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RESEARCH ARTICLE

Limited evidence for species-specific sensitivity of temperature-dependent fractionation of oxygen stable isotope in biominerals: A meta-analysis

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Abstract

1. Water temperature is key to the study of aquatic ectotherm ecology, but precise measurements of individual-based thermal experience remain difficult to validate. The stable isotope composition of oxygen in biominerals acts as a natural thermometer due to the temperature dependence of isotopic fractionation between water and mineral phases. Coefficients of published temperature-dependent fractionation equations, however, vary among taxa (the so-called 'vital effect') without apparent consistent predictors, implying that species-specific experimental validation may be needed before inferring temperature from biomineral oxygen isotope thermometry.
2. Here, we describe a meta-analysis conducted to assess the influence of biological and experimental sources of variation on the coefficients of published isotope thermometry equations.
3. We observed that the thermal sensitivity (equation slope) was resistant to any biological or experimental factors, while the isotopic spacing between water and biomineral (equation intercept) showed consistent variation. Experimental conditions and phylogeny were the two main sources of variation in equation coefficients, where experiment approaches influenced both equation intercepts and the fit of the linear regression.
4. Our results suggest that the use of common equation slopes and generalized taxa-specific equation intercepts may be appropriate under some circumstances. We additionally suggest that processes related to oxygen balance and osmoregulation may influence equation intercepts, and suggest further experimental work in this area. Finally, our observations provide ground for improvement for future design and reporting of biomineral thermometry experiments.

KEYWORDS
aragonite, biochronology, calcite, calcium carbonate, isotope ratio, otolith, oxygen stable isotopes, thermal habitat

1 | INTRODUCTION

Responses of animals to individually experienced environmental conditions define the viability and distributions of populations (Faillace et al., 2021). For aquatic ectotherms, water temperature is a key driver of individual behaviour and condition, due to its direct and indirect effects on physiological rates and the availability of oxygen and food (Rubalcaba et al., 2020). Acquiring precise and accurate data on the thermal experience of individual organisms remains a challenge. In mobile organisms such as fish, the temperature experienced by an individual may differ markedly from temperature estimates derived from fixed location data loggers or remotely sensed data (Collas et al., 2019). Consequently, individual and time-resolved records of thermal exposure histories are needed to accurately assess the responses of organisms to thermal variations in their environment, to understand life-stage thermal habitat partitioning and to predict their vulnerability in future climate change scenarios. Electronic data recorders (e.g. tags) implanted into or attached onto individual animals can provide high-resolution information on experienced temperatures (Block et al., 2001). Most data recorders, however, can only be attached to larger individuals and may have a limited battery life. Data storage tags often require physical recovery to download the data, and the rate of successful recovery is often low (De Pontual et al., 2012). Loggers are also limited in their contribution to reconstruct past temperature earlier than the 1980s, corresponding to the beginning of their widespread use. The associated costs mean that relatively few animals can be monitored/tagged, and retrospective analysis is impossible (Gallagher et al., 2018).

The ratio of oxygen stable isotopes (expressed as $\delta^{18}O$ values) in biominerals, especially calcium carbonate biominerals such as mollusc shells, coral skeletons or fish otoliths, acts as a natural temperature proxy due to the temperature dependence of equilibrium fractionation of oxygen stable isotopes (^{18}O and ^{16}O) during precipitation (Kim et al., 2007; Urey et al., 1951). Consequently, oxygen-stable isotope ratios in biominerals vary in relation to the ambient water isotopic ratio modulated by the temperature experienced at the time of deposition. For example, $\delta^{18}O$ thermometry in biomineral carbonates of unicellular foraminifera is used as the primary information source for the reconstruction of the deep ocean temperature records (Zachos et al., 1994), underpinning models of global climate sensitivity. As many biomineral carbonates grow continuously throughout the individual's lifetime, the variation of composition in the studied structure represents a chronological record of this past condition. Oxygen isotope thermometry had also been extensively used to reconstruct temperature experienced by individual fish (Dorval et al., 2011; Godiksen et al., 2012), cephalopods (Martino et al., 2022) and many other taxa. In the absence of a full mechanistic model of isotopic exchanges in those taxa, the use of $\delta^{18}O$ thermometry is dependent on a statistical determination of the isotopic relationship between ambient water and mineral. Isotopic dynamics of abiotic, inorganic mineral growth have been determined through experimental precipitation experiments, providing a statistical model linking the oxygen isotope composition of the ambient water and the mineral. This relationship is expressed by a negative linear model with the intercept describing the isotopic separation between water and mineral ratios and the slope describing the thermal sensitivity (Kim et al., 2007). In multicellular organisms, however, biomineralization typically occurs in a compartmentalized space, more or less separated from the ambient water (Gilbert et al., 2022), with potential for additional physiological and/or kinetic influences on the isotopic composition of oxygen ultimately expressed in the biomineral. Such influences (often packaged as 'vital effects') include, but are not limited to, biomineral growth rate and organisms' growth rate (e.g. metabolism), fractionation of isotopes during transport across membrane boundaries and mixing of isotopically distinct sources of water within an individual's body.

Experimental studies have yielded differences in the slope, intercept and linearity of biomineral thermometry equations among various organisms, leading researchers to argue that species- or genus-specific fractionation equations should be used when attempting to reconstruct experienced temperature using biomineral oxygen isotope thermometry (Darnaude et al., 2014; Morissette et al., 2020). Temperature-dependent fractionation of oxygen isotopes during biomineral precipitation can be expressed in many equation formulations, first as the response of fractionation factor (α) to ambient temperature (T) (Equation 1):

$$10^3 \ln\alpha = b \times 10^3 T(K)^{-1} + a. \quad (1)$$

The oxygen isotope ratios, when expressed relative to the same standard material (i.e. Vienna Peedee Belemnite, VPDB, or Vienna Standard Mean Ocean Water, VSMOW), can be used to estimate the fractionation factor (α) using Equation 2:

$$\alpha_{\text{carbonate-water}} = \frac{\delta^{18}O_{\text{carbonate}} + 1000}{\delta^{18}O_{\text{water}} + 1000}. \quad (2)$$

The temperature-dependent equations can also be expressed as the absolute differences between carbonates and water isotopic ratios, expressed in relation to their respective standard material (Equation 3):

$$\delta^{18}O_{\text{carbonate,VPDB}} - \delta^{18}O_{\text{water,VSMOW}} = b \times T(^\circ C) + a. \quad (3)$$

Equation 3 is empirically derived from Equation 1, as $\delta^{18}O_{carbonate,VPDB} - \delta^{18}O_{water,VSMOW}$ is approximately equal to 1000 * ln(α) when differences between both isotopic ratios are small. In some cases, the temperature-dependent fractionation equations derived in experimental conditions are non-linear and can be expressed as more complex polynomial equations (Godiksen et al., 2011). However, most temperature reconstruction studies rely on linear relationships for simplicity and our meta-analysis has only included these equations.

While the potential for consistent variation in oxygen isotope dynamics between water and biomineral exists, to date there is a limited consensus on the strength of the contribution from the different sources. If isotopic fractionation does indeed vary consistently among taxa (or life stages), specific thermometry equations will be needed for accurate temperature calculations, and deviation from inorganic temperature-dependent estimates may hold information on organism physiology. Conversely, if oxygen isotopic fractionation is essentially conserved across organisms, the application of isotope thermometry to estimate individual temperature experience is simplified, but at the cost of potential metabolic or physiological signals. Here, we address this problem drawing on published relationships between ambient water and biomineral $\delta^{18}O$ values, across a wide range of taxa.

In the context of this study, we proposed two main sources of variation in published $\delta^{18}O$ fractionation equations: species biology and experimental conditions. For species biology, sources of variation are inherent to the species and should have emerged from the multiple evolutive origins of the species' biomineralization process. Hence, the mechanisms that could introduce variability in equation variables are (1) the fractionation of oxygen isotopes during transport across membranes, (2) the differential fractionation of oxygen isotopes during carbonate precipitation associated with crystal forms and growth rates and (3) the mixing of oxygen from isotopically distinct sources. First, in vertebrates such as fish, oxygen (primarily in the form of dissolved oxygen, water or bicarbonate ions) must initially pass through numerous barriers such as the gill membrane and the gut lining. In the blood plasma, dissolved oxygen, water and carbonate are exchanged with products of cellular respiration, influencing the resulting isotopic values. In the case of fish and cephalopods, water and carbonate ions are then exported across the saccular epithelium into the endolymph before finally being incorporated into the growing surface of the otolith or statoliths (Campana, 1999; De Pontual & Geffen, 2003). Secondly, during biomineralization, temperature-driven kinetics of carbonate deposition should follow the predictions made for the thermodynamics of fractionation in inorganic carbonate (Kim et al., 2007), unless physical–chemical factors such as crystal strain and imperfections or crystal growth rate significantly disrupt equilibrium fractionation, which was potentially identified in corals (Juillet-Leclerc, 2020). Finally, while most studies assume only a single source of $\delta^{18}O$ (ambient water), body water actually contains oxygen molecules from three main sources; ambient water, water in diet and oxygen released from cellular respiration. The oxygen in these sources may be more or less isotopically distinct and present in differing proportions depending on the physiology of the organism and environmental or experimental conditions, but quantification of their respective influence remains to be better defined (Magozzi et al., 2019).

Experimental conditions can additionally influence apparent interspecific variability of oxygen isotope fractionation equations. Thus far, three experimental approaches (or type) have dominated the literature, (1) the rearing of studied organisms under differing controlled water temperatures (Owen et al., 2002), (2) the use of captive populations in continuously monitored in situ mesocosm, cage or aquaculture pens (Bugler et al., 2009) or (3) the capture of wild specimens experiencing divergent—and preferably well-monitored—thermal conditions (Aharon, 1983). While wild capture is more likely to replicate the conditions experienced by the target species in future studies, captive populations or laboratory rearing offer more controlled and stable environmental conditions. Other experimental conditions include the range of temperatures investigated, the analytical methods used to measure $\delta^{18}O$ in the biomineral and environment (e.g. water temperature and salinity) and the removal of organic material (especially protein) in the carbonate. Organic removal, depending on the selected method (e.g. heating or peroxide digestion), has been shown to have a potential effect on stable isotope values (Key Jr et al., 2020), but no consistent effect directionality was identified. Diet is another potential factor influencing experimental results, but the isotopic composition of oxygen in diet is generally not reported in experimental studies and is not explicitly considered here.

In this study, we performed a meta-analysis to assess the influence of biological and experimental sources of variation on published temperature-dependent fractionation equations. Specifically, we tested four hypotheses:

- H1: The thermal sensitivity of isotopic fractionation (i.e. equation slope) is not influenced by phylogenetic or physiological factors, and is indistinguishable from that seen in inorganic carbonate deposition.
- H2: There are species (or taxa)-specific influences on equation intercepts, given that distant species groups may have evolved different physiological barriers and pathways to the biomineralizing fluid, including variable mixing of oxygen sources.
- H3: Laboratory-based equation estimations are more precise than those estimated from wild-collected samples.
- H4: Ambient salinity influences the equation variables among marine and freshwater species from the same taxonomic group (in this case teleost fishes), due to higher flux rates of ambient water in marine fishes.

With this work, we aim to identify systematic sources of variation in published temperature-dependent fractionation equations to increase the understanding of $\delta^{18}O$ dynamics during biomineralization. Our study also aims to refine the use and estimation of $\delta^{18}O$ temperature-dependent fractionation equations, which represent a useful tool in the assessment of individual temperature histories and the impact of climate change on aquatic ecosystems.

2 | MATERIALS AND METHOD

We conducted a systematic review of the literature using the 'Web of Science' search engine (WOS) in January 2022 (range 1950–2022). The search query was built on three concepts; biogenic carbonates, oxygen stable isotopes, and temperature estimation, resulting in the following search string: (otolith OR carbonate OR bone OR shell OR aragonite) AND ('oxygen isotope*' OR δ18O OR d18O OR 'oxygen 18') AND (thermal* or temperature). This search provided 989 records, 12 additional articles were added based on cross-referencing, which consisted of an examination of the list of references and citing articles ('cited by' section of the publisher's website or the article's Google Scholar record).

A study's suitability for inclusion/exclusion from the meta-analysis was evaluated based on predetermined criteria (Figure 1) following the preferred reporting items for systematic reviews and meta-analyses (PRISMA) best practices statement (Moher et al., 2009). Of the 1001 records, suitability was first evaluated based on articles' record for title and abstract, where we evaluated whether the aims included estimating a temperature-dependent oxygen stable isotope fractionation equation (896 excluded). The remaining articles (105) were retrieved and assessed at the full text level to confirm that the objectives stated in the abstract were concordant with those described in the full text (53 excluded), which minimally required the expression of a temperature-dependent equation. Finally, full texts were read entirely (52 articles) and the final selection was made on two pre-determined eligibility criteria; (1) equation formulation: the calculation of a linear temperature-dependent fractionation equation of oxygen stable isotopes (either as Equation 1 or Equation 3) and (2) water fractionation: the equation formulation considered fractionation among ambient water and biogenic carbonates, and not merely the response of carbonate oxygen stable isotope ratios to temperature (19 excluded). The criteria of equation formulation and explicit consideration of water isotope values were critical for the subsequent meta-analytical models, as the comparison of equation coefficients from two different formulations, especially if the nature of regression strongly diverts from a linear regression (e.g. polynomial equations), risks inducing errors in meta-analysis conclusions. Hence, a total of 37 studies (27 articles from the original WOS search, 6 from the cross-referencing and 4 suggested by reviewers) were retained for data extraction and subsequent analyses (Figure 1).

Details of experimental conditions were extracted using information reported in the materials and methods or the results sections of each article. Specifically, the life stage (larvae, juveniles or adults), type of carbonate structure analysed (e.g. shell, otolith, statolith), carbonate form (aragonite or calcite), experimental approach (wild sampling, captive rearing or laboratory rearing), procedure used for removal of organic matter in the carbonate matrix (e.g. none, heating, peroxide), number of studied specimens (study size), maximum and minimum temperature, temperature range and experiment habitat (freshwater or saltwater). Temperature-dependent fractionation equation slopes, intercepts, and their respective standard error (both for Equations 1 and 3, when available) were extracted from the study results. The regression coefficients of Equation 3 were estimated for the Patterson (1998) study, as raw data were published in the article in which only Equation 1 was reported. Additionally, fractionation equations for four studies (Burbank et al., 2020; Kastelle

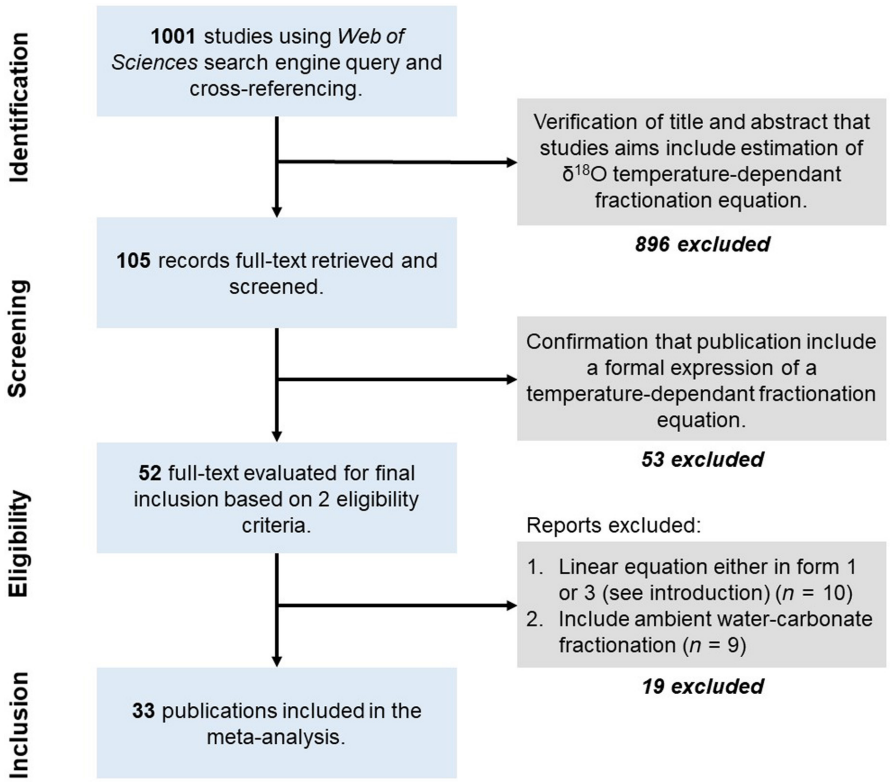

FIGURE 1 PRISMA flowchart of systematic literature review showing records from databases and other sources.

et al., 2022; Storm-Suke et al., 2007; Willmes et al., 2019) were corrected from the published version, linked to a divergent calculation of Equation 3. Those studies based their estimation of both carbonate and water $\delta^{18}O$ values relative to the same standard material (Vienna Peedee Belemnite, VPDB), rather than using VSMOW for water samples as commonly conducted. This resulted in a large difference in the intercepts compared to the rest of the dataset. We estimated a correction factor by using a linear regression of the Equation 1 intercepts—which were not influenced by this error—and Equation 3 intercepts from all of the studies that presented both forms of equations (14 studies). This resulting negative regression ($b_{corrected} = b * -0.044 + 2.53$, $R^2 = 0.69$) was used to convert the biased intercepts to a *post-hoc* approximation of a similar intercept. As the computation error does not have any impact the estimated slopes, they were extracted as published.

Phylogenetic distances among studied species were estimated using consensus COI sequences from the Genebank repository. We used species-specific difference in the gene sequence as a proxy of time since divergence, to test for evolutionary effects accounting for variation in the carbonate biomineralization process among all studied taxa. Sequences were aligned using the MSA R package (Bodenhofer et al., 2015) and the squared root of the pairwise distances between sequences identity was estimated for each species using the *seqinr* package (Charif & Lobry, 2007). The distance matrix was transformed into a continuous distance metric using the species-specific values on the first axis of a nonmetric multidimensional scaling (NMDS), computed using the function metaMDS from the VEGAN package (Oksanen et al., 2017).

Six meta-analysis models were used to test the effects of either species biology or experimental conditions on equation slopes (meta-analysis 1 and 2), intercepts (meta-analysis 3 and 4) and correlation coefficients (meta-analysis 5 and 6). The meta-analyses assessing the influence of species biology (1,3 and 5) were mixed effects models fitted via restricted maximum-likelihood where moderators were the high-level taxa name (i.e. coral, crustacean, fish, mollusc, foraminifera and sponge), a binary categorical variable of environment during the experiment (freshwater [<2] or saltwater [>30]) and life stage (i.e. larva, juvenile or adult). A unique study identifier was included as a random effect to consider the non-independence of multiple equations generated from the same study. The meta-analyses assessing the influence of experimental conditions (2, 4 and 6) were mixed effects models fitted via restricted maximum-likelihood and included four moderators which were experimental approaches (laboratory rearing or wild capture), calcium carbonate form (aragonite or calcite), experimental temperature range (numeric, range 3.8–27.1) and sample pre-treatment of organic matter (no or yes) along with the study random effect to consider non-independence among multiple equations from the same study.

The estimation of effect sizes for regression slopes was based on unbiased correlation coefficients (Olkin & Pratt, 1958). Effect sizes for equation intercepts were based on a log-transformed mean effect size (Nakagawa et al., 2015) and missing sampling variance terms (vi, $n = 24$ missing) for meta-analysis were imputed as the mean of estimated vi ($8.71*10^{-4}$, $n = 19$) divided by the study sample size (Ne) (Koricheva et al., 2013). Finally, the regression correlation coefficients' effect sizes were calculated as a Fisher's *r*-to-*z* transformed correlation coefficient based on published Pearson's correlation coefficients or transformed R^2.

Two additional meta-analyses were carried out on a subset of the dataset, limited to fishes ($n = 18$ studies), to test a finer-scale effect of three moderators; phylogenetic distance, environment during the experiment (freshwater [<2] or saltwater [>30]) and life stage (larval, juvenile and adult) on the regression slopes (meta-analysis 7) and intercept (meta-analysis 8). Effect sizes were estimated as unbiased correlation coefficients (meta-analysis 7) and log-transformed mean effect size (meta-analysis 8). Sampling variance in meta-analysis 8 was imputed as the mean of estimated vi ($8.71*10^{-4}$, $n = 19$). Meta-analyses 7 and 8 were fitted with restricted maximum-likelihood meta-analytic linear models. All calculations of effect sizes and meta-analysis models were computed using the R package METAFOR (Viechtbauer, 2010).

3 | RESULTS

After literature review and data extraction, we retrieved 53 temperature-dependent oxygen stable isotope fractionation equations from 37 studies (Figure 2). The most frequently studied taxa were teleost fishes ('fish', 18 equations), molluscs (including cuttlefish, 14 equations), corals (12 equations) and foraminifera (6 equations). Comparatively few studies provided equations for other groups such as sponges (two equations based on spicules). A single study on the statocysts of *Cyprideis torosa* (Bodergat et al., 2014) was included, representing 'crustacea'. Most experiments were conducted in a saltwater environment (43 equations) compared to freshwater (10 equations). No experiments were conducted in brackish water (see Supporting Information S1). Slightly more than half of the equations were estimated from wild-sampled individuals (28 equations). Of the 25 equations estimated from controlled rearing experiments, only one equation was based on a captive rearing experiment and one equation was based on a combined dataset of three approaches (Bugler et al., 2009). The average study size—which is the number of specimens analysed for stable isotopes—was 54 (SD = 22.2, ranging from 10 to 470). Our phylogenetic distance metric ranged from −0.17 to 0.16, with fish (mean = −0.12), crustacean (mean = 0.04), mollusc (mean = 0.06), sponge (mean = 0.09) and coral (mean = 0.15) species ordered along the first NMSD axis.

We checked for any artefacts of the meta-analysis first. Effect sizes were not correlated with the date of publication either for equation slopes ($F_{1,49} = 1.14$, $p = 0.29$), equation intercepts ($F_{1,49} = 1.30$, $p = 0.526$), or correlation coefficient ($F_{1,47} = 0.31$, $p = 0.58$), suggesting no temporal trends in effect size (e.g. temporal bias). Observation of funnel plots for all meta-analyses did not show any sign of pronounced asymmetry linked to potential publication bias, precluding the necessity of imputing missing effect sizes.

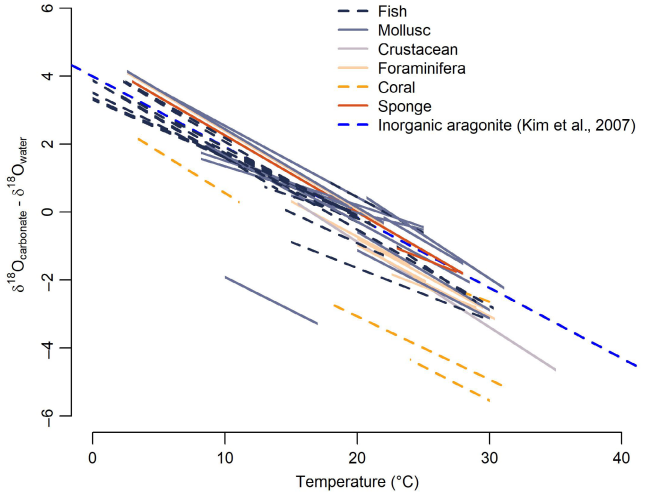

FIGURE 2 Published temperature-dependent oxygen stable isotope fractionation equations of each study included in the meta-analysis. The line colour represents the higher-level taxonomic group included in the meta-analyses and the line length represents the temperature range of the corresponding study. The blue dashed line is the fractionation equation for inorganic aragonite (Kim et al., 2007).

Meta-analysis 1 and 2 (effect of species biology and experimental conditions on slopes) showed no significant effects of moderators, either species groups, environment (freshwater/saltwater) or life stage on the estimated regression slopes (Figure 3). The among-studies variance (σ^2) was 0.0, and residual heterogeneity was not significant (Cochran's $QE_{39} = 2.42$, $p = 1.00$). Similarly, neither experiment type (laboratory/captive rearing, or wild capture), type of carbonate, temperature range or removal of organic content in biomineral had an effect on equation slopes.

The influence of species biology on equation intercepts was significant only for coral, with a negative effect on equation intercept. Life stage, linked to the use of adult specimens, had a small significant positive effect on equation intercepts (meta-analysis 3). When using raw data, phylogenetic distance had a significant negative effect on equation intercept (ANOVA, $F_{1,38} = 28.86$, $p < 0.0001$). Unlike the slopes, the equation intercepts were influenced by experimental conditions (meta-analysis 4). Experiment type had a positive effect on intercepts, with wild-capture experiments having higher values. The temperature range had a small, yet significant negative effect on intercept.

No species biology moderators had a significant effect on correlation coefficients, our proxy for accuracy (meta-analysis 5). However, accuracy was significantly affected by experimental conditions (meta-analysis 6), with a significant reduction in correlation coefficients for wild sampling experiments (compared to laboratory rearing), linked to a lower predictive power of these equations (Supporting Information S2).

In meta-analysis 7, limited to fish studies, neither phylogenetic distance, rearing environment (freshwater or saltwater) nor life stage had any significant effect on the slopes of the temperature-dependent equations (Figure 4). There was a non-significant residual heterogeneity (Cochran's $QE_{12} = 0.33$, $p = 1.00$) of equation slopes. Phylogenetic distance had a significant negative effect on the equation intercept (meta-analysis 8), where lower intercepts were linked to taxa more closely related to marine benthic predators (e.g. Atlantic Cod, *Gadus morhua*), and higher intercepts were linked to taxa more closely related to diadromous or freshwater taxa (e.g. freshwater salmonids, e.g. Arctic Char, *Salvelinus alpinus*, and cyprinids). Additionally, the environment showed a significant, negative effect on the equation intercept where rearing in saltwater was linked to a lower intercept (Supporting Information S3). Life stage had a significant negative effect on the equation intercept; adults had lower intercepts than larvae and juveniles (Supporting Information S3).

4 | DISCUSSION

Using a meta-analysis framework, our study evaluated the systematic effects of species biology and experimental conditions on variations observed in the parameters of published temperature-dependent $\delta^{18}O$ fractionation equations. We aimed to provide a better understanding of the sources of species-specific variations in published estimates of the $\delta^{18}O$ fractionation between biomineral and ambient water. Thermal sensitivities of oxygen isotopic fractionation (equation slopes) were highly conserved across taxa and experimental conditions. We observed that taxa and experimental conditions were the two main sources of variation. Specifically, the experiment approach (e.g. captive rearing or wild sampling) influenced both equation intercepts and the accuracy of the linear regressions. Equation intercepts, overall, were subject to only limited systematic influence by taxa, except for corals that showed a significant negative effect, resulting in lower-than-average values.

Analyses of a subset of the data that only included fish species showed that phylogenetic distance between taxa, as well as life stage and rearing environment (freshwater or saltwater), significantly influenced the intercepts in published $\delta^{18}O$ fractionation equations. These results may offer insights into the mechanistic process of oxygen-stable isotope mixing in biomineral across a wider taxonomic spectrum. We consider that various observations during the review help to identify knowledge gaps in biomineral thermometry.

4.1 | Temperature-dependent fractionation is resistant to species-specific variations

Our results showed that the temperature sensitivity of $\delta^{18}O$ fractionation between water and biomineral (i.e. the slope of the equation) was not affected by aspects of species biology—including taxa, life stage and environment—and experimental conditions (consistent with hypothesis H1). This highlights the weaknesses in using the term 'vital effects' to explain species-specific differences in thermometry equations. The observed median slope of published equations (−0.209‰*T) was indistinguishable from the estimation based on synthetic aragonite (−0.21‰*T; Kim et al., 2007) given uncertainties but was different from dissolved bicarbonate (−0.288‰*T; Beck et al., 2005), strongly suggesting that equilibrium fractionation thermodynamics dominate temperature

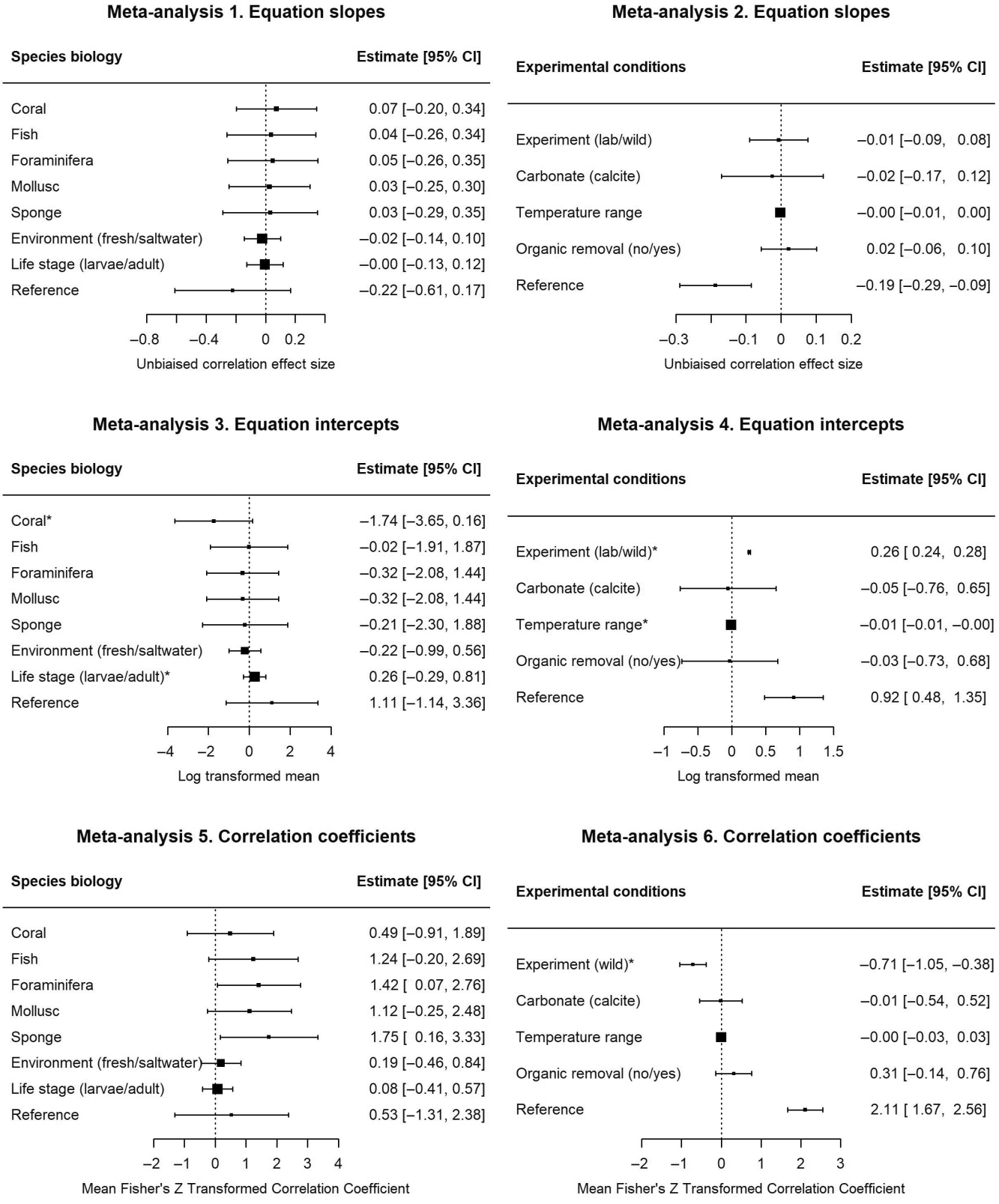

FIGURE 3 Forest plots for meta-analysis on the effects of species biology (1) and experimental conditions (2) on slopes, the effects of species biology (3) and experimental conditions (4) on equation intercepts, and the effects of species biology (5) and experimental conditions (6) on correlation coefficients. The position of the points represents the influence on the common effect size for each moderator and standard error (whiskers). Asterisks next to moderators show significant influence on the different effect sizes ($p < 0.05$).

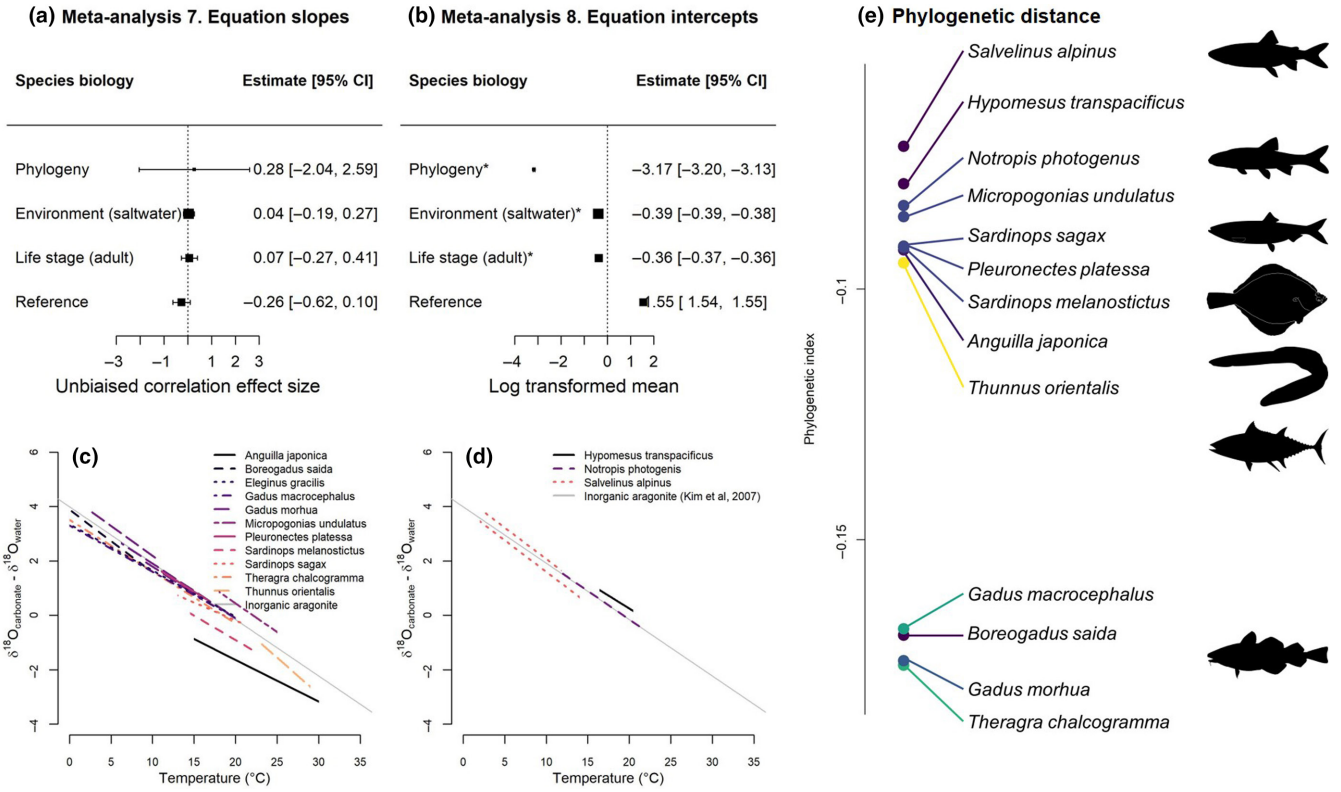

FIGURE 4 Forest plots for meta-analysis on the effects of species biology on regression slopes (a meta-analysis 7) and intercepts (b meta-analysis 8) for the fish-specific subset of data. Published temperature-dependent oxygen stable isotope fractionation equations for marine (c) and freshwater (d) fish species included in the meta-analyses. Grey solid line is the fractionation equation for inorganic aragonite (Kim et al., 2007). Visual depiction of fish phylogenetic distance index (e), fish silhouettes are from Phylopic database.

dependency of oxygen isotope fractionation during biomineral precipitation across taxa. If a biological or disequilibrium factor does influence biomineral $\delta^{18}O$ temperature sensitivity, our results suggest that these effects are not systematic and probably negligible, at least among the taxa included in this study. The main practical implication of this result is that relative temperatures (i.e. differences in experienced temperature among individuals) can be estimated with confidence from inorganic equilibrium fractionation equations. These results also suggest that, for future experiments estimating $\delta^{18}O$ temperature-dependent fractionation equation, slopes strongly deviating from the synthetic aragonite estimation (Kim et al., 2007) should be considered with caution. Any observed strong deviation may indicate an unknown or hidden variable or process at play, or an experimental condition having a marked effect on estimated $\delta^{18}O$ values. Notably, we consider that biological variables like individual growth rate, or analytical variables like IRMS laboratory facilities and carbonate sampling procedure (e.g. micro-milling, sectioning or others), acid digestion reaction temperature and calcium carbonate to CO_2 fractionation factors are variables that are inconsistently reported and could have influence on estimated equations.

4.2 | The importance of experimental conditions in among-study variations

Variations of the experimental conditions reported in different studies influenced equation coefficients and predictive power (accuracy), expressed as the correlation coefficient. Experimental conditions differ widely between studies, and the variety of conditions is difficult to capture in a meta-analysis (Koricheva et al., 2013). In many cases, the experimental details are missing, or are partially reported with very variable precision, and the lack of detail often precludes a clear understanding and quantification of those factors. For example, less than 80% of the 14 studies of fish otoliths we assessed specified which otolith pair (i.e. sagitta, lapillus or asteriscus) was used. The sagitta is usually the largest of the otolith pairs, and when not specified, it is usually assumed that these have been analysed, however, there are exceptions (Burbank et al., 2020; Morissette et al., 2021). The choice of otolith could have significant implications for the results since different otolith pairs can be composed of different crystal forms (i.e. aragonite, vaterite or calcite) that exhibit different chemical affinity to trace elements and isotopic fractionation (Budnik et al., 2020; Campana, 1999; Macdonald et al., 2012). Missing details, which can be found in other experimental conditions, could be responsible for a substantial proportion of the unexplained variation observed for correlation coefficients. According to our results, experimental approaches and temperature range were the factors that exerted a significant effect on the intercepts and correlation coefficients, with the main effect being that laboratory-based studies provided higher predictive power compared to studies based on wild-caught specimens. This result is consistent with our hypothesis H3 and emphasizes that captive rearing offers finer control and monitoring of environmental variability, which results

in lower uncertainty. Better reporting of experimental conditions is needed for further large-scale reviews.

Other sources of variation, both biological and experimental, remain beyond the variables included in our analysis, often because of reporting constraints noted above. It is important to note that numerous authors had applied an erroneous formulation of $\delta^{18}O$ conversion equation from VSMOW to VPDB reference material ($\delta^{18}O_{VPDB} = 0.99978^{*}\ \delta^{18}O_{VSMOW} - 0.22$, the incorrect equation) which they attributed to Friedman and O'Neil (1977). This is significantly different from the original Friedman and O'Neil (1977) formulation: $\delta^{18}O_{VPDB} = 0.970068 * \delta^{18}O_{VSMOW} - 29.94$. The error appears to have been propagated following a typographical error in Høie et al. (2004) and that was subsequently reused by other studies. Unfortunately, the effect of this error could not be tested because details of the conversion equation(s) used, if any, was missing from 56% of the studies included in the present analysis. The International Union of Pure and Applied Chemistry (IUPAC) guideline equation $\delta^{18}O_{VPDB} = 0.97001 * \delta^{18}O_{VSMOW} - 29.99$ (Brand et al., 2014; Kim et al., 2015) is a more recently adopted standard that should be applied in accordance with a suite of IUPAC best practices in stable isotope science.

Additionally, we noted relatively frequent use of $\delta^{18}O$ values in relation to the incorrect standard material (VSMOW vs. VPDB), which we addressed post hoc when possible (see Section 2). Use and reporting of the appropriate conversion equations and standards is critical, especially when analysing aragonite samples with the calcite NBS19 standard, as calcite and aragonite exhibit different acid fractionation factors and different reaction-temperature dependencies (Kim et al., 2007). Future studies reporting isotopic data should fully describe the standard reference material, reaction temperature with phosphoric acid, with or without correction of acid fractionation factor, and the values used for any corrections made. Finally, the emerging use of secondary ion mass spectrometry (SIMS) in addition to isotope ratio mass spectrometry (IRMS) could influence fractionation equations, as surface-based analyses such as SIMS unavoidably sample oxygen contained in the organic matrix as well as carbonate-bound oxygen, contributing to a matrix effect that can have a significant offset effect on resulting $\delta^{18}O$-derived temperature estimates (Hane et al., 2020; Rollion-Bard & Marin-Carbonne, 2011). As only two studies in our dataset used SIMS over IRMS for data acquisition (Shirai et al., 2018; Willmes et al., 2019), the effect of this experimental choice, if any, could not be tested here.

4.3 | Insight into consistent variation of intercepts in biomineralization dynamics

The largest effect observed in our meta-analysis was in the intercept term and its association with differences between taxa, which is consistent with H2. The total range in intercept terms exceeded 3‰, equivalent to a difference in inferred temperature of c.12°C if a common temperature equation was used. This effect, although it could not be consistently identified for all taxa, seems to support an effect of phylogenetic distance between taxa in oxygen isotopic dynamics. Corals, in particular, showed a large difference in intercepts when compared to other groups. The difference we observed between shallow-water corals and other taxa is concordant with the striking difference in $\delta^{13}C$ and $\delta^{18}O$ equilibrium with ambient water observed between autotrophic and heterotrophic taxa (Gilbert et al., 2022). Biomineralization is widespread across taxa, and undoubtedly evolved independently on multiple occasions, but conclusions in one taxonomic group could also influence our understanding of the process in others. Isotope dynamics associated with biomineralization processes have been well-studied in corals (Aharon, 1983; Bohm et al., 2000) and recent work implies that species-specific differences between oxygen isotope thermometry equations primarily arise from processes occurring during calcification (the calcifying fluid to carbonate fractionation) more than the biomineral (or organism) growth rate per se. These processes may include (1) the thermodynamics of calcification (lower $\delta^{18}O$ values at higher temperature), (2) the mixing of within-organism source of water and (3) the contribution of oxygen released from photosynthesis (increasing $\delta^{18}O$ values at higher temperature), a behaviour well observed at the microstructural scale (Juillet-Leclerc, 2020). Since temperature sensitivity was not affected by any predictors in our study, we suggest that those other mechanisms should be investigated as sources of variation in $\delta^{18}O$ temperature-dependent fractionation equation in corals.

When considering only fishes, differences in intercept terms still exceeded 1‰ (equivalent to range of inferred temperatures of *c*. 4°C based on Kim et al.'s (2007), showing potential for species-specific variation. The difference in intercepts among taxa has long been observed in oxygen stable isotope thermometry, routinely referred to as 'vital effects' (Darnaude et al., 2014; Kozdon et al., 2009). Equation intercept terms describe the overall isotopic spacing between water and biomineral. Meta-analyses 7 and 8 compared factors influencing equation terms when controlling for a large part of phylogenetic variation by reducing the data to a subset of closely related species, in this case, teleost fish. Both analyses suggested that phylogenetic distance, life stage and rearing environment (freshwater or saltwater) all had significant effects on intercepts (but not slopes), which is consistent with H4.

Two of those factors (phylogeny and environment) were at least partly correlated, as lower phylogenetic index corresponded to marine species and higher values corresponded to mostly freshwater species. Our interpretation highlights an important combined effect of environment (freshwater or marine) and phylogenetic origin on temperature-dependent fractionation, which is probably linked to their diverging osmotic state and process of water exchange (Knezovich, 1992; Loewen et al., 2016). Marine fishes ingest seawater, leading to a large flux of ambient water—which usually had an average $\delta^{18}O$ value of 0 ± 0.6‰—and, thus the internal body water pool would have a low proportion of body water from metabolic sources. By contrast, freshwater fishes are hypertonic and limit their ingestion of freshwater. The ambient water for freshwater fish has generally lower $\delta^{18}O$ values (-6.1 ± 4.2‰; Pfister et al., 2019)

Taxa	Generalized equations
Fish – Freshwater	$\delta^{18}O_{carbonate,VPDB} - \delta^{18}O_{water,VSMOW} = -0.21 * T(°C) + 4.05$
Fish – Saltwater	$\delta^{18}O_{carbonate,VPDB} - \delta^{18}O_{water,VSMOW} = -0.21 * T(°C) + 3.72$
Mollusc – Freshwater	$\delta^{18}O_{carbonate,VPDB} - \delta^{18}O_{water,VSMOW} = -0.21 * T(°C) + 2.55$
Mollusc – Saltwater	$\delta^{18}O_{carbonate,VPDB} - \delta^{18}O_{water,VSMOW} = -0.21 * T(°C) + 4.02$
Foraminifera – Saltwater	$\delta^{18}O_{carbonate,VPDB} - \delta^{18}O_{water,VSMOW} = -0.21 * T(°C) + 3.32$
Coral – Saltwater	$\delta^{18}O_{carbonate,VPDB} - \delta^{18}O_{water,VSMOW} = -0.21 * T(°C) + 0.77$
Crustacean – Saltwater	$\delta^{18}O_{carbonate,VPDB} - \delta^{18}O_{water,VSMOW} = -0.21 * T(°C) + 4.14$
Sponge – Saltwater	$\delta^{18}O_{carbonate,VPDB} - \delta^{18}O_{water,VSMOW} = -0.21 * T(°C) + 3.49$
Inorganic aragonite (Kim et al., 2007)	$\delta^{18}O_{carbonate,VPDB} - \delta^{18}O_{water,VSMOW} = -0.21 * T(°C) + 3.99$

TABLE 1 Taxa and environment (freshwater and marine) -specific generalized $\delta^{18}O$ temperature-dependent fractionation equations. Here, fish refer only to teleosts.

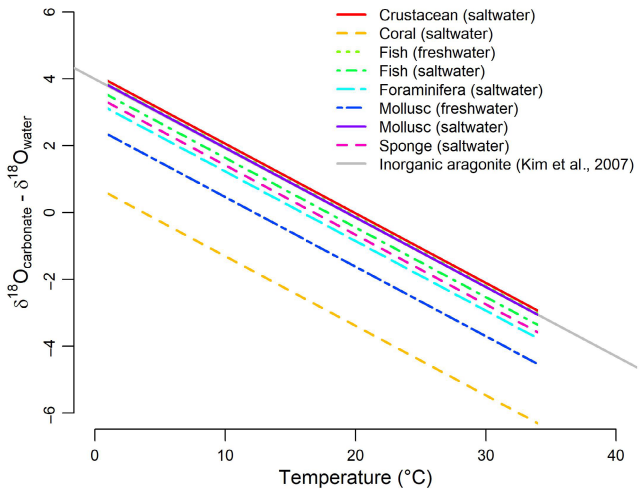

FIGURE 5 Generalized temperature-dependent oxygen stable isotope fractionation equations for the different taxa and their environment (freshwater and saltwater), see Table 1 for exact formulations. Grey solid line is the fractionation equation for inorganic aragonite (Kim et al., 2007).

compared to seawater (~0‰ ± 0.6‰), resulting in a greater relative contribution of metabolic water to the body water flux. As metabolic water is expected to have a constant $\delta^{18}O$ value of −3.5‰ (Kreuzer-Martin et al., 2005; Li et al., 2016), freshwater taxa would be predicted to have a higher fractionation intercept, which is consistent with our results. The position of diadromous fishes in this continuum, however, is not clear, as our available dataset did not include any experiments conducted in brackish water. Variation in osmotic state of diadromous species may result in variable fractionation among life stages or environments. Experiments estimating temperature-dependent fractionation dynamics for the same species in divergent salinity treatments may shed light on this phenomenon and clarify the effect of the osmotic state in oxygen isotope flux and biomineralization. We, therefore, argue that differences in oxygen flux and isotope mixing within organisms, potentially related to oxygen balance and osmoregulation, are likely to be the principal biological mechanisms responsible for inter-specific differences in temperature-dependent fractionation.

4.4 | Generalization of taxon-level equations

The conservation of slopes among published equations and the variation of intercepts observed within broad taxonomic groups implies that generalized equations could be formulated based on variables representing information about the high-level taxonomic group (e.g. fish, mollusc or coral) and the environment (freshwater or saltwater). Based on our results, these generalized equations should draw on the slope term estimated for inorganic carbonate (Kim et al., 2007), which represents a realistic common term. Those generalized equations (Table 1) could provide a reasonable substitute where species- or taxon-specific equations are lacking. This is also a reasonable substitute when the use of published species- or taxon-specific equations produces unrealistic estimations of experienced temperature. However, the use of a species-specific intercept term, especially if produced via laboratory/captive rearing, may remain the preferred method for maximum accuracy of temperature estimation (Figure 5).

5 | CONCLUSIONS

In summary, we find strong support for the argument that thermal sensitivity of oxygen isotope fractionation between ambient water and biomineral aragonite is statistically indistinguishable from inorganic aragonite precipitation across taxa. By contrast, we confirm that large variations in intercept terms were linked to systematic taxon-related differences. Among teleost fish studies, the variations in intercepts are consistent with functional traits associated with osmoregulation in marine compared to freshwater fishes. It is not possible at this stage, however, to identify mechanisms underpinning variations in intercept terms. Our analyses suggest that relative temperature differences within taxa are relatively robust, given the consistency in thermal sensitivity terms across systems and taxa, and therefore it may be appropriate to use one of the taxon-specific generalized equations to provide relative changes in temperature in species that have not been tested experimentally. With additional focussed study, systematic variations in oxygen isotope thermometry intercept terms identified here may provide a tool to explore

aspects of aquatic animal physiology, particularly related to water balance and osmoregulation.

This is, to our knowledge, the first attempt to generalize factors influencing $\delta^{18}O$ temperature-dependent fractionation across a large group of both related and unrelated aquatic taxa. Our analytical framework, like many meta-analyses, remained limited to the variables that we could consistently extract from the descriptions of each study. We observed that a non-negligible proportion of the variation in published fractionation equations originated from experimental design and analytical choices rather than from systematic biological variation. Other factors that likely contribute to the remaining variation in equation parameters include the use of erroneous formulae, conversion and calculation errors, matrix effects associated with mass spectrometer type or laboratory protocol. This study demonstrates the importance of implementing best practices, and the importance of full and consistent reporting of the experimental conditions, calculation methods and results in all scientific reporting media (articles or talks), to promote data sharing and accurate, open science.

AUTHOR CONTRIBUTIONS

All the authors conceived the ideas and designed methodology; Olivier Morissette realized the systematic review, and extracted the data; all the authors conceptualized the statistical analyses and Olivier Morissette coded them and analysed the data; Olivier Morissette led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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CONFLICT OF INTEREST STATEMENT

None of the authors have a conflict of interest to declare.

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DATA AVAILABILITY STATEMENT

All the R codes, raw datasets and figures are available on the freely accessible Borealis repository, following this link: https://doi.org/10.5683/SP3/JRSOO8.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Table S1. Information on studies used in meta-analysis, listing taxa, common name, latin name, studied carbonate structures, experiment types, water environment and temperature range used for estimation of temperature dependant fractionation equations.

Table S2. Outputs of meta-analyses of general influences of species biology (meta-analyses 1, 3 and 5) and experimental conditions (meta-analyses 2, 4 and 6) on oxygen stable isotope temperature-dependent fractionation equations, showing mean moderators' effects on common effect size, standard error (SE), *z* values, confidence interval (CI) lower and higher bounds and *p* values.

Table S3. Outputs of meta-analyses on influences of species biology (meta-analysis 7 and 8) on fish otolith oxygen stable isotope temperature-dependent fractionation equations, showing mean moderators' effects on common effect size, standard error (SE), *z* values, confidence interval (CI) lower and higher bounds and *p* values.

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