The fundamental niche of blood-oxygen binding in the pelagic ocean

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Abstract

Marine species ranging in size from microscopic zooplankton to large predatory fish move vertically in the ocean water column to forage for food and avoid predators. Oxygen and temperature decrease, often rapidly, from shallow to deeper depths, restricting the ability of species to use the vertical habitat. One physiological trait that determines the tolerance of organisms to low oxygen is the oxygen affinity of oxygen carrier proteins, hemoglobin and hemocyanin, in the blood. To quantify the range of oxygen affinities for marine organisms, we surveyed the literature for measurements of oxygen binding to blood at multiple temperatures to account for its temperature sensitivity. Oxygen affinity is mapped within the ocean environment using the depth at which oxygen pressure decreases to the point at which the blood is 50% oxygenated (P_{50} depth) as organisms move from the surface to depth in the ocean water column. We find that vertical gradients in both temperature and oxygen impact the vertical position and areal extent of P_{50} depths. Shifts in P_{50} due to temperature cause physiological types with the same P_{50} in the surface ocean to have different P_{50} depths and physiological types with different P_{50}'s in the surface ocean to have the same P_{50} depth. The vertical distances between P_{50} depths are spatially variable, which may determine the frequency of ecological interactions, such as competition and predation. In summary, P_{50} depth, which represents a key physiological transition point between dexoxygenated and oxygenated blood, provides mechanistic insight into organism function within the water column of the global ocean.

Introduction

Physiological functions adjust as organisms move within complex environments, and mechanisms underlying habitat utilization by species are tied to physiological tolerance (Andrewartha and Birch, 1954). Therefore, the geographies of physiological functions provide insights for understanding the patterns of habitat utilization and species interactions in complex environments. The pelagic ocean is an ideal system for analyzing physiological function and tolerance in the environment because oceanographic conditions create steep vertical gradients in oxygen and temperature, and many species move vertically from shallower to deeper depths on daily and sub-daily time scales.

Hypoxia, defined as oxygen concentrations below 60 μmol kg^{-1} (Rabalais et al., 2001), occurs in large regions of the coastal and open ocean (e.g. Keeling et al., 2010). Oxygen is supplied to the ocean by air-sea exchange at the surface and as a byproduct of photosynthesis by marine microbes. Ocean circulation transports oxygenated water from the surface to deeper depths. Hypoxia develops at depths where supply of oxygenated waters is slow and oxygen is extensively utilized in-situ by heterotrophic organisms consuming dissolved and sinking organic matter. Regions of the ocean where hypoxia is a permanent feature are called Oxygen Minimum Zones and include the Equatorial Pacific and the Arabian Sea. Observations indicate that hypoxic regions are expanding and shoaling in the global ocean (e.g. Stramma et al., 2008; Diaz and Rosenberg, 2008; Gilly et al., 2013). Climate warming is projected to decrease the supply of oxygen to deeper waters in some regions though models disagree considerably on the impact this will have in the tropics, particularly with respect to the size of Oxygen Minimum Zones (Bopp et al., 2013). Expansion of Oxygen Minimum Zones has been hypothesized to alter marine ecosystems by compressing overlying habitats (e.g. Stramma et al., 2010; Koslow et al., 2011; Gilly et al., 2013).

Characterization of hypoxia with a single oxygen concentration, however, is fraught with complications. Pelagic marine species swim daily between shallower and deeper depths in the ocean (e.g. Vinogradov, 1970; Block et al., 2001). Around Oxygen Minimum Zones, the vertical movements of some species are restricted while other species are able to utilize the entire water column (e.g. Childress and Seibel, 1998; Stramma et al., 2011; Wishner et al., 2013). Organisms are able to detect and avoid hypoxia while swimming and even make decisions on whether to enter hypoxic zones based on the availability of an adjacent refuge with higher oxygen levels (Herbert et al., 2011). Once in hypoxic zones, thresholds for survival vary greatly because marine species have a large range of hypoxia tolerances (e.g. Vaquer-Sunyer and Duarte, 2008; Ekau et al., 2010). Temperature also needs to be considered because higher temperatures lower hypoxia tolerance for most, but not all, species (Vaquer-Sunyer and Duarte, 2011; Deutsch et al. 2015). Temperature differences between the surface and deep ocean vary more than 10°C in tropical Oxygen Minimum Zones, exposing vertical swimmers to a large range of temperatures and oxygen levels. The surface to deep gradients in oxygen and temperature counterbalance each other such that the hypoxia tolerance of organisms in warmer well-oxygenated surface waters is lower, and the hypoxia tolerance of organisms in colder less-oxygenated deep waters is higher. Temperature is known to influence behavioral responses to hypoxia - organisms increase hypoxia tolerance by actively selecting lower temperatures during hypoxia (Schurmann et al., 1991). As climate change is warming the ocean surface, temperature differences between the surface and deep ocean are increasing (e.g. Rhein et al., 2013). Therefore, the effect of temperature on hypoxia tolerance and behavioral responses to hypoxia are important factors to consider for organisms moving vertically in the ocean.

Hypoxia tolerance is quantified using critical oxygen pressure, P_{crit}, which is the oxygen pressure in the environment below which oxygen uptake can no longer be regulated (e.g. Farrell and Richards, 2009). To measure P_{crit}, individual organisms are placed in vessels and oxygen consumption is recorded across a range of oxygen concentrations (e.g. Speers-Roesch et al., 2012). This method works well for small, sedentary organisms but is more difficult to use for large, active organisms. Mandic et al. (2009) measured P_{crit} as well as a suite of potential underlying adaptations for hypoxia tolerance for twelve closely-related species of sculpins, and found a strong statistical relationship between P_{crit} and the oxygen pressure in the blood at which whole blood is 50% oxygenated, hereafter called P_{50}. The percent oxygenation of whole blood changes as blood cells pass through respiratory surfaces where oxygen diffuses from the environment into the organism. Oxygen binds to proteins, referred to as respiratory pigments, in a reversible reaction which equilibrates relative to oxygen pressure inside blood cells (Hochachka and Somero, 2002). A low P_{50} means that respiratory pigments in the blood of an organism equilibrate to 100% oxygenation at lower oxygen pressures, and the organism is more hypoxia tolerant.

The temperature of blood at respiratory surfaces of water-breathing marine species is the same temperature as the local environment. Blood-oxygen binding is sensitive to temperature because the binding reaction absorbs energy or releases energy, called the heat of oxygenation (Hochachka and Somero, 2002). If energy is released during blood-oxygen binding, lower temperatures decrease P_{50}, and, if energy is absorbed during blood-oxygen binding, lower temperatures increase P_{50}. For most species, the reaction between oxygen and blood releases energy but notable exceptions are pelagic species, including the tuna *Thunnus maccoyii* and the northern krill *Meganyctiphanes norvegica* (Power et al., 1979; Brix et al., 1989; Clark et al., 2008). Oceanographic conditions are typically colder with depth such that P_{50} either increases or decreases with increasing depth depending, respectively, on whether energy is absorbed or released during blood-oxygen binding.

While the hypoxia tolerance of a marine organism is determined by multiple parameters, including respiratory surface area and metabolic requirements, blood-oxygen binding is the first step that needs to occur for oxygen to be transported within an organism and is likely a key underlying mechanism for acute responses to hypoxia. The temperature sensitivity of the reaction adds additional complexity to predicting the percent oxygenation of respiratory pigments and understanding how blood-oxygen binding affects hypoxia tolerance, metabolism, and behavioral responses to hypoxia in the environment. In this study, our goal is to assess how vertical gradients in oxygen and temperature affect the rates of blood-oxygen binding across pelagic ocean habitats.

Methods

Meta-analysis of blood-oxygen binding traits

We conducted a literature search for whole blood measurements of P_{50}, the oxygen pressure when blood is 50% oxygenated, for at least two temperatures. We then used the van't Hoff integration to calculate the heat of oxygenation (ΔH), which is the energy released or absorbed when oxygen binds with an oxygen carrier protein, either hemoglobin or hemocyanin depending on the species (e.g. Clark et al., 2008).

$$\Delta \mathrm{H} = 2.303\mathrm{R}\frac{\log(\mathrm{P}_{50})_1 - \log(\mathrm{P}_{50})_2}{1/\mathrm{T}_1 - 1/\mathrm{T}_2} \tag{1}$$

R is the universal gas constant, 0.008314 kJ K^{-1} mol^{-1}. P_{50} measurements at two temperatures, T_1 and T_2 in K are also needed as input for Equation 1. For our analysis, we converted the units for P_{50} to kPa. A negative (positive) ΔH indicates that energy is released (absorbed) when oxygen binds with hemoglobin or hemocyanin. For negative ΔH, oxygen binding to hemoglobin is more favorable at low temperatures and less favorable at high temperatures. For positive ΔH, the effect of temperature is reversed.

The meta-analysis to determine the range of oxygen-binding traits in the marine environment included both benthic and pelagic marine organisms. ΔH changes over large temperature ranges. If the study included measurements of P_{50} at more than two temperatures, we selected measurements that included the acclimation temperature, which is the environmental temperature experienced by the organism in the laboratory or field prior to sampling.

Ocean data

We used oxygen, temperature, and salinity data from World Ocean Atlas 2009 (WOA 2009) (García et al., 2010; Locarnini et al., 2010; Antonov et al., 2010) with a bias-correction for the lowest oxygen concentrations (Bianchi et al., 2012). We report oxygen concentration in μmol kg^{-1} as a geochemical metric of hypoxia, and oxygen pressure in kPa as a more biologically relevant metric for organism function (Seibel, 2011). To calculate oxygen pressure, oxygen concentration from the World Ocean Atlas 2009 data was converted to oxygen saturation using the equations from García and Gordon (1992) and divided by 0.21, which is the atmospheric composition of oxygen, to get oxygen pressure, pO_2, in atm units. The units for pO_2 were then converted from atm to kPa. Temperature and salinity are required for the conversion from oxygen concentration to oxygen saturation (García and Gordon, 1992).

P_{50} depth calculation

We developed a metric called the P_{50} depth to map blood-oxygen binding thresholds in the pelagic ocean. The P_{50} depth is defined as the shallowest depth in the ocean where $pO_2 = P_{50}$. For $\Delta H \neq 0$, P_{50} is altered by shifts in temperature, so the effect of temperature was also included in the analysis. We made the assumption that organisms are acclimated to temperature at 10 m depth, $T_{(x,y,10)}$, and dive or migrate to deeper depths for shorter intervals. We assumed that the oxygen carrier proteins of animals do not re-acclimate to hypoxia or temperatures at deeper depths during foraging because the process of acclimation for oxygen carrier proteins requires several days (Johansen and Weber, 1976; Weber and Lykkeboe, 1978). The $P_{50(x,y,z)}$ in the water column was thus determined by rearranging Equation 1.

$$P_{50(x,y,z)} = 10^{\left(\log P_{50(x,y,10)} - \frac{\Delta H(1/T_{(x,y,10)} - 1/T_{(x,y,z)})}{2.303R} \right)} \tag{2}$$

where $P_{50(x,y,10)}$ is the P_{50} at 10 m, $T_{(x,y,z)}$ are temperatures at depth intervals below 10 m in the water column, ΔH is the heat of oxygenation, and R is the universal gas constant.

Results

Meta-analysis of blood-oxygen binding traits

Marine organisms have many combinations of P_{50} and ΔH (Figure 1, Table 1, Table 2). P_{50} ranges from 0.26 to 9.5 kPa, and ΔH ranges from -109 to 132 kJ mol^{-1}. In order to explore geographic patterns of blood-oxygen binding in the ocean environment, three different combinations of low versus high P_{50} and negative versus positive ΔH characteristics were selected. A physiological type with high P_{50} and positive ΔH was not included in the geographic analysis because there are no species in the meta-analysis with a high P_{50} and positive ΔH (Figure 1). The low P_{50} and negative ΔH type (A in Figure 1) is the average of the values within the $P_{50} < 5$ and $\Delta H < 0$ quadrant in Figure 1, which includes 71% of species in the meta-analysis (Table 3). The low P_{50} and positive ΔH type (B in Figure 1) **has the same P_{50}** as the low P_{50} and negative ΔH type (A in Figure 1). The high P_{50} and negative ΔH type (C in Figure 1) **has the same ΔH** as the low P_{50} and negative ΔH type (A in Figure 1). The ΔH and P_{50} values of the different physiological types were selected to contrast with each other but still be representative of multiple species. The low P_{50} and negative ΔH type has a P_{50} of 2 kPa and a negative ΔH of -40 kJ mol^{-1}. Many pelagic organisms have blood-oxygen binding characteristics with low P_{50} and negative ΔH including longfin inshore squid (*Doryteuthis pealeii*), nautilus (*Nautilus pompilius*), Atlantic herring (*Clupea harengus*), and migrating shrimp (*Systellaspis debilis*). The low P_{50} and positive ΔH type has a P_{50} of 2 kPa and a positive ΔH of 20 kJ mol^{-1}. Chub mackerel (*Scomber japonicus*), southern bluefin tuna (*Thunnus maccoyii*), and Atlantic bluefin tuna (*Thunnus thynnus*) have similar blood-oxygen binding characteristics to the low P_{50} and positive ΔH type. The high P_{50} and negative ΔH type has a P_{50} of 8 kPa and a negative ΔH of -40 kJ mol^{-1}. European flying squid (*Todarodes sagittatus*) and giant squid (*Architeuthis dux*) have blood-oxygen binding characteristics similar to the high P_{50} and negative ΔH type. There are no species with $P_{50} > 4$ and $\Delta H > 0$ (Figure 1). To highlight the differences among the traits in the ocean, we compare P_{50} depths for physiological types in Figures 2, 3, 4, and 5. Additional comparisons are made with the oxygen concentration of 60 μmol kg^{-1}, which is used as a threshold to indicate hypoxia (Rabalais et al., 2001; Keeling et al., 2010) (Figures 2 and 3).

Distribution of P_{50} depths in the ocean

P_{50} depths primarily occur in the North Pacific, Equatorial Pacific, Arabian Sea, and Bay of Bengal for all the physiological types (Figure 2abc). Any area without a P_{50} depth indicates a lack of hypoxia throughout the water column. A shallow P_{50} depth indicates shallow hypoxia and deep P_{50} depth indicates deep hypoxia. Assuming there is a connection between P_{50} depth and vertical habitat utilization, then the vertical habitat dimension is more restricted when P_{50} depth is shallow than when it is deep. There are differences in P_{50} depths among the low P_{50} and negative ΔH type, low P_{50} and positive ΔH type, and high P_{50} and negative ΔH type. The low P_{50} and negative ΔH type A has P_{50} depth over a much smaller geographic area than the other two physiological types (Figure 2abc). There is regional variability in the vertical separation among the P_{50} depths. Along 140°W in the Pacific, the P_{50} depth for the low P_{50} and negative ΔH type C is always deeper than the other two physiological types, and there are sections along the transect where the low P_{50} and negative ΔH type C does not have a P_{50} depth (Figure 3a). The P_{50} depths of the low P_{50} and positive ΔH type B and the high P_{50} and negative ΔH type C are similar between 10°S and 30°N (Figure 3). North of 30°N, the P_{50} depth of the low P_{50} and positive ΔH type B is much deeper than the high P_{50} and negative ΔH type C (Figure 3a).

Average temperature at 10 m along the 140°W transect decreases by 8.6°C between 20°N and 40°N (Figure 3c). North of 40°N, lower temperatures in the surface ocean decrease the difference in temperature between the surface ocean and the deep ocean (Figure 3c). The ocean thermocline causes differences in P_{50} depths. If temperature does not alter blood-oxygen binding (i.e. $\Delta H = 0$) in the ocean water column, the P_{50} depth for organisms with P_{50} of 2 kPa would be 180 m in the Equatorial Pacific (10°N, 140°W) and 550 m in the North Pacific (55°N, 140°W). If temperature does alter blood-oxygen binding in the ocean water column, at 10°N, 140°W, the P_{50} when $\Delta H = -40$ kJ mol^{-1} decreases from 2 kPa to 0.8 kPa, and the P_{50} when $\Delta H = 20$ kJ mol^{-1}

increases from 2 kPa to 3.2 kPa between 10 m and 200 m depth (Figure 4a). An organism with a $\Delta H = -40$ kJ mol^{-1} does not have a P_{50} depth at this location because the decrease in temperature in the ocean thermocline decreases P_{50} (Figure 4a). The P_{50} is low enough that the oxygen pressure in the water column is always higher than the P_{50} (Figure 4a). In contrast, the P_{50} depth of an organism with $\Delta H = 20$ kJ mol^{-1} is shallower, 140 m, due to the effect of temperature on P_{50} (Figure 4a). At 55°N, 140°W, the P_{50} of an organism with $\Delta H = -40$ kJ mol^{-1} decreases from 2 kPa to 1.6 kPa and the P_{50} of an organism with $\Delta H = 20$ kJ mol^{-1} increases from 2 kPa to 2.2 kPa between 10 m and 200 m depth (Figure 4b). The P_{50} depth of an organism with a $\Delta H = -40$ kJ mol^{-1} is deeper, 670 m, and the P_{50} depth of an organism with $\Delta H = 20$ kJ mol^{-1}, 500 m, is shallower than if there were no effect of temperature on blood-oxygen binding (Figure 4b).

Oxygen pressure or temperature could be causing vertical separation between the organisms with both different P_{50} and different ΔH values along the 140°W transect (B and C in Figure 1). Oxygen pressure decreases with increasing depth and the gradients are the steepest, 0.18 ± 0.06 kPa m^{-1}, between 10°N and 20°N (Figure 3b). The gradients are less steep, 0.07 ± 0.04 kPa m^{-1}, north of 20°N (Figure 3b). The effect of oxygen gradient on P_{50} determines the separation in P_{50} depths when ΔH is 0 kJ mol^{-1}. In the Equatorial Pacific (10°N, 140°W) when ΔH is 0 kJ mol^{-1}, the P_{50} depth is 180 m for a P_{50} of 2 kPa and 110 m for a P_{50} of 8 kPa which is equal to 70 m in vertical separation. In the North Pacific (55°N, 140°W) when ΔH is 0 kJ mol^{-1}, the P_{50} depth is 550 m for a P_{50} of 2 kPa and 210 m for a P_{50} of 8 kPa which is equal to 340 m in vertical separation. Steep oxygen gradients decrease vertical separation in P_{50} depths.

There are also opposite effects on blood-oxygen binding of a positive ΔH of 20 kJ mol^{-1} and a negative ΔH of -40 kJ mol^{-1}, which means that a decrease in temperature in the ocean thermocline increases the P_{50} when $\Delta H = 20$ kJ mol^{-1} and decreases the P_{50} when $\Delta H = -40$ kJ mol^{-1}. In the Equatorial Pacific (10°N, 140°W), the P_{50} when $\Delta H = 20$ kJ mol^{-1} increases from 2 kPa to 3.2 kPa and the P_{50} when $\Delta H = -40$ kJ mol^{-1} decreases from 8 kPa to 3.2 kPa between 10 m and 200 m depth as the temperature decreases from 27.0°C to 10.8°C (Figure 4a). The decrease in the P_{50} when $\Delta H = -40$ kJ mol^{-1} and concurrent increase in the P_{50} when $\Delta H = 20$ kJ mol^{-1} shrinks the vertical separation in P_{50} depths to <10 m (Figure 4a). In the North Pacific (55°N, 140°W), where temperature decreases from 8.4°C to 5.1°C between 10 and 200 m depth, the vertical separation between organisms with $\Delta H = 20$ kJ mol^{-1} and $\Delta H = -40$ kJ mol^{-1} is greater, 250 m, because there are smaller shifts in O_2 affinity due to temperature (Figure 4b). P_{50} shifts from 2 kPa to 2.2 kPa when $\Delta H = 20$ kJ mol^{-1} and from 8 kPa to 6.5 kPa for Type C when $\Delta H = -40$ kJ mol^{-1} at 55°N, 140°W (Figure 4b). In summary, the P_{50} depths can be further separated or drawn closer together by steep ocean thermoclines.

The P_{50} depth of the low P_{50} and negative ΔH type (A in Figure 1) is the same or deeper than the other two physiological types (B and C in Figure 1) in regions of the ocean where the low P_{50} and negative ΔH type has a P_{50} depth (Figure 5ab). In the Equatorial Pacific, the Arabian Sea, and the Bay of Bengal, the vertical separation between P_{50} depths with opposite sign ΔH (A and B in Figure 1) and different P_{50} (A and C in Figure 1) are relatively small, 0 to 100 m (Figure 5ab). In the North Pacific, the vertical separation between the P_{50} depths for physiological types A and C with different P_{50} values at 10 m but the same ΔH is >200 m (Figure 5a). In contrast, the vertical separation between the P_{50} depths for physiological types A and B with opposite sign ΔH and the same P_{50} value at 10 m is <200 m throughout much of the North Pacific (Figure 5b). Vertical separation between the P_{50} depths of the low P_{50} and positive ΔH type A and the high P_{50} and negative ΔH type B is regionally variable (Figure 5c). The P_{50} depth of the low P_{50} and positive ΔH type B is deeper than the high P_{50} and negative ΔH type C in the North Pacific

(Figure 5c). The P_{50} depths of the low P_{50} and positive ΔH type B and the high P_{50} and negative ΔH type C are similar in the Bay of Bengal, the Arabian Sea, and the Northern Equatorial Pacific (Figure 5c). The P_{50} depth of the high P_{50} and negative ΔH type C is deeper than the low P_{50} and positive ΔH type B in the center of the North Pacific Gyre (Figure 5c).

The 60 μmol kg^{-1} hypoxia threshold covers a geographic area larger than the P_{50} depth area of the low P_{50} and negative ΔH type and similar to the P_{50} depth areas of the low P_{50} and positive ΔH type and the high P_{50} and negative ΔH type (Figure 2). Along 140°W in the Pacific, the 60 μmol kg^{-1} hypoxia threshold is similar to the P_{50} depths of the low P_{50} and positive ΔH type and the high P_{50} and negative ΔH type between 10°N and 30°N (Figure 3a). The 60 μmol kg^{-1} hypoxia threshold is different from P_{50} depths south of 10°N and north of 30°N (Figure 3a).

Physiological comparison of P_{50} depths

The term "P_{50} restricted depth" refers to the proposed constraint on vertical habitat utilization to the water column above the P_{50} depth. The geographic extent of P_{50} restricted depths is highly variable, ranging from <1% to >80% of the global ocean area, depending on P_{50} and ΔH (Figure 6). Low P_{50} combined with negative ΔH has the lowest percentage of ocean area with a P_{50} restricted depth, and high P_{50} combined with positive ΔH has the highest percentage of ocean area with a P_{50} restricted depth (Figure 6). For the hemoglobins and hemocyanins of pelagic organisms in the meta-analysis, the majority have <30% of the global ocean area with a P_{50} restricted depth (Figure 6). The outlier in Figure 6, which has a P_{50} restricted depth over >70% of the ocean area is the northern krill, *Meganyctiphanes norvegica*.

The pattern in P_{50} depths varies across the physiological spectrum of P_{50} and ΔH values (Figure 7). The potential minimum P_{50} depth ranges from 0 to 380 m depth (Figure 7a). High P_{50}

combined with positive ΔH, which has no natural analogue, results in the shallowest minimum P_{50} depths, and low P_{50} combined with negative ΔH (Type A) results in the deepest minimum P_{50} depths. As P_{50} increases from 1 kPa to 2 kPa, there is a deepening of the median P_{50} depth and an increase in the interquartile range of P_{50} depths. The reason for this pattern is related to the distribution of oxygen in the ocean environment. High oxygen affinity, $P_{50} \leq 1$ kPa, combined with negative ΔH has a P_{50} depth covering approximately 1% of the global ocean area which means that the P_{50} depth area is limited to the core oxygen minimum zone regions in the Equatorial Pacific and Arabian Sea which have little to no oxygen at oxygen minimums in the water column. As P_{50} increases from 1 kPa to 2 kPa, the percent ocean area with a P_{50} depth increases (Figure 6). Most of the increase in area is in the North Pacific. Oxygen minimums in the water column of the North Pacific are deep (740 m) relative to those in the core of the Eastern Tropical Pacific oxygen minimum zone (490 m), characteristics that cause the deepening of the median P_{50} depth and the expansion of the interquartile range of P_{50} depths. There is another deepening of the median P_{50} depth and an increase in interquartile range of P_{50} depths as the geographic area with a P_{50} depth increases from 60% to 70% (Figure 7bc). This represents an expansion of the geographic area of P_{50} depths to the entire tropical and temperate oceans as P_{50} increases. As the geographic area of P_{50} depths reaches 80%, polar regions become the only regions without P_{50} depths.

Discussion

The ubiquity of oxygen carrier proteins and diversity of P_{50} and ΔH traits across metazoan species suggest that these proteins were critical in the evolution of metazoans but malleable in response external conditions (Figure 1) (Mangum, 1998; Terwilliger, 1998). The diversity of P_{50} and ΔH traits translates into regional variability in the vertical zonation of the physiological threshold, P_{50} depth (Figures 2 and 3). Measurements of species abundance at different depths indicate that vertical zonation is an important feature of pelagic habitats in oxygen minimum zone regions (e.g. Vinogradov and Voronina, 1962; Longhurst, 1967; Saltzman and Wishner, 1997). Pelagic species are found at depths where the oxygen pressure is equal to but is not below the critical oxygen pressure, P_{crit} (Childress, 1975; Torres et al., 1979). P_{50} is a determinant of P_{crit}, which is the key trait of the organism governing hypoxia tolerance (Mandic et al., 2009). A low P_{50} means that even when oxygen is low, arterial blood can still be 100% oxygen saturated, ensuring oxygen delivery to tissues. While P_{50} depth is yet another proxy for hypoxia tolerance, it is one that is derived from P_{50} and oceanographic temperature and oxygen data, thus integrating relevant physiological traits with environmental gradients. We suggest that P_{50} depth provides a more mechanistic perspective on habitat suitability and zonation in hypoxic regions.

Vertical gradients in oxygen and temperature in the water column impact P_{50} depth and consequently the ability of an organism with a particular physiology to extract oxygen from the environment when moving from shallower to deeper depths. There is more vertical separation between the P_{50} depths of high P_{50} and low P_{50} physiological types when the oxygen gradients are gradual than when the oxygen gradients are steep (Figure 3). The structure of oxygen and temperature gradients together determine whether the P_{50} depths converge or diverge as modulated by ΔH. In the Equatorial Pacific, an organism with $P_{50} = 2$ kPa and $\Delta H = 20$ kJ mol^{-1} at 10 m and an organism with $P_{50} = 8$ kPa and $\Delta H = -40$ kJ mol^{-1} at 10 m have the same P_{50} depths because temperature increases the P_{50} of organisms with $\Delta H = 20$ kJ mol^{-1} and decreases the P_{50} of organisms with $\Delta H = -40$ kJ mol^{-1} as the organisms move from warmer shallower depths to cooler deeper depths (Figure 4). Therefore oxygen-binding traits may have particularly important implications for the frequency of ecological interactions among species in regions with steep oxygen and temperature gradients.

Predation and competition are ecological interactions which have been linked to patterns of zonation in marine habitats (e.g. Connell, 1961; Paine, 1974). If the P_{50} depth of a prey is deeper than the P_{50} depth of its predator, then the prey might be able to take advantage of a pelagic refuge by swimming deeper than the P_{50} depth of the predator. This would be the case if the prey species has a low P_{50} and negative ΔH and the predator species has either a low P_{50} and positive ΔH or high P_{50} and negative ΔH (Figure 5). Midwater shrimp and Atlantic herring are examples of prey species capable of this strategy as they have both a low P_{50} and negative ΔH, giving them the potential for a large pelagic refuge in hypoxic zones. However, low P_{50} and negative ΔH are not universal characteristics of prey species. The krill *M. norvegica* has a low P_{50} and the highest positive ΔH, which is 102 kJ mol^{-1} higher than any other species in the analysis (Figure 1) (Brix et al., 1989a), and the krill, *E. superba*, has a high P_{50} of 8.2 kPa and the lowest negative ΔH in the analysis (Bridges et al., 1983). These krill species appear to be exceptions, and, in general, the other pelagic species with low P_{50} and positive ΔH or high P_{50} and negative ΔH are predators (Figure 1, Table 2). Squids, *Architeuthis dux* and *Todarodes sagittatus*, are pelagic predators with high P_{50} and negative ΔH (Brix et al., 1989b). Tunas, *Thunnus maccoyii* and *Thunnus thynnus*, and the chub mackerel, *Scomber japonicus*, are pelagic predators with low P_{50} and positive ΔH (Brill and Bushnell, 2006; Clark et al., 2008; Clark et al., 2010). Although predators with low P_{50} and positive ΔH or high P_{50} and negative ΔH are at a disadvantage around oceanic hypoxic zones, these characteristics likely confer other advantages either for environmental conditions in well-oxygenated water or other life characteristics.

Competition also might be influenced by P_{50} depth, and there are differences in P_{50} and ΔH among closely related tuna species. The P_{50} depth of *Thunnus obesus*, which has low P_{50} and negative ΔH, is deeper than the P_{50} depths of *T. maccoyii* and *T. thynnus*, which have low P_{50} and positive ΔH (Figure 1, Figure 5) (Lowe et al., 2000; Brill and Bushnell, 2006; Clark et al., 2008). *T. obesus* spends considerable time foraging in the deep ocean around Oxygen Minimum Zones where having a deeper P_{50} depth would be advantageous (Howell et al., 2010). Prey, predators, and competitors have different P_{50} and ΔH traits but whether the traits influence the rates of predation or competition in particular regions or at certain depths would need to be determined from field observations, experiments, and measurements of P_{50} and ΔH traits for interacting species from different trophic levels living in the same pelagic ecosystem.

Vertical migrators swim between the surface and deep ocean daily and cross environmental gradients in oxygen and temperature so P_{50} and ΔH traits may be adapted for migration. Sanders and Childress (1990b) investigated the oxygen-binding properties of the hemocyanin of several species of deep-sea shrimp that live in the pelagic ocean near Hawaii. The hemocyanins of migrating shrimp were more exothermic (i.e. more negative ΔH) than non-migrating shrimp and the hemocyanins of non-migrating shrimp had a lower P_{50} than migrating shrimp, which confers advantages to the migrators crossing a temperature gradient and non-migrators living permanently at depths with low oxygen concentrations (Sanders and Childress, 1990b). For migrating shrimp, colder temperatures decrease the P_{50} of hemocyanin in the hypoxic deep ocean, and warmer temperatures increase the P_{50} of hemocyanin in the well-oxygenated surface ocean where shrimp actively feed and need delivery of oxygen to tissues (Sanders and Childress, 1990b). However, the P_{50} and ΔH traits of the migrating shrimp, *Acanthephyra smithi* (34 in Figure 1), *Oplophorus gracilirostris* (47 in Figure 1), and

Systellaspis debilis (50 in Figure 1), are similar to other species, including ones that are not migrators. Measurements of P_{50} and ΔH for more species and environmental data from habitats are necessary to fully understand the adaptive significance of P_{50} and ΔH during migration in the pelagic ocean.

Hemoglobin and hemocyanin have a wide range of temperature sensitivities (Figure 1). An interesting finding of the meta-analysis is that there are no species with blood-oxygen binding traits that have a $P_{50}>4$ and $\Delta H>0$ (Figure 1). The meta-analysis relied on published measurements of P_{50} and ΔH, which only included a subset of species, so it is possible that species with $P_{50}>4$ and $\Delta H>0$ exist. However, a species with $P_{50}>4$ and $\Delta H>0$ would not be well adapted for survival because the shallow P_{50} depths, which cover >80% of the global ocean, would severely limit the ability of species with these blood-oxygen binding traits to extract oxygen in the water column (Figure 7).

While we argue that the P_{50} depth metric is a more relevant hypoxia indicator than a threshold oxygen concentration, it also has limitations. Organisms have adaptations such as a large gill surface area to enhance oxygen extraction and the ability to suppress metabolism to decrease oxygen utilization (e.g. Childress and Seibel, 1998; Pauly, 2010). In addition, the temperature of the environment alters metabolic rates. As organisms move from the surface to deeper depths, the decrease in temperature with depth decreases metabolic rates, and organisms need less oxygen. Some organisms also have the ability to switch to anaerobic metabolism, reducing the need for extracting oxygen from the environment, for periods of time (e.g. Childress and Seibel, 1998). These and other adaptations may allow organisms to swim deeper than a P_{50} depth and remain there for a limited time. Also, organisms spend time at many depths in the water column, and are not necessarily acclimated to temperature and oxygen pressure at 10 m depth. For example, species that migrate may actually be acclimated to conditions in the deep ocean or a weighted average of their recent environmental history. However, organisms shift P_{50} by gradually changing the concentration of nucleoside triphosphates (NTPs) in the blood over more than 6 days so acclimation may take many days to occur (Johansen and Weber 1976, Weber and Lykkeboe 1978). Also, some species have multiple types of respiratory pigments, which have different sensitivities to temperature and hypoxia (e.g. Gillen and Riggs, 1973; Brix et al., 2004). Cod (*Gadus morhua* L.) with two types of hemoglobin increased the relative concentration of the hemoglobin type best suited for the acclimation temperature after one year of exposure (Brix et al., 2004). Future investigations in the field and laboratory are needed to determine the effect of acclimation on P_{50} depth.

In summary, we suggest that geographic analyses of blood-oxygen binding traits provide an enlightening and more mechanistic view of the vertical habitat of pelagic species in the ocean. We demonstrate that current concentration-based hypoxia thresholds (i.e. 60 μmol kg^{-1}) ignore key regional variations in the effect of temperature on a mechanism, blood-oxygen binding, underlying the hypoxia tolerance of different species (Figure 2). For example, the ocean area with the 60 μmol kg^{-1} hypoxia threshold is 4 times larger and 220 m shallower than the P_{50} depth threshold when P_{50} = 2 kPa and ΔH = -40 kJ mol^{-1}. The ecological ramifications of this diversity are an important topic for future research on the physiology, behavior, survival, growth, and reproduction of organisms relative to the P_{50} depth. One of the benefits of assessing the environmental impacts on particular traits is being able to assess the potential for future adaptation. The environment influences respiratory pigments over evolutionary time scales (Verde et al., 2006), so respiratory pigments have the potential to be an indicator of adaptations occurring in response to climate change. Geographic analyses of habitat changes based on blood-oxygen binding and additional key physiological traits such as metabolism will provide mechanistic understanding and added confidence in projections of the effect of climate change on habitat compression.

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Table Legends

Table 1: Benthic marine species with P_{50} measurements at multiple temperatures.

ID	Species	Common Name	Reference
1	*Abarenicola affinis*	intertidal lugworm	Chadwick et al. (1984)
2	*Alitta virens*	sandworm	Economides and Wells (1975)
3	*Atelecyclus rotundatus*	circular crab	Taylor et al. (1985)
4	*Busycon canaliculatus*	channeled whelk	Mangum and Lykkeboe (1979)
5	*Carcinus maenus*	european shore crab	Weber et al. (2008)
6	*Cephaloscyllium isabellum*	draughtsboard shark	Tetens and Wells (1984)
7	*Enteroctopus dofleini*	giant Pacific octopus	Lenfant and Johansen (1965)
8	*Eurytium albidigitum*	crab	Burnett et al. (1988)
9	*Forsterygion malcolmi*	mottled triplefin	Brix et al. (1999)
10	*Forsterygion varium*	variable triplefin	Brix et al. (1999)
11	*Glyphocrangon vicaria*	deep sea shrimp	Arp and Childress (1985)
12	*Goneplax rhomboides*	angular crab	Taylor et al. (1985)
13	*Grahamina capito*	spotted triplefin	Brix et al. (1999)
14	*Haliotus corrugata*	pink abalone	Burnett et al. (1988)
15	*Hyas araneus*	great spider crab	Morris and Bridges (1989)
16	*Hyas coarctatus*	arctic lyre crab	Morris and Bridges (1989)
17	*Limulus polyphemus*	Atlantic horseshoe crab	Burnett et al. (1988)
18	*Liocarcinus depurator*	sandy swimming crab	Taylor et al. (1985)
19	*Lopholithodes foraminatus*	brown box crab	Burnett et al. (1988)
20	*Megaleledone setebos*	Antarctic octopod	Zielinski et al. (2001)
21	*Metacarcinus anthonyi*	yellow rock crab	Burnett et al. (1988)
22	*Metacarcinus gracilis*	graceful rock crab	Burnett et al. (1988)
23	*Metacarcinus magister*	Dungeness crab	Burnett et al. (1988)
24	*Myliobatis californica*	bay ray	Hopkins and Cech Jr. (1994)
25	*Neotrypaea californiensis*	bay ghost shrimp	Miller and Van Holde (1974)
26	*Octopus vulgaris*	common octopus	Brix et al. (1989b)
27	*Palaemon elegans*	intertidal prawn	Morris et al. (1985)
28	*Scophthalmus maximus*	turbot	Samuelsen et al. (1999)
29	*Sepia officinalis*	common cuttlefish	Zielinski et al. (2001)
30	*Stenoplax conspicua*	chiton	Burnett et al. (1988)
31	*Terebella haplochaeta*	intertidal polychaete	Wells et al. (1980)

Table 2: Pelagic marine species with P_{50} measurements at multiple temperatures

ID	Species	Common Name	Reference
32	*Acanthephyra acutifrons*	shrimp non-migrator	Sanders and Childress (1990b)
33	*Acanthephyra curtirostris*	shrimp non-migrator	Sanders and Childress (1990b)
34	*Acanthephyra smithi*	shrimp migrator	Sanders and Childress (1990b)
35	*Acipenser medirostris*	green sturgeon	Kaufman et al. (2006)
36	*Architeuthis dux*	giant squid	Brix et al. (1989b)
37	*Clupea harengus*	Atlantic herring	Everaarts (1978)
38	*Dissostichus mawsoni*	Antarctic toothfish	Qvist et al. (1977)
39	*Doryteuthis pealeii*	longfin inshore squid	Redfield and Ingalls (1933)
40	*Dosidicus gigas*	jumbo squid	Seibel (2013)
41	*Euphausia superba*	Antarctic krill	Bridges et al. (1983)
42	*Gnathphausia ingens*	mysid	Sanders and Childress (1990a)
43	*Katsuwonus pelamis*	skipjack tuna	Brill and Bushnell (1991)
44	*Loligo vulgaris*	European squid	Brix et al. (1989b)
45	*Meganyctiphanes norvegica*	northern krill	Brix et al. (1989a)
46	*Nautilus pompilius*	nautilus	Johansen et al. (1978)
47	*Oplophorus gracilirostris*	shrimp migrator	Sanders and Childress (1990b)
48	*Pagothenia borchgrevinki*	bald notothen	Tetens et al. (1984)
49	*Scomber japonicus*	chub mackerel	Clark et al. (2010)
50	*Systellaspis debilis*	shrimp migrator	Sanders and Childress (1990b)
51	*Thunnus albacares*	yellowfin tuna	Brill and Bushnell (1991)
52	*Thunnus maccoyii*	southern bluefin tuna	Clark et al. (2008)
53	*Thunnus obesus*	bigeye tuna	Lowe et al. (2000)
54	*Thunnus thynnus*	Atlantic bluefin tuna	Brill and Bushnell (2006)
55	*Todarodes sagittatus*	European flying squid	Brix et al. (1989b)

Table 3: A summary of the percent of characteristics in each of the low P_{50} and negative ΔH, low P_{50} and positive ΔH, and high P_{50} and negative ΔH quadrants from Figure 1. There are no species in the high P_{50} and positive ΔH quadrant. The categories of non-migrator and migrator refer to vertical movement in the water column.

<table>
<tr><th colspan="3">Low P_{50}, Negative ΔH:
$0 < P_{50} < 5$ kPa, $-140 < \Delta H < 0$ kJ mol^{-1}</th></tr>
<tr><td>Variable</td><td>% Quadrant</td><td>% Total</td></tr>
<tr><td>Number of species</td><td></td><td>71</td></tr>
<tr><td>benthic/pelagic</td><td>59/41</td><td>42/29</td></tr>
<tr><td>hemocyanin/hemoglobin</td><td>72/28</td><td>51/20</td></tr>
<tr><td>invertebrate/vertebrate</td><td>79/21</td><td>56/15</td></tr>
<tr><td>non-migrator/migrator</td><td>69/31</td><td>49/22</td></tr>
<tr><td colspan="3">Low P_{50}, Positive ΔH:
$0 < P_{50} < 5$ kPa, $0 < \Delta H < 140$ kJ mol^{-1}</td></tr>
<tr><td>Variable</td><td>% Quadrant</td><td>% Total</td></tr>
<tr><td>Number of species</td><td></td><td>14.5</td></tr>
<tr><td>benthic/pelagic</td><td>38/63</td><td>5/9</td></tr>
<tr><td>hemocyanin/hemoglobin</td><td>38/63</td><td>5/9</td></tr>
<tr><td>invertebrate/vertebrate</td><td>38/63</td><td>5/9</td></tr>
<tr><td>non-migrator/migrator</td><td>38/63</td><td>5/9</td></tr>
<tr><td colspan="3">High P_{50}, Negative ΔH:
$5 < P_{50} < 10$ kPa, $-140 < \Delta H < 0$ kJ mol^{-1}</td></tr>
<tr><td>Variable</td><td>% Quadrant</td><td>% Total</td></tr>
<tr><td>Number of species</td><td></td><td>14.5</td></tr>
<tr><td>benthic/pelagic</td><td>63/38</td><td>9/5</td></tr>
<tr><td>hemocyanin/hemoglobin</td><td>63/38</td><td>9/5</td></tr>
<tr><td>invertebrate/vertebrate</td><td>63/38</td><td>9/5</td></tr>
<tr><td>non-migrator/migrator</td><td>63/38</td><td>9/5</td></tr>
</table>

Figure Legend

Figure 1: There is a range in oxygen affinity (P_{50}) and heat of oxygenation (ΔH) traits among marine species. The circles (○) are hemoglobin and the triangles (△) are hemocyanin. The number next to each symbol identifies the species and common name which are listed in Table 1 and Table 2. A, B, and C represent physiological types that will be explored in more detail and correspond to the following characteristics, A = low P_{50} with negative ΔH, B = low P_{50} with positive ΔH, and C = high P_{50} with negative ΔH. Low P_{50} means high oxygen affinity and more hypoxia tolerant. Blood-oxygen binding of species with $\Delta H=0$ is independent of temperature. There are no species with traits that correspond with a positive ΔH and a high P_{50}. View an interactive version of the graph (with information from Table 1, Table 2, and Table 3 embedded): http://www.kallisonsmith.us/D3/P50/Figure1.html

Figure 1:

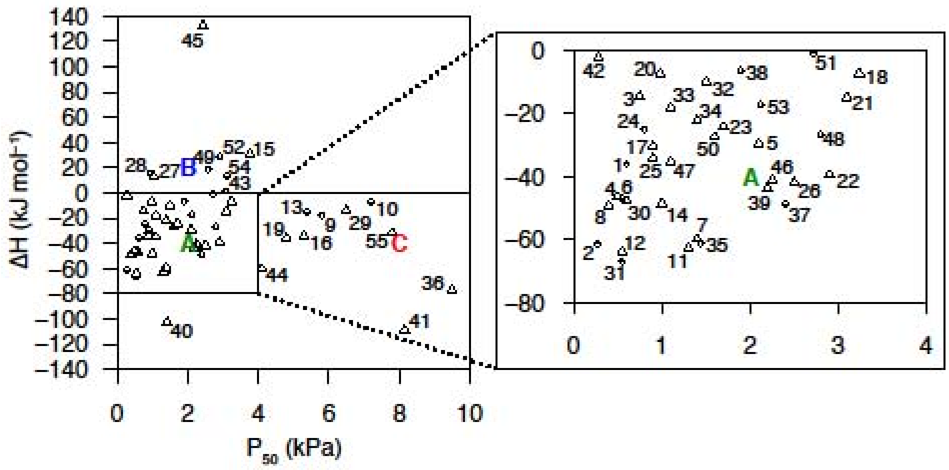

ΔH (kJ mol⁻¹)
P₅₀ (kPa)
140
120
100
80
60
40
20
0
−20
−40
−60
−80
−100
−120
−140
0
2
4
6
8
10
45
28
27
B
49
52
15
54
43
A
13
10
19
9
29
16
55
C
44
36
41
40
0
−20
−40
−60
−80
0
1
2
3
4
42
20
38
51
18
3
33
32
21
24
34
53
23
17
5
50
48
1
25
47
A
46
22
4
6
26
39
8
30
14
37
7
2
12
35
11
31

Figure 2: The distribution of P_{50} depths, z, in the global ocean for different physiological types compared to the depth of the 60 μmol kg^{-1} concentration, a threshold used for assessments of hypoxia. White indicates areas where there is no P_{50} depth or hypoxia threshold. The P_{50} depth for low P_{50} with negative ΔH type A occurs over a much smaller geographic area than P_{50} depths for low P_{50} with positive ΔH type B and high P_{50} with negative ΔH type C. The 60 μmol kg^{-1} hypoxia threshold occurs over the largest geographic area.

Figure 2:

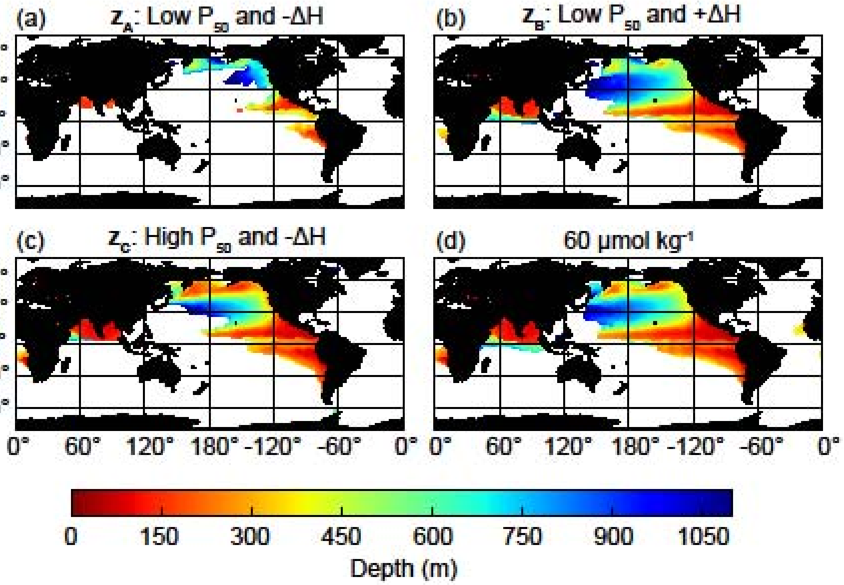

(a)
z_A: Low P_{50} and -ΔH
(b)
z_B: Low P_{50} and +ΔH
(c)
z_C: High P_{50} and -ΔH
(d)
60 µmol kg^{-1}
60°
30°
0°
-30°
-60°
0°
60°
120°
180°
-120°
-60°
0°
0
150
300
450
600
750
900
1050
Depth (m)

Figure 3: A transect along 140°W in the central north Pacific showing the influence of oxygen pressure, pO_2 , and temperature on P_{50} depth. The 60 μmol kg^{-1} hypoxia threshold, [60], is included for comparison. The white lines in (b) and (c) are the P_{50} depths and hypoxia threshold shown in (a). The relative separation between the P_{50} depths changes with latitude. The hypoxia threshold coincides with the P_{50} depths of low P_{50} with positive ΔH type B and high P_{50} with negative ΔH type C between 10 and 30°N, but is different from the P_{50} depths at other latitudes.

Figure 3:

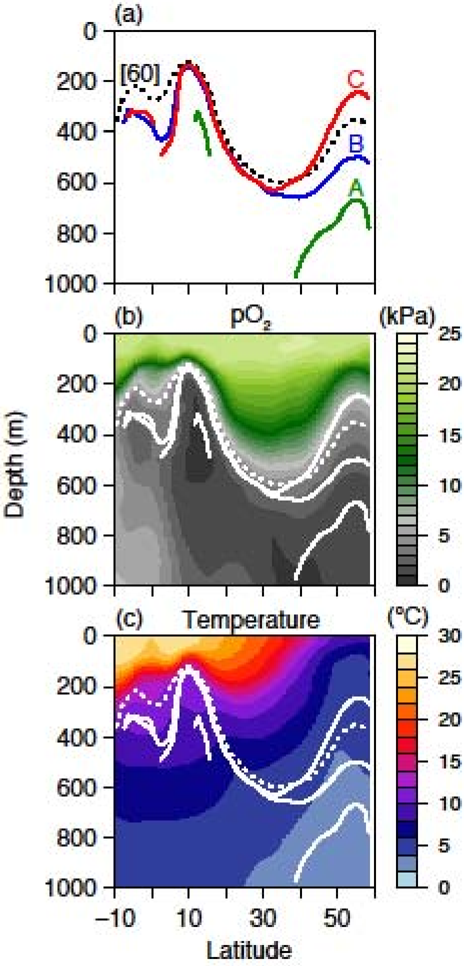

(a)
[60]
C
B
A
(b)
pO$_2$
(kPa)
25
20
15
10
5
0
Depth (m)
(c)
Temperature
(°C)
30
25
20
15
10
5
0
0
200
400
600
800
1000
–10
10
30
50
Latitude

Figure 4: P_{50} changes due to decreasing temperature between shallower and deeper depths. Locations are in the (a) Equatorial Pacific (10°N, 140°W) and (b) North Pacific (55°N, 140°W). The plotted lines are oxygen (grey), temperature (black), and the P_{50} of low P_{50} with negative ΔH type A (green), low P_{50} with positive ΔH type B (blue), and high P_{50} with negative ΔH type C (red). The dotted lines indicate the depths at which environmental $pO_2 < P_{50}$. The P_{50} depth occurs at the shallowest depth at which $pO_2 < P_{50}$ (i.e. the depth at which the solid line becomes the dotted line). The changes in P_{50} with depth at 10°N, 140°W are greater than at 55°N, 140°W because of higher temperatures in the shallower depths at 10°N, 140°W.

Figure 4:

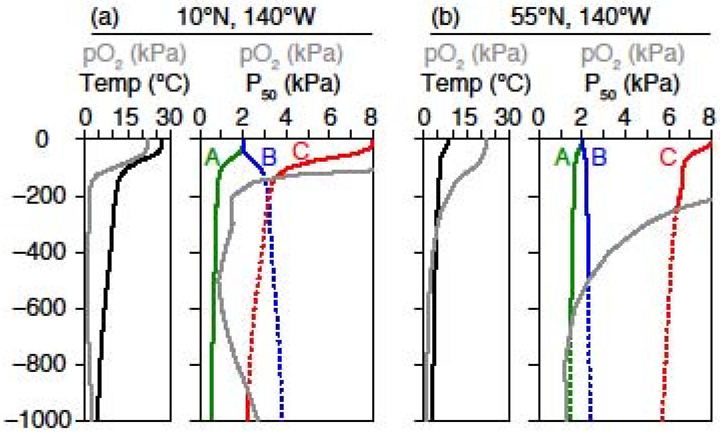

(a) 10°N, 140°W
pO₂ (kPa)
Temp (°C)
pO₂ (kPa)
P₅₀ (kPa)
0 15 30
0 2 4 6 8
0
−200
−400
−600
−800
−1000
A
B
C
(b) 55°N, 140°W
pO₂ (kPa)
Temp (°C)
pO₂ (kPa)
P₅₀ (kPa)
0 15 30
0 2 4 6 8
A
B
C

Figure 5: Vertical separation, s, between the P_{50} depths of the low P_{50} with negative ΔH type A, low P_{50} with positive ΔH type B, and high P_{50} with negative ΔH type C. White indicates areas where there is no P_{50} depth for either physiological type. Grey indicates areas where there is a P_{50} depth for one type and no P_{50} depth for the other type (Figure 2). Note that the color bar for (c) has a different scale. The P_{50} depth for the low P_{50} with negative ΔH type A occurs at the same depth or deeper than the low P_{50} with positive ΔH type B or the high P_{50} with negative ΔH type C. The relative position (shallower or deeper) of the P_{50} depth is regionally variable in the comparison of the low P_{50} with positive ΔH type B with the high P_{50} with negative ΔH type C.

Figure 5:

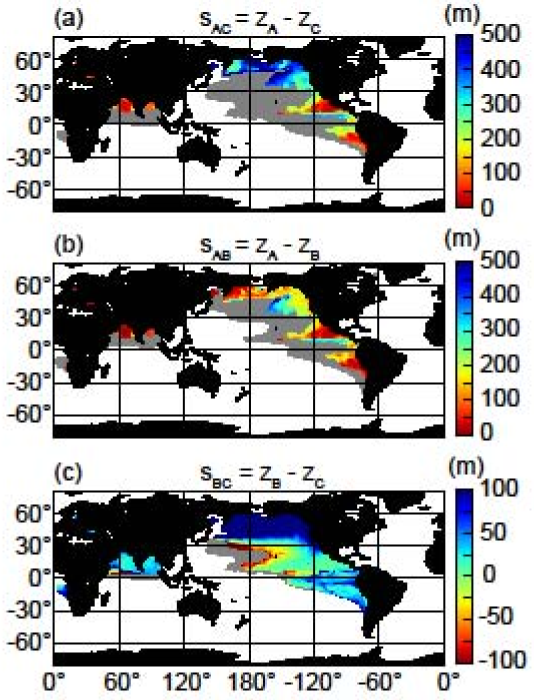

(a)
s_AC = Z_A - Z_C
(m)
500
400
300
200
100
0
(b)
s_AB = Z_A - Z_B
(m)
500
400
300
200
100
0
(c)
s_BC = Z_B - Z_C
(m)
100
50
0
-50
-100
60°
30°
0°
-30°
-60°
0°
60°
120°
180°
-120°
-60°
0°

Figure 6: A comparison of the percentage of the ocean area with a P_{50} depth across the entire range of ΔH and P_{50} traits. The points from Figure 1 for pelagic marine species from Table 2 are plotted for reference. The percentage of the ocean area with a P_{50} depth is lower for marine organisms with negative ΔH. Positive ΔH and high P_{50} have the greatest percent ocean area with a P_{50} depth.

Figure 6:

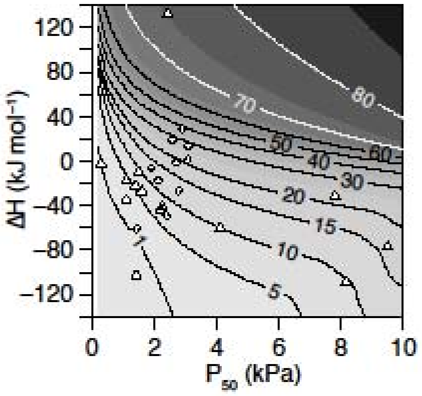
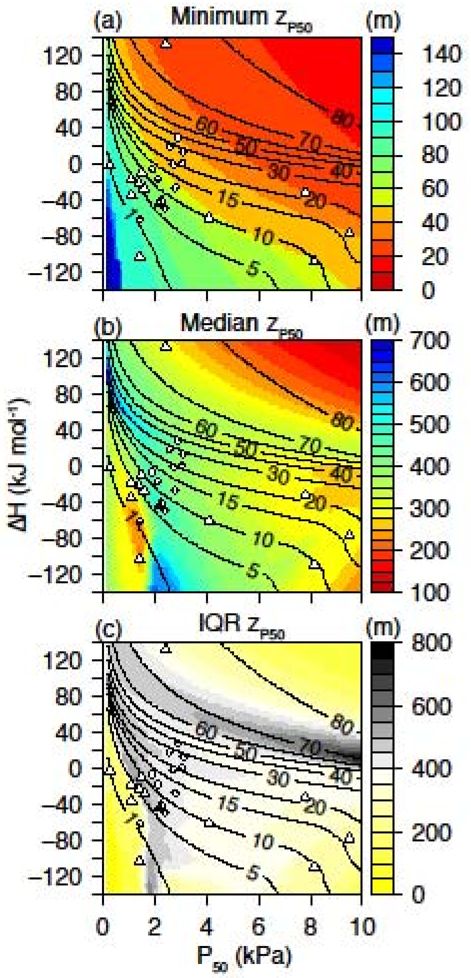

ΔH (kJ mol⁻¹)
120
80
40
0
−40
−80
−120
P50 (kPa)
0
2
4
6
8
10
70
80
50
40
60
30
20
15
10
5
1

Figure 7: The minimum, median, and interquartile range (IQR) of P_{50} depths, z, in the ocean across the entire range of ΔH and P_{50} traits. IQR is plotted to show P_{50} depth variability in the global ocean. The points from Figure 1 for the pelagic species from Table 2 and the contours of percent ocean area with P_{50} depth from Figure 6 are plotted for reference. Positive ΔH and high P_{50} have the shallowest minimum and median P_{50} depths. Negative ΔH and low P_{50} have the deepest minimum P_{50} and the lowest IQR.

Figure 7:


(a)
Minimum z_{P50}
(m)
(b)
Median z_{P50}
(m)
(c)
IQR z_{P50}
(m)
ΔH (kJ mol^{-1})
P_{50} (kPa)
120
80
40
0
−40
−80
−120
0
2
4
6
8
10
140
120
100
80
60
40
20
0
700
600
500
400
300
200
100
800
600
400
200
0
80
70
60
50
40
30
20
15
10
5
1