates gas diffusion across gills/lungs, blood oxygen binding and mitochondrial oxygen uptake. I think one problem is that Hofmann et al view the issue as “the ocean’s capacity to supply oxygen to organisms”. Physiologists view the problem as the animal’s ability to extract oxygen from the ocean. The latter view accurately reflects the evolution of mechanisms that substantially alter flow rates and oxygen gradients such that the environmental oxygen levels are, to a point, irrelevant. At the same time, existing oxygen levels are everything. Below about 5 kPa, organisms are adapted to the lowest oxygen level they experience.

C4871

So it doesn't matter what the current oxygen level is, any departure from it requires further evolutionary enhancement of oxygen extraction ability. Short-term acclimation is largely unknown. There is a lower limit beyond which further enhancement is apparently not possible (~0.5 kPa). If oxygen drops below that value, organisms must migrate or die. So a particular C_f value is no more informative than a concentration limit.

Line 27: "simple concentrations have served us well in a steady state ocean"

I disagree. Specific values, whether presented as concentration or partial pressure, have always been useless as a metric for aerobic organismal limits because oxygen tolerances are species specific. Again, the physiologists have known this and don't typically use concentration, or partial pressure, to propose limits to life generally. There has been an important communication gap between physiologists and oceanographers that is exacerbated in this manuscript.

Page 13820 Line 4: "This concept of kinetic limitation is not new to marine biologists" It is also not new to the problem of oxygen minimum zones (Childress and Seibel, 1998). The point of decades of research on animal physiology in oxygen minimum zones has been that oxygen gradients must be maintained for diffusion via changes in oxygen affinity of blood proteins, flow rate (ventilation), barrier thickness (gill membranes) and oxygen demand. This literature is completely ignored in this paper. The authors state that they are only interested in what the ocean can supply to organisms, but that, to an extent, doesn't matter. The only thing that matters is whether organisms can extract sufficient oxygen from the environment. The amount of oxygen is not limiting, only its availability to organisms not appropriately adapted. It doesn't matter what the maximum supportable oxygen flux is (E_{max}). What matters is whether the required oxygen flux can be extracted from the environment. The latter question can only be answered by measuring the critical oxygen partial pressure. There is, at best, a weak relationship between the evolved oxygen demand and the critical oxygen level.

C4872

Line 11: "We include only the organism-independent physical properties" Then this paper is, again, no more useful than the simple oxygen concentration limits that it criticizes. The limits on organisms are set by evolved physiological properties. If you don't include those, then you've not identified a limit at all.

For example, line 16, the venous blood PO_2 may influence the rate at which oxygen can diffusive across gills, but blood oxygen binding affinity sets the limit on how low venous PO_2 can be while still carrying sufficient oxygen.

This paper merely points out that oxygen minimum zones have the least oxygen availability. Not a big surprise or a big improvement over previous concentration profiles.

In reviewing this paper, I attempted to identify specific uses for the analysis or original predictions that the paper makes that might push the field forward. Unfortunately, I can't imagine how this paper would be used beneficially by oceanographers. As already pointed out, oceanographers rely on oxygen concentrations even though PO_2 is better... a thoroughly reported fact. So why would they switch to using an even more complicated metric that won't get them any closer to a real physiological limit. More importantly, I could imagine a few predictions that this paper makes that could mislead researchers and policy makers.

For example, the suggestion that, when taking temperature and diffusivity into account, some regions appear to gain a net benefit from warming that over-compensates for oxygen loss, can be very misleading. When taking into account increased metabolism due to increased temperature, there will still be a net loss to the organism. More importantly however, in most regions where this dichotomy becomes an issue (e.g. Med Sea), oxygen is nowhere near a limiting value and most organisms will not suffer from small changes in oxygen or temperature-mediated oxygen delivery.

Hofmann et al state that the effect of temperature on metabolic demand is "very organism specific and beyond the scope of this paper" (page 13829, line 15). However, unlike adaptations for oxygen uptake (gill surface areas, blood O_2 binding etc), the

C4873

effect of temperature on metabolic rate is fairly consistent across species (Q10 ~2-3). Some even consider the effect of temperature on metabolism to be universal (see Clarke, A. for discussion of universal temperature dependence models). So the effect of temperature could actually be easily modeled with reasonable accuracy in this paper. However, given the species-specific nature of oxygen uptake parameters and of metabolic rate itself, the resulting metric will still not provide insight into critical oxygen levels for marine species.

Specific Comments:

I'm confused about the use of the term "L". In section 3.1 it is stated that respiratory exchange can be treated as a two-step process. The first step is oxygen transfer across a boundary layer. The second step is transfer across animal exchange tissues. L in the first step is the thickness of the boundary layer. . .the boundary layer being just stagnant water? In the second step, L refers to gill SA and thickness. They go on to say that the first step is rate limiting and that total oxygen flux, E, approaches E of the boundary layer step. But then on page 13825 (line 6) they state that the DBL thickness L is an organism-specific quantity depending on gill SA and thickness. This must be clarified.

It seems to me that the assumption that the boundary layer step is the limiting step is fundamental to the entire argument. But they provide no evidence that that is generally true. If its not the limiting step, then the conclusion is that environmental oxygen is not limiting metabolism. I don't know why it has to be viewed as a two-step process. Water diffuses from seawater, across the gill (membrane), into the blood (cytoplasm). Ventilation and circulation maintain the gradient required. The oxygen gradient from water to blood required to support a particular oxygen demand can be calculated = oxygen demand/ diffusion capacity. A higher affinity respiratory protein ensures high blood oxygen content with a low venous PO₂ (thus a high gradient to maintain diffusion). Thin gill membranes and high gill surface area ensure high diffusion capacity and seawater PO₂, if adequately ventilated, maintains the high gradient relative to the blood (Krogh, 1941). Without knowing the physiological properties of the animals (or

C4874

Pcrit as a measure that integrates these properties), the seawater oxygen tells you nothing.

If I've done the math right, an animal with a gill surface area of 10 cm²/gram (typical of a high-performance animal), at $80 \times 10^{-7} \mu\text{mol/s} \cdot \text{cm}^2$ (red line, right side of Fig. 5), would have a metabolic rate of $\sim 0.3 \mu\text{mol/g}\cdot\text{h}$. Figure 5 suggests that that animal would require at least 60-120 $\mu\text{mol/kg}$ to support that rate. 0.3 is a very low rate for an animal, typical of low rate deep-sea shrimps and fishes and jellies. In fact, the example metabolic rate chosen for animals in this paper is a vampire squid which has a very low rate. This species requires far less oxygen than most (critical oxygen levels near 10 $\mu\text{mol/kg}$ because it is adapted to the OMZ in the California Current). Even some high performance, high rate animals require only $\sim 20 \mu\text{mol/kg}$. Jellyfish with similar rates do not require specific oxygen uptake mechanisms and have low critical oxygen levels as well. All of this suggests that the diffusive boundary layer is not limiting aerobic performance down to a very low oxygen level. In fact, above a PO₂ of about 5 kPa ($\sim 60 \mu\text{mol/kg}$ at 10°C), no specific adaptations are required to meet routine oxygen demand. Most animals in the ocean can regulate their routine metabolic rate to this level regardless of the oxygen content surrounding them.

Moreover Figure 5 suggests that as you go deeper, because of the dependence of diffusivity on temperature, that more oxygen is required to meet demand. In fact, because of the temperature dependence of metabolic rate, going deeper usually requires far less oxygen.

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C4875