

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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Response to comment by B. Seibel

General reply

We thank the reviewer for his comments, but we wish to point out that there are several misunderstandings here. The goal of the paper is not (review comment, paragraph 1) that of “providing information on aerobic limits to marine life”, but to find better ways to link the changing physical properties of the ocean under climate change (temperature, and declining O₂), to the boundary layer environment experienced by marine animals. And to do so in a way that permits the use of physico-chemical units that can be

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quantified and the properties mapped. The basis for the work, use of well known boundary layer theory and experiment, has been successfully applied to the problem of air-sea gas exchange, mineral dissolution, and phytoplankton gas and nutrient uptake. The calculation of the animal boundary layer fluxes is essentially no different and is equally powerful in quantifying the processes at work. That is our goal.

We have already noted that there is a legacy here of physiological work that extends over many decades. But we must also note that this has been applied quite unevenly, and most often in a manner that describes only a species of animal and not the properties of the ocean. Where descriptions of the ocean are given this legacy of work is unfortunately often ignored and the result is confusion.

Thus the concept of hypoxia (see Hofmann et al., 2011) has been applied in widely varying form, and almost always as a temperature, or species, independent term, thereby frustrating any formal climate connection. For example widely cited papers in major journals such as that by Diaz and Rosenberg (2008) states that “As DO declines to <0.7 ml of O₂/liter and extends through time mass mortality . . . occurs.” Unfortunately no temperature dependent terms are present, and as pointed out by Seibel there are vast areas of the ocean that contain marine life adapted to such low levels and there “mass mortality” is not found; the regional, or depth etc distinctions are not made. This concept of a single temperature independent concentration was also used by Vaquer-Sunyer and Duarte (2008) who found “the conventional definition of 2 mg O₂/liter to designate waters as hypoxic” to be too high “to conserve fisheries resources.” And when physical models of the ocean are developed and the implications for hypoxia are explored (Shaffer et al., 2009) it is concluded that for 3 °C warming “up to 61% of the total ocean volume is hypoxic ($\leq 80 \mu\text{mol kg}^{-1}$), suboxic, or anoxic, compared with 9.1% for the present ocean.” The comment by Seibel does not address this literature.

Where physiological processes are described they support the arguments given here linking supply of O₂ and temperature as critical, but most often in conceptual and non-numeric form making progress in describing future ocean conditions and impacts difficult. For example Pörtner (2010) describes “oxygen supply to tissues and the resulting aerobic performance characters thus form a primary link between organismal fitness and its role and functioning at the ecosystem level”, but only as a “conceptual analysis” with no physical units. It is this very “oxygen supply to tissues” that is described here in terms familiar to all ocean chemists.

Specific replies

“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.”

Exactly right. And the “barrier” that the diffusive boundary layer **around** an organism constitutes, exactly influences this “availability”. Not only the amount (i.e concentration) matters from the oceanic “supply side” – therefore we define our quantities.

“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.”

We describe the limits imposed by the oceanic environment. Whether those will be the actual limits for a given organism, is of course depending on the limitations of the organism – only if the organism would be “capable of more”, then the limits imposed

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by the oceanic environment would be the actual hard limits. However, that is not the point here. Here we just want to investigate what **potential** (or “ultimate” if you will) limitation the oceanic environment imposes.

“The limits on organisms are set by evolved physiological properties.”

Still, organisms live in a physico-chemical environment. This environment always interacts with the organism and can under given circumstances pose limitations on it. This is just common sense. All we do here is trying to describe and quantify this potential limitation of the physico-chemical environment.

“So why would they switch to using an even more complicated metric that won’t get them any closer to a real physiological limit.”

We are *not* after a “physiological limit”. We are after the contribution of the oceanic environment to the total limitations imposed on organisms. This “environmental” part of the limitations might be dominant, or the “physiological properties” might be dominant in determining the total limitation. We are not discussing this here, we just want to describe the “environmental” part. We do this to gain more understanding by quantifying contributions of different origin, but mainly to be able to compare and describe changes in the oceanic environment.

“The effect of temperature on metabolic rate is fairly consistent across species ... So the effect of temperature could actually be easily modeled with reasonable accuracy in this paper.”

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We are **not** looking at the effect of temperature on the metabolic rate E in our treatment here — since we want to investigate the role of the **oceanic environment**. We separate two facets of the problem here, and we explicitly want to show the different contributions to oxygen limitation. More specifically, we show the role and contribution of the oceanic environment. Of course the organismic side is variable, too, however, by keeping it constant, we can isolate and visualize the oceanic contribution, which fosters understanding, allows for comparison and is the whole point here. However, our quantities **can** be used with variable and organism specific parameters (e.g. E , L etc.) as well.

“...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?”

L refers to the thickness of the diffusive-boundary layer (DBL) in the medium **around** any gas exchange surface. The DBL is the layer across which transport of chemical species can be described solely by diffusion.

“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.”

No we don't. We say that, for our deliberation and purposes (to find metrics to describe the medium **around** organisms, i.e. the ocean), we **assume** the first step to be rate limiting — since this is the step we want to describe and investigate. This is the only case we are looking at. We assume the organism itself to operate “with

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maximal efficiency” — so much that the tissue transfer step is not rate limiting. Under those **assumptions** the total flux approaches the flux of the boundary layer step. We explicitly want the quantities we define to be properties of the surrounding medium. That is the reason why we make this assumption. This is common scientific (and especially mathematical!) practice — no mystery there.

“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.”

L_{tissue} we define in Eq. 3 is indeed the thickness of the gas exchange tissue. However, as mentioned above, we do not take the step of transport of chemical species across the tissue itself into account — since we want to explicitly limit ourselves to processes **outside** the organism. That is why we consider (i.e. **assume** the respective case) the DBL transfer step to be rate limiting and only look at L in the remainder of the paper. L is defined in Eq. 5 as the thickness of the DBL in the medium **around** gas exchange tissues and is always used that way. However, also L is an organism specific quantity, as it is depending on the gas exchange tissue shape, pumping rate of the organism and so on. Here, again for our purposes of describing the ocean in a not organism-specific way, we consider a generic description of L . That we mention explicitly that the DBL thickness L is also an organism-specific quantity, is a concession we make to physiologists, as physiologists have stressed this fact when confronted with our work many many times.

In a nutshell: L is the thickness of the DBL in the medium **around** an organism. We assume a generic description of L to compare various oceanic regions in a non-species specific way. Nevertheless, the real value of L is also a species specific quantity. Respective values or even model descriptions can be used. No confusion there.

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"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."

It seems here, that there is a fundamental misunderstanding of what we are doing. What we are doing is general mathematical practice and can be readily applied to ocean chemistry. Again, since we want to describe the oceanic environment and the fundamental barrier it provides for oceanic gas exchange, we **assume** the boundary layer step to be limiting. We are not claiming that this is always the case in reality – we assume it, such that we can devise properties that can describe the oceanic environment only – in a not-species specific way. We actually assume the organism to be maximally efficient, such that we can look at possible limitations the oceanic environment **might** pose, **if**, in fact the boundary layer step **might** be the limiting step in a specific case.

"If its not the limiting step, then the conclusion is that environmental oxygen is not limiting metabolism."

Yes of course. Again, we are **not** claiming the boundary step **is** always the limiting step. We just want to describe what limitations it would yield if it **was** the limiting step. Or better, to describe the **contribution** of the oceanic environment to the total limitation of the organism. Whether this contribution is the dominant contribution is not discussed here.

"I don't know why it has to be viewed as a two-step process."

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See also the final remark below. We look at gas exchange as a two step process, since we want to isolate (as best as possible) influences of the oceanic environment and organism specific influences. This is just common scientific practice: divide the problem into sub-problems. Our division here is very intuitive, as there is in fact first a transition across the DBL around an organism and then the transition through tissue etc. into an organism.

"Water diffuses from seawater, across the gill (membrane), into the blood (cytoplasm). Ventilation and circulation maintain the gradient required. . . . Without knowing the physiological properties of the animals (or Pcrit as a measure that integrates these properties), the seawater oxygen tells you nothing."

That an organism lives in a physico-chemical environment is a fact. That fundamental laws of physics apply is a fact. Furthermore, that oceanic properties need to be described and mapped in a non-species specific way, not only for management purposes, but also to describe changes to the oceanic environment (in which in turn, also changed organisms live), is common sense. So, again, here we assume the processes **inside** the organism as well as the properties **of** the organism (e.g. gill tissue thickness etc.) to be as **optimal as possible**, to look at the contribution or the **potential for** limitation that the oceanic environment provides. This **potential** oceanic limitation might be in fact the **real effective** limit, **if** in fact, all organismic properties are **as optimal as possible**. In reality, this will often not be the case – but this is not the point here. Here we want to look at the **potential** limitation of the oceanic environment only.

"If I've done the math right, . . . of the oxygen content surrounding them."

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The right panel of Figure 5 shows the dependency of Cf on E, but with constant u100 of 2 cm-s (which is not yet explicitly stated in the caption – this will be added in a revised version) — so if one looks at the **left** panel as well and takes into account that the animal may pump at let's say 8 cm/s, then the whole "calculation" given in the above remark is off. In fact, varying the flow across gas exchange tissues is a mechanism with which an animal can regulate gas exchange. Species-specific values can be included here by using different flow values for the calculation of Cf. Again, Figure 5 is an example of visualizing the influences of specific variables to one of our quantities (Cf here), by showing its variation with some variables being varied, while others are held constant.

"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."

We are **not** looking at a changed metabolic rate E – we **assume** constant E in Figure 5. The purpose of Cf is to investigate the potential of the oceanic environment to support a given E. Figure 5 shows Cf as a function of the oceanic environment, i.e. of variables **other** than E. Again, this approach separates a combined problem into two separate problems: the change of the potential of an oceanic environment to supply oxygen (Cf), and the (change in) oxygen demand (E). So – E might (or will) change as well, one can then consider e.g. a profile of variable E values as well, even for the calculation of Cf profiles. However, holding E constant, separates out the contributions of the oceanic environment. This is our point here and is very valuable and common scientific practice.

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Final remark

There is a physico-chemical environment around every organism. There is interaction between this physico-chemical environment and every organism. Both the organism **and** the physico-chemical environments change due to global change. Eventually, changes of both and changes of the interactions between both need to be understood. On this road, a separate treatment between both (albeit an "artificial" separation since in reality it all occurs simultaneously), constitutes a very beneficial "divide and conquer" approach to understanding the whole thing. This is how understanding is generated. Both physiologists and chemical oceanographers (and thus the whole field of ocean sciences) benefit more from communicating, trying to at least partially understand processes in each others domain, and working together to finally obtain knowledge of the whole system, than from arguing about importance of fields and trying to block each other's ideas and findings to enter the open scientific discourse.

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