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Research Article

Predicting oxygen thresholds of marine taxa to improve ecological forecasts

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Species' ranges are shifting in response to increasing temperature and decreasing oxygen in coastal oceans. Predicting these shifts is limited by information on physiological oxygen thresholds and how they depend on temperature. Here we collate laboratory-derived measurements of a common oxygen threshold, p_{crit} , for 148 animal species that span six phyla, and fit a hierarchical model based on taxonomy to impute threshold values for all based on taxonomy, body size, and environmental temperature. As expected, p_{crit} increased with increasing temperature and body size, and these temperature- and body size effects were broadly similar among species. Generally, variation in p_{crit} measurements was estimated to be most pronounced at the taxonomic family and species level, although the partitioning of variance was relatively imprecise. We demonstrate application of these estimates for species distribution modeling of six groundfish species that reside in the coastal waters of the US and Canadian Pacific coast, finding that models that used imputed values sometimes – but not always – improved the performance of species distribution models compared to models that use environmental pO_2 alone. This modeling framework and data can support species distribution modeling for marine species by providing an alternative way to consider the role of shifting oxygen levels and temperatures on species ranges.

Keywords: marine fish, oxygen, spatial modeling, species distribution modeling, taxonomic imputation

Introduction

Anthropogenic greenhouse gas emissions are causing widespread changes to marine ecosystems worldwide (IPCC 2022). While average temperatures increased, so have the frequency of severe events such as marine heatwaves and storms (IPCC 2022). These same processes also deoxygenate the ocean because of the reduced solubility of gases in warmer water, and the increased strength of thermal and saline stratification that reduces gas exchange beyond the mixed layer (Stramma et al. 2008,



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Breitburg et al. 2018). These changes are already having detectable impacts on the species phenology (Asch et al. 2019), productivity (Free et al. 2019), and species distributions (Deutsch et al. 2015, Pinsky et al. 2020), which are causing management organizations and coastal fishing communities to take action to enhance their ability to adapt to these changes (McClanahan et al. 2008).

Ecological forecasting (Clark et al. 2001) is one way to generate knowledge and identify pathways to sustain natural systems and the people that depend on them (Bennett et al. 2016). However, predicting the dynamics of complex adaptive systems is challenging (Schindler and Hilborn 2015), particularly as anthropogenic stressors move systems far from previously observed states (Brodie et al. 2022). Nonetheless, policymakers, communities, and industries that rely on marine living resources continue to call for tools that can provide predictions over decision-relevant timelines (Tommasi et al. 2017). These predictions can be made more robust by explicitly linking predicted marine taxa responses to changing temperature and oxygen via well-known and generalizable mechanisms (Lefevre et al. 2017, Brodie et al. 2022).

There has been a growing application of ecophysiology and metabolic theory to explain biogeography and species distribution shifts in a changing ocean (Pörtner and Knust 2007, Pörtner and Peck 2010). This work is based on the principle that increased ocean temperature and decreased oxygen availability act synergistically to limit the ability of aquatic life to meet aerobic metabolic demands. This joint effect arises from the temperature dependence of oxygen demand versus oxygen supply (Deutsch et al. 2015), which means that the consequences of temperature and oxygen changes cannot be considered in isolation, i.e. the range of tolerable thermal environments depends on oxygen availability and vice versa (Pörtner and Knust 2007, Pörtner et al. 2017, Rubalcaba et al. 2020; but see Jutfelt et al. 2018 for counter-arguments). If these co-dependences can be well predicted from experimental or other means, then metabolic theory can provide a mechanistic basis to explain and forecast species distribution shifts in a warmer, less oxygenated ocean.

These concepts are operationalized in the so-called 'metabolic index' (Deutsch et al. 2015), which may provide the mechanistic linkage that ecological forecast models need. The index estimates an organism's oxygen supply relative to demand (Deutsch et al. 2015). Deutsch et al. (2015) found that the range edges of four species corresponded to metabolic index values (termed ϕ^{crit}) between 2 and 5, and they predicted that by the late century, the volume of these species' current distribution that is physiologically tolerable will decline by 9 to 42%. Penn et al. (2018) expanded this analysis by collating experimental data from marine taxa and used those to simulate the diversity of metabolic index in traits and explain the mass extinction event that occurred at the end of the Permian era.

There are two main challenges in applying the metabolic index to predict range shifts. Oxygen tolerance – and the effect of temperature and body size therein – appears to be

highly variable across marine animals (Vaquer-Sunyer and Duarte 2008, Rogers et al. 2016), meaning detailed information on a species level is needed to predict range shifts. Yet, there are limited species-specific trait values derived from controlled laboratory studies. Penn et al. (2018) compiled a dataset of critical oxygen partial pressures (p_{crit}) to estimate species-specific metabolic index parameter values. While this dataset had high taxonomic breadth, including taxa within several Phyla within Kingdom Animalia (including Annelida, Arthropoda, Chordata, Cnidaria and Mollusca), its taxonomic coverage was sparse, containing fewer than 70 marine species. The second challenge is the applicability of laboratory-based estimates to predict taxa distributions in situ. Wood (2018) describes several limitations to contemporary lab methods used to measure the critical oxygen pressure, and how its meaning has changed, sometimes unknowingly through time. Consequently, different laboratory procedures may be measuring different physiological thresholds (Wood 2018). Moreover, many marine taxa have an exceptional ability to acclimate to challenging metabolic conditions (Tetens and Lykkeboe 1981, Sollid et al. 2003, Mandic et al. 2009), and experiments differ with respect to the extent that organisms are granted the opportunity to acclimate to experimental conditions.

In comparison, there is extensive information on species distributions that might be used to evaluate the combinations of temperature and oxygen that define species' range limits and thereby draw inferences on metabolic index parameters (Deutsch et al. 2020). This method presumes that range limits provide information that defines the Grinnelian niche (Hirzel and Le Lay 2008). However, high dimensionality of the Grinnelian niche combined with the high covariance of environmental conditions that define those dimensions, means that a two-dimensional analysis (e.g. temperature and oxygen, or a single combined metric such as the metabolic index) might inadvertently attribute range limits to temperature and oxygen when other covarying conditions limit them. For instance, many marine taxa have distinct patterns of distribution across depths, which could reflect the effect of depth (pressure) itself or the associated changes in temperature, oxygen, light, prey or predator abundances, or bottom substrates (Essington et al. 2022, Bandara et al. 2024). Separating the contributions of temperature and oxygen from other environmental conditions will require advanced species distribution modeling techniques (Thorson et al. 2015, Anderson et al. 2021, Indivero et al. 2025) and causal statistics (Pearl and Mackenzie 2018, Ferraro et al. 2019, Addicott et al. 2022).

One solution to these problems is to combine statistical species distribution modeling with information on metabolic index traits (Indivero et al. 2025). To be applied at a wide scale, information on metabolic index traits for a wider range of taxa is needed. Phylogenetic trait imputation is a common method to use information from well-studied taxa to provide informed estimates for less-studied taxa (Penone et al. 2014, Goolsby et al. 2017). While this has been done in an ad hoc manner for decades, more formalized methods

have been developed and used to predict life history traits (Thorson 2020), demographic rates (James et al. 2021), and physiological traits (Garland and Ives 2000). These phylogenetic comparative methods and phylogenetic trait imputation typically have seen less use for marine fishes than other major taxa (Thorson 2024a). This is surprising, given that the large number of marine species (e.g. > 24 000 fishes and > 18 400 marine invertebrates; Ah Yong et al. 2023) makes measuring traits for all marine species infeasible. Further, estimated trait values derived from phylogenetic trait imputation can reveal similarities and differences in traits not readily discerned from individual sources alone.

Here, we modify the phylogenetic imputation method described by Thorson (2020) to estimate metabolic index traits from laboratory data on p_{crit} and predict p_{crit} for taxa that lack extensive experimental data. We use taxonomy rather than phylogeny to represent relatedness, given that no dated tree is available across the range of marine vertebrates and invertebrates considered here. We demonstrate how these estimates can be used to identify metabolically inhospitable environments in the northeast Pacific Ocean.

Methods

The data

We collated laboratory-derived measurements of p_{crit} from published studies and theses. To permit a standardized comparison, we only considered methods that estimated p_{crit} from measured respiration rate and how it varies with pO_2 . This meant that other measures of oxygen sensitivity (lethal levels; LC50, or behavioral shifts) were not included. The latter are difficult to standardize, in part because lethal levels vary with duration of exposure and are therefore not easily comparable.

We used the compilations of experimental studies from Deutsch et al. (2020), and from Rogers et al. (2016). We also conducted a literature review for additional taxa using Web of Science (with search terms { p_{crit} OR oxygen tolerance} AND temperature), and filtered results according to whether they 1) included an unambiguous measurement of p_{crit} ; 2) used respirometry to derive their p_{crit} measurement at two or more temperatures; 3) described the experimental set up and the method of p_{crit} determination; and 4) reported the body mass of experimental organisms.

Overall, the compiled dataset included 434 p_{crit} measurements spanning 148 animal taxa identified to species and two identified to genus, spanning six phyla, 13 classes, 38 orders and 73 families (Fig. 1). In general, only a subset of orders (Calanoida, Cyprinodontiformes, Decapoda, Eupercaria, Ovalentaria and Perciformes) had three or more families represented, and 48 families had only a single species represented (Fig. 1). Thus, the database had relatively high taxonomic breadth but limited depth of species coverage. Of these species, 35 and 44 had p_{crit} measurements for more than one body size or temperature, respectively. All data and corresponding sources can be found in the Supporting information.

The metabolic index model

The metabolic index (ϕ) is the ratio of the rates of metabolic supply to metabolic demand (Deutsch et al. 2015). When both metabolic supply and demand are expressed as Arrhenius equations, the resulting ratio also takes the form of an Arrhenius equation:

$$\phi = pO_2 \frac{1}{V} \left(\frac{W}{W_{ref}} \right)^n - \exp \left(\frac{E_o}{k_b} \left(\frac{1}{T} - \frac{1}{T_{ref}} \right) \right) \quad (1)$$

Where all variables are described in Table 1. Briefly, the parameters V , n and E_o are estimated parameters, T and W are temperature (K) and body size (g), k_b is Boltzmann's constant, and W_{ref} and T_{ref} are scaling parameter set to improve estimation convergence and interpretability of the model parameters.

By assuming that the experimental p_{crit} is the value of pO_2 that makes $\phi = 1$, we can re-arrange Eq. 1 as follows to estimate V , n and E_o from the data:

$$\log(p_{crit,i}) = \log(V_{[s]}) - n_{[s]} \log \left(\frac{W_i}{W_{ref}} \right) - E_{o,[s]} T'_i + \epsilon_i \quad (2)$$

Where, i indexes a single experimental outcome, $[s]$ indicates the species identity for each experimental outcome, ϵ_i is a Gaussian random error term with mean 0 and standard deviation σ for each study i measurement, and logarithms are in base e . The term T'_i equals:

$$T'_i = \left(\frac{1}{k_b} \left(\frac{1}{T_i} - \frac{1}{T_{ref}} \right) \right) \quad (3)$$

The p_{crit} estimates were derived from laboratory studies that used different measurement proxies. The most common approach was to measure oxygen uptake as a function of pO_2 , and then to identify the threshold value of pO_2 above which oxygen uptake is independent of pO_2 (termed 'oxyconformity'). Other studies estimated p_{crit} as the pO_2 at which respiration rate dropped below the standard metabolic rate. For most mobile taxa and experimental setups, the former can be conceptualized as the pO_2 at which routine metabolism cannot be supported. Both methods were used to estimate p_{crit} among taxa within phylum Chordata, but oxyconformity was the primary method used among other phyla (Fig. 1). We therefore modified Eq 2. to account for variation in experimental protocols so that the fitted model was:

$$\log(p_{crit,i}) = \log(V_{[s]}) - n_{[s]} \log \left(\frac{W_i}{W_{ref}} \right) - E_{o,[s]} T'_i + \epsilon_i + \beta_m M_i \quad (4)$$

Where M_i is a dummy variable equal to 1 if the measurement was based on standard metabolic rate, and 0 otherwise. The

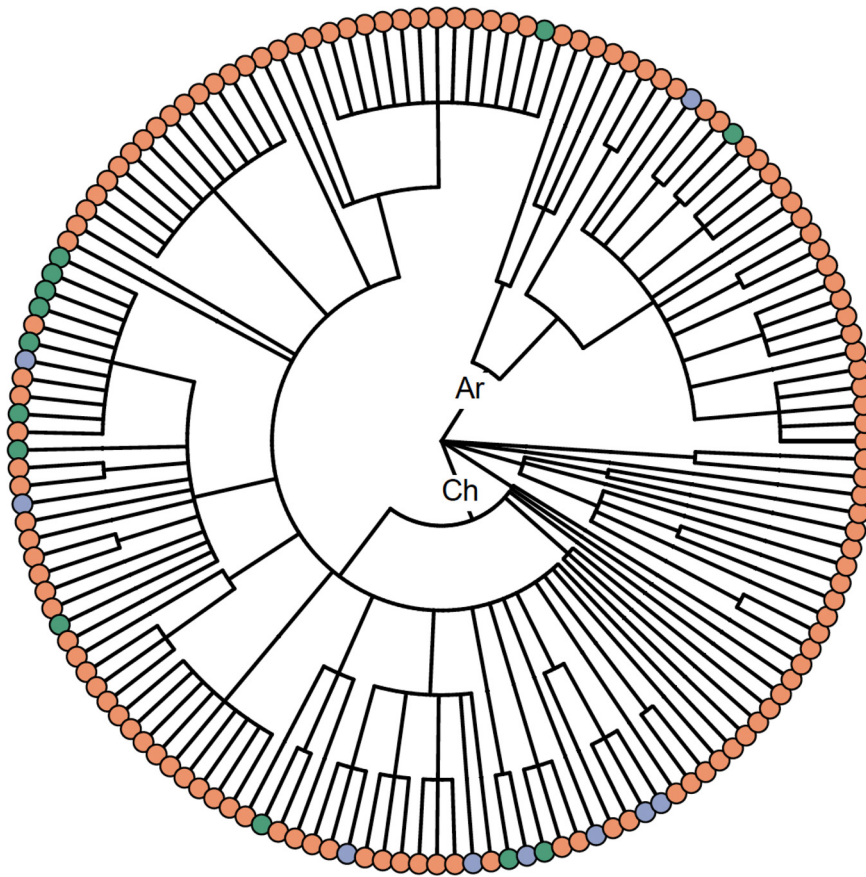


Figure 1. Taxonomic representation of species in the data set. Phyla Arthropoda and Chordata are labeled as Ar and Ch, respectively. Other Phyla arranged clockwise from Arthropoda are Echinodermata, Cnidaria, Mollusca and Annelida. Circle colors denote the p_{crit} estimation method(s) used for each species, where red, blue and green represent taxa for which estimation was based on oxyconformity, standard metabolic rate, or both, respectively.

parameter β_m is therefore the difference in $\log(p_{crit})$ between estimates based on standard metabolic rate compared to estimates based on oxyconformity.

Parameter estimation

To estimate these parameters hierarchically, we apply phylogenetic factor analysis (Thorson et al. 2017b, Tolkoﬀ et al. 2018) using a Brownian motion (evolutionary random walk) model for the vector of species-specific traits V , n and E_0 . We approximate taxonomic distance (i.e. evolutionary relatedness) by defining a tree with nodes representing taxonomic levels (e.g. class, order, family, genus and species), and estimating the branch length (i.e. trait variance) associated with each taxonomic level. This is inspired by Thorson (2020), who used taxonomy as a proxy of evolutionary relatedness because there is no consensus tree that includes the wide range of fishes and marine invertebrates analyzed here.

Our model analysis used all taxonomic levels from phylum to species. The model assumes that the mean values of any taxonomic grouping (the ‘child’) are a function of the mean values of the higher taxonomic group (the ‘parent’) in which each taxon is nested. For instance, the mean value for a particular species will depend on the mean value for that species’

genus. A multivariate normal distribution describes the distribution of mean trait values within a taxonomic grouping:

$$X_{[g]} \sim MVN(x_{p(g)}, \Sigma_{l(g)}) \quad (5)$$

where we define vector $\mathbf{x}_{[g]}$ as the mean trait values ($\log(V)$, n , E_0) for child taxonomic group g , and $\mathbf{x}_{p(g)}$ is the vector of mean trait values for the parent taxonomic grouping for child taxonomic group g . $\Sigma_{l(g)}$ is the trait (evolutionary) covariance, and $l(g)$ indicates the taxonomic level of group g . For reference $l(g)=1$ refers to class, 2 refers to order, etc.

The estimation procedure estimates a vector of elements of the lower triangular matrix, $\mathbf{L}_\Sigma$, such that:

$$\Sigma_{l(g)} = \lambda_l (\mathbf{L}_\Sigma \mathbf{L}_\Sigma^T + \mathbf{D}) \quad (6)$$

where $\mathbf{D}$ is a diagonal matrix of the additional and independent evolutionary variance in traits (σ_j^2) for each of the j traits, the parameters $\lambda_{l(g)}$ are the relative amount of covariance expressed at a taxonomic level $l(g)$ relative to taxonomic level Order (e.g. $\lambda_{l(g)=0} = 1$), and the superscript T denotes the

Table 1. Parameters of the metabolic index and estimation model.

Parameter	Description	Units
ϕ	Ratio of oxygen supply to demand	Unitless
V	p_{crit} for taxa at reference temperature and body size	kPa
W	body mass	g
W_{ref}	reference body mass	g
T	temperature	K
T_{ref}	reference temperature	K
n	effect of $\log(W)$ on $\log(p_{crit})$	Unitless
E_o	effect of inverse-temperature ($^{\circ}K$) on $\log(p_{crit})$	eV^{-1}
k_b	Boltzmann's constant	$eV K^{-1}$
ϵ_i	Residual for observation i	$\log(kPa)$
σ	standard deviation of the residuals	$\log(kPa)$
β_m	Effect of estimating p_{crit} from estimated standard metabolic rate	Unitless
i	Index for individual observation	Unitless
$[s]$	Index for species identity for each observation	Unitless
$\mathbf{x}[g]$	Vector of mean traits for taxonomic group g	Varies
$\Sigma_{l(g)}$	variance-covariance matrix of traits among child taxa $l(g)$ within its parent taxa	Varies
$\lambda_{l(g)}$	scaling of relative variance-covariance of traits at child group $l(g)$, relative to taxonomic level class	Unitless

transpose of $\mathbf{L}_2$. The diagonal elements of $\mathbf{D}$ are not explicitly included in the estimation but are set at 0.001 to aid in model convergence. Because we had three traits, $\mathbf{L}_2$ was a 3×3 matrix, having six lower triangular elements to estimate.

The model, therefore, included multiple fixed-effects parameters. These were: $\mathbf{x}_{l(g)=0}$, the mean trait values from which the taxonomic phylum – level traits are drawn; the six elements of $\mathbf{L}_2$; λ , the array of covariance multiplier terms for class, orders, family, genera, and species relative to the covariance among phyla; σ , the standard deviation of the experimental observations; and β_{method} , the effect of estimation method = standard metabolic rate on measured p_{crit} . All other parameters (specifically, the $\mathbf{x}_{[g]}$) are random effects.

We fit one model with, and one without the p_{crit} estimation method as a predictor variable, and judged model support using conditional AIC (Vaida and Blanchard 2005) and the empirical degrees of freedom calculation method described by Thorson (2024b).

Parameter estimation was conducted using template model builder (TMB; Kristensen et al. 2016), which uses the Laplace approximation to integrate over joint likelihood of the data and random effects. This estimation approach has been thoroughly tested elsewhere for use in phylogenetic comparative methods (Thorson and van der Bijl 2023, Thorson et al. 2023). Taxonomic structure was based on the World Register of Marine Species (www.marinespecies.org, accessed 5 June 2025; Ahlyong et al. 2023).

Furthermore, we calculated standard graphical diagnostics of models deemed to be well supported by the data. These were Q–Q plots, predicted versus observed, residuals versus predicted, and kernel density smoothers of residuals.

Generating distributions of out-of-sample species

One purpose of this analysis was to provide information for taxonomic groups for which there are no experimental data to inform the metabolic index parameters (hereafter called ‘out-of-sample species’). One approach to that end would be to include additional parameters for V , E_o and n for all species

represented in a full dataset of marine taxa. However, because the model does not consider the influence of any other traits that might be available from other sources on metabolic index parameters, this level of detail is unnecessary because in the taxonomic hierarchical model, the only information used to generate estimates for out-of-sample species is taxonomic relatedness. We therefore used a simpler approach that involved creating ‘blank’ species within each represented taxonomic group, and estimating the metabolic index parameters for each. Specifically, we added a blank species within each represented genus, a blank genus and species within each represented family, etc. Because these ‘blank’ species had no measured p_{crit} in the data, these estimates are based purely on taxonomic relatedness and the model’s estimate of similarity of traits within these taxonomic groups. The maximum likelihood estimates were then used to estimate the standard error of prediction of the estimated p_{crit} for species that are not within the dataset by identifying the lowest taxonomic group that was represented in the data, and identifying the estimates for the corresponding ‘blank’ species. Estimated p_{crit} is then based on the maximum likelihood parameters and their covariance. We assume that the residuals reflect observation error, not true taxonomic differences, so our estimate of the standard error of p_{crit} did not include the estimated σ . This assumption can be relaxed by including any proportion of σ in the prediction interval (p_o), depending how much one assumes that variability in observed p_{crit} derive from measurement error. The method accounts for uncertainty (and covariance) in the p_{crit} measurement method, allowing us to generate p_{crit} estimates based on standard metabolic rate or oxyconformity.

Application to species distribution modeling

We wished to assess whether these estimates of p_{crit} improve species distribution models. To that end, we used the predicted p_{crit} and its standard errors, applied to data on four groundfish species distributions along the US and Canadian continental shelf and slope. Here, we used the above

estimation routine to generate the maximum likelihood estimate of $\log(p_{crit})$ for each observed temperature and its standard error, assumed that $\log(p_{crit})$ was normally distributed around the maximum likelihood estimate, and then calculated the probability that the observed pO_2 exceeded p_{crit} ($P(pO_2 > p_{crit})$) from a cumulative normal probability function. Here, we based p_{crit} on standard metabolic rate, and assumed a body mass of 1 kg. Data derive from trawl surveys conducted by US NOAA fisheries and Canada Department of Fisheries and Oceans, and from longline surveys conducted by the International Pacific Halibut Commission. These data provide information on catch rate, temperature and oxygen at over 6700 sampling events from 2010–2022, the only years with extensive oxygen data available. Details of the fitted species distribution model is provided in the Supporting information. Briefly we fit generalized linear mixed-effects models with spatio-temporal random effects to account for latent environmental features, a smoothed function of log-depth, temperature², and survey type (Thorson et al. 2017a, Ward et al. 2024). We did this for six species that provide contrasts in depth ranges and to span three common taxonomic groups (flatfishes, Pleuronectidae; cods and hakes, Gadiformes; rockfishes, Scorpaenidae). Pacific halibut *Hippoglossus stenolepis*, Pacific cod *Gadus macrocephalus*, and Canary rockfish *Sebastes pinniger* inhabit relatively shallow habitats while Dover sole *Microstomus pacificus*, Pacific hake *Merluccius productus*, and longspine thornyhead *Sebastolobus altivelis* inhabit deeper habitats where oxygen is often low. Of these, only Pacific cod have measured p_{crit} within our database. We used the species distribution models to ask whether the probability that pO_2 exceeds p_{crit} enhances the ability to predict species' occurrences at sample sites over models that lack pO_2 or models that use pO_2 directly as a predictor variable. We fit two models each for p_{crit} and pO_2 , one with a standard linear effect, and another with a linear breakpoint function whereby levels above some estimated threshold have no additional effect on species' presence or absence. Model selection was conducted using blocked cross validation with five folds, and 65 km block size. The latter was chosen to be larger than the maximum autocorrelation distance of the response variables, temperature, and oxygen-related variables. Cross

validation was repeated 10 times for each model to generate the mean and standard error of the predictive log-likelihood. Model performance was based on the mean predictive log-likelihood, where models with high predictive log-likelihood are better supported (Supporting information).

Analysis was conducted using R ver. 4.2.1 (www.r-project.org).

Results

The measured p_{crit} from published sources varied widely among species, and generally increased with temperature and body mass (Fig. 2). The measured p_{crit} spanned nearly two orders of magnitude, ranging from 0.3 to 21.3 kPa, with both the smallest and largest measured values deriving from species in phylum Arthropoda (*Gennadas* spp. and *Goniotropis cruentata*, respectively). Generally, the largest measured p_{crit} tended to be associated with the warmest temperatures (e.g. 35°C) and largest body sizes. There was little apparent difference among phyla in the p_{crit} measurements (Fig. 2). The smallest measured p_{crit} tended to be associated with zooplankton that reside in oxygen minimum zones (Wishner et al. 2018).

The data provided strong support for models that accounted for analysis method i.e. the method of determining p_{crit} from the data. The ΔAIC of the model that did not include an estimation method effect was 30.2. As expected, p_{crit} was lower when based upon standard metabolic rate, equaling, on average, 0.72 (SE=0.05) times the value measured from oxyconformity. The best fitting model had good diagnostic properties, apart from having more large underestimates (< -0.5) of $\log(p_{crit})$ than expected under the model assumption (Supporting information).

The model could not reliably identify the relative evolutionary variance arising at different taxonomic levels. While the maximum likelihood estimates pointed to the greatest trait variance at family and species level (i.e. families within orders, species within genus), the standard errors of the estimates were large (Supporting information). Consequently, confidence intervals of estimated λ broadly overlapped and all contained 1.

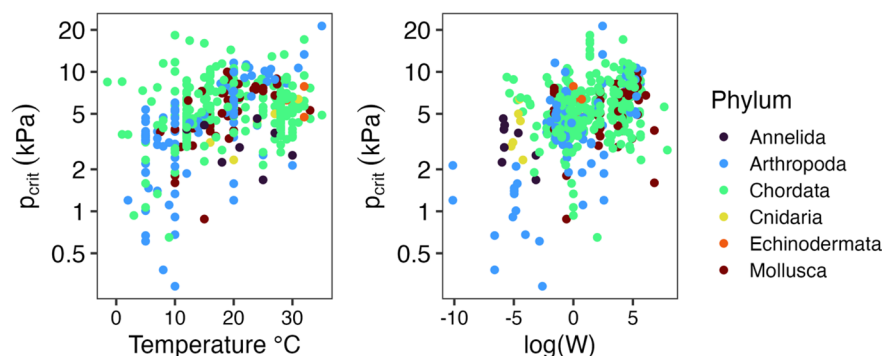


Figure 2. Measured p_{crit} values as a function of temperature and body size (right). Each point represents a single reported value in a paper source. Points are color coded by phylum. Y-axis is plotted on a log-10 scale.

Across all taxonomic groups, the estimated mean (SE) values of the three parameters – species baseline vulnerability, $\log(V)$; allometry of p_{crit} , n ; and temperature sensitivity, E_o – were 1.27 $\log(\text{kPa})$ (0.135), -0.071 (0.029) and 0.26 eV^{-1} (0.058), respectively. The allometry and temperature sensitivity parameters are consistent with expectations that p_{crit} declines with increasing body size and temperature. The mean values of traits varied little among phyla (Fig. 3), classes, or orders (Supporting information), but showed more variation among families (as expected given Table 2 variance for family). Generally, phyla with greater taxonomic representation had more precise estimates, specifically Chordata and Arthropoda. The differences in mean values were small compared to their standard errors. In comparison, mean trait values show more variation among taxonomic families (Fig. 4), especially in the estimates of V and E_o . For example, Euphausiidae had lower mean baseline vulnerability ($\log(V)$) but higher temperature sensitivity (E_o) than Gadidae. In contrast, estimates of the allometric exponent n were broadly similar among families, except for Pomacentridae which had the highest estimated mean n .

We demonstrate how the estimates of p_{crit} estimates change for species at greater taxonomic distance from those in the dataset, using a representative species, *Clinocottus globiceps* (using $W=25 \text{ g}$, approximate mean of body sizes of *Clinocottus globiceps*, and $T=20^\circ\text{C}$, the largest experimental temperature for data for this species). The estimated p_{crit} based on oxyconformity was roughly 7.1 (SE=1.15) kPa and the p_{crit} based on standard metabolic rate 5.14 (SE 1.14) kPa (Fig. 5). Note that the standard error of the estimate is larger for p_{crit} based on standard metabolic rate. The predicted value for a species within *Clinocottus* (but not in our dataset), increases slightly to 7.6 kPa, and the standard error increases (Fig. 5). This pattern continues for predicted p_{crit} of species within family Cottidae. The increasing predicted

p_{crit} represents shrinkage of the estimates towards the family level mean, which was larger than the estimate for *Clinocottus globiceps*. For predictions at the family level, the standard errors were relatively large, 1.8 kPa for oxyconformity and 2.2 kPa for standard metabolic rate, representing the increased uncertainty of predictions for species that are taxonomically distant from those represented in the data (Fig. 5).

Application to coastal ecosystems

While cross validation of fitted species distribution models to groundfish revealed effects of oxygen on spatial distributions, it did not reveal that outputs from our taxonomic hierarchical model consistently outperformed pO_2 alone (Table 2). Among the three shallower-dwelling species, two (Pacific cod and Pacific halibut) showed evidence for an effect of oxygen on spatial distribution, and for both, the models that used $P(pO_2 > p_{crit})$ as a predictor outperformed those that used pO_2 as a predictor. Canary rockfish, did not show strong evidence for an effect of either oxygen predictor on species distribution, as the best model's cross validation score (linear effect of pO_2) did not exceed that of the base model by more than one standard error. Among the deep dwelling species, only Dover sole showed evidence for an effect of oxygen on spatial distribution, where model with pO_2 (breakpoint) outperformed those that used $P(pO_2 > p_{crit})$. For Pacific hake and longspine thornyhead, neither of the oxygen models had any support, because the estimated effect sizes either exactly equaled or slightly exceed 0 for all cross-validation folds.

Discussion

Here we synthesized estimates of a common oxygen threshold, p_{crit} , for 148 taxa in six phyla, and fit a model to impute oxygen thresholds for all marine species. Oxygen thresholds

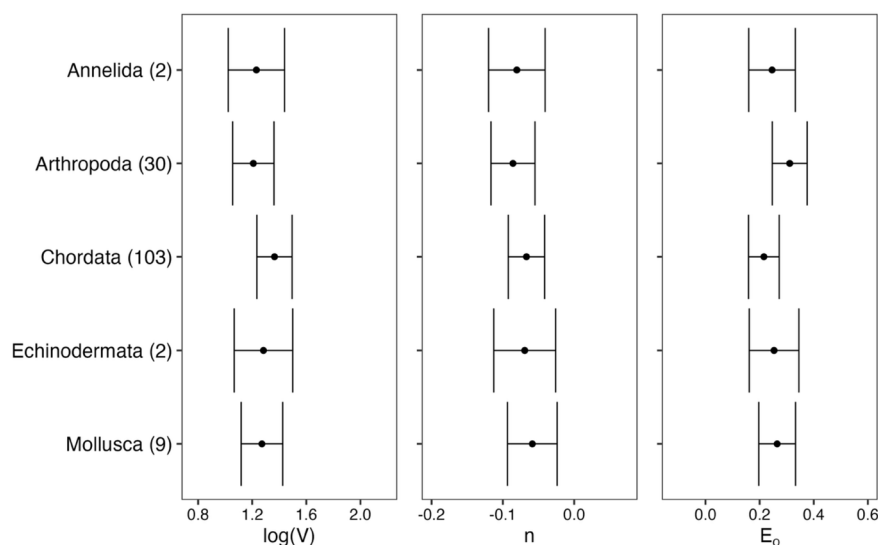


Figure 3. Estimated mean metabolic index trait values ($\pm$ SE) by phyla. $\log(V)$ is the log of the p_{crit} for a 5 g individual at 15°C , n is the allometric exponent, and E_o describes the effect of inverse temperature on p_{crit} (Table 1). Numbers in parenthesis indicate the number of species in the dataset within each phylum.

Table 2. Difference in model prediction log-likelihood (standard error) between the best model and each candidate model by species. Smaller values mean better prediction performance. The base model only includes smoothers on depth and temperature, and spatio-temporal random effects. Cells denoted – indicate where the oxygen-related predictors equaled 0.

	Base	$P(pO_2 > p_{crit})$, breakpoint	$P(pO_2 > p_{crit})$, linear	pO_2 , breakpoint	pO_2 , linear
Pacific cod	40.1 (2)	0 (0)	40.6 (1.7)	11 (0.6)	43.6 (1.9)
Pacific halibut	22.5 (1.7)	2.2 (0.6)	0 (0)	3.7 (0.7)	7.9 (1.3)
Canary rockfish	0.2 (0.8)	8.7 (1.6)	2.1 (0.6)	3.6 (0.7)	0 (0)
Pacific hake	0 (0)	–	–	–	–
Dover sole	28.2 (3.1)	3.7 (2)	26.2 (2.3)	0 (0)	30.5 (3.2)
Longspine thornyhead	0 (0)	–	–	–	–

increased with temperature and body size, although the magnitude of the former varied among taxa, and we did not observe consistent differences in parameters among high level taxonomic groups. Predicted p_{crit} levels for species not represented in our data lost precision with greater taxonomic distance from those in the data. Furthermore, p_{crit} estimates shifted towards the average values of higher taxonomic groups (e.g. Class, Order) as the further a species was mode distantly related to other species in the dataset. Our demonstrated application of imputed p_{crit} values did not reveal that these values consistently outperformed more direct measures of oxygen in the environment, but when they did, the benefit was large. These findings support the continued development and testing of quantitative imputation methods for key traits used in species distribution models.

The data come from short-term laboratory experiments, yet laboratory-derived oxygen thresholds may not accurately predict species distributions in situ. For example, Moriarty et al. (2020) showed that Pacific herring *Clupea pallasii* were abundant in locations having oxygen levels that were close to their estimated p_{crit} values (ca 4.2 kPa). Short-term acute laboratory studies do not permit organisms to acclimate or adapt to low pO_2 , although there is abundant evidence of phenotypic plasticity in oxygen transport and oxygen demand, from physiological adaptation (Tetens and

Lykkeboe 1981, Sollid et al. 2003, Mandic et al. 2009) to epigenics and evolution (Audzijonyte et al. 2019). On the other hand, p_{crit} (especially when based on standard metabolic rate) is a lower bound for distribution, and most species require higher oxygen levels to meet activity requirements (Penn et al. 2018, Deutsch et al. 2020). Thus, when applying these estimated to field environments, one should apply the same cautions as one would for a laboratory experiment. Oxygen sensitivity is subject to adaptation on a variety of temporal scales: from physiology (acclimation), epigenetic, to evolution (e.g. local adaptation) (Audzijonyte et al. 2019).

The imputation model might be improved by considering additional traits that might provide information on oxygen thresholds. For instance, the imputation model struggled to predict p_{crit} for taxa with exceptionally low oxygen thresholds (Supporting information). The residuals had a heavy left-handed tail (Supporting information), and the plot of p_{crit} versus temperature and body size reveals several data points where p_{crit} was considerably lower than expected based on these two covariates (Fig. 2). Several of these measurements derived from species that inhabit oxygen minimum zones (Wishner et al. 2018), where pO_2 is commonly below 0.5 kPa. Future imputation models might use structural equation modeling to incorporate data on habitat use (demersal versus pelagic), maximum depth, minimum pO_2 where species

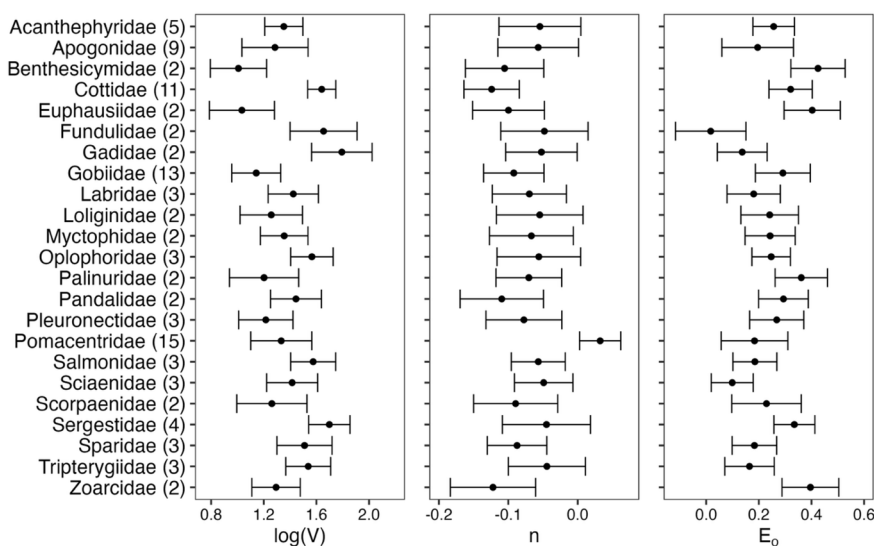


Figure 4. Estimated mean metabolic trait values ($\pm$ SE) by taxonomic family. Numbers in parenthesis indicate the number of taxa within each family that are included in the dataset. Only families with at least two species represented are plotted.

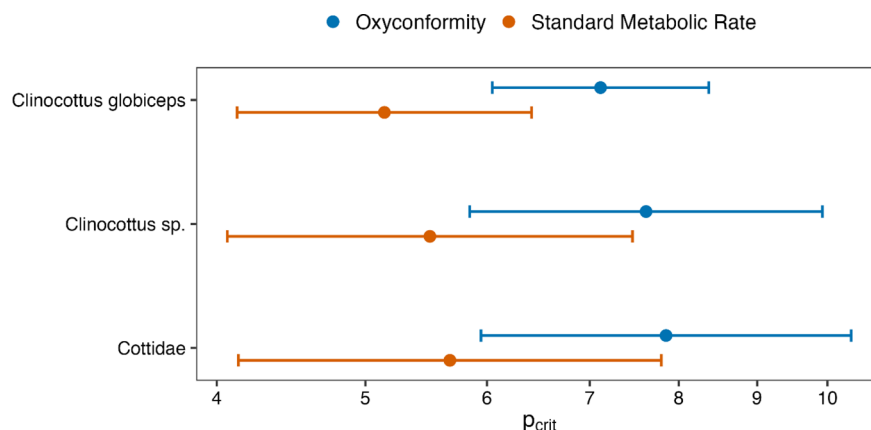


Figure 5. Predicted p_{crit} ($\pm$ SE) based on oxyconformity (blue) or standard metabolic rate (orange) at three different taxonomic levels. *Clinocottus globiceps* are represented in the data set, and estimated labeled *Clinocottus* spp. and Cottidae represent estimates for species not in the dataset within taxonomic groups *Clinocottus* or within Cottidae.

are observed, and measures of plasticity (i.e. range area, or difference in latitude between range edges) to improve predicted oxygen thresholds. Previous simulation and cross-validation experiments confirm that trait imputation can be aided both by correlations among related taxa (phylogenetic signal) as well as covariation among traits (Penone et al. 2014, Debastiani et al. 2021, Thorson et al. 2023). However, imputation performance can also degrade when traits are not missing at random (Johnson et al. 2021). We therefore recommend further research regarding ‘preferential sampling’ (Diggle et al. 2010), where a structural equation model could estimate the relationship between traits (e.g. body size) and data availability (e.g. count of trait measurements per species) to correct for this source of bias (Conn et al. 2017).

We see at least three ways that this work could be used to improve species distribution models for prediction. First, it provides a quantitative basis to estimate likely values for p_{crit} , or analogously, the metabolic index, for any species, regardless of whether it has been the subject of experimental work. For instance, the metabolic index parameters combined with past oxygen and temperature could be used as a covariate to explain past distributions (Deutsch et al. 2015, 2020, Penn et al. 2018, Essington et al. 2022, Bandara et al. 2024), and the estimated effect size combined with projections of environmental change can predict species distribution shifts (Clarke et al. 2021, Thompson et al. 2023). Two, the imputation model can be used for species distribution models as we have done here, as a probabilistic measure of p_{crit} or the metabolic index. Three, the results from the current study could be used as Bayesian prior probabilities of parameters for estimation efforts that use different data to identify eco-physiological thresholds of oxygen and temperature (Ellison 2004). For instance, species distribution models applied to in situ survey data could be used to estimate the parameters of the metabolic index and the threshold values therein that limit taxa ranges. Because many relevant environmental controls of taxa range limits covary in time and space, these prior probabilities might improve estimation performance (Indivero et al. 2025).

Our analysis also contributes to the ongoing discussion of the role of oxygen supply and demand in generating the well-known temperature size rule (Atkinson 1994). Much has been written on this topic, as different research groups have used different models and methods either to support a role for oxygen, or to deny it (Audzijonyte et al. 2019, 2020, Verberk et al. 2021). However, Deutsch (2022) showed a mathematical treatment of Eq. 1 could predict empirically observed effects of temperature on body size. Importantly, their model predicted that these effects are among taxa whose allometric scaling of metabolic index is close to 0. Because we found evidence that on average, the allometric scaling coefficient, n , is near 0 and negative, then those modeling results suggest a high potential for reductions in body size in a warmer ocean when oxygen is a leading cause of the temperature-size rule.

Our estimation model also made many assumptions that might affect its predictions. For instance, we assumed that the relative variance and covariance of traits were identical across taxonomic levels and only differed by a scaling coefficient that either increased or decreased the variance/covariance relative to what was estimated at the phylum level (Thorson 2020). This assumption is common in phylogenetic factor analysis, path analysis, structural equation models, and phylogenetic trait imputation (von Hardenberg and Gonzalez-Voyer 2013, Thorson and van der Bijl 2023) – it is unlikely that the data could provide information to estimate a separate variance-covariance matrix at each taxonomic level. It is possible that the variance-covariance structure could differ among taxonomic groups depending on unique trade-offs related to physiological adaptations within those groups. Furthermore, this analysis presumes that taxonomic similarity is an approximate proxy for evolutionary processes, and we estimate different ‘branch lengths’ (i.e. variance contributions) associated with different taxonomic levels. However, speciation rates vary widely among taxonomic groups (Rabosky et al. 2018), such that additional transformations of the taxonomic tree might have different performance. Finally, we assumed that p_{crit} scales with body size linearly in log-space, and that the

effect of temperature on p_{crit} is monotonic. Although that assumption seems warranted given the patterns in the raw data (Fig. 1), others have found that over larger size ranges (Deutsch et al. 2022) or temperature ranges (Endress et al. 2024), these assumptions may not be upheld.

Because of the limited taxonomic coverage of the data, we did not attempt formal skill-testing of the taxonomic imputation method. However, the residual analysis and comparison of estimates for species represented and unrepresented in the data give an indication of where skill is likely to be limited. Clearly, imputed values for species distantly related will have limited precision, as evidenced by the substantial standard errors shown in Fig. 5. This uncertainty is related to the fact that the imputation model found that there is high divergence of metabolic index parameters for species within the same genus. Additionally, imputed values will tend to be centered at group – level means which may not well represent particularly vulnerable or tolerant species. Indeed, the model struggled to predict the very low p_{crit} values for mesopelagic zooplankton that inhabit oxygen minimum zones. For that reason, this method might best be used to impute taxa that live in similar environments than those that are present in the data.

Future elaborations of this method hold promise for improved prediction of oxygen thresholds and thereby enhancing our understanding of how oxygen shapes species distributions in a changing ocean. For instance, our method here used single type of data for purposes of standardization: respirometry-based measurements of p_{crit} . Future data synthesis and models may incorporate additional types of oxygen threshold measurements, including laboratory based lethal exposure limits or behavioral response assays. Moreover, there is a vast amount of information in records of species occurrence (e.g. OBIS: <https://obis.org>) and ocean oxygen levels (e.g. World Ocean Atlas: www.ncei.noaa.gov/products/world-ocean-atlas), as well as surveys that synoptically record local density with oxygen and temperature (Indivero et al. 2025). By integrating these diverse data sources, not only will these future models greatly expand the taxonomic representation within the data, but they may also lead a greater understanding of thresholds vary from laboratory to the field.

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Author contributions

Timothy E. Essington: Conceptualization (lead); Data curation (lead); Formal analysis (lead); Funding acquisition (lead); Investigation (lead); Methodology (equal); Project administration (lead); Visualization (lead); Writing – original draft (lead); Writing – review and editing (lead). **James T. Thorson:** Formal analysis (equal); Methodology (equal); Writing – original draft (supporting); Writing – review and

editing (supporting). **Curtis Deutsch:** Data curation (supporting); Writing – original draft (supporting).

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Data availability statement

Data are available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.vhhmgqp7w> (Essington et al. 2025). All R and TMB scripts are available at Github: https://github.com/tessington/metabolic_index.

Supporting information

The Supporting information associated with this article is available with the online version.

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