Article

Unique thermal sensitivity imposes a cold-water energetic barrier for vertical migrators

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Alterations of marine species' ranges with climate change are often attributed to oxygen limitation in warming oceans. Here we report unique metabolic temperature sensitivities for the myriad of vertically migrating oceanic species that daily cross depth-related gradients in temperature and oxygen. In these taxa, selection favours high metabolic activity for predator–prey interactions in warm shallow water and hypoxia tolerance in the cold at depth. These diverging selective pressures result in thermal insensitivity of oxygen supply capacity and enhanced thermal sensitivity of active metabolic rate. Aerobic scope is diminished in the cold, well beyond thermodynamic influences and regardless of ambient oxygen levels, explaining the native distributions of tropical migrators and their recent range expansions following warming events. Cold waters currently constitute an energetic barrier to latitudinal range expansion in vertical migrators. As warming due to climate change approaches, and eventually surpasses, temperatures seen during past warming events, this energetic barrier will be relieved.

A myriad of oceanic species, from diminutive krill to jumbo squids, descend to depth in the daytime, seeking refuge from predators, and return to surface waters at night to feed. These synchronous daily movements may be the largest animal migration, and the midwater environment they traverse is potentially the largest ecosystem on the planet[1]. Vertical migrators are critical components of pelagic ecosystems worldwide, especially in regions with pronounced oxygen minimum zones (OMZ)[2]. Their metabolism and vertical displacements contribute substantially to elemental fluxes from surface to depth and to oxygen depletion in the OMZ[3–6]. Although this migration spans only a few hundred metres, it often crosses strong, correlated gradients in light, temperature and oxygen. Warm surface temperatures impose physiological stress on some vertical migrators[7–9], while extreme hypoxia at depth triggers metabolic suppression and constrains habitable space in others[10–12]. Thus, compression between climate change-induced warming surface waters, where light renders zooplankton more vulnerable to predation, and de-oxygenating deeper waters is a growing concern[13–17].

Latitudinal range shifts in marine animals are commonly linked to climate warming[18]. However, ranges for some species contract while others expand and the rates of population movement often differ at the leading and trailing edges[19]. The precise mechanisms imposing latitudinal range shifts are uncertain, especially for oceanic species, including vertical migrators. In recent decades, the abundance of tropical zooplankton increased in North Pacific temperate waters during warming events (for example, El Niño and warm-water anomalies[20–22]. At the same time, the jumbo squid, *Dosidicus gigas*, expanded its tropical range into temperate waters[23]. The tropicalization of the temperate community that resulted from range expansion of zooplankton and the squid had cascading effects throughout food webs[23,24]. Latitudinal range shifts for vertical migrators have been attributed to a combination of productivity changes, ecological and life-history influences and altered circulation patterns and chemical and physical changes in the environment[20,25]. However, the role of temperature is often dismissed because migrators appear to tolerate a broad temperature

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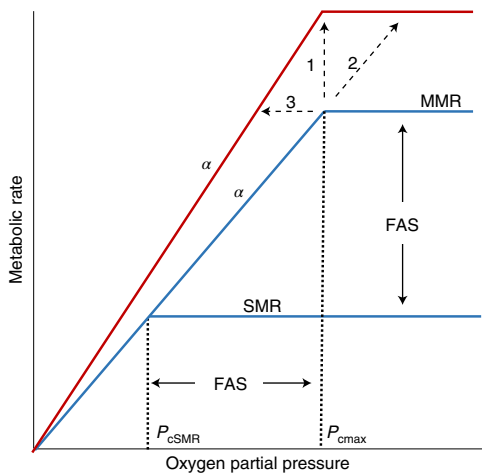
Fig. 1 | Oxygen and temperature dependency of oxygen supply and demand.
Maximum (MMR) and standard (SMR) metabolic rate, their critical oxygen
pressures (P_{cmax} and P_{cSMR}), factorial aerobic scope (FAS) and the oxygen
supply capacity (α, the slope of the relationship between MR and PO_2) change
with temperature and oxygen in several ways. (1) MMR and α increase with
temperature while the P_{cmax} is constant. (2) The α is insensitive to temperature and
P_{cmax} changes in proportion to MMR. (3) Adaptation to low oxygen increases α and
preserves FAS.

range between their day and night habitat[23]. Regardless, their distributions and contributions to biogeochemical cycles are a function of the temperature sensitivities of the underlying physiological traits, which remain poorly described[26].

Deep, dark tropical waters convey distinct selective pressures from shallow well-lit temperate waters, despite similarly cold temperatures.

We argue that these differences play a key role in the temperature sensitivity of metabolic capacity with consequences for latitudinal range limits. Using the *Metabolic Index* framework[27–29] (Fig. 1), we show that for vertical migrators (oceanic species with distinct day and night depth ranges), cold, rather than warm, waters impose an energetic barrier to their distributions. This cold-water barrier results from strong selection for predator–prey interactions in warm surface waters and the relaxation of that selection at cold, mesopelagic depths[30,31]. This ecological reality is cemented into the migrator's physiological capacity to supply oxygen, which must be high to support high oxygen demands near the surface and must remain high at depth, despite much lower oxygen demands, to tolerate the extreme hypoxia in the OMZ. Thus, in migrators, oxygen supply capacity is high and invariant across the depth and temperature range (Fig. 2). Here we used laboratory-derived temperature sensitivities of metabolic traits and recently derived relationships between them[28] to map aerobic scope for several dominant vertical migrators, including euphausiids (krill) and the jumbo squid, *Dosidicus gigas*, inferring energetic constraints and opportunities that influence current and future habitat.

For a population to sustain itself, oxygen supply must meet demand. Oxygen demand is the metabolic rate (MR), measured as a rate of oxygen consumption. Oxygen supply is the product of environmental availability (PO_2) and the physiological capacity to extract oxygen from the environment and to transport it to respiring tissues (α, the physiological oxygen supply capacity per unit time, mass and PO_2; $\mu mol\ g^{-1}\ h^{-1}\ kPa^{-1}$). The α depends on the respiratory (that is, gill) surface area, blood-oxygen binding and cardiac output among other traits. As environmental PO_2 declines and/or as metabolic rate increases, physiological oxygen supply increases towards its capacity, α, which is quantifiable as the ratio of metabolic rate and the critical PO_2 for that rate (P_c, the lowest PO_2 that can sustain a given metabolic rate; Fig. 1, Supplementary Figs. 1 and 2 and equation (1)[28,32]. The α can be viewed from two equivalent perspectives:
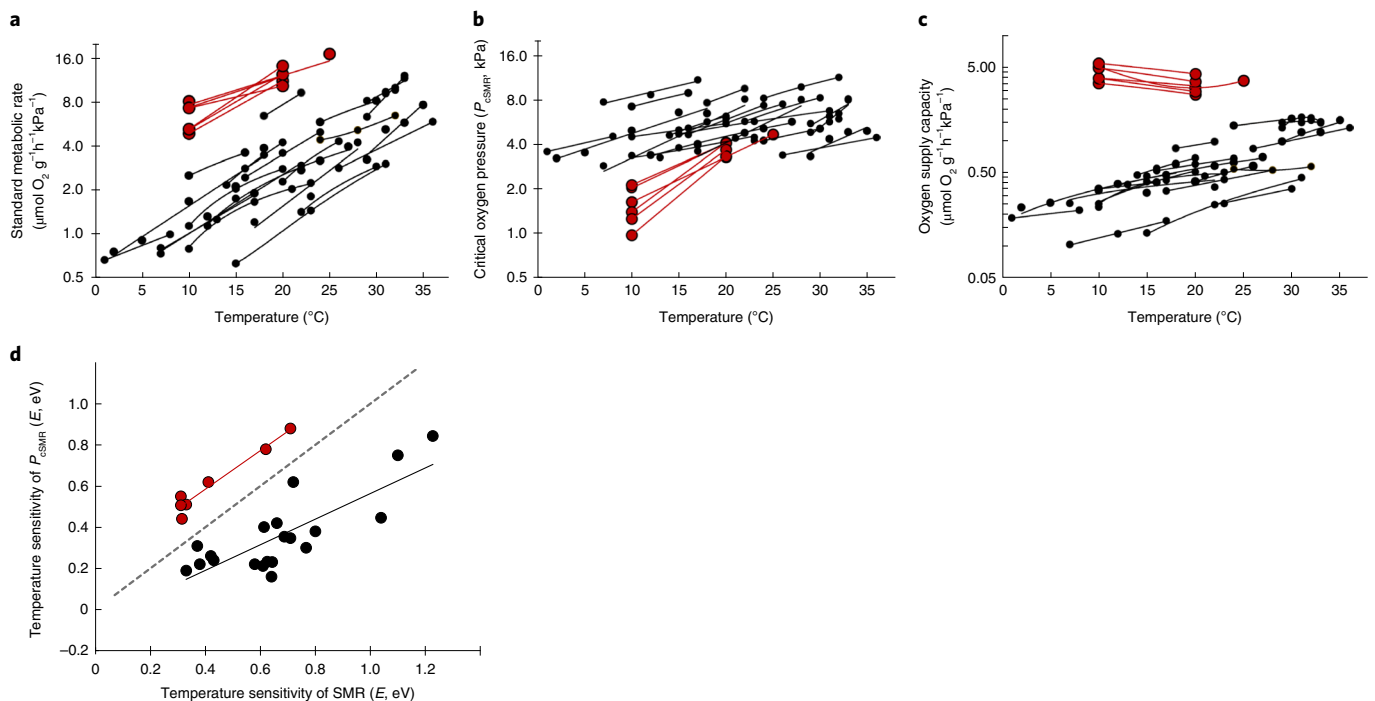

Fig. 2 | Unique temperature sensitivities of metabolic traits in vertical migrators. **a**–**c**, Standard metabolic rates (Y, SMR; **a**), critical oxygen pressures (Y, P_{cSMR}; **b**) and the oxygen supply capacity (Y, α = SMR P_{cSMR}^{-1}; **c**) as a function of temperature (X) in tropical vertical migrators (red) and diverse coastal species (black; Supplementary Table 2). **d**, The temperature sensitivities (E) for SMR (X) and P_{cSMR} (Y) are similar to each other (y = 0.94X + 0.21, n = 7 species; P = 0.06,

two-tailed *t*-test; Supplementary Table 2), falling just above the dashed unity line. For coastal species, the SMR is more temperature sensitive than P_{cSMR} (Supplementary Table 2; y = 0.62X - 0.06, n = 20 species; P = 4.3 × 10⁻⁵, two-tailed *t*-test). Thus, in migrators, the oxygen supply capacity is higher (P = 1.76 × 10⁻⁹; two-tailed *t*-test) and relatively insensitive to temperature (P = 3.06 × 10⁻¹⁰, two-tailed *t*-test) compared with coastal marine animals.
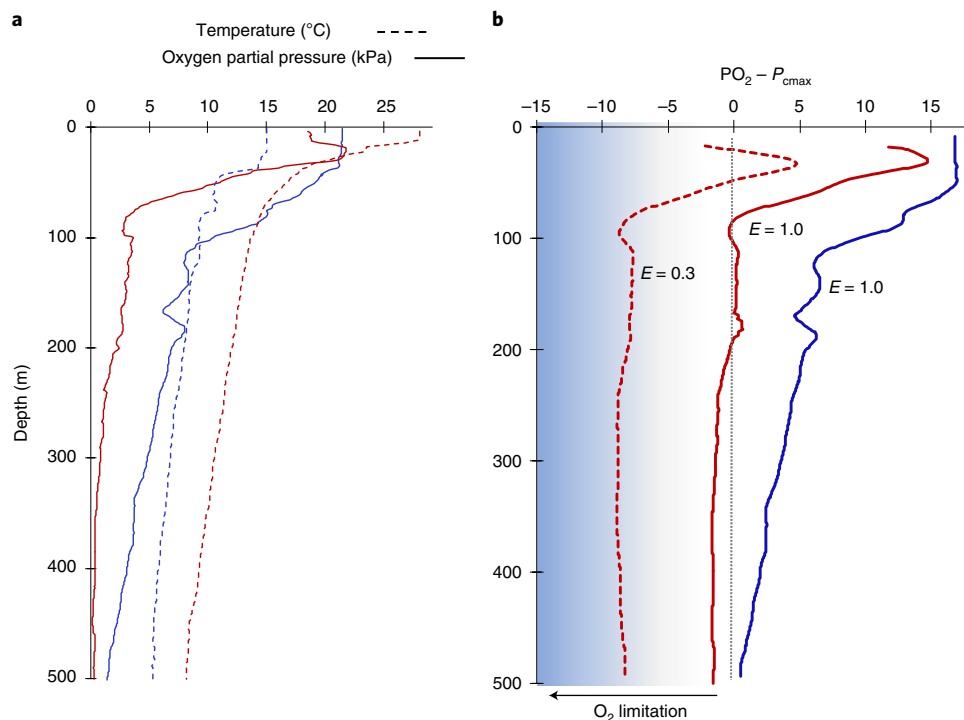
Fig. 3 | Oxygen and temperature limitation of MMR and its P_{cmax} for *Dosidicus gigas*. a, Representative oxygen and temperature profiles in the upper 500 m depth in the Gulf of California (red) and the California Current System (blue) were used to calculate P_{cmax}. **b**, The difference between PO_2 and P_{cmax} indicates depths at which MMR is increasingly oxygen limited (negative values, blue shading), which only occurs in the tropics (Gulf of California) and only if the temperature coefficient is less than 1.0 eV (dashed line indicates P_{cmax} calculated with a temperature coefficient of 0.3 eV, which is near the mean for MMR).

(1) it determines the lowest environmental PO_2 that can support a given metabolic rate (that is, P_c) and (2) it determines the maximum metabolic rate (MMR) achievable at a given environmental PO_2. Metabolism cannot increase with oxygen indefinitely, however, and above a certain environmental PO_2, the ability to both supply and utilize oxygen are maximized and MR cannot further increase. This limit is P_{cmax} (the P_c for MMR). Oxygen supply has evolved such that P_{cmax} approximates the lowest PO_2 that an organism persistently (longer than a diel or tidal cycle) encounters at a given temperature[23]. Thus, for most species measured to date, P_{cmax} is near air saturation (21 kPa) (ref. [28]), and any decline in PO_2 will result in a decrement in metabolic capacity.

The MR is typically measured either at rest in a fasted state (standard, SMR) or under maximum exertion (MMR), and aerobic scope is the factorial difference between these two rates (factorial aerobic scope, FAS; equation (2) and Fig. 1). A FAS greater than 1 permits metabolic rate to increase by that factor above SMR, and environmental PO_2 must exceed the P_c at that rate (P_{cSMR}) by that same factor to ensure sufficient oxygen availability. While FAS ranges between 1 and ~7 in acute temperature trials, a critical FAS value of ~3 is coincident with warm (Equatorward) range boundaries for a variety of species, providing a benchmark for metabolically available habitat[29].

$$\alpha = \frac{MR_1}{P_{c1}} = \frac{MR_2}{P_{c2}} \quad (1)$$

$$FAS = \frac{MMR}{SMR} = \frac{P_{cmax}}{P_{cSMR}} \quad (2)$$

The temperature sensitivity of metabolic traits is described here by the slope of an Arrhenius function (*E*, the temperature coefficient; Supplementary Information). Because the metabolic traits are related to each other, the temperature coefficients are also related (equation (3) and Extended Data Fig. 1a)[28,29].

$$E_a = E_{MMR} - E_{Pcmax} = E_{SMR} - E_{PcSMR} \quad (3)$$

Metabolic traits and their temperature sensitivity

We report SMR, P_{cSMR} and α at temperatures approximating day and night habitats for six vertically migrating euphausiids (krill) and for the jumbo squid, *Dosidicus gigas* (Supplementary Tables 1 and 2 and Fig. 2). For *D. gigas*, the compiled data include MMR (Supplementary Table 1). We further compile metabolic traits for a diversity of coastal marine animals (Supplementary Table 2). Across this diversity of species, α, the physiological capacity to extract oxygen from the environment and transport it to respiring tissues, spans two orders of magnitude. Among coastal species, the P_{cSMR} is much less variable than SMR between species or across temperatures (Fig. 2). Thus, most of the interspecific variability in α (SMR:P_{cSMR}) is accounted for by differences in metabolic rate, whether driven by temperature and size effects or by ecological differences (that is, activity)[28,29]. However, specific adaptation to low oxygen among mesopelagic species in oxygen minimum zones, such as the vertical migrators studied here, also drives an increase in α (refs. [12,33]). Across the measured temperature range, the mean α for the Eastern Pacific vertical migrators (3.84 μmol O_2 g^{-1} h^{-1} kPa^{-1}; Supplementary Table 1) is much higher than that for coastal marine species (0.64 ± 0.45 μmol O_2 g^{-1} h^{-1} kPa^{-1}).

For coastal species, the P_{cmax} is typically near air saturation and is independent of temperature[28]. Furthermore, the SMR is more temperature sensitive than P_{cSMR} (Supplementary Table 2), such that α increases with temperature with a similar coefficient to MMR (mean $E_\alpha = 0.31$ eV, $n = 20$ species; mean $E_{MMR} = 0.27$, $n = 7$ species (ref. [28])). Thus, in coastal species, as temperature increases, SMR approaches MMR, P_{cSMR} approaches the P_{cmax} and FAS declines towards 1, where the scope
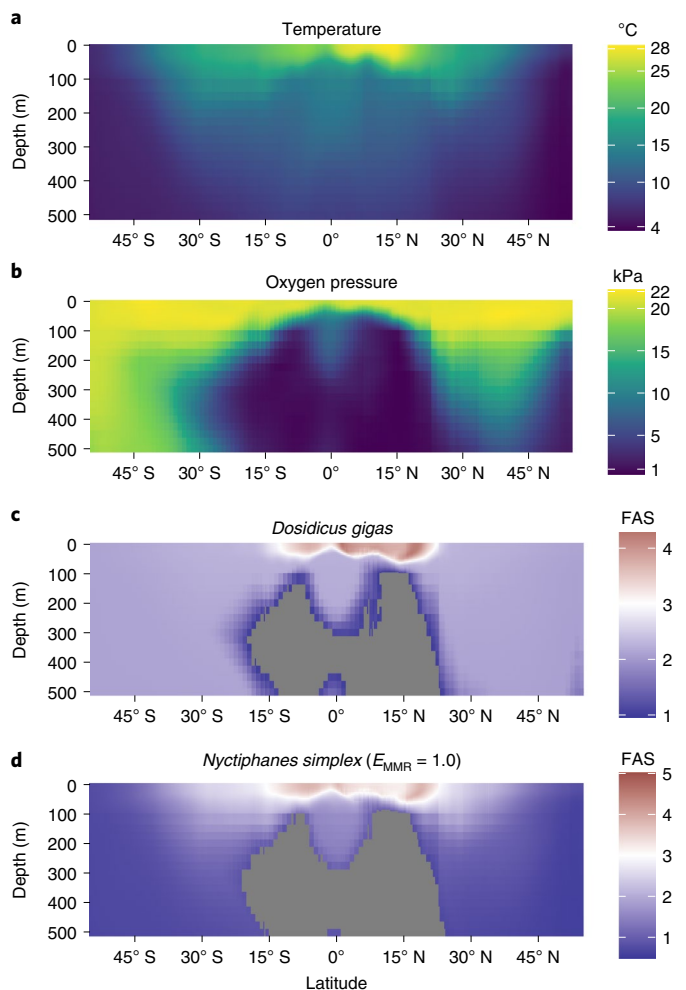
Fig. 4 | FAS and metabolically available habitat. a,b, Seawater temperature (**a**) and oxygen (**b**) profiles from 500 km to 2,000 km off the coast of the eastern Pacific Ocean (Extended Data Fig. 4; World Ocean Atlas 2018). **c**, Colour map of *Dosidicus gigas* FAS calculated using measured rates and temperature coefficients (Supplementary Table 1 and Extended Data Fig. 1) and environmental profiles (**a**,**b**). **d**, FAS of the euphausiid, *Nyctiphanes simplex*, estimated with a high (E_{MMR} = 1.0 eV) temperature coefficient for MMR. Calculations are anchored at 25 °C assuming that P_{cmax} is 21 kPa (air saturation) at that temperature. Grey shading indicates FAS < 1.

for activity beyond basic maintenance is nil. In these coastal species, the similar temperature coefficients for α and MMR suggest that oxygen supply evolves within air-saturated waters to match maximum oxygen demand across the temperature range[28].

The thermal sensitivity of tropical migrators is fundamentally different. The P_{cSMR} in the tropical migrators studied here is highly temperature sensitive with a coefficient equal to or greater than SMR. Thus, α (= SMR P_{cSMR}^{-1}) is relatively insensitive to temperature. In fact, α actually decreases slightly from 10 °C and 20 °C in all migrators (mean E_{α} = −0.21 eV, n = 7 species; Supplementary Table 2 and Fig. 2b). The relative temperature insensitivity means that the temperature coefficients for MMR and P_{cmax}, regardless of their absolute values, must be similar to each other (equation (3)). Thus, as MMR decreases with temperature, a lower environmental oxygen pressure is sufficient to meet that demand. If, due to a high temperature coefficient, P_{cmax} drops below ambient PO₂ at any depth, then MMR and FAS will depend only on temperature, and oxygen has no effect. In contrast, if P_{cmax} remains higher than environmental PO₂ at depth, then MMR and FAS will be oxygen limited.

Among migrators, the temperature sensitivity of MMR has been measured only in *D. gigas*. In this species, MMR does not scale in a typical exponential temperature-dependent manner. Instead, MMR is nearly insensitive to temperature between 10 °C and 20 °C (E_{MMR} = 0.21) and extremely temperature sensitive between 20 °C and 25 °C (E_{MMR} = 1.65; Extended Data Fig. 1). As a result, FAS increases dramatically in warm, shallow water and is very low at depth due to cold, regardless of ambient oxygen levels. In migrators, a high oxygen supply capacity in warm water supports high activity during migration to shallow, oxygenated water at night, while some residual aerobic capacity remains at cold depths in the pronounced OMZ.

Modelling aerobic scope and metabolically available habitat

To calculate FAS across latitudinal and depth gradients, we extracted temperature and dissolved oxygen (World Ocean Atlas 2018[34,35]) for a geographic band 500 km to 2,000 km off the western coast of the Americas between 55° S and 55° N and from 0 m to 500 m depth. Below the surface mixed layer, the oxygen and temperature gradients vary with latitude (Figs. 3a and 4a,b), being most pronounced in tropical OMZs[36]. We also modelled FAS across a latitudinal gradient using sea surface temperature data for the 1997–1998 El Niño and for Coupled Model Intercomparison Project (CMIP) 6 Shared Socioeconomic Pathway (SSP) 5–8.5 climate projections for the years 2021–2040, 2041–2060 and 2081–2100.

Throughout the native range for tropical diel migrators, surface waters are characterized by temperatures >25 °C and air-saturated waters (Fig. 4a,b). Using this as a starting point, we calculated MMR at 25 °C (from equation (2)), assuming P_{cmax} is air saturation (21 kPa) at that temperature, as has been shown in *D. gigas*. At 25 °C, the measured MMR for *D. gigas* was very similar to that calculated for air-saturated waters at that temperature based on equations (1)–(3) (ref. [37]) (Supplementary Table 2). The calculated P_{cmax} very closely matches the environmental PO₂ across the depth range in the squid's native habitat (Fig. 3b) despite being calculated from metabolic traits measured in air-saturated water. For euphausiids, the calculated MMR resulted in FAS ranging from 4 to 6, which is at the upper end of the range measured for a diversity of species[28,38,39], supporting the approach.

From the 25 °C and 21 kPa starting points, we modelled FAS using measured temperature coefficients for SMR and P_{cSMR}. FAS was calculated for every latitudinal and depth bin. For *D. gigas*, we used measured temperature coefficients for MMR while, for euphausiids, we used a continuous range of possible coefficients to assess their effects on modelled FAS (Fig. 3 and Supplementary Fig. 3d). Within the native tropical range, any temperature coefficient (E_{MMR}) less than -1.0 eV resulted in modelled P_{cmax} values that were higher than the ambient PO₂ for all migrators at all depths below the shallow mixed layer (Fig. 3a and Supplementary Fig. 3d). In that case, MMR would be oxygen limited, declining in proportion to PO₂. In contrast, higher temperature coefficients (E_{MMR} > 1.0 eV), such as that measured for *D. gigas*, result in a P_{cmax} below the ambient PO₂ across the inhabited depth range (Fig. 3a). The MMR is not oxygen limited in that scenario, but it declines with depth due to temperature to values that are as low or lower at all depths than they would be if they were oxygen limited (Figs. 4c,d and 5). Thus, FAS for these tropical migrators must decline with depth at least as fast as ambient PO₂ regardless of its temperature sensitivity.

For all migrators studied, FAS currently reaches values greater than 3 (the benchmark for population viability based on warm boundaries in marine species) only in the upper -200 m of the water column, coincident with the known nighttime distribution for most migrators, throughout their native range (-20° N to 20° S; Fig. 4c,d and Supplementary Fig. 4). FAS declines below 1 at deeper daytime depths (200–400 m) in some regions. Survival at such depths is achieved via metabolic suppression which reduces total energy demand by 50–80% relative to SMR[10,11,40,41]. The prevalence of daytime metabolic
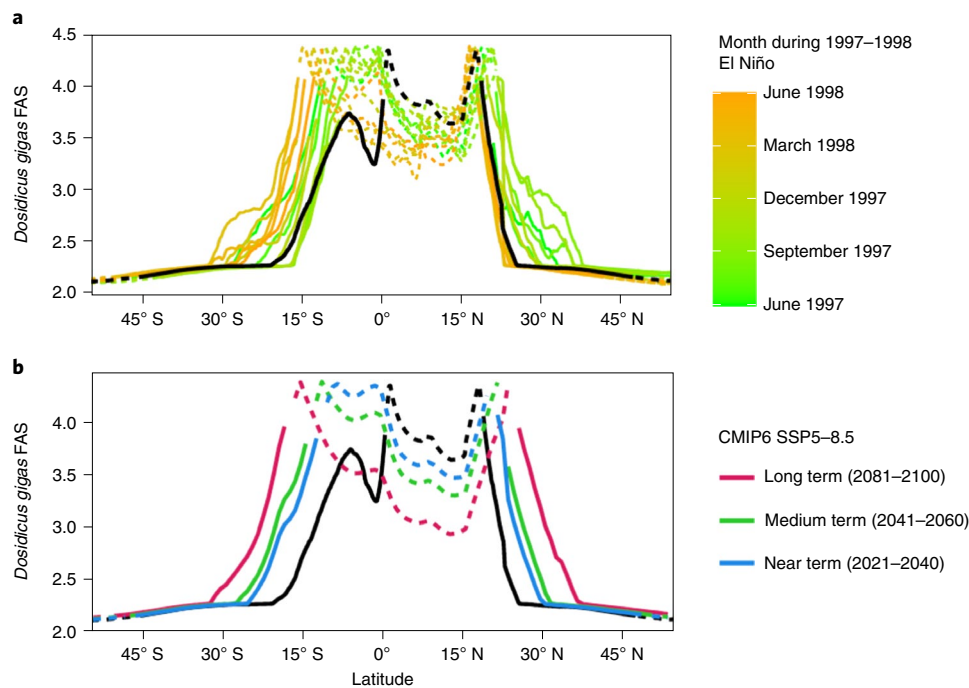
Fig. 5 | FAS and metabolically available habitat. a, *Dosidicus gigas* FAS in surface waters plotted for the current condition (thick black line) and for the 1997–1998 El Niño (orange to green coloured lines). Dashed lines indicate extrapolation beyond the measured temperature range (10–25 °C). **b**, *D. gigas* FAS in surface waters plotted for the current condition (thick black line) and for near, medium and long-term projections of anticipated sea-surface temperatures (SST) from the CMIP6 SSP5–8.5 model.

suppression among migrators supports our argument that high metabolic rates are not required at depth.

FAS in surface waters declined below 2–3 at the edge of their native latitudinal range, a pattern that was robust across a 95% confidence band of Monte Carlo simulations of the measured physiological traits for *D. gigas* (Extended Data Figs. 2 and 3). Higher latitudes are metabolically unavailable (FAS < 3) for *D. gigas* due to persistent cold and the squid's high thermal sensitivity of MMR. For other migrators, the thermal sensitivity of MMR has not been directly measured. However, temperature coefficients for MMR less than 1.0 eV (Extended Data Fig. 1d) would suggest excess metabolic capacity at cold temperatures that could never be utilized in their native habitat due to oxygen limitation at depth. Thus, low-temperature sensitivity of MMR is unlikely to have evolved, consistent with the direct measurements in *D. gigas*. A coefficient greater than -1.0 eV will nevertheless result in low aerobic scope across the entire depth range in temperate waters, acting as an energetic barrier to range expansion (Figs. 4–6 and Extended Data Fig. 4). Notably, FAS also increases with temperature in at least one euphausiid from the California Current[42], suggesting that similar cold-water barriers to range expansion also exist for temperate migrators. However, our model shows that warmer waters, such as those experienced during the El Niño in 1997–1998 and that will be reached with climate change over the next several decades, are sufficient to expand metabolically available habitat by ~10–20° N and S (Fig. 5).

Analysis of climate change effects on the native habitat requires extrapolation beyond the measured temperature range and ignores the potential for other mechanisms to set critical temperatures. Noting those caveats, modelled aerobic scope does decline in the native tropical habitat as temperatures exceed 25 °C in surface waters due to a continual increase in oxygen demand while supply is constrained by atmospheric PO$_2$ (Figs. 4c and 5). However, even under the climate change projections, FAS never declines to values near those currently achieved in temperate waters (~2.2; Fig. 5b).

Ocean de-oxygenation due to climate change[10] would have to lower PO$_2$ by more than 50% in temperate waters to limit FAS (Fig. 6). Even if oxygen were limiting (that is, if PO$_2$ < P_{cmax}), FAS would decline by only 1 P$_{cmax}^{-1}$ (that is ~5% per kPa PO$_2$ in surface waters). Such small changes will have a negligible effect on these migrators in temperate waters and are unlikely to have much effect at any latitude because PO$_2$ would have to decline beyond any reasonable projections to reduce FAS to values currently observed at cold temperatures (Fig. 6). Thus, in the context of de-oxygenation, the most likely effect of climate change is a modest compression of the native habitat between warming surface waters and the potentially expanding OMZ (Fig. 6b).

Discussion

Oceanic species that migrate daily across strong, persistent and correlated gradients in light, temperature and oxygen possess a unique metabolic temperature sensitivity. Our results suggest that the capacities for oxygen supply and demand are driven by ecological pressures rather than thermodynamic influences or environmental limitations. Low light levels at depth restrict visual predator–prey interactions, reduce selection for metabolic capacity[31] and provide a daytime refuge from predation for vertical migrators[43]. Locomotory activities have been estimated for vertical migrators across the depth range using biologging[44], acoustics[45,46], in situ observations[47,48] and laboratory measurements[37,42]. This mounting evidence suggests that most vertically migrating species are largely inactive at depth during the daytime. Selective pressure for metabolic capacity to support activity for predator–prey interactions in warm, shallow water and the absence of such selection at depth result in enhanced temperature sensitivity of active metabolism in vertical migrators.

At low temperature, aerobic scope is low, even when measured in air-saturated waters, because low temperature is experienced only at depth where high metabolic capacity is not required and has not evolved. Thus, temperature appears to act as a metabolic regulator beyond thermodynamic constraints. Physiological oxygen supply
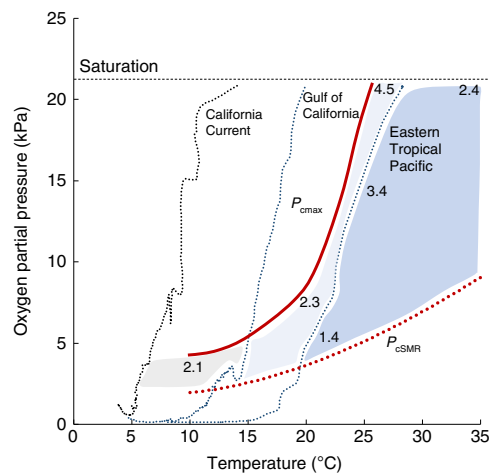
Fig. 6 | Critical oxygen pressures for standard and maximum metabolism for _Dosidicus gigas_ as a function of temperature. Representative regional oxygen pressure profiles are shown (dashed lines). Where P_{cmax} > PO_2 in a given region, aerobic scope is oxygen limited (shading). Numbers and their placement on the plot indicate the FAS at that temperature, oxygen pressure and region. In the California Current (black line and shading), FAS is low due to temperature, and oxygen is not limiting until temperatures near 5 °C in the core of the OMZ there (~600 m depth). In the Gulf of California (light blue line and shading) oxygen becomes limiting only below 15 °C. In the Eastern Tropical Pacific (dark blue line and shading), oxygen is limiting at all depths, but aerobic scope is nevertheless high at high temperatures.

capacity is high in migrators at all temperatures, reflecting the extreme temperature sensitivity of the underlying oxygen transport mechanisms[49,50] and supporting high activity in warm, aerated surface waters and the diminished oxygen requirements in the OMZ at depth.

We propose that the low aerobic scope in cold water precludes persistent occupation of temperate waters by tropical migrators. There, FAS is low across the typically inhabited depth range due to temperature while oxygen has no effect on tropical migrators in temperate waters (Figs. 3 and 4 and Extended Data Figs. 5–7). At these higher latitudes, FAS does not surpass 3, even at the surface, probably rendering this habitat metabolically unavailable (Fig. 4c,d and Extended Data Figs. 6 and 7). If so, the reported range expansions to high latitudes by squids[23] and krill[20] could occur only following warming events (for example, El Niño; Fig. 4a). Modest warming, such as that occurring during the 1997–1998 El Niño, elevated aerobic scope throughout temperate waters and expanded metabolically viable habitat by 10–20° N and S (Fig. 5). Ocean warming due to climate change may similarly expand metabolically available habitat at these higher latitudes, permanently altering oceanic ecosystems.

We have shown for tropical vertical migrators that (1) the oxygen supply capacity is high and relatively independent of temperature, (2) accordingly, MMR and its critical PO_2 change with temperature in proportion to each other and (3) FAS declines with depth throughout the native habitat due to temperature. Low oxygen may further restrict FAS at depth in extreme OMZs, but high oxygen confers no benefit in cold water. These findings imply that temperature mediates metabolism in response to ecological demands for activity beyond simple thermodynamic effects on biochemical reaction rates.

Ocean warming is believed to cause a poleward drift in the thermal performance window for marine ectotherms and extirpation of animals from their native range[51]. Ocean de-oxygenation is predicted to compress available habitat, especially where the OMZ is shallow and intruding on the daytime habitat of vertical migrators[52]. In contrast to these predictions, we suggest that a modest increase in temperature, such as that associated with the 1997–1998 El Niño or projected with climate

change (Fig. 5a), will result in a dramatic expansion of available habitat at higher latitudes for vertical migrators. While we lack measurements beyond 25 °C, our model predicts minimal loss of habitat in their native tropical range, despite ongoing warming and de-oxygenation (Fig. 6 and Extended Data Fig. 6). These opposing views predict different timing and extent of species' distributional shifts due to climate change with consequences for the resulting community assemblages.

Online content

Any methods, additional references, Nature Research reporting summaries, source data, extended data, supplementary information, acknowledgements, peer review information; details of author contributions and competing interests; and statements of data and code availability are available at https://doi.org/10.1038/s41558-022-01491-6.

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Methods

Data compilation

The metabolic traits (SMR, P_{cSMR}, α) and their temperature coefficients (E) are derived from laboratory measurements at multiple temperatures. These metabolic traits are reported in Supplementary Table 1 (*Dosidicus gigas*, including maximum metabolic rate) and 2 (vertical migrators and coastal species). Measurements for four euphausiid species are reported here for the first time. All others are from published literature (Supplementary Table 2). Coastal species are those known to live predominantly in shallow, well-oxygenated waters over the continental shelf. Only crustaceans, cephalopods and fish are considered here as they possess reasonably comparable oxygen transport systems, inclusive of gills, respiratory proteins and at least partially closed circulatory systems. Except for *D. gigas*, all species' metrics are reported only within a narrow body size range, insufficient for confident scaling analysis. Metabolic rates typically decline with body mass (M) according to MR = aM^b, where a is a normalization constant and b is a scaling coefficient that describes the slope of the relationship. The scaling coefficients for metabolic traits are related to each other as in equation (4). If SMR declines with size but P_c does not, oxygen supply capacity will decline with size (equation (4) (ref. [28])). P_{cSMR} is insensitive to body mass for *D. gigas*. However, b for SMR is also relatively shallow ($b \sim -0.1$; Extended Data Fig. 1c) compared with most species ($b \sim 0.25$). If P_{cmax} does not change with size, oxygen supply capacity will match MMR regardless of size (equation (4)). In any case, *D. gigas* metabolic rates were normalized to 100 g body mass using measured scaling coefficients (Extended Data Fig. 1c).

$$b_{\alpha} = b_{MMR} - b_{Pcmax} = b_{PSMR} - b_{Pc} \qquad (4)$$

Animal capture

For four zooplankton species (euphausiids), live experiments were conducted according to ref. [12]. Animals were collected using a modified Tucker trawl, which used standard MOCNESS control software and sensors and had a large insulated cod end to maintain species at their ambient (capture) temperatures when brought to the surface alive. A month-long research expedition from Manzanillo, Mexico, to San Diego, California, on the *R/V Sikuliaq*, cruise number SKQ201701S, occurred from 19 January to 15 February 2017 and was centred at 21.6° N, 117.8° W, an area with a strong OMZ.

Respirometry

Shipboard respiration measurements of key species (euphausiids) determined their oxygen supply[25] at 10 °C and 20 °C. Following 6- to 12-hour acclimation at experimental temperature and air-saturated water, animals were placed in darkened sealed chambers filled with 0.2 μm filtered seawater treated with antibiotics (25 mg l^{-1} each of streptomycin and ampicillin) to minimize microbial respiration. Chamber size ranged from 2 ml to 50 ml, resulting in a ratio of chamber volume to animal mass of ~10 to 100. Seawater PO_2 (oxygen partial pressure) was measured optically with a Loligo Systems Witrox 4 or PyroScience FireSting O_2 meter. Animals were allowed to consume the ambient oxygen until the PO_2 declined to a level insufficient to support their oxygen-consumption rate. Individual trial durations ranged from 6 hours to 48 hours. Temperature was maintained with Lauda E100 and Thermo Fisher Scientific NESLAB RTE-7 water baths. Oxygen meters were calibrated with air-saturated seawater and concentrated $NaSO_3$ solution. Chambers were stirred with magnetic stirrers (Cole–Parmer Immersible Stirrer EW-04636-50). After the experiments were completed, animals were frozen at −80 °C before being weighed.

Oxygen supply capacity

Oxygen supply capacity was calculated as SMR P_c^{-1} for species with available published rates. For four euphausiid species, oxygen supply capacity was directly determined[32]. The MR, measured as above, was monitored as oxygen declined. Each trial was divided into discrete time bins to calculate multiple MR values over each trial. Bins of 1/10th the trial duration were used at the highest PO_2 values (where precise rate measurement was a priority) and 1/100th the trial duration at the lowest PO_2 values (where good PO_2 resolution was a priority). For each measurement period, MR was divided by the corresponding PO_2 to provide the concurrent oxygen provision (α_0 = MR PO_2^{-1}). The average of the highest three α_0 values was designated as α, the oxygen supply capacity. In each trial, the α is the slope of a line describing the rate dependence of P_c (P_c = MR α^{-1}). The same value of α is reached at P_c for any MR regardless of previous or subsequent metabolic activity. Six representative trials, including three at each temperature, are provided for each of four species (Extended Data Figs. 7–10).

Mapping physiological parameters for all species

To calculate FAS plots, environmental data (temperature and dissolved oxygen) were pulled from the World Ocean Atlas 2018[34,35] for a geographic band 500 km to 2,000 km off the western coast of the Americas between 55° S and 55° N and across 37 depth bins from 0 m to 500 m depth. This range covered temperatures from 2.7 °C to 29 °C and oxygen levels from 0.1 kPa to 22.5 kPa. Measured SMR, P_{cSMR} and α values and their temperature dependencies (E values) were drawn from Supplementary Table 2 for each species examined here. Then, these values were computed at any given temperature within the geographic range by the 'adj_by_temp()' function from the respirometry v.1.4.0 R package[53]. For all species, P_{cmax} at 25 °C was assumed to be 21 kPa, because this is the average sea surface temperature in the eastern tropical Pacific, and marine animals that live in the mixed layer have a P_{cmax} near 21 kPa (ref. [28]). MMR at 25 °C was estimated by 21 kPa × $\alpha_{25°C}$, and its temperature sensitivity (E_{MMR}) was defined as either 0.3, which is the approximate mean value for coastal fish in Supplementary Table 2, or 1.0 eV, a value chosen as the minimum that avoids oxygen limitation (Extended Data Fig. 1d). E_{MMR} has not been determined in any species examined here except *Dosidicus gigas* (below). Temperature-dependent MMR (MMR$_T$) was defined for any given temperature based on this starting value and E_{MMR}.

From these primary metrics, the following additional metrics were derived for every cell in the environmental array:

$$MMR_{PO_2} = \frac{P_{O_2}}{P_{cSMR}} \times SMR$$

$$MMR_{T*} = \frac{SMR}{P_{cSMR}} \times P_{cmax}$$

*using measured or modelled temperature coefficients for each metric.

$$FAS_{PO_2} = \frac{MMR_{PO_2}}{SMR}$$

$$FAS_T = \frac{MMR_T}{SMR}$$

$$MMR_{min} = \min\{MMR_{PO_2}, MMR_T\}$$

$$FAS_{min} = \min\{FAS_{PO_2}, FAS_T\}$$

$$P_{cmax} = FAS_T \times P_{cSMR}$$

The average of all observations at a given 0.25° latitude bin and depth ($n \approx 50$–90 depending on latitude) was computed for all metrics.

Mapping physiological parameters for *Dosidicus gigas*

Mapping of physiological parameters to the environmental data was similar for *Dosidicus gigas* as for other species, except that MMR data (in addition to SMR) are available for this species and thus measured MMR and E_{MMR} were used rather than computed metrics. Interestingly,

MMR does not scale in a typical exponential temperature-dependent manner. Instead, MMR is quite temperature insensitive between 10 °C and 20 °C ($E_{MMR} = 0.21$) and extremely temperature sensitive between 20 °C and 25 °C ($E_{MMR} = 1.65$; Extended Data Fig. 1). Thus, when mapping FAS in relation to the environmental data, $E_{MMR} = 0.21$ was used when $T < 20$ °C and $E_{MMR} = 1.65$ was used when $T \geq 20$ °C to most accurately align to the measured characteristics of the species.

Mapping *Dosidicus gigas* FAS during the 1997–1998 El Niño and climate change

Sea surface temperature was pulled from the National Oceanic and Atmospheric Administration's (NOAA) Daily Optimum Interpolation Sea-Surface Temperature (DOISST) v2.1 dataset for the first day of each month from June 1997 through June 1998[54]. The CMIP6 SSP5–8.5 projection for the years 2021–2040, 2041–2060 and 2081–2100 were similarly used to project sea surface temperature. Mapping of physiological metrics for *Dosidicus gigas* to these datasets was identical to that described above for the WOA data except that oxygen data were not available so were assumed to be 21 kPa at the surface. The FAS for the El Niño and climate change time series was then compared with the surface FAS values from the World Ocean Atlas (WOA) data.

Mapping model sensitivity analysis

A Monte Carlo simulation was run to determine the sensitivity of the mapping model to underlying variation in physiological measurements for the squid *Dosidicus gigas* (Extended Data Fig. 2). For each measured physiological trait (SMR, MMR and P_{cSMR}), 5,000 draws were made from a normal distribution with mean and standard deviation matching the mean and standard error of that trait (Supplementary Table 1). In each iteration, the complete mapping model described above was simulated. The 2.5 and 97.5 percentiles of each derived trait (for example, FAS, P_{cmax}) at each latitude and depth bin across all 5,000 iterations were compiled, thus representing a 95% confidence interval for each spatial bin.

The results of this analysis indicate that while the absolute values may shift, the trend remains constant across the 95% confidence interval that FAS is ≥ 3 at the surface between about 15° S and 20° N and falls below 3 at higher latitudes (Supplementary Fig. 5a–c), matching well to the native range boundary for this species.

We also ran this sensitivity analysis with a 'normal' exponential temperature dependence (fixed E value across all measured temperatures) to ensure that the reliability of our model was not over-estimated in cold-water regions where the low-temperature dependence of metabolism may underestimate variability. In nearly all latitude and depth bins, the use of fixed E values for metabolic rates would have led to confidence intervals that were nearly the same or smaller than the model using changing E values to best fit the observed data. The code used in our analysis is available on Github[47].

Reporting summary

Further information on research design is available in the Nature Research Reporting Summary linked to this article.

Data availability

World Ocean Atlas temperature and oxygen data (woa18_decav_t00_04.nc and woa18_all_O00_01.nc, respectively) are available at https://www.ncei.noaa.gov/access/world-ocean-atlas-2018/. CMIP6 climate projections are available at https://interactive-atlas.ipcc.ch/39965d78-e97e-42af-b488-b1e1f4d32f75. NOAA's DOISST v2.1 dataset is available at https://www.ncei.noaa.gov/data/sea-surface-temperature-optimum-interpolation/v2.1/access/avhrr/.

Code availability

All code used in the production of this manuscript are available at https://github.com/matthewabirk/DVM_temp_sensitivity (https://zenodo.org/badge/latestdoi/506078504).

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Author contributions

B.A.S. conceived of the project and wrote the original draft. Both B.A.S. and M.A.B. contributed to all other aspects of the manuscript including methodology, validation, formal analysis, data curation and review and editing.

Competing interests

The authors declare no competing interests.

Additional information

Extended data is available for this paper at https://doi.org/10.1038/s41558-022-01491-6.

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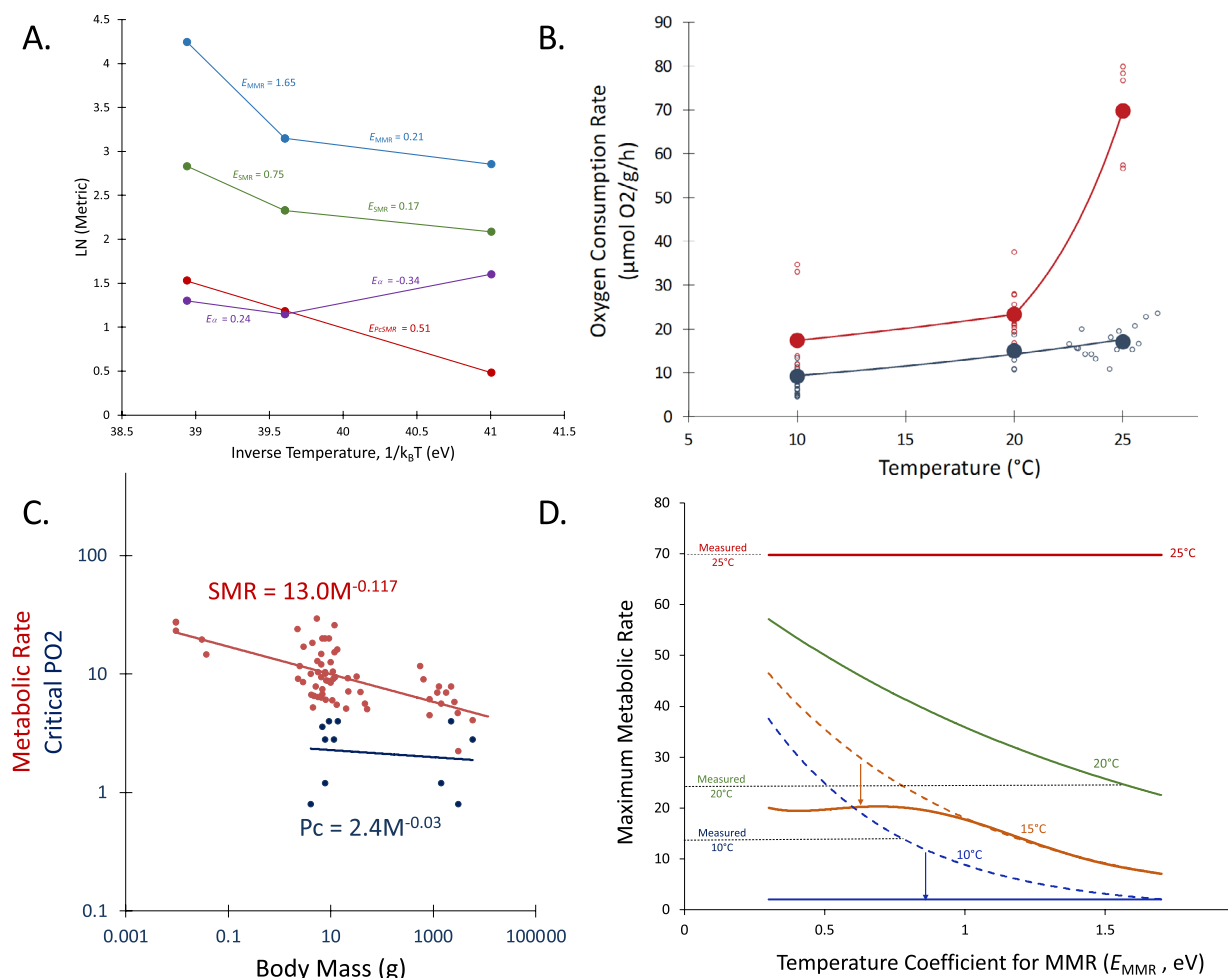
Extended Data Fig. 1 | *Dosidicus gigas*: Temperature and mass effects on metabolic traits. a. The temperature dependence, *E* (eV), of each metric (SMR, MMR, P_{cSMR} and α, was determined from the slope of the linear regression of $1/k_BT$ versus the natural logarithm of each metric (for *Dosidicus gigas*), where T is absolute temperature (K) and k_B is the Boltzmann constant. Note that, to avoid the confusion when using inverse temperature plots, the sign for each temperature coefficient is reversed (that is temperature coefficients are positive when a metric increases with temperature). **b**. Oxygen-consumption rates recorded at rest (blue, mass-normalized, SMR) and during exercise (MMR, red). The effect of temperature between 10 and 20 °C is similar for MMR and SMR. The effect of temperature is much higher for MMR compared to SMR between 20 and 25 °C. The metabolic rates are normalized to a common body mass (100 g) using

the scaling coefficients in panel C. **c**. SMR and P_{cSMR} as a function of body mass (M) at 10 °C (SMR = 13.03 $M^{-0.12}$ and P_{cSMR} = 2.44 $M^{-0.03}$). **d**. The effect of temperature coefficient on MMR in the Gulf of California (solid lines) and in the California Current System (dashed lines) at different temperatures. The difference between dashed and solid lines at a given temperature (arrows) is due to oxygen limitation in the Gulf of California and the lack of oxygen limitation in the California Current. The measured rates are indicated by black dashed lines. This figure indicates that a temperature coefficient for MMR less than 1.0 eV results in oxygen limitation of maximum metabolic rate whereas a coefficient greater than 1.0 eV results in temperature depression of metabolism at cold temperatures and no effect of low oxygen except at the coldest, deepest daytime depths (-300 m, 10 °C, PO_2 < 0.5 kPa).
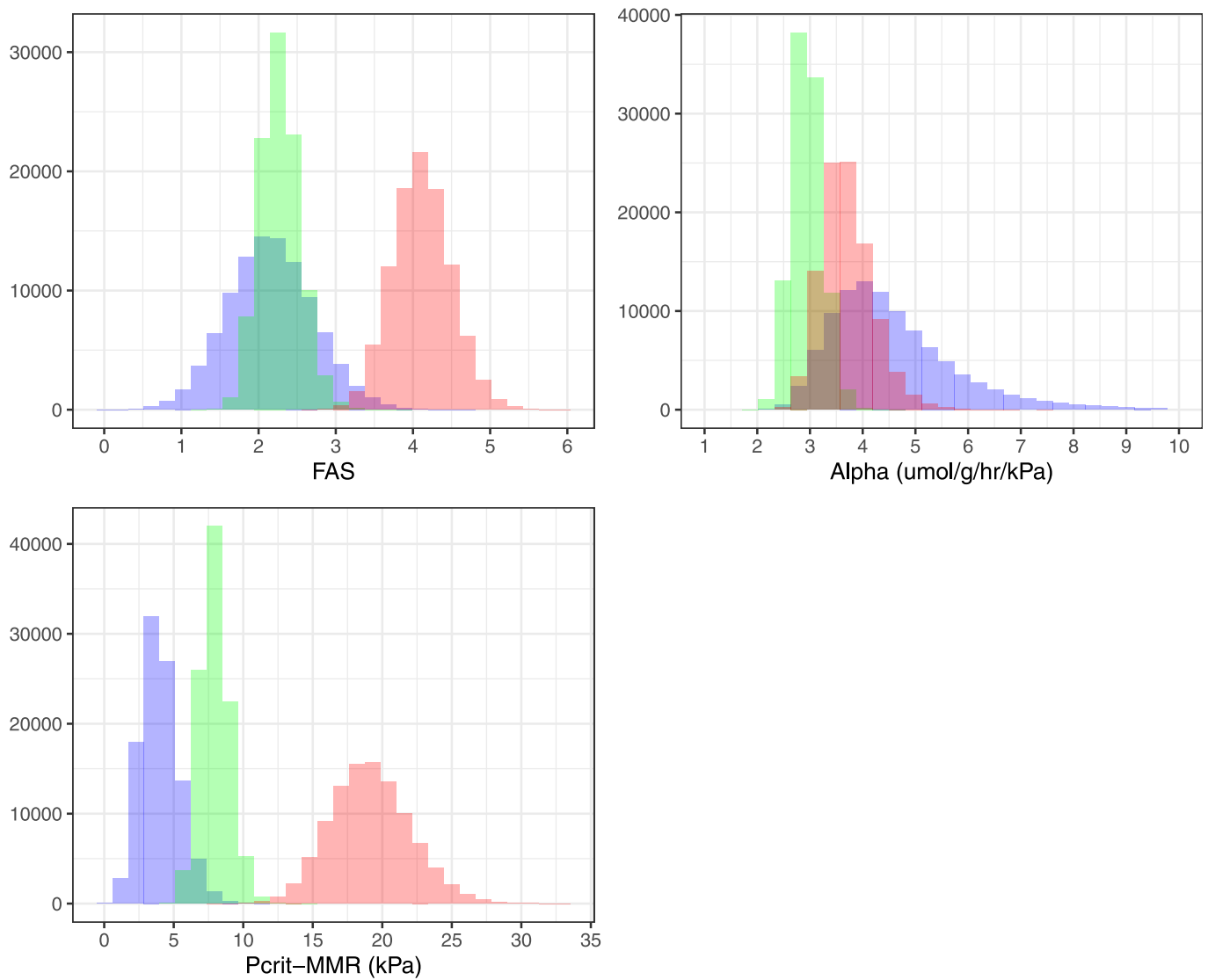
Extended Data Fig. 2 | The precision of derived metrics based on the variability of measured physiological metrics. A Monte Carlo simulation was conducted for each measured metric (that is SMR, MMR, and P_{cSMR}) of 100,000 draws from a normal distribution with each measured metric's mean and standard error. For each simulation, FAS = MMR/SMR, alpha = SMR/P_{cSMR}, and P_{cmax} = MMR/α. FAS is higher at 25 °C (red) than 10 (blue) or 20 °C (green), and P_{cmax} at 10 and 20 °C is much lower than at 25 °C where it averages near air saturation.
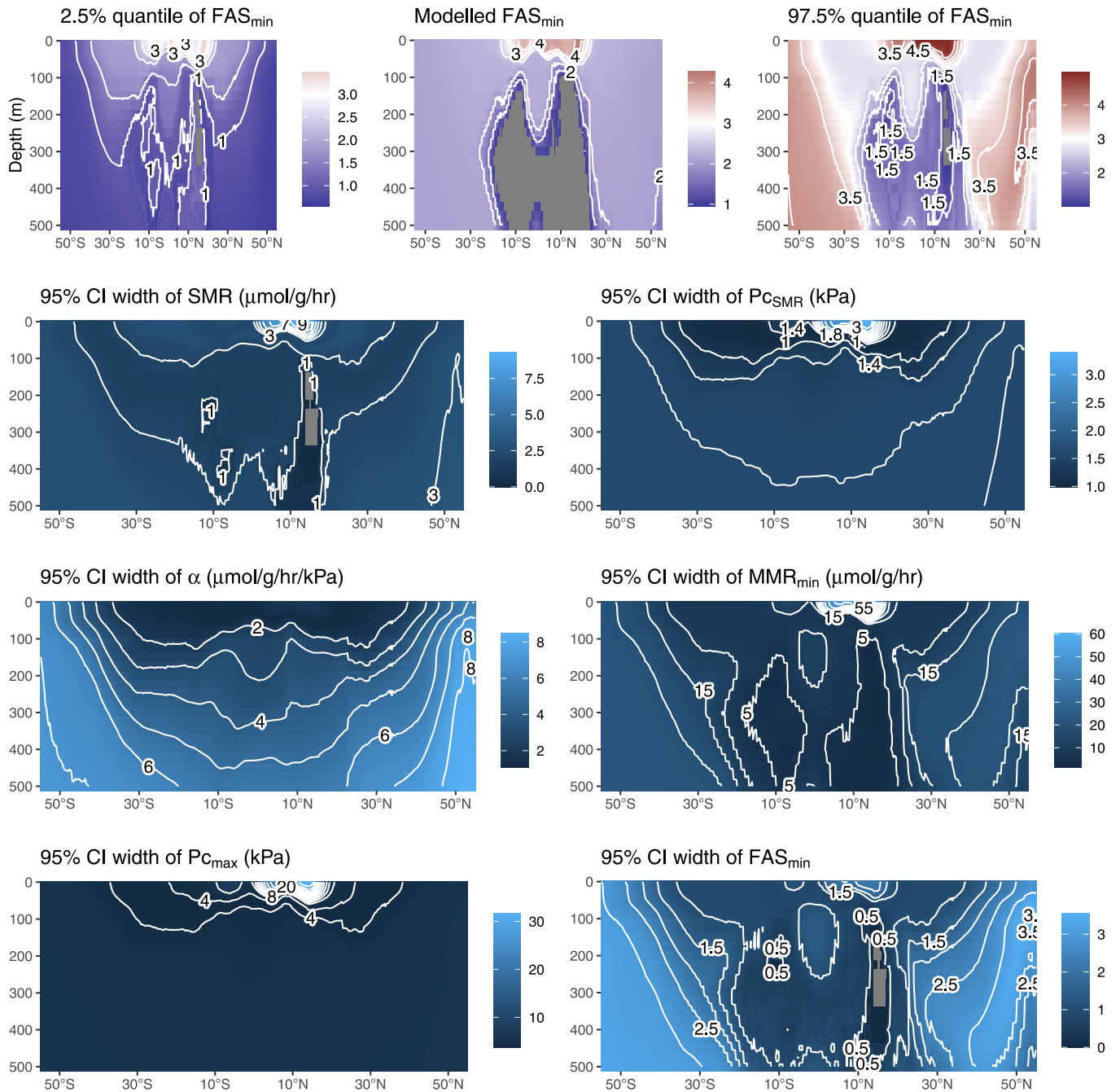
Extended Data Fig. 3 | Sensitivity analysis for each measured metabolic metric. Top row, the modelled factorial aerobic scope (FAS; centre) and the lower (left) and upper (right) confidence band. The lower panels show confidence interval isolines for each metric. In surface waters at low latitudes, for example,
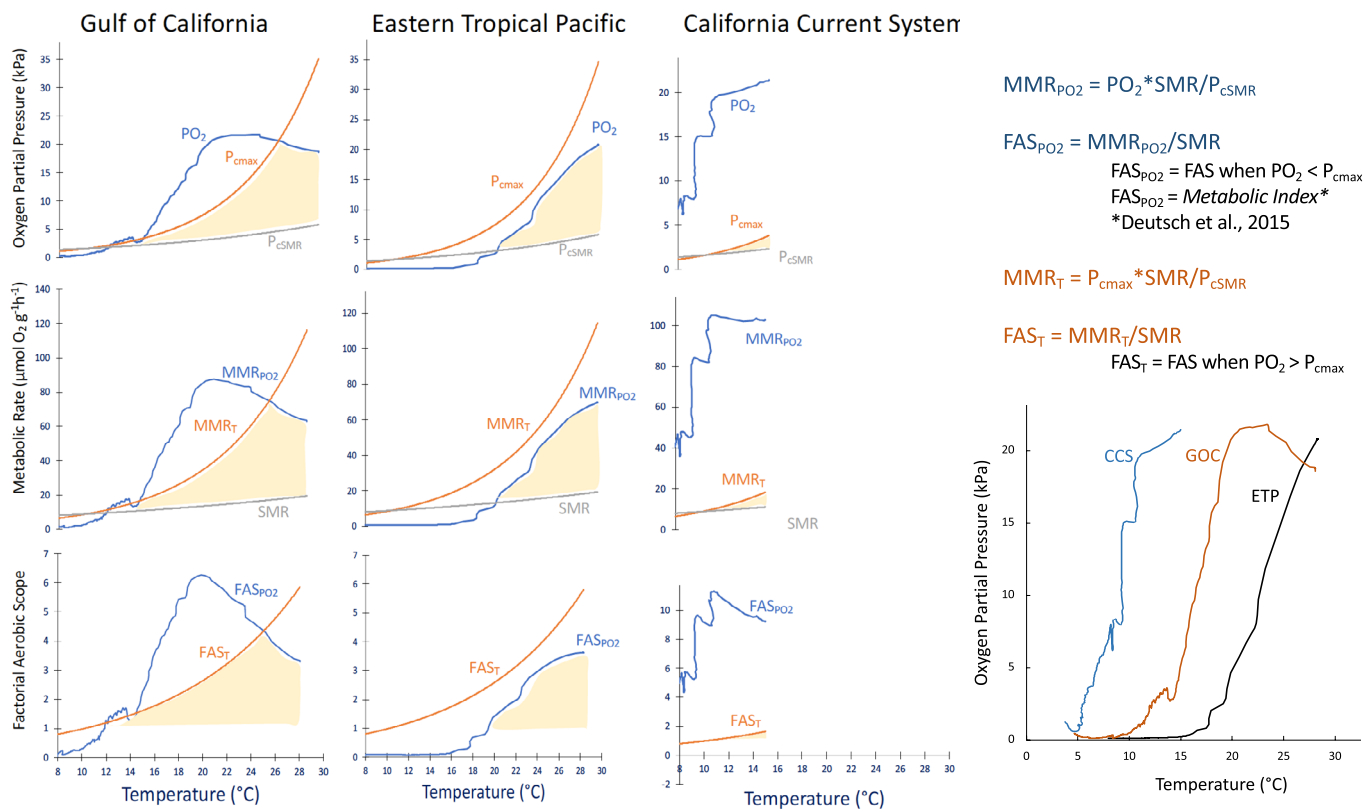
the modelled P_{cSMR} used to create Fig. 4c has a 95% CI range of 2.6 kPa (that is ± 1.3 kPa). For most of the metrics, the greatest variability is at higher temperatures where the underlying physiological measurements are higher and more variable and temperature sensitivities (E) are high.
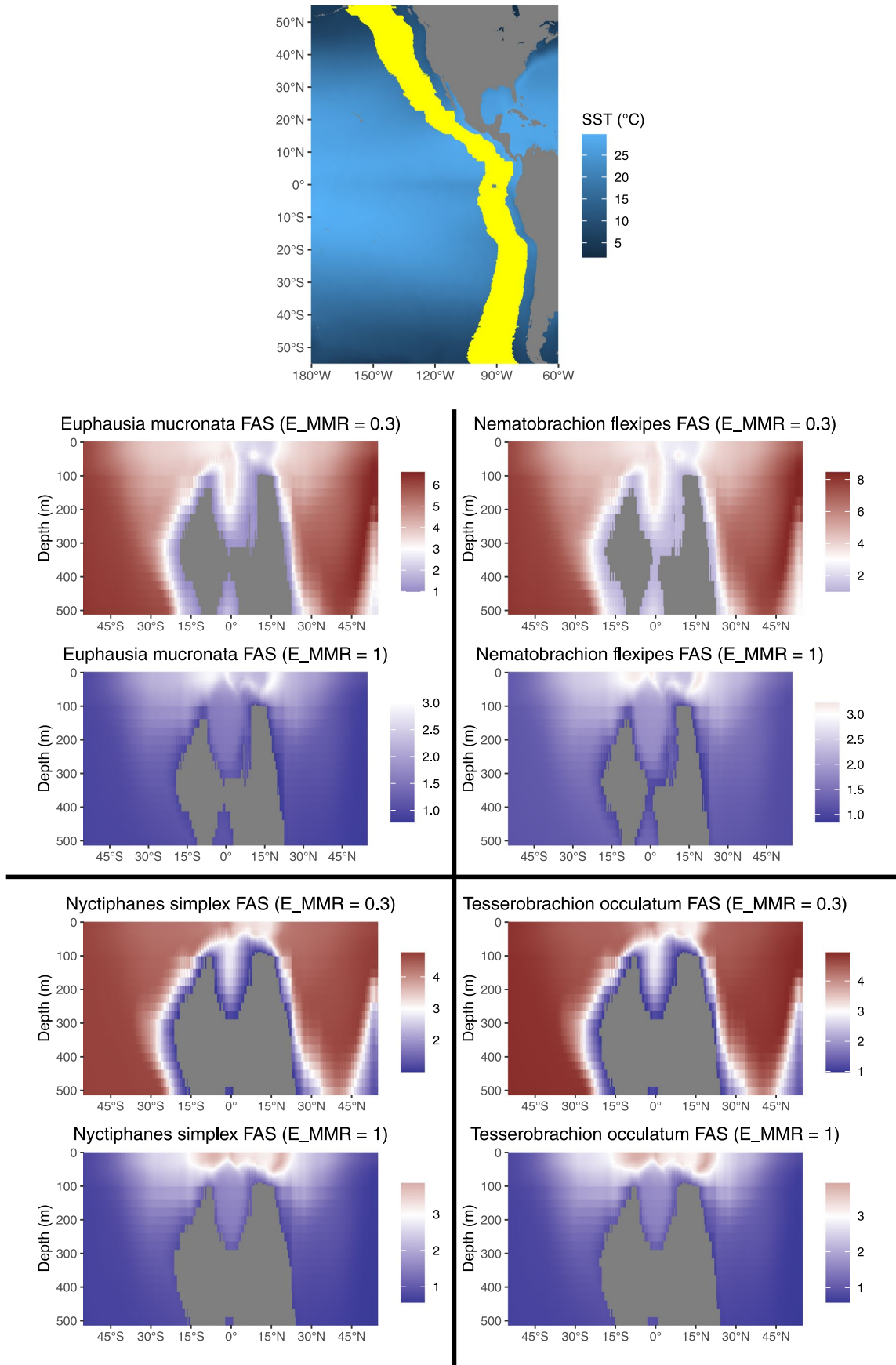
**Extended Data Fig. 4 | See next page for caption.**

Extended Data Fig. 4 | Modelled factorial aerobic scope (FAS) across a latitudinal and depth transect for four euphausiid species. Top) Yellow band shows the geographic area included in analysis 500 to 2000 km off the western coast of the Americas between 55°S and 55°N. In each subsequent panel pair, the top panel is calculated assuming the temperature coefficient (E) for MMR is 0.3 eV and the bottom panel assumes $E_{MMR} = 1.0$. The grey regions indicate that

PO_2 is less than P_{cSMR} and metabolic scope is nil. With the higher temperature coefficient, metabolically suitable habitat (FAS > 3) is present only in the upper 200 m from about 15°S to 30°N, with highest FAS achieved only in the native range. More poleward habitat is constrained due to the high temperature coefficient. With a low-temperature coefficient, the poleward latitudes are metabolically available but underfilled by these tropical migrators.

$$MMR_{PO2} = PO_2 * SMR/P_{cSMR}$$

$$FAS_{PO2} = MMR_{PO2}/SMR$$

FAS_{PO2} = FAS when $PO_2 < P_{cmax}$
FAS_{PO2} = *Metabolic Index**
**Deutsch et al., 2015*

$$MMR_T = P_{cmax} * SMR/P_{cSMR}$$

$$FAS_T = MMR_T/SMR$$

FAS_T = FAS when $PO_2 > P_{cmax}$

Extended Data Fig. 5 | The interrelationships between metabolic traits provides quantitative projection of aerobic scope. P_{cmax} and P_{cSMR} (top); MMR and SMR (middle) and FAS (bottom) as a function of temperature in three different regions using representative oxygen and temperature profiles (inset, right). Yellow shading represents the achievable factorial aerobic scope (lower of FAS_T or FAS_{PO2}). MMR_{PO2} and FAS_{PO2} (equivalent to the *Metabolic Index*[27]; blue lines) are accurate when PO_2 is less than P_{cmax} (O_2-limited). MMR_T and FAS_T (orange lines) are accurate when PO_2 is greater than P_{cmax} (not O_2-limited). Temperature trends (orange lines) are calculated using measured rates and coefficients for

Dosidicus gigas. Note that, in all three regions, FAS is low at low temperature due to the strong effect of temperature. In the California Current (CCS), FAS is driven by temperature at all depths. In the most hypoxic regions of the Eastern Tropical Pacific (ETP), PO_2 is consistently lower than P_{cmax} and MMR and FAS are, thus, oxygen limited at all depths. In the Gulf of California (GoC), oxygen becomes limiting at depth (cold) or at high temperatures where P_{cmax} is projected to exceed air saturation. No measurements have been made at temperatures beyond 25 °C. Dashed black lines indicate FAS = 1, where MMR = SMR and $P_{cmax} = P_{cSMR}$.
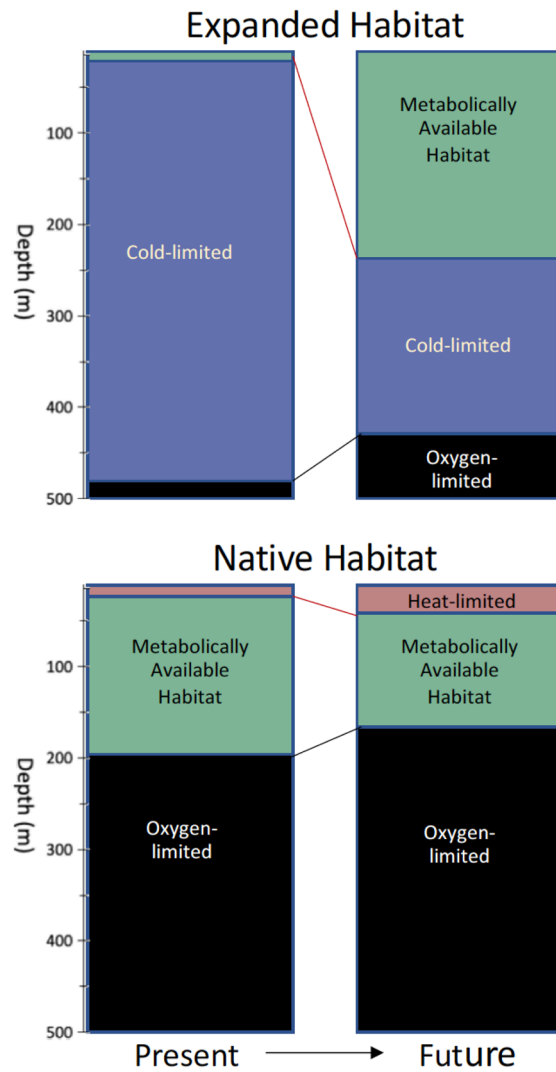
Extended Data Fig. 6 | Schematic projections of current and future metabolically available habitat in tropical vertical migrators. The restriction on habitable space imposed by cold (upper left) in temperate waters is relaxed with future warming (upper right). Temperature and oxygen currently impose minimal restrictions on shallow and deep habitat, respectively, at tropical latitudes (lower left). Climate change may exacerbate these constraints to some extent by compressing metabolically available habitat (lower right). Metabolically available habitat refers to temperature and oxygen conditions resulting in FAS > 3. Oxygen limited (black shading, $PO_2 < P_{cmax} < 21$ kPa); cold limited (blue shading, $P_{cmax} < PO_2$); heat-limited (red shading, MMR constrained at temperatures > 25 °C by constant $PO_2 = 21$ kPa).
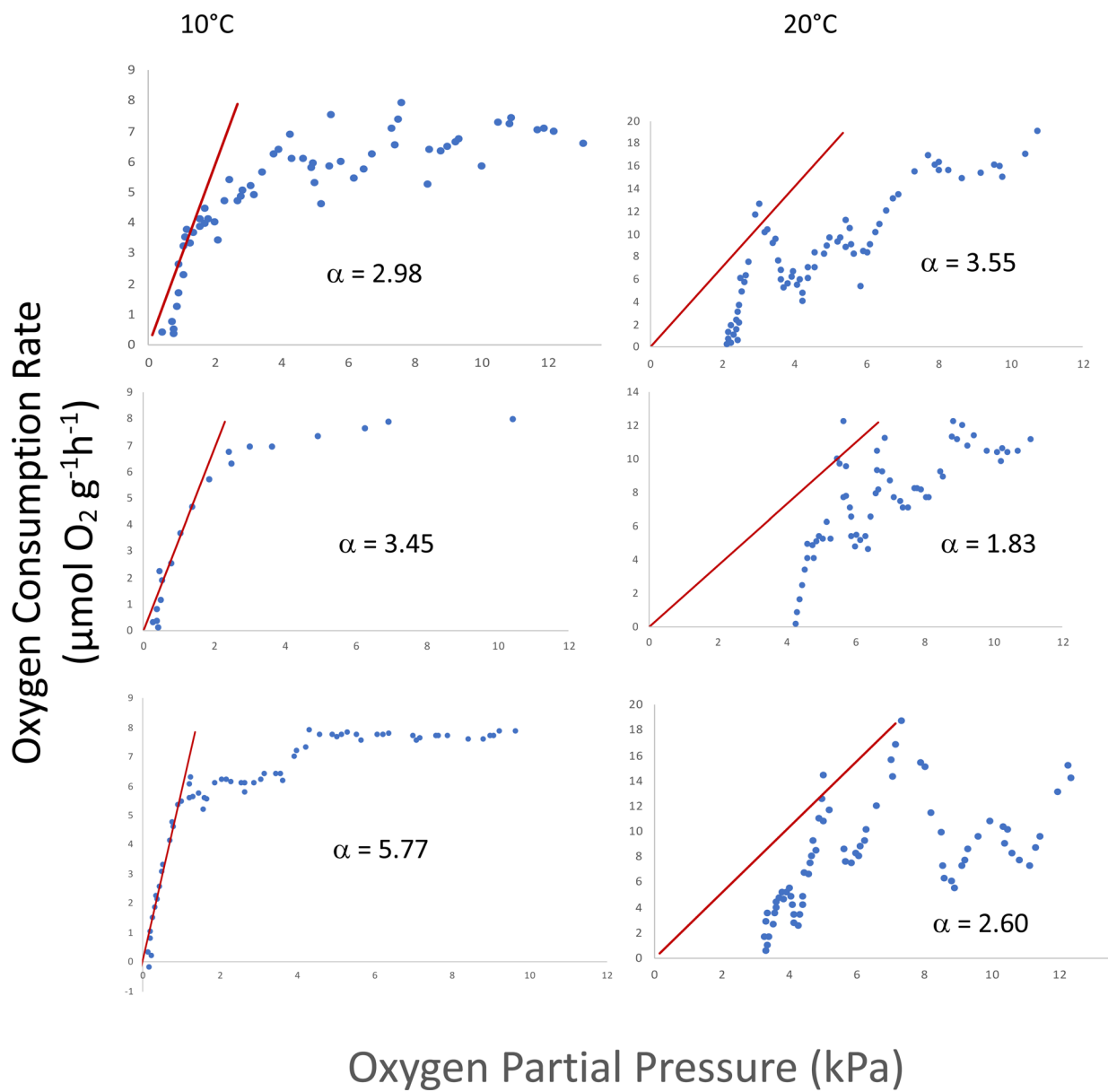
Tessarabrachion oculatum
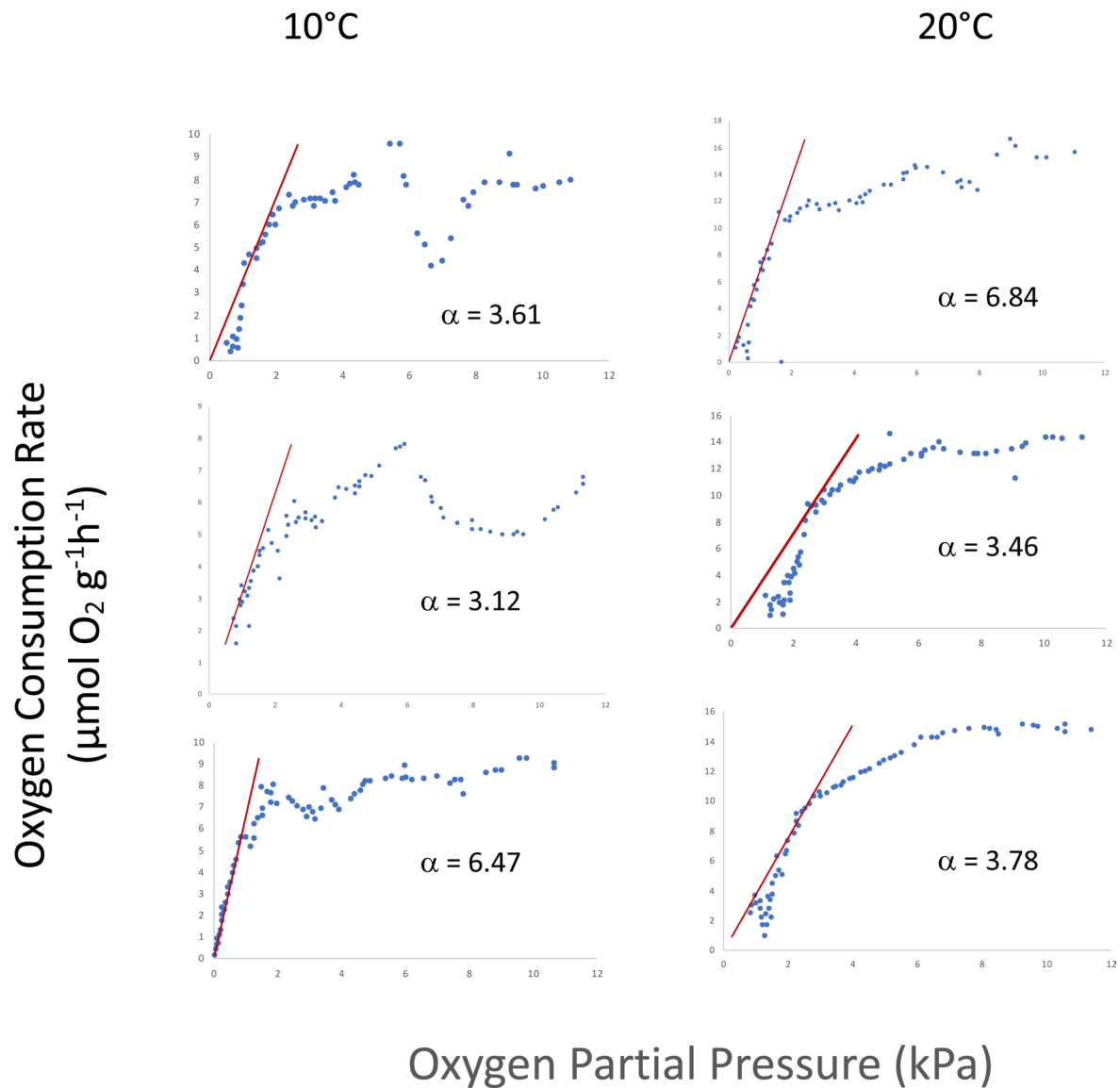
Extended Data Fig. 7 | Representative respirometry trials for *Tessarabrachion oculatum* (Euphausiidae; krill), showing six trials, three at each temperature (10 and 20 °C). In each trial, the red line, with slope, α (oxygen supply capacity), describes the metabolic rate dependence of P_{cSMR} ($P_{cSMR} = MR/\alpha$).
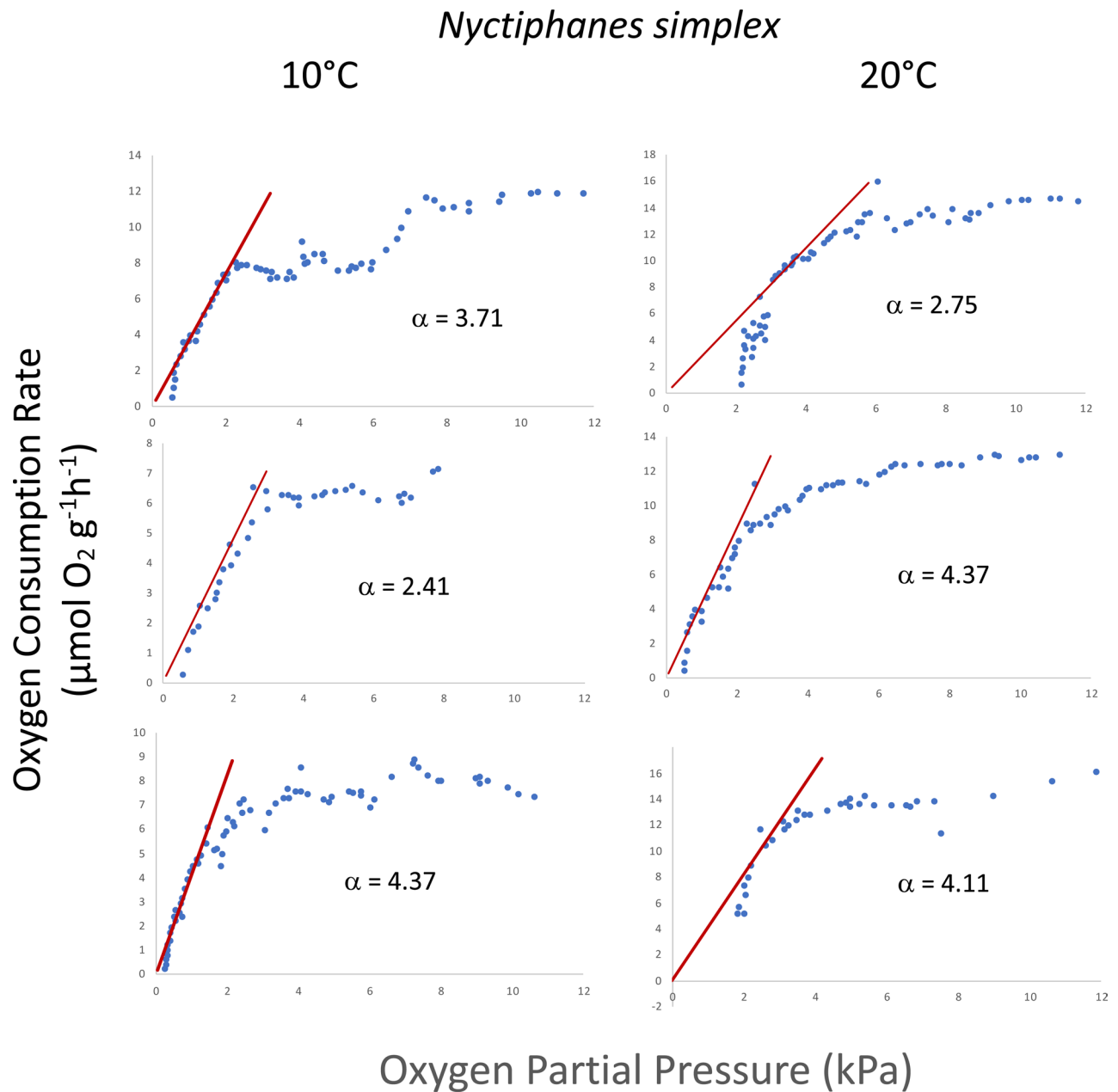
Extended Data Fig. 8 | Representative respirometry trials for *Nyctiphanes simplex* (Euphausiidae; krill), showing six trials, three at each temperature (10 and 20 °C). In each trial, the red line, with slope, α (oxygen supply capacity), describes the metabolic rate dependence of P_{cSMR} ($P_{cSMR} = MR/\alpha$).

Nematobrachion flexipes
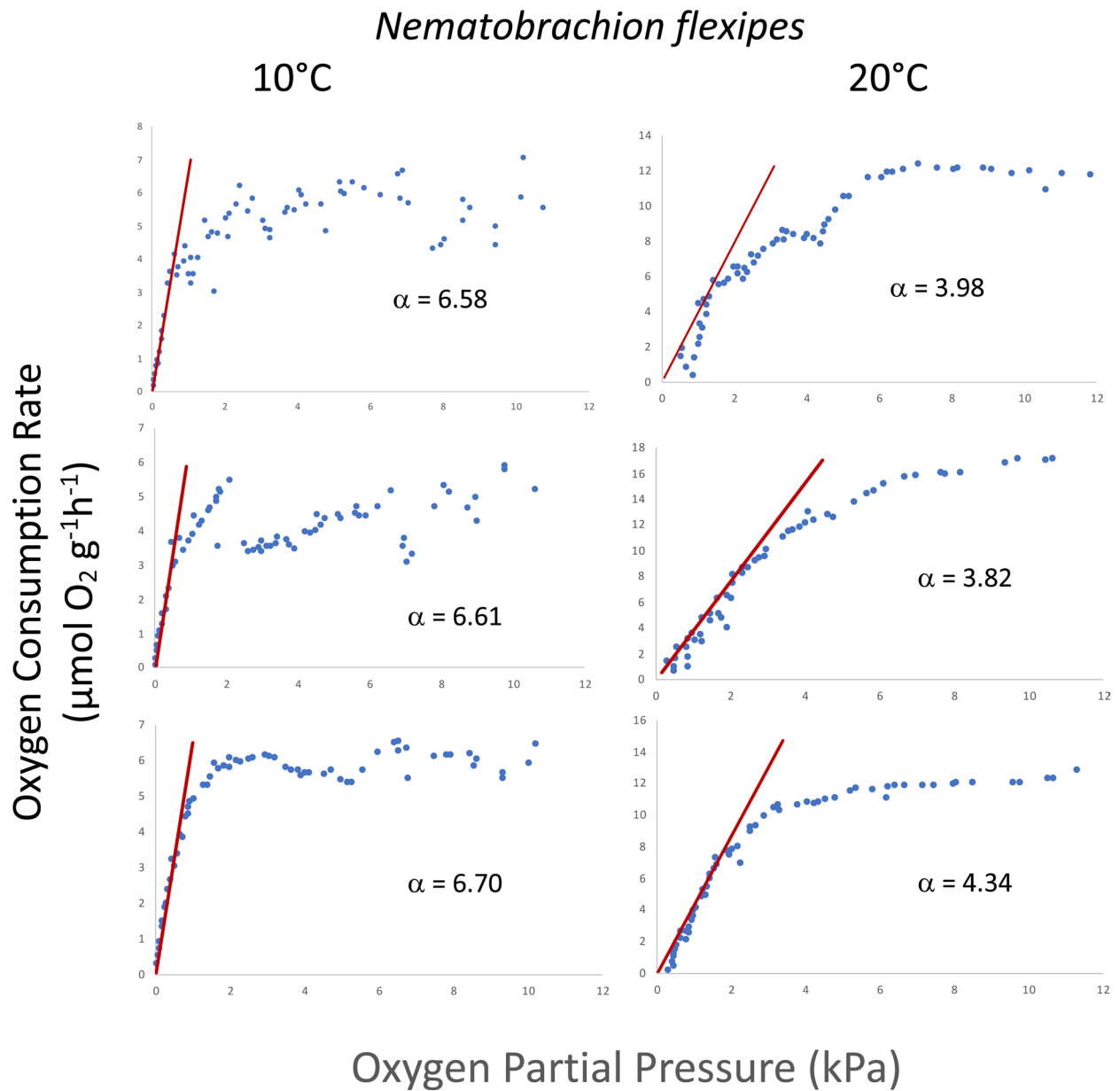
Extended Data Fig. 9 | Representative respirometry trials for *Nematobrachion flexipes* (Euphausiidae; krill), showing six trials, three at each temperature (10 and 20 °C). In each trial, the red line, with slope, α (oxygen supply capacity), describes the metabolic rate dependence of P_{cSMR} ($P_{cSMR} = MR/\alpha$).

Euphausia mucronata

Extended Data Fig. 10 | Representative respirometry trials for *Euphausia mucronata* (Euphausiidae; krill), showing six trials, three at each temperature (10 and 20 °C). In each trial, the red line, with slope, α (oxygen supply capacity), describes the metabolic rate dependence of P_{cSMR} ($P_{cSMR} = MR/\alpha$).

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☐	☒	The statistical test(s) used AND whether they are one- or two-sided *Only common tests should be described solely by name; describe more complex techniques in the Methods section.*
☐	☒	A description of all covariates tested
☐	☒	A description of any assumptions or corrections, such as tests of normality and adjustment for multiple comparisons
☐	☒	A full description of the statistical parameters including central tendency (e.g. means) or other basic estimates (e.g. regression coefficient) AND variation (e.g. standard deviation) or associated estimates of uncertainty (e.g. confidence intervals)
☐	☒	For null hypothesis testing, the test statistic (e.g. *F*, *t*, *r*) with confidence intervals, effect sizes, degrees of freedom and *P* value noted *Give P values as exact values whenever suitable.*
☒	☐	For Bayesian analysis, information on the choice of priors and Markov chain Monte Carlo settings
☒	☐	For hierarchical and complex designs, identification of the appropriate level for tests and full reporting of outcomes
☒	☐	Estimates of effect sizes (e.g. Cohen's *d*, Pearson's *r*), indicating how they were calculated

Our web collection on statistics for biologists contains articles on many of the points above.

Software and code

Policy information about availability of computer code

Data collection	Respirometry (oxygen) data was collected using Pyroscience and Presens commercial systems. The MOCNESS net system used to collect animals is a Visual Basic 3.0 program operating on Windows 95.
Data analysis	All code is available at: https://gitfront.io/r/user-5680682/7b3d1707e82e906f1092e13de9d4a75d8aa106fe/DVM-temp-sensitivity/

For manuscripts utilizing custom algorithms or software that are central to the research but not yet described in published literature, software must be made available to editors and reviewers. We strongly encourage code deposition in a community repository (e.g. GitHub). See the Nature Research guidelines for submitting code & software for further information.

Data

Policy information about availability of data

All manuscripts must include a data availability statement. This statement should provide the following information, where applicable:
- Accession codes, unique identifiers, or web links for publicly available datasets
- A list of figures that have associated raw data
- A description of any restrictions on data availability

Data availability: All data generated or analysed during this study are included in this published article (and its supplementary information files). World Ocean Atlas temperature and oxygen data (woa18_decav_t00_04.nc and woa18_all_O00_01.nc, respectively) are available at https://www.ncei.noaa.gov/access/world-ocean-atlas-2018/. CMIP6 climate projections are available at https://interactive-atlas.ipcc.ch/39965d78-e97e-42af-b488-b1e1f4d32f75. NOAA's DOISST v2.1 dataset is available at https://www.ncei.noaa.gov/data/sea-surface-temperature-optimum-interpolation/v2.1/access/avhrr/.

Field-specific reporting

Please select the one below that is the best fit for your research. If you are not sure, read the appropriate sections before making your selection.

☐ Life sciences   ☐ Behavioural & social sciences   ☒ Ecological, evolutionary & environmental sciences

For a reference copy of the document with all sections, see nature.com/documents/nr-reporting-summary-flat.pdf

Ecological, evolutionary & environmental sciences study design

All studies must disclose on these points even when the disclosure is negative.

Study description	The goal of the study was to determine "metabolically available habitat", defined as that with temperature and oxygen values sufficient to provide aerobic scope for growth as described in Deutsch et al., 2020 (Nature).
Research sample	Species and sample sizes were based on availability in deep-water trawls conducted during multiple research cruises in the Eastern Pacific. This study measured metabolic traits in diel vertical migrators (euphausiids, n = 4 species) from the Eastern Tropical Pacific. Temperature sensitivity was measured across 2 temperatures for euphausiids and 3 temperatures for squids. Additional euphausiid data and data for squid (Dosidicus gigas) was taken from published literature. The temperature sensitivity of metabolic traits for migrators were compared to that for diverse marine animals from the literature.
Sampling strategy	Sample sizes were limited by time at sea and availability in trawls. No specific sample size calculation was performed as no additional samples were possible within the funded project. We supplemented our samples with additional species from published literature.
Data collection	Respiration measurements were made at sea by students, postdocs and PI of the NSF-funded project.
Timing and spatial scale	Timing of data collection was determined by shiptime availability. The scale was oceanic, comparing populations native to the eastern tropical pacific with species found globally over the shelf (coastal regions of oceans word wide).
Data exclusions	No data were excluded.
Reproducibility	No replication of the experiment was possible due to limitations of ship time and expense.
Randomization	Experiments were run simultaneously at two treatment temperatures using animals collected from the same trawls.
Blinding	Data analysis was performed on trials labeled only by specimen number and were thus blinded from experiment conditions.

Did the study involve field work?   ☒ Yes   ☐ No

Field work, collection and transport

Field conditions	Environmental parameters in species' habitat were measured and reported in Wishner et al., 2018, Sci. Adv. A month-long research expedition from Manzanillo, Mexico, to San Diego, CA, on the R/V Sikuliaq, cruise number SKQ201701S, occurred from 19 January to 15 February 2017 and was centered at 21.6°N 117.8°W, an area with a strong OMZ.
Location	21.6°N 117.8°W
Access & import/export	The study took place in international waters. No permits were required.
Disturbance	No disturbance was caused by this study.

Reporting for specific materials, systems and methods

We require information from authors about some types of materials, experimental systems and methods used in many studies. Here, indicate whether each material, system or method listed is relevant to your study. If you are not sure if a list item applies to your research, read the appropriate section before selecting a response.

Materials & experimental systems

n/a	Involved in the study
☒ ☐	Antibodies
☒ ☐	Eukaryotic cell lines
☒ ☐	Palaeontology and archaeology
☐ ☒	Animals and other organisms
☒ ☐	Human research participants
☒ ☐	Clinical data
☒ ☐	Dual use research of concern

Methods

n/a	Involved in the study
☒ ☐	ChIP-seq
☒ ☐	Flow cytometry
☒ ☐	MRI-based neuroimaging

Animals and other organisms

Policy information about studies involving animals; ARRIVE guidelines recommended for reporting animal research

Laboratory animals	The study did not involve laboratory animals.
Wild animals	Euphausiids (krill, n = 4 species in Table S1) were captured using nets in the Eastern Tropical Pacific. Specimens were incubated in respirometry chambers, subsequently flash frozen or preserved for identification and mass in home laboratory. All other species data is derived from published literature.
Field-collected samples	Animals were captured and immediately incubated in glass respirometry chambers. No additional housing was necessary.
Ethics oversight	No approval is required for invertebrate species in the US.

Note that full information on the approval of the study protocol must also be provided in the manuscript.