

# The universal imprint of oxygen isotopes can track the origins of seafood

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## Abstract

Identifying the source of seafood is critical for combatting seafood fraud, but current tools are predominantly developed and applied on a species-specific basis. This study investigates how multiple marine taxa could be geolocated at global scales by exploiting stable oxygen isotope compositions in carbonate biominerals ( $\delta^{18}\text{O}_{\text{biomin}}$ ), where we expect to see universally expressed and predictable spatial variation in  $\delta^{18}\text{O}_{\text{biomin}}$  values across taxa. We constructed global ocean isoscapes of predicted  $\delta^{18}\text{O}_{\text{biomin}}$  values specific to fish (otoliths), cephalopod (statoliths) and shellfish (shells), and a fourth combined “universal” isoscape, and evaluated their capacity to derive  $\delta^{18}\text{O}_{\text{biomin}}$  values among known-origin samples. High correspondence between isoscape-predicted  $\delta^{18}\text{O}_{\text{biomin}}$  values and a compiled database of measured, georeferenced values (3954 datapoints encompassing 68 species) indicated that this  $\delta^{18}\text{O}_{\text{biomin}}$  approach works effectively, particularly in regions with highly resolved projections of seawater  $\delta^{18}\text{O}$  composition. When compared to taxon-specific isoscapes, the universal isoscape demonstrated similar accuracy, indicating exciting potential for universal provenance applications. We tested the universal framework via a case study, using machine-learning models to identify sample origins amongst regions of divergent (Tropical Asia vs Temperate Australasia) and similar (Temperate Asia vs Temperate Australasia) climates and latitudes. Classification accuracy averaged 75.3% between divergent regions, and 66% between similar regions. When endothermic tuna species were excluded from the analysis, the accuracy between divergent regions increased up to 90% between divergent regions. This study presents the first empirical step towards developing universal chemical markers, which have the potential to support a more inclusive and global approach of validating provenance of seafood.

## KEYWORDS

authentication, biominerals, fingerprinting, global model, isoscape, provenance

## 1 | INTRODUCTION

A healthy and sustainable food system is underpinned by knowing where food comes from, and how it is produced. However, wild-caught

seafood is a hard-to-monitor shared resource, and seafood supply chains are often opaque and complex (Fox et al., 2018; Kittinger et al., 2017), which in turn makes seafood particularly vulnerable to fraud. Provenance fraud occurs when consumers or businesses

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are intentionally deceived about where seafood is caught or its production method, with products often substituted with lower-quality and lower-value options, or harvested from locations with fewer regulations regarding sustainability or ethics concerns. Such substitution threatens our food system by jeopardising sustainability, safety, and consumer confidence (Lindley, 2020; van Ruth et al., 2017). Provenance fraud can also result in over-exploitation of stocks, which undermines the long-term viability of fisheries, the balance of marine ecosystems, and ultimately, harms seafood businesses that rely on these resources (Jacquet & Pauly, 2008; Kompas et al., 2010). Substitute seafood products may also pose safety and health risks for consumers, by containing hidden pathogens, banned contaminants, unlisted allergens or reduced nutrient profiles (Gopi et al., 2019). While many factors influence fisheries sustainability, validating the provenance of seafood empowers authorities to combat seafood fraud and ensures consumers can make an informed choice about the seafood they eat.

The provenance of food can be authenticated using a range of techniques, including DNA profiling (Calosso et al., 2020; Rasmussen & Morrissey, 2008), paper-based and digital tracing, such as block-chain (Howson, 2020), and chemical profiling (Duarte et al., 2022; Martino et al., 2022). While chemical methodologies for provenance testing are well-established in terrestrial food forensics, adoption in the aquatic food sector has been slower but is increasingly indicated to have wide potential (Gopi et al., 2019). Natural chemical tracers bound within seafood tissues can be effective at identifying harvest source as they are carried unaltered within the product itself and are difficult to falsify. However, existing provenance tools can be prohibitively expensive for many seafoods due to the high cost of developing reference databases, which are typically optimised for specific species, regions, or supply chains (Kelly et al., 2005). Reference databases are more commonly adopted as standard practise in terrestrial food systems, as land-owning producers have more economic incentive to characterise and protect produce originating from land they own (Monahan et al., 2018; Soares et al., 2017). In marine systems with common access to waters and the presence of migratory species, there is less financial incentive for producers to fund chemical or genetic characterisation of specific geographic areas. Furthermore, small-scale fisheries comprise an estimated 70% of the total world catch (Kolding et al., 2014), with many targeting low-value stocks, operated by independent fishers with no access to forensic tools, and located in exploited waters of developing countries. Traceability methods that rely on development and maintenance of costly fishery-specific databases are thus largely inaccessible to these producers. Therefore, a shared provenance system capitalising on consistent inherent properties across taxa could ease the burden of species-specific, cost-prohibitive provenance systems, and improve accessibility of seafood provenance for lower-income regions, smaller industries, or lower-value seafood species.

A shared provenance system could be developed using *universal* chemical markers. Here, we define a universal chemical marker as having predictable spatial variation coupled with common expression among taxa (Doubleday et al. *in review*). Essentially, a universal marker

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is primarily influenced by the environment whilst species-specific modifications of the environmental signal (e.g., physiological 'vital effects' that vary across taxa) are minimal, so that different taxa living in the same region would share a common chemical value in their tissues. The stable isotope composition of oxygen in calcium carbonate ( $\text{CaCO}_3$ ) biominerals (expressed as  $\delta^{18}\text{O}_{\text{biomin}}$  values) exhibits such properties, making it a promising candidate for universal provenance applications across broad geographic scales (100s to 1000skm). Oxygen is incorporated into marine animals from seawater with an isotopic composition ( $\delta^{18}\text{O}_{\text{water}}$ ) that is relatively constrained and predominantly varies as a function of salinity, water mass identity, and surface evaporation rate (Craig & Gordon, 1965). In general, typically lower  $\delta^{18}\text{O}_{\text{water}}$  values are found in higher latitudes due to discharge of river water and glacial meltwater with low  $\delta^{18}\text{O}$  values, and higher  $\delta^{18}\text{O}_{\text{water}}$  values are observed in highly evaporative regions, such as some sub-tropical zones (Conroy et al., 2014; Singh et al., 2010; Voelker et al., 2015). Global compilations of seawater  $\delta^{18}\text{O}_{\text{water}}$  values have been constructed (LeGrande & Schmidt, 2006), further constraining region-specific relationships between  $\delta^{18}\text{O}_{\text{water}}$  values and salinity. Consequently, with high-resolution salinity data,  $\delta^{18}\text{O}_{\text{water}}$  values can be predicted with confidence on global scales. During biomineralisation, oxygen isotopes are fractionated with preferential incorporation of the lighter  $^{16}\text{O}$  isotope. The extent of this fractionation depends on the temperature of mineral growth (Kalish, 1991; Kim et al., 2007), which in marine ectothermic organisms is the ambient seawater temperature. The form of the temperature-dependent equation of  $\delta^{18}\text{O}_{\text{biomin}}$  has been extensively studied as it serves as the foundation for temperature reconstructions (Zachos et al., 1994), with  $\delta^{18}\text{O}_{\text{biomin}}$  thermometry equations experimentally derived for a range of fish (Geffen, 2012; Godiksen et al., 2010; Høie et al., 2004; Sakamoto et al., 2019; Thorrold et al., 1997), gastropod and bivalve species (Grossman & Ku, 1986; Nishida et al., 2015; Owen et al., 2008; Wanamaker et al., 2007), as well as a single cephalopod

species (Chung et al., 2020). However, there remains some debate on whether  $\delta^{18}\text{O}_{\text{biomin}}$  values reflect ambient temperatures in fish with regional endothermy, such as some shark and tuna species (Graham & Dickson, 2004; Hane et al., 2020).

Given global scale predictions of  $\delta^{18}\text{O}_{\text{water}}$  values and temperatures in the ocean alongside the well-established biogeochemical relationships, it is possible to create spatial models ("isoscapes") of predicted  $\delta^{18}\text{O}_{\text{biomin}}$  values in tissues of marine animals (Trueman et al., 2012). Isoscapes are typically displayed as spatial maps of isotopic distributions and can be used to predict the most likely geographic origins of an organism by matching the isotopic composition of its tissue to area(s) on the isoscape with similar values. Isoscapes have been used in both terrestrial and aquatic ecology to investigate animal movements and environmental histories (Artetxe-Arrate et al., 2021; Pearson et al., 2020; Trueman & Glew, 2019), but have had little application in marine food provenance.

Here, we propose that globally predicted, universal  $\delta^{18}\text{O}_{\text{biomin}}$  markers are effective indicators of provenance for multiple marine taxa. Our taxa of interest included teleost fish, bivalves and gastropods (hereafter called shellfish), and coleoid cephalopods, which are critical components of the world's seafood supply. Our specific objectives were to (1) develop and compare three global ocean isoscapes of predicted  $\delta^{18}\text{O}_{\text{biomin}}$  values in fish, cephalopods and shellfish, with a fourth "universal" multi-taxa isoscape, (2) evaluate isoscape-predicted  $\delta^{18}\text{O}_{\text{biomin}}$  values through comparing against a global database of measured, georeferenced  $\delta^{18}\text{O}_{\text{biomin}}$  values, and assess predictors of variation in residuals; and (3) in a case study, test the isoscape performance for geolocating multiple taxa between regions with divergent (Tropical Asia vs Temperate Australasia) or similar (Temperate Asia vs Temperate Australasia) climatic profiles.

## 2 | MATERIALS AND METHODS

### 2.1 | Development of isoscapes

Mechanistically predicted global ocean isoscapes of  $\delta^{18}\text{O}_{\text{biomin}}$  values were constructed using environmental datasets and established biogeochemical relationships from the literature. Three isoscapes were built specific to aragonitic calcium carbonate ( $\text{CaCO}_3$ ) biominerals of fish (otoliths), shellfish (exoskeleton shells of bivalve and gastropod molluscs), and cephalopods (statoliths). A fourth "universal" isoscape was then created via an average of the taxon-specific isoscapes. All modelling and analysis was done in R (R Development Core Team, 2013), with isoscapes developed using R packages raster (Hijmans et al., 2015), gstat (Pebesma, 2004), and rasterVis (Lamigueiro et al., 2022; Liaw & Wiener, 2002).

$\delta^{18}\text{O}_{\text{biomin}}$  values were derived using literature datasets of sea surface temperature and  $\delta^{18}\text{O}_{\text{water}}$  values. Sea surface temperatures ( $^{\circ}\text{C}$ ,  $0.05^{\circ}$  resolution) representing a depth of 20 cm were taken at weekly intervals from the ESA Sea Surface Temperature Climate Change Initiative through the Copernicus E.U. Copernicus Marine Service Information (Merchant et al., 2019). Data across a 4-year

period (February 2017–January 2021) were extracted and averaged across this period and transformed to  $1^{\circ} \times 1^{\circ}$  resolution using bilinear resampling. A global gridded dataset of  $\delta^{18}\text{O}_{\text{water}}$  values ( $\text{‰}$ ,  $1^{\circ} \times 1^{\circ}$  resolution) were also obtained (LeGrande & Schmidt, 2006). This gridded dataset was constructed from direct  $\delta^{18}\text{O}_{\text{water}}$  measurements combined with estimates calculated from regional  $\delta^{18}\text{O}_{\text{water}}$  to salinity relationships in areas of sparse data.

The terms used in the thermometry equations for predicting the  $\delta^{18}\text{O}$  values in biominerals included:  $\delta^{18}\text{O}_{\text{biomin.VPDB}}$  indicating the predicted values of  $\delta^{18}\text{O}$  in carbonates reported relative to Vienna Pee Dee Belemnite (VPDB),  $\delta^{18}\text{O}_{\text{water.VSMOW}}$  indicating the  $\delta^{18}\text{O}$  of seawater relative to Vienna Standard Mean Ocean Water (VSMOW), and SST indicating the sea surface temperature in Celsius ( $^{\circ}\text{C}$ ).

A single experimentally derived thermometry equation for statoliths of cephalopods has been published and was used to predict  $\delta^{18}\text{O}$  values in statoliths (Chung et al., 2020):

$$\delta^{18}\text{O}_{\text{biomin.VPDB}} = -0.20 (\pm 0.005) \times \text{SST} (^{\circ}\text{C}) + 2.88 (\pm 0.14) + \delta^{18}\text{O}_{\text{water.VSMOW}} \quad (1)$$

A range of thermometry equations for otoliths of teleost fish species have been experimentally validated (Table S1). An averaged thermometry equation was derived from these published experimental studies in order to construct an isoscape that could be widely applicable across species. The selection aimed to include a range of functional algebraic forms (Geffen, 2012; Høie et al., 2004; Kitagawa et al., 2013; Nakamura et al., 2020; Radtke et al., 1996; Sakamoto et al., 2017; Thorrold et al., 1997). The averaged thermometry equation used to predict  $\delta^{18}\text{O}$  values in otoliths was:

$$\delta^{18}\text{O}_{\text{biomin.VPDB}} = -0.2143 (\pm 0.012) \times \text{SST} (^{\circ}\text{C}) + 4.056 (\pm 0.28) + \delta^{18}\text{O}_{\text{water.VSMOW}} \quad (2)$$

For shellfish, we first compared the suitability of two equation forms, 1) an averaged thermometry equation constructed from a range of experimentally validated equations specific to aragonitic shells and 2) one of the most widely used thermometry equation for shellfish, the biogenic aragonite calibration from Grossman and Ku (1986) which is derived from a range of species. The Grossman and Ku model was subsequently chosen due to lower residual sum of squares when comparing predicted  $\delta^{18}\text{O}_{\text{biomin}}$  values against measured values (see Figure S1). The version of the Grossman and Ku equation used included a modification by Hudson and Anderson (1989), alongside a 0.38 ‰ offset applied to compensate for differences in acid fractionation factors between calcite and aragonite (Caldarescu et al., 2021). The modified equation used to predict  $\delta^{18}\text{O}$  values in shells was:

$$\delta^{18}\text{O}_{\text{biomin.VPDB}} = \frac{\text{SST} (^{\circ}\text{C}) - 19.7}{-4.34} + \delta^{18}\text{O}_{\text{water.VSMOW}} - 0.38 \quad (3)$$

For each taxon-specific isoscape, predicted  $\delta^{18}\text{O}_{\text{biomin}}$  values were calculated for each  $1^{\circ}$  by  $1^{\circ}$  cell, and plotted as a global map using ggplot2 in R (Wickham, 2011). The universal biomineral isoscape

was constructed by averaging the predicted  $\delta^{18}\text{O}_{\text{biomin}}$  values per cell across the three taxon-specific isoscapes.

## 2.2 | Evaluation of isoscapes

To evaluate how the isoscape models compare against actual measured data, we compiled a database of  $\delta^{18}\text{O}_{\text{biomin}}$  values measured in fish, coleoid cephalopods and shellfish, that were collected alongside geographical harvest coordinates (See Appendix S1). The database comprised of published  $\delta^{18}\text{O}_{\text{biomin}}$  values, representing individual datapoints of  $\delta^{18}\text{O}_{\text{biomin}}$  where available, as well as a smaller number of unpublished values, provided by the authors. This database represented wild-caught, wholly marine, subtidal taxa collected between 1995 and 2021, and from depths of <500m. However, due to the spatial resolution of the isoscapes along coastlines, some datapoints from coastal zones were ultimately excluded. As such, 3954 datapoints derived from 68 species were ultimately used to represent the measured values. The data represented isotopic values measured from either the whole carbonate structure or the period corresponding to the area of capture (i.e., marginal increment of otoliths of migratory species) where appropriate. To assess regional-specific trends in the isoscapes, measured values were assigned to groups corresponding to 10 ocean ecoregions – Arctic, Central Indo-Pacific, Mediterranean, Temperate Australasia, Temperate Northern Atlantic, Temperate Northern Pacific, Temperate South America, Tropical Atlantic, Tropical Eastern Pacific, and Western Eastern Pacific (Spalding et al., 2007). As one of the main objectives of this study is the universal and practical application of the isoscape, shellfish species that had a range of  $\text{CaCO}_3$  polymorphs were all included and assessed. The shells of bivalves and gastropods can comprise of either calcite, aragonite, or a combination of both, which can influence the relationship between  $\delta^{18}\text{O}_{\text{biomin}}$  and temperature due to different fractionation factors. The other carbonate structures, otoliths and statoliths, were characterised as aragonite.

For each measured value in the database, a matching predicted  $\delta^{18}\text{O}_{\text{biomin}}$  value was extracted from the isoscapes as a  $1^\circ$  by  $1^\circ$  cell mean around the coordinate of capture. Residuals (differences) between the measured  $\delta^{18}\text{O}_{\text{biomin}}$  values from the database and isoscape-predicted values were calculated to investigate divergence. Global maps of residuals were constructed using inverse distance-weighting interpolation and evaluated.

To investigate the potential sources of variation between isoscape-predicted  $\delta^{18}\text{O}_{\text{biomin}}$  values and measured values, linear models were used to explore partitioning of the residuals among potential predictor variables. Model predictors included ocean ecoregion, taxa, latitude, longitude, and year of capture. For shellfish models, the  $\text{CaCO}_3$  polymorph (aragonite, calcite, or combined) was also included as a predictor. Model residuals were checked for normal distribution and homogeneity of variance, while collinearity of predictors was assessed using variance inflation factors below >2.5. Due to geographical predictors being highly collinear, two models were compared either excluding longitude and latitude or excluding ocean region using Akaike's information criterion corrected for small sample sizes (AICc; Burnham & Anderson, 2004). Relative importance weights were derived to

assess the proportional contribution of each predictor to the variability of the dependent value (Grömping, 2006). Estimated Marginal Means derived from the optimal model was then used to investigate whether the residuals differed significantly ( $p < .05$ ) between ocean ecoregion, taxa, and polymorph after accounting for the influence of all other predictors using package emmeans (Lenth et al., 2018). Pairwise comparisons were conducted using a Tukey adjustment. Subsequently, otolith isoscape-predicted values were rerun in a separate linear model to assess if residuals for endothermic tuna species (*Thunnus* sp.) were significantly different to ectothermic fish. The tuna species tested included albacore tuna (*Thunnus alalunga*, Scombridae), Atlantic bluefin tuna (*Thunnus thynnus*, Scombridae), Pacific bluefin tuna (*Thunnus orientalis*, Scombridae), southern bluefin tuna (*Thunnus maccoyii*, Scombridae), and yellowfin tuna (*Thunnus albacares*, Scombridae).

## 2.3 | Case study: Testing isoscape performance for seafood geolocation across Asia and Australia

A case study was conducted to test the application of  $\delta^{18}\text{O}_{\text{biomin}}$  values for geolocating seafood to source in a real-world scenario, and to compare efficacy between regions of divergent or similar climatic profiles and latitudes. Regions in eastern Asia and Australasia were selected as they represent markets with high levels of seafood trade and suitable environmental profiles. "Temperate Asia" and "Temperate Australasia" were selected to represent similar climatic profiles and latitudes, while "Tropical Asia" was selected to represent a divergent climate profile from the temperate regions. A machine-learning approach using random forest was used to classify geographical origins of measured  $\delta^{18}\text{O}_{\text{biomin}}$  values harvested within the boundaries of study regions. The random forest algorithm determines classifications using the aggregated results of an ensemble of individual classification and regression trees built using a random bootstrap of the data. Random forest models was built using R package randomForest (Liaw & Wiener, 2002) for each taxon-specific isoscape and the universal biomineral isoscape. Grid values of  $\delta^{18}\text{O}_{\text{biomin}}$  representing  $1^\circ$  mean latitude and longitude steps within regions of interest (Temperate Australasia, Temperate Asia, and Tropical Asia) were extracted from each isoscape and then used to train each model with k-fold cross-validation incorporated. Out-of-bag (OOB) errors were derived to measure the predictive capacity of the trained model using bootstrap aggregating, whilst Cohen's kappa coefficient was calculated as an additional metric of classifier performance. Subsequently, random forest models predicted the region of origin of individual measured  $\delta^{18}\text{O}_{\text{biomin}}$  values and model accuracies were derived through comparing the resulting matrix of class probabilities to the known regional classifications. The universal and otolith-isoscape models were rerun without *Thunnus* sp to see if model accuracy increased with the removal of endothermic species.

### 3 | RESULTS

#### 3.1 | Development of isoscapes

Isoscapes of mechanistically predicted  $\delta^{18}\text{O}_{\text{biomin}}$  values were successfully constructed for fish, cephalopod, and shellfish, as well as a universal average isoscape (Figure 1). Isotopic trends were similar among taxa, and at global scales spatial variance was dominated by thermal effects with more positive  $\delta^{18}\text{O}_{\text{biomin}}$  values towards the poles and more negative  $\delta^{18}\text{O}_{\text{biomin}}$  values nearer to the equator (Figures S2B, S3).

#### 3.2 | Evaluation of isoscapes

The trends in model residuals, derived from comparing isoscape-predicted values and measured  $\delta^{18}\text{O}_{\text{biomin}}$  values from the database, provided an understanding of the variation between regions and taxa (Table S2). The measured  $\delta^{18}\text{O}_{\text{biomin}}$  values spanned between  $-5.3$  and  $3.9\text{‰}$ , corresponding well with the isoscape ranges (Figure 2a). Although the residual sum of squares was similar between the universal and taxon-specific isoscapes when separating out the taxa ( $\pm 1$ ), the universal isoscape produced lower average residuals for statoliths ( $1.2$  vs  $1.6\text{‰}$ ) and otoliths ( $-0.07$  vs  $-0.4\text{‰}$ ), but higher residuals for shells ( $0.5$  vs  $0.4\text{‰}$ ) (Figures 2b, 3).

Linear regressions uncovered the key influences on the residuals of  $\delta^{18}\text{O}_{\text{biomin}}$  values. The linear model derived from the universal

isoscape explained 41.0% of the variance ( $p < .001$ ). Ocean region was the dominant predictor, responsible for 82.2% of the model variance. This regional variation was also demonstrated through significant differences ( $p < .05$ ) between many regions (Table S3). The estimated marginal means of residuals were the most negative in the Arctic ( $-0.96\text{‰}$ ) and Mediterranean ( $-0.73\text{‰}$ ), whilst the most positive estimated marginal means were found in Temperate South America ( $1.32\text{‰}$ ) and the Central Indo-Pacific ( $1.49\text{‰}$ ) (Figure 4). The estimated marginal means of residuals in the Temperate Northern Atlantic ( $0.09\text{‰}$ ) had values closest to 0, indicating the predicted values closely aligned with the measured values. Taxon was responsible for 15.2% of the model variance. Cephalopods ( $0.75\text{‰}$ ) and shellfish ( $0.8\text{‰}$ ) had similar positive estimated marginal means of residuals, whilst the estimated marginal means for fish were significantly lower ( $-0.06\text{‰}$ ). Polymorph was responsible for 1.9% of the variance but was not significantly different between aragonite, calcite, or combined mixes of the two. Year of capture was responsible for 0.5% variation but was also not significant.

The linear model assessing the taxon-specific isoscapes explained 46.7% of the variance ( $R^2$ ) of the residuals ( $p < .001$ ). Compared to the universal model, taxon was a more dominant influence in these individual isoscapes. While ocean region remained the dominant influence of variation in residuals at 66.3%, taxon was also responsible for 31.0% of variance, with minor contributions from polymorph at 1.9%, and year of capture at 0.6%. The estimated marginal means of the residuals for ocean regions largely aligned with those described for the universal model, however, the estimated marginal means for

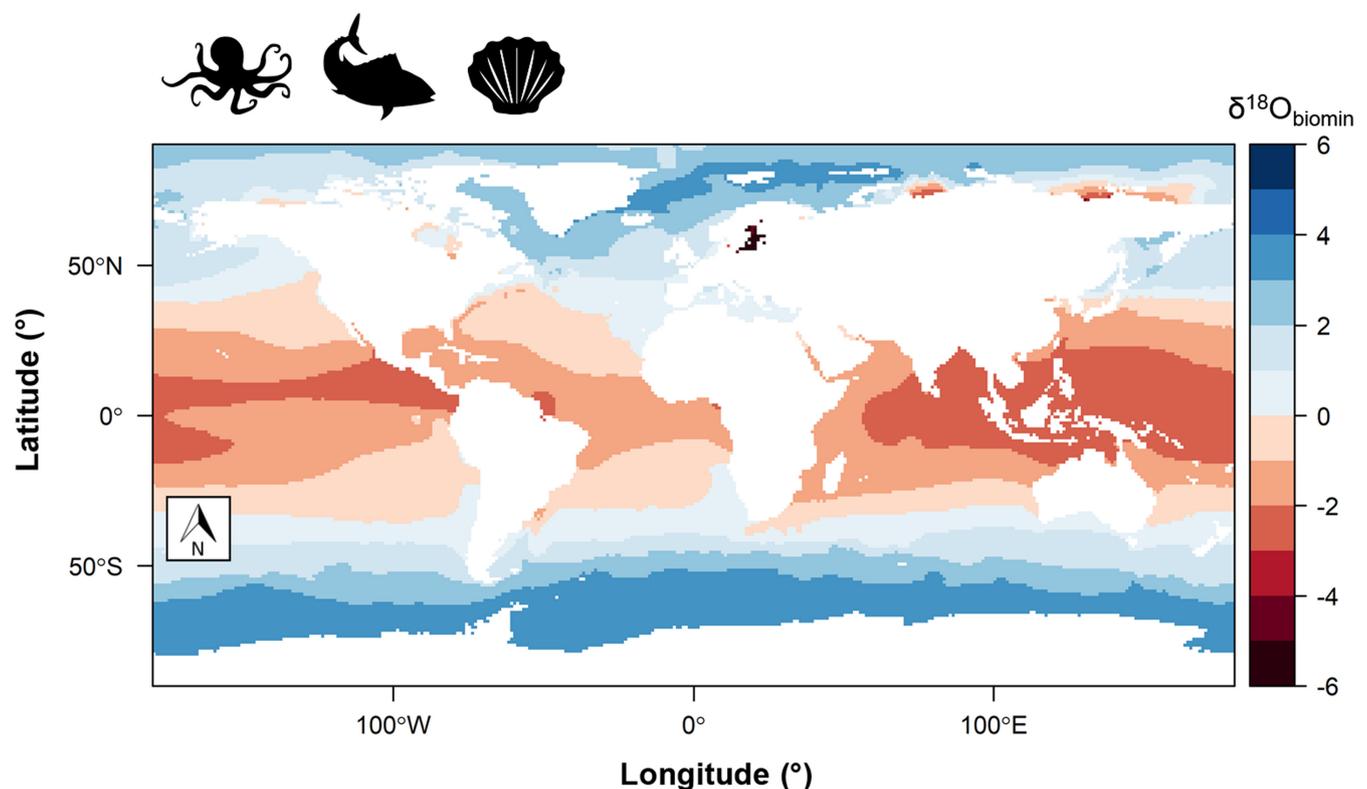
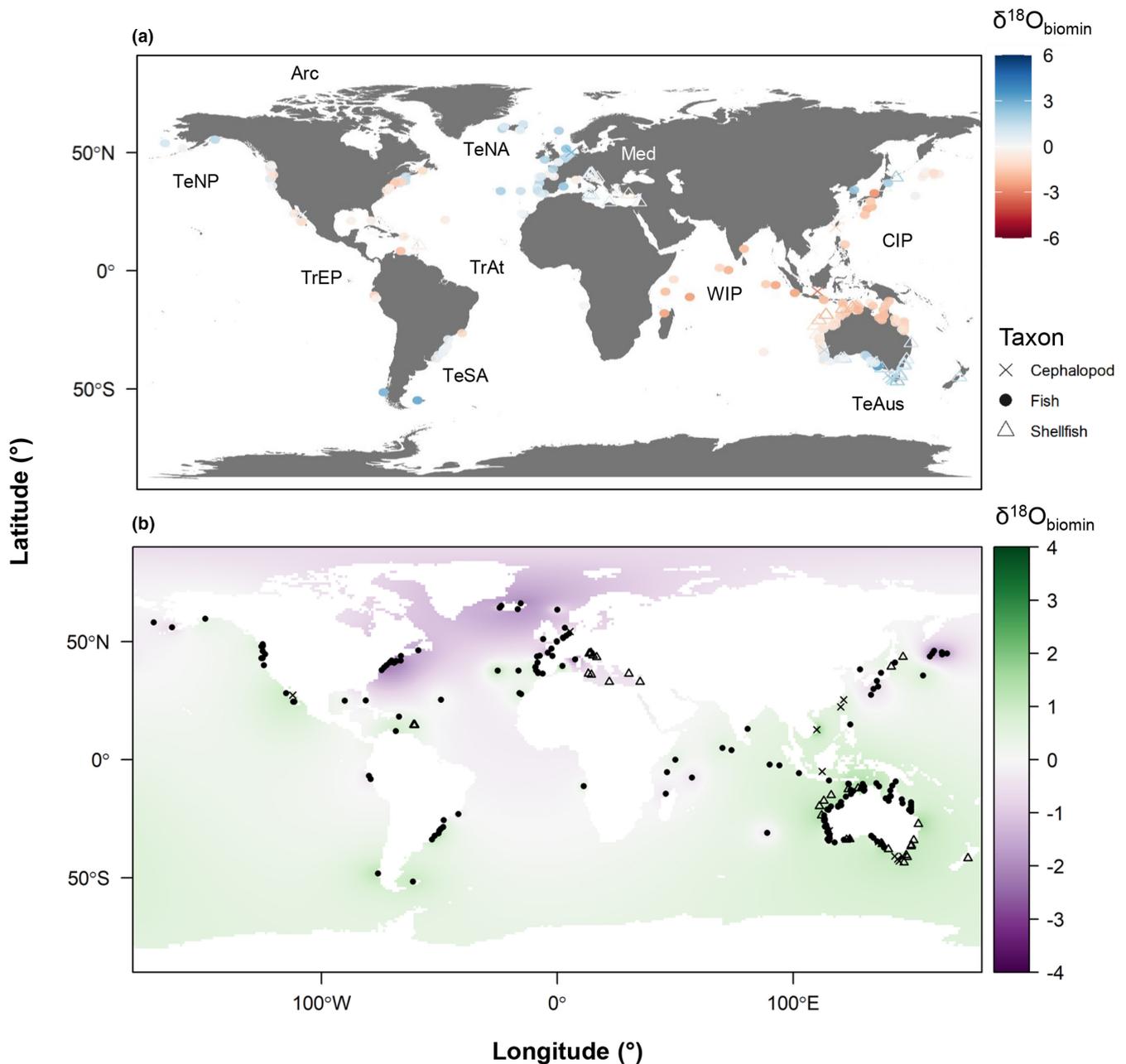


FIGURE 1 A universal isoscape of predicted oxygen isotopes in biominerals ( $\delta^{18}\text{O}_{\text{biomin}}$ ) of marine organisms. This isoscape is built from an averaging of temperature-dependent fractionation equations of  $\delta^{18}\text{O}_{\text{biomin}}$  from the statoliths of cephalopods, otoliths of fish, and exoskeleton shells of shellfish (bivalves and gastropods). Taxon-specific isoscapes are found in Figure S3



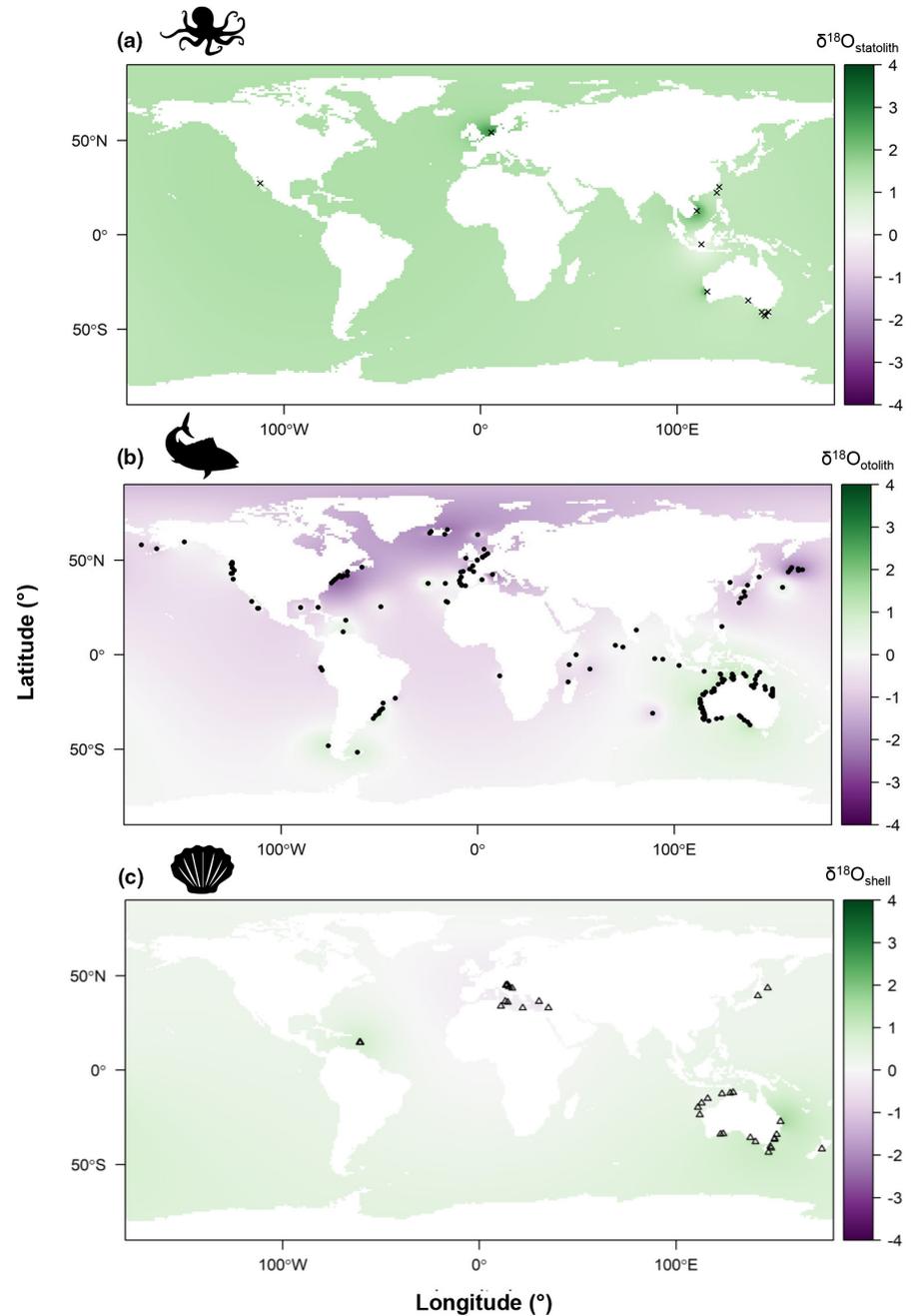
**FIGURE 2** Global maps depicting (a) measured oxygen isotopes ( $\delta^{18}\text{O}_{\text{biomin}}$ ) values of geo-referenced samples ( $n = 3954$ , 68 species) from compiled database with ocean ecoregions labelled, and (b) the residuals between measured and universal isoscape-derived predicted  $\delta^{18}\text{O}_{\text{biomin}}$  values calculated per datapoint, and then interpolated as a continuous surface onto a global map. The ocean ecoregions defined here include the Arctic (Arc), Temperate Northern Pacific (TeNP), Temperate Northern Atlantic (TeNA), Mediterranean (Med), Tropical Eastern Pacific (TrEP), Tropical Atlantic (TrAt), Central Indo-Pacific (CIP), Western Indo Pacific (WIP), Temperate Australasia (TeAus), and Temperate South America (TeSA) (Spalding et al., 2007)

taxon were significantly different between all groups. Compared to the universal models, estimated marginal means of residuals was closer to zero (0.62 vs 0.8‰) for the shell isoscape, more negative but further from zero (−0.39 vs −0.06 ‰) for the otolith isoscape, and more positive but similarly further from zero (1.25 vs 0.75 ‰) for the statolith isoscape. Like the universe isoscape regression models, the polymorph and year of capture did not significantly influence the residuals.

### 3.3 | Case study: Testing isoscape performance for seafood geolocation across Asia and Australia

In the case study, measured test samples ( $n = 1097$ , species = 16) were classified back to geographical source between regions of both divergent (Tropical Asia) and similar (Temperate Asia, Temperate Australasia) climatic profiles and latitudes (Figure 5). Lower values of Cohen's kappa coefficients compared to classification accuracies were observed, primarily due to class imbalances. For the universal

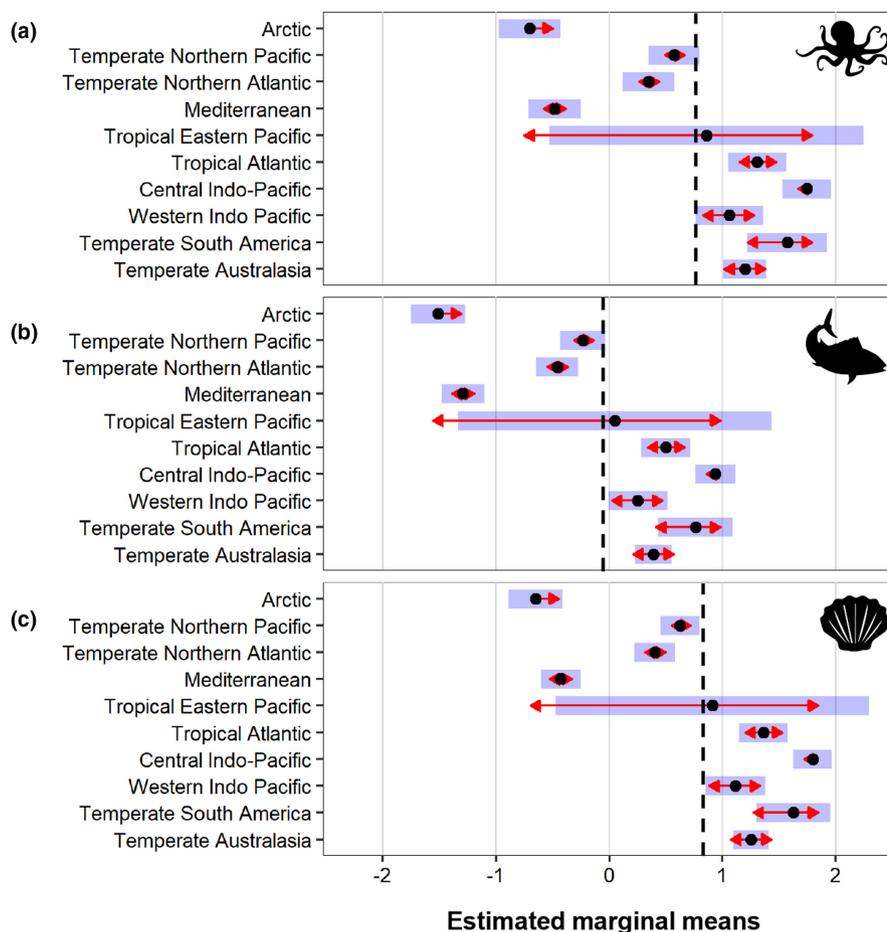
**FIGURE 3** The residuals between measured and taxon-specific isoscape-predicted oxygen isotope values in biominerals ( $\delta^{18}\text{O}_{\text{biomin}}$ ) calculated per datapoint and then interpolated as a continuous surface onto a global map for the (a) statoliths of cephalopods, (b) otoliths of fish and (c) exoskeleton shells of shellfish (bivalves and gastropods)



isoscape model (OOB: 15.6%, Kappa: 0.2), overall accuracy at classifying samples back to source across the three regions was 50.5% (554 out of 1097 samples) (Table 1). Samples could be successfully distinguished between tropical and temperate zones with 72.6% (796 out of 1097 samples) accuracy, but this accuracy rate dropped to 63.4% (434 out of 684 samples) when distinguishing between the two temperate zones (Kappa: 0.56). For the taxon-specific models (mean OOB 13.5%, Kappa: 0.17), the mean overall accuracy across all models and all three regions was 54.4% (Table 1). For the otolith isoscape model, samples could be distinguished between tropical and temperate zones with a 58.5% (304 out of 520 samples) success rate. When discriminating between the two temperate zones, accuracy was 84.2% (107 out of 127 samples; Kappa: 0.55). For the statolith isoscape model, samples were distinguished between

tropical and temperate zones with a 70% (28 out of 40 samples) success rate, and between the two temperate zones with 50% (10 out of 20 samples) correctly distinguished (Kappa: 0.53). For the shell isoscape model, no measured Tropical Asia samples from the database were available, so only temperate samples were tested against the model. These included temperate samples were 100% correctly classified as temperate rather than tropical (537 out of 537 samples), whilst 62% (333 out of 537 samples) of these samples were correctly distinguished between the two temperate zones (Kappa: 0.5).

The inclusion of tuna species in the dataset was found to influence both the linear models and accuracy of the classification models. The otolith isoscape linear model that included a *Thunnus* sp. predictor variable showed that the estimated marginal means of



**FIGURE 4** Estimated marginal means of residuals between measured and universal isoscape-derived predicted oxygen isotope values in biominerals ( $\delta^{18}\text{O}_{\text{biomin}}$ ) separated into ocean bioregions and taxon of (a) cephalopods (b) fish, and (c) shellfish. The bars represent confidence intervals, while the red arrows represent group comparisons with overlaps across the horizontal axis indicating that groups are not significantly different ( $p > .05$ ). Dashed vertical lines represent the estimated marginal mean of residuals averaged across regions for each taxon.

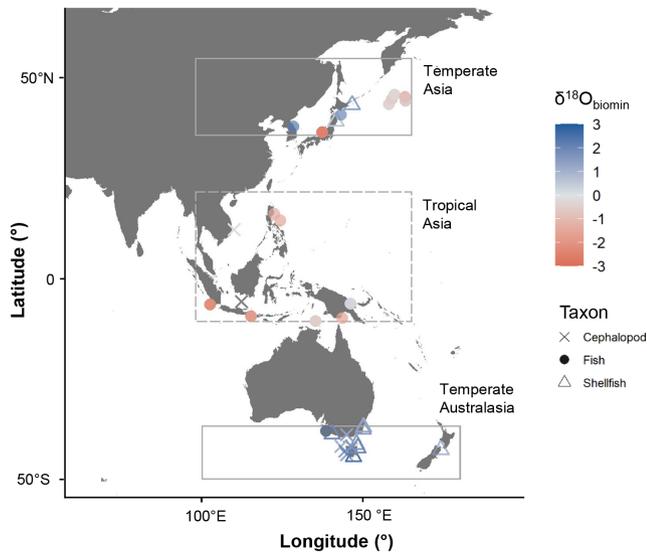
residuals between predicted and measured  $\delta^{18}\text{O}_{\text{biomin}}$  values were significantly more negative ( $-1.08\text{‰}$ ) for the tuna group than the other teleost fish ( $0.2\text{‰}$ ). When the classification models from universal and otolith isoscapes were rerun with *Thunnus* samples excluded, successful classifications increased when distinguishing between the temperate and tropical zones. The universal model increased from 72.6% to 90% (689 out of 766 samples) accuracy, and the otolith model increased from 58.5% to 69.3% (131 out of 189 samples) accuracy. However, excluding *Thunnus* samples did not alter the classification success between the two temperate zones.

## 4 | DISCUSSION

Oxygen isoscapes were successfully demonstrated to identify the geographical origins of a broad range of marine species. The universal isoscape predicted geographic origin more accurately than the taxon-specific isoscapes for cephalopods and fish, whilst the shell isoscape predicted geographic origin more accurately for shellfish. When assigning animals back to their region of origin, classification models developed from the isoscapes generally performed best between test regions with high temperature and latitudinal contrast (i.e., tropical versus temperate waters). Our results indicate that oxygen isoscapes are particularly effective for geolocating animals over wider latitudinal gradients (100s to 1000skm), where there

are known regional differences in water temperature and salinity. While most traceability tools are species or supply chain-specific, our findings demonstrate that oxygen isotopes have the potential to be used in a universal and combined provenance approach for marine animals.

The promising implication of the universal isoscape being comparable, and sometimes more accurate, at predicting  $\delta^{18}\text{O}_{\text{biomin}}$  than the taxon-specific isoscapes is that it demonstrates its suitability for a wide range of species without the need for prior taxon-specific compilation of reference data. This comparable accuracy of the universal isoscape likely in part stems from its construction via an averaging of a range of thermometry equations. While negative linear relationships are consistently demonstrated between  $\delta^{18}\text{O}_{\text{biomin}}$  values and temperature, there are minor species and taxonomy variation in equation coefficients, particularly intercepts (Chung et al., 2020; Kitagawa et al., 2013; Shirai et al., 2018), potentially owing to differences in haemoglobin oxygen-binding affinity, or oxygen sources within body fluids (Macdonald et al., 2020). Differences in experimental setup, such as experimental temperature range, alongside measurement and statistical errors, may also have had a minor influence on equation coefficients between species. While there are examples of isoscapes being effectively developed and applied using a thermometry equation validated for a single-species (Artetxe-Arrate et al., 2021; Pearson et al., 2020; Trueman et al., 2012), the idea here is that a combined equation may be more likely to be physiologically-relevant



**FIGURE 5** Measured oxygen isotope values ( $n = 1097$ , species = 16) in biominerals ( $\delta^{18}\text{O}_{\text{biomin}}$ ) of fish, shellfish, and cephalopods used in case-study to geolocate animals back to source between regions with climates and latitudes that are divergent (tropical Asia) and similar (temperate Asia, temperate Australasia). Also indicated are the boundary boxes of the case-study regions where predicted  $\delta^{18}\text{O}_{\text{biomin}}$  values were extracted from isoscapes and used to train random forest classification models

to a randomly chosen species on average. Further testing will help to refine the averaged equation for optimal applications across species and taxa. In particular, most experimental studies validating the relationship between temperature and  $\delta^{18}\text{O}_{\text{biomin}}$  values were derived from temperate or sub-arctic temperature ranges and study species (Geffen, 2012; Høie et al., 2004; Radtke et al., 1996), although there are a couple of exceptions (Chung et al., 2020; Kitagawa et al., 2013). It is evident that more experimental research is needed to define thermometry equations specific to tropical species, which would allow for more effective use of  $\delta^{18}\text{O}_{\text{biomin}}$  as a universal proxy.

Our results indicate that  $\delta^{18}\text{O}_{\text{biomin}}$  values need to be used with caution in endothermic fish such as tuna. Residuals between measured and predicted  $\delta^{18}\text{O}_{\text{biomin}}$  values were significantly more negative for *Thunnus* species in our database compared to the other fish species, and subsequently, when these samples were excluded from the classification models, the model accuracy improved. Many tuna species are considered endothermic as they can elevate their muscular, visceral, and cranial temperatures using counter-current heat exchangers known as retia mirabilia (Graham & Dickson, 2004; Malik et al., 2020). As a result, rather than solely reflecting environmental temperatures as in ectothermic animals,  $\delta^{18}\text{O}_{\text{biomin}}$  values in tuna are also likely to represent elevated internal temperatures, though the extent of this likely varies as the use of thermoregulatory mechanisms are influenced by somatic size and ambient ocean temperatures (Kitagawa et al., 2006). While further research is needed to assess how endothermy affects  $\delta^{18}\text{O}_{\text{biomin}}$  values and the implications for provenance applications, at least endothermy is a rare

phenomenon in fish and only relevant to tuna, billfish and a small number of shark species (Madigan et al., 2015).

The use of different  $\text{CaCO}_3$  polymorphs for shellfish was indicated to have a minimal impact on using  $\delta^{18}\text{O}_{\text{biomin}}$  as a provenance tool. No significant differences were found in  $\delta^{18}\text{O}_{\text{biomin}}$  values between calcitic, aragonitic or mixed  $\text{CaCO}_3$  structures of bivalves and gastropods. While the coefficients of the oxygen thermometry equation vary between polymorphs, we found that for broader scale provenance purposes, the variation in  $\delta^{18}\text{O}_{\text{biomin}}$  values owing to polymorph type was minor compared to the dominant spatial variation. Supporting this result, a previous field study found minimal isotopic differences between calcite and aragonite layers in different gastropod and bivalves species growing in the same environment (Lécuyer et al., 2012). While identifying and separating the polymorphs prior to isotopic analysis can be achieved (i.e., using x-ray diffraction and mechanically separating calcite and aragonite layers), this can be a time-consuming and costly process. The consistency of results here across calcite and aragonite structures indicates that for universal applications, where the aim is to reduce time and effort for industry and research, a combined system is likely appropriate.

We were also interested in identifying whether universal geolocation is equally applicable across regions. Predictions of  $\delta^{18}\text{O}_{\text{biomin}}$  values were most accurate in the Temperate Northern Pacific and Temperate Northern Atlantic regions, whereas Central Indo-Pacific and Temperate South America were the least accurate. These differences in accuracy may stem from the variability in the number of measurements between regions used to derive the gridded data of  $\delta^{18}\text{O}_{\text{water}}$  (LeGrande & Schmidt, 2006). While the dataset was developed with a relatively consistent coverage of directly measured  $\delta^{18}\text{O}_{\text{water}}$  values in the northern Pacific and northern Atlantic Oceans, areas of sparse coverage are also clearly evident including around tropical Asia and the southern coastline of South America. This insight highlights that isoscape applications work best for regions with highly resolved current projections of  $\delta^{18}\text{O}_{\text{water}}$  values. For regions with high residuals, predicted accuracies could be improved by integrating localised seawater measurements of  $\delta^{18}\text{O}_{\text{water}}$  or coupling detailed salinity projections with specific regional  $\delta^{18}\text{O}_{\text{water}}$  – salinity relationships.

While we demonstrate the promising potential of universal oxygen isoscapes to geolocate seafood, there are still limits. As the oxygen isoscapes developed here cover fully marine surface conditions, it is necessary to have a thorough understanding of the life history, habitat use, and movement and migratory patterns of the study species, particularly identifying taxa with nearshore, subtidal or estuarine habitats or life stages. Chemical markers may also potentially reflect the migratory path rather than the harvest location for highly migratory species, such as tuna. Using age data alongside targeted sampling of new otolith growth is recommended to isolate  $\delta^{18}\text{O}_{\text{biomin}}$  values that represent the harvest location. Furthermore, when compared to samples from inshore or shelf sea settings, the compiled database of measured georeferenced samples used to test the isoscape was relatively scarce in offshore pelagic samples (Figure 2a). This is likely driven by coastal marine ecosystems accounting for

Isoscape	Predicted class	True class		
		Tropical Asia	Temperate Australasia	Temperate Asia
Universal biominerals	<b>Tropical Asia</b>	<b>120</b>	0	8
	<b>Temperate Australia</b>	7	<b>89</b>	216
	<b>Temperate Asia</b>	286	26	<b>345</b>
	Class accuracy (%)	29.1	77.4	60.6
	Overall accuracy (%)			50.5
Cephalopod statoliths	<b>Tropical Asia</b>	<b>8</b>	0	0
	<b>Temperate Australia</b>	10	<b>10</b>	0
	<b>Temperate Asia</b>	2	10	<b>0</b>
	Class accuracy (%)	40.0	50.0	-
	Overall accuracy (%)			45
Fish otoliths	<b>Tropical Asia</b>	<b>185</b>	0	8
	<b>Temperate Australia</b>	1	<b>25</b>	0
	<b>Temperate Asia</b>	207	12	<b>82</b>
	Class accuracy (%)	47.1	67.6	91.1
	Overall accuracy (%)			63
Shellfish shells	<b>Tropical Asia</b>	<b>0</b>	0	0
	<b>Temperate Australia</b>	0	<b>30</b>	176
	<b>Temperate Asia</b>	0	28	<b>303</b>
	Class accuracy (%)	-	51.7	63.3
	Overall accuracy (%)			62.0

Note: This case study investigated whether measured samples can be classified back to region of origin between divergent (tropical Asia) or similar (temperate Asia, temperate Australasia) climates and latitudes. The total number of accurately classified samples per class are indicated in bold.

95% of the biomass of fisheries catch, likely in part due to greater accessibility and lower costs for fishers, despite covering only 22% of ocean area (Stock et al., 2017). As such, the assignment potential estimates presented should be applied with caution to open ocean species. Similarly, our isoscape models represent shallow ocean depths and further development and testing is needed for deeper water species. However, previous research indicates that predicted  $\delta^{18}\text{O}_{\text{biomin}}$  values in otoliths are highly consistent in depths between 0 and 50 m, and while values became more positive in deeper depths, spatially driven variation in  $\delta^{18}\text{O}_{\text{biomin}}$  values still remained dominant (Artetxe-Arrate et al., 2021). Lastly,  $\delta^{18}\text{O}_{\text{biomin}}$  approaches are clearly inapplicable to seafood taxa without calcitic or aragonitic tissues. While most seafood taxa have  $\text{CaCO}_3$  tissues, sharks and other elasmobranch fish constitute a notable exception. However, phosphate and structural carbonate ions within bioapatite of skeletal structures of vertebrate animals are potential targets for investigating universal oxygen isotope markers (e.g., Bryant et al., 1996). Furthermore, more study is needed to better understand oxygen thermometry relationships in decapod crustaceans, which form a significant component of the seafood supply. As crustacean exoskeletons are comprised of a mixture of organic matrices, calcite or Mg-calcite, and amorphous polymorphs of  $\text{CaCO}_3$  (Luquet, 2012), oxygen thermometry models developed for fish and molluscs may not be as accurate.

In addition to these taxonomic considerations, the isoscapes presented here are constructed using annual means in temperature and salinity. However, seasonal fluctuations of temperature and salinity can influence  $\delta^{18}\text{O}_{\text{biomin}}$  values, and the magnitude of this influence varies between regions. For example, when global  $\delta^{18}\text{O}$  values in barnacle calcite were predicted for individual seasons, mid-latitude regions ( $30^\circ$  to  $60^\circ$ ) with large annual temperature gradients exhibited the greatest variance in isotope values (up to  $1.9 \pm 0.7$  ‰) (Pearson et al., 2020). Conversely, in the tropics and southern polar regions where temperature fluctuations between seasons are limited, minimal variance in isotopic values were found. While higher residuals were not seen in mid-latitude zones in the current study, addressing season of capture remains a topic for future research. Local variations in time-resolved  $\delta^{18}\text{O}_{\text{biomin}}$  values may indeed provide finer-scale assignment potential, particularly for shellfish where high-resolution time-resolved sampling is relatively simple across the shell, and their sessile nature ensures that variation through time is directly linked to local variations in temperature (and possibly salinity).

Additional isotopic or elemental layers with universal properties could be introduced to the isoscape to improve the predictive capacity and spatial resolution of  $\delta^{18}\text{O}_{\text{biomin}}$  values as a provenance tool, particularly among samples collected from similar latitudes. Like  $\delta^{18}\text{O}_{\text{biomin}}$  values, complementary universal chemical markers

TABLE 1 Confusion matrix of class classifications of measured sample alongside accuracies from random forest models, derived from a universal biomineral oxygen isoscape and isoscapes specific to statoliths of cephalopods, otoliths of fish, and exoskeleton shells of shellfish (bivalves and gastropods).

require predictable spatial variation coupled with common expression amongst species. While carbon isotopes ( $\delta^{13}\text{C}$ ) in biominerals are commonly analysed concurrently with  $\delta^{18}\text{O}$ , they are unsuitable in this context as  $\delta^{13}\text{C}$  values in seawaters are generally homogeneous ( $\sim 0\text{‰}$ ) and carbonate values can vary between individuals due to diet and metabolic influences (Chung et al., 2019, 2021; Martino et al., 2020). By contrast, neodymium isotopes ( $^{143}\text{Nd}/^{144}\text{Nd}$  ratios expressed as  $\epsilon_{\text{Nd}}$  values) are indicated to be governed by continental geology, resulting in distinct geographic ocean profiles with high spatial resolution (Jeandel et al., 2007). Recent research demonstrated that  $\epsilon_{\text{Nd}}$  values in the soft and hard tissues of bivalve molluscs are highly effective at identifying the origins of individuals at even small spatial scales (10s km) (Saitoh et al., 2018; Tanaka et al., 2022; Zhao et al., 2019). Concentrations of barium ratioed to calcium (Ba/Ca) are an additional candidate for universal provenance, as signatures reflect seawater composition (Bath et al., 2000; Walther & Thorrold, 2006), and are little affected by individual life history factors, such as physiology or diet (Grammer et al., 2017; Hüseyin et al., 2021; Martino et al., 2021). However, significant work first needs to be undertaken to quantify spatial variations in these potential universal markers. Chemical markers could be used in conjunction with taxon-specific provenance methods, such as DNA analysis or fatty acid profiling. While the additional time and financial costs need to be balanced against the potential benefit, using multiple methods and biomarkers can strengthen the accuracy and precision of provenance assignments (Cazelles et al., 2021). For example, a recent meta-analysis of provenance testing using DNA and isotopic markers, found that a combined DNA-isotope approach reduced the chance of misassignment (Cusa et al., 2021). The study thus concluded that using both DNA and isotopes would be most effective where the regions of interest include isotopically similar water bodies (i.e., between Temperate Asia and Australasia in this study) or where populations are genetically similar.

Chemical markers are used extensively in ecological and fisheries applications (e.g., defining stock structure or identifying natal origins), but their application to address seafood provenance fraud, as well as their integration into associated management and policy decisions, is scarce (Camin et al., 2016; Cusa et al., 2021). This is also true for DNA-based approaches, whereby uptake by managers and policymakers for seafood authentication has stagnated (Bernatchez et al., 2017; Cusa et al., 2021; Martinsohn et al., 2019). For DNA-based approaches, roadblocks to adoption include limited awareness on the true costs and benefits of DNA analyses (e.g., perceived analytical costs versus the value of confiscated catches and associated fines), as well as poor communication about the relevant methods among scientists, managers, and policymakers (Bernatchez et al., 2017; Martinsohn et al., 2019). We suggest that, alongside demonstrating tangible outcomes, raising awareness and communication about chemical markers and the efficiencies that could be achieved using a universal approach, is key to uptake. For instance, universal markers could be applied to distinguish multiple marine taxa from protected designations of origin (PDO), as has been successfully accomplished using a species-specific marker approach, for example, the authentication of mussels from Galicia (Costas-Rodríguez

et al., 2010), or between key trade partners, as demonstrated here between Southeast Asia and Australia. Furthermore, a universal marker approach negates the requirement for developing time-consuming reference databases for individual species and target regions (Li et al., 2016), which is a drawback of current chemical marker methods and a barrier to adoption by industry (Camin et al., 2016). However, incentives to employ provenance technology to support sustainable seafood practices are inconsistent, with seafood labelling standards and regulations varying by jurisdiction (Lindley, 2021). Involvement from PDO protection consortia, producer associations, or eco-certification organisations can all play a role in driving real-world implementations (Camin et al., 2016). For example, the Marine Stewardship Council used DNA barcoding to verify the species of 100s of seafood products sampled from multiple countries (Barendse et al., 2019). Chemical markers, alongside DNA-based approaches, are well-regarded methods for delineating population structure for fisheries management applications, therefore, we are optimistic that the universal approach outlined here could be realised for seafood provenance applications through ongoing communication with stakeholders and a coordinated international approach to method development.

## 5 | CONCLUSIONS

Here, we demonstrate how universal chemical markers and isoscape mapping techniques can successfully geolocate a diverse range of seafood back to their geographical source. These techniques have the potential to change the way we verify the provenance of seafood on a more unified, global, and equitable scale. Oxygen isotope compositions in biominerals are indicated to be effective for geolocating samples across large latitudinal and thermal gradients, but the framework's spatial resolution and precision could be improved through augmenting with additional isotopic and elemental layers or species-specific approaches (e.g., DNA markers). Furthermore, we highlight the unique characteristics of biomineral structures for seafood provenance applications: they permanently retain lifetime chemical fingerprints; do not decay; are frequently discarded or low-valued by the seafood industry; and are commonly retained for other purposes, such as ageing of stocks (e.g., otoliths). Additionally, we can draw upon the extensive ecological and fisheries literature already developed using chemical profiling of biominerals for reconstructing environmental or movement histories. Validating the provenance of seafood products on a global scale is a vast and complex undertaking due to the diversity of species, fisheries, and socio-economic drivers. Here, we present a more universal strategy that is applicable to multiple taxa and seafood products, and may provide access to provenance for smaller or lower-income producers, as well as to species with lower commercial value. Provenance fraud continues to be a significant issue that threatens food security, equitable access to resources, food safety, and consumer trust in seafood products. The development of universal chemical markers, such as oxygen isotopes, represent a valuable step towards a more inclusive, global approach for authenticating seafood.

## CONFLICT OF INTEREST

The authors declare no competing interests.

## DATA AVAILABILITY STATEMENT

Data is available in Appendix S1, except unpublished data which is available from the corresponding authors upon reasonable request.

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## SUPPORTING INFORMATION

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