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Perspective Article

# Harnessing universal chemical markers to trace the provenance of marine animals

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ABSTRACT

Identifying the provenance of marine animals yields fundamental data on a species' ecology and life history and enables the geolocation of individuals for food forensic applications. However, many provenance methods are resource-intensive and developed on a species-specific basis. Here we discuss how natural chemical markers with predictable spatial patterns and common expression among species could be used as provenancing tools that are universally applicable to many species. To demonstrate the universal marker concept, we focus on stable oxygen isotopes bound within calcium carbonate biominerals. In doing so, we compiled a global database of oxygen isotope values to illustrate universal latitudinal patterns across key marine taxa. We then discuss how this concept could be integrated within a spatial modelling framework and applied to tackle the environmental challenge of seafood provenance. By developing universal markers we have the opportunity to trace a greater range of species to support their conservation and management.

## 1. Introduction

Natural chemical markers are powerful tools used to trace the movement and provenance of animals with applications across ecology, conservation, archaeology, and food forensics (Carter and Chesson, 2017; Grupe and McGlynn, 2016; Rubenstein and Hobson, 2004). They are based on the premise that isotope or trace element values in the environment (e.g. values in seawater, diet, or underlying geology) are reflected in the biological tissues of animals. An array of isotopes and trace elements have been used to trace marine animals; however, chemical markers are typically variable among species or life history stages due to the influence of ecological and physiological factors on chemical incorporation (such as trophic transfer and metabolic rate) (Arkhipkin, 2005; Hüssy et al., 2020; Trueman and St John Glew, 2019). Thus, chemical markers are typically optimised and applied on a species-specific basis.

Here we bring together knowledge from the fields of ecology, geochemistry, and paleoclimatology to discuss the concept of *universal* chemical markers. In other words, a chemical marker that is incorporated consistently and predictably in tissues across a wide range of marine taxa. For instance, if a marker is truly universal, different taxa living in the same region, such as fish, octopus and gastropods, will share a common value for a given chemical marker in their tissues. We then discuss how universal markers could be applied to help address a pressing environmental challenge: validating the provenance of seafood species to support sustainable harvest practices.

## 2. Stable oxygen isotopes in biominerals: A unifying chemical marker

A chemical marker with "universal" marine applications needs to 1) vary geographically in a predictable fashion across oceans and 2) be minimally influenced by biological processes, diet, and species-specific effects (i.e. physiological regulation) so that the chemical values, representing a given geographic region, are relatively homogenous across taxa. Strontium isotopes, specifically $^{87}Sr/^{86}Sr$ ratios, fulfil these criteria in terrestrial and freshwater systems and have been used to trace the movement of modern and ancient taxa, as well as the provenance of food products (Bentley, 2006; Carter and Chesson, 2017; Holt et al., 2021). However, ocean waters have essentially uniform $^{87}Sr/^{86}Sr$ values because of the long residence time of dissolved Sr ions compared to rates of ocean mixing, and thus cannot be applied to marine systems.

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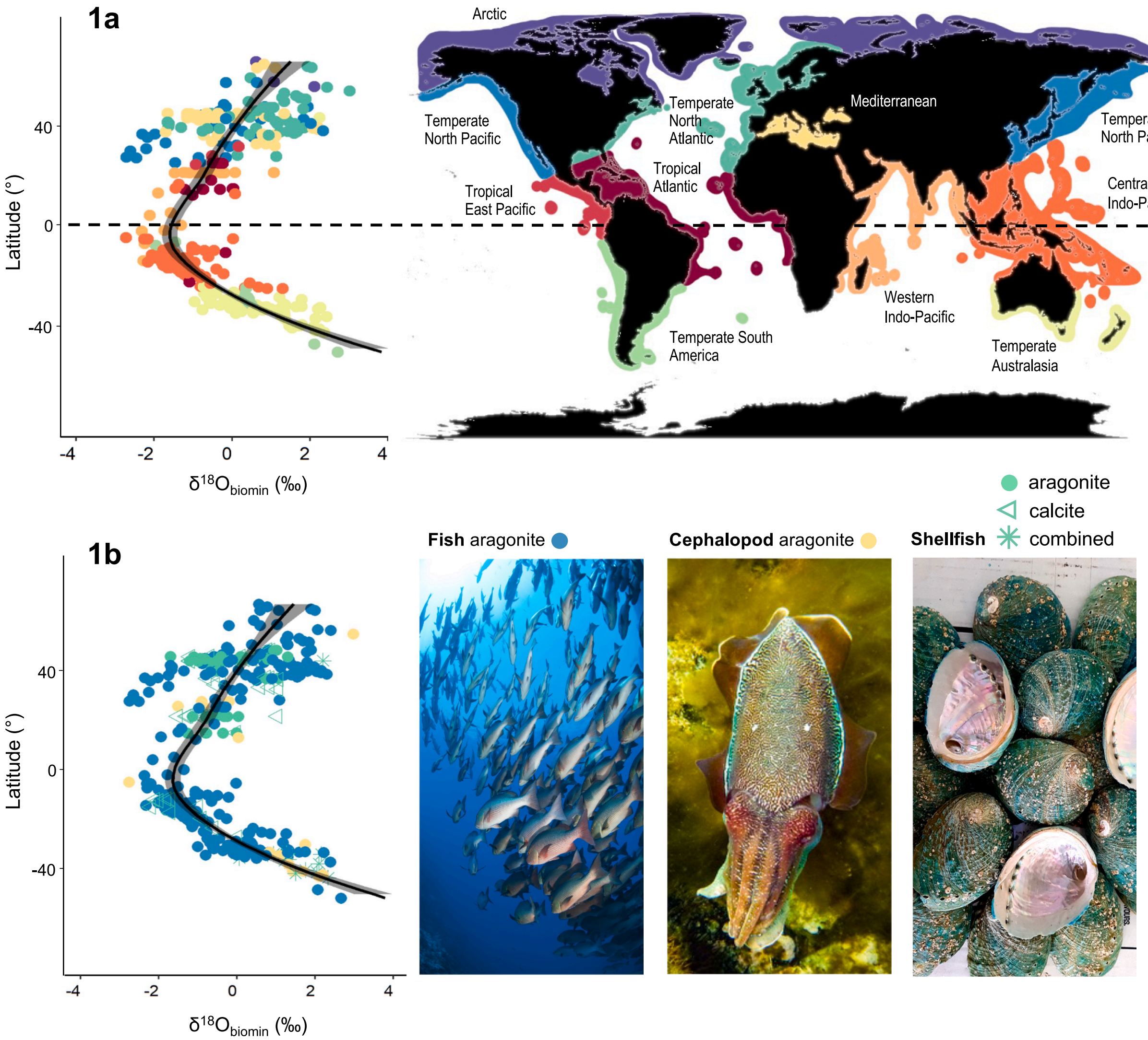


**Fig. 1. Global patterns of $\delta^{18}O$ analysed in the calcium carbonate tissues of marine animal taxa to illustrate the universal marker concept.** Data are visualised by a) marine ecoregion and b) taxa (fish, cephalopod, and shellfish) and biomineral (aragonite and calcite). Oxygen isotopes are presented in per mil (‰) using delta notation ($\delta^{18}O$) relative to Vienna Pee Dee Belemnite and trends are visualised using a local polynomial regression (LOESS) curve. Marine ecoregions in Fig. 1a are based on Spalding et al. (2007) and the equator is shown by a dashed line. Images from Fig. 1b are sourced from the authors (cephalopod and shellfish) and Anna Segeren/Shutterstock (fish).

In contrast, stable isotopes of oxygen, specifically $^{18}O/^{16}O$ ratios expressed as $\delta^{18}O$ values, vary weakly but predictably in oceans as a function of salinity, the isotopic composition of freshwater inputs, and evaporation rates (LeGrande and Schmidt, 2006). However, stable isotopes of oxygen are fractionated during their incorporation into calcium carbonate biominerals, and the extent of this fractionation is dependent on water temperature, with relatively little physiological influence in ectothermic animals (Epstein et al., 1953; Kim et al., 2007; Trueman and St John Glew, 2019). In other words, biominerals, which are produced by ectothermic marine species, magnify the geographic variation of $\delta^{18}O$ values in seawater based on predictable spatial or latitudinal temperature gradients. The predictable relationships between water temperature and $\delta^{18}O$ in marine biominerals has long been exploited by geochemists and paleoclimatologists to reconstruct past ocean temperatures and the thermal histories of marine animals (e.g.Grossman and Ku, 1986; Pearson, 2012; Trueman and St John Glew, 2019). Here, we discuss how these predictable relationships can be exploited to universally trace the provenance of a wide range of marine taxa.

To illustrate the universal marker concept, we compiled a global database of published $\delta^{18}O_{biomin}$ values (with the addition of an unpublished dataset provided by the authors) and then plotted these $\delta^{18}O_{biomin}$ values against latitude. Specifically, the $\delta^{18}O_{biomin}$ values were derived from the calcium carbonate biominerals of wild-caught fish, bivalves and gastropods (collectively called "shellfish" hereafter), and cephalopods with the search restricted to wholly marine and subtidal species at depths of less than 500 m. We aimed to illustrate the "universal concept" at the broadest of levels with data spanning 26 years (1995 to 2021), 10 major marine ecoregions, and 79 species ($n = 349$ total values). Regional coordinates were extracted or estimated from the information provided in each published paper. If multiple years of data were present at a single location, the mean of those values is presented. We included data from both aragonite and calcite biominerals in this analysis, as shelled molluscs produce both calcium carbonates, either singularly or in combination within the same shell. Fractionation factors can differ between calcite and aragonite (by about 0.6 ‰, see Kim et al., 2007 for review of studies), however, field studies have also shown minimal isotopic distinctions between calcite and aragonite layers within individual shellfish or from different shellfish species growing in the same environment (Lécuyer et al., 2012).

The data reveals a striking latitudinal gradient in $\delta^{18}O_{biomin}$ values, which aligns with the global patterns observed for seawater $\delta^{18}O$ values (LeGrande and Schmidt, 2006) (Fig. 1a). This pattern was observed despite a dataset spanning 25 years and the potential effects associated with environmental change, as well as variations in analytical methodology, accuracy, and precision over time. The relationship is particularly consistent in the Southern Hemisphere, and less so for the Mediterranean Sea and the temperate north Pacific, which may be explained by local variation in salinity and temperature gradients. However, such local variations may provide higher spatial resolution for provenance applications. Further, when these data are visualised by the three taxa and two biominerals represented, the results are relatively consistent, even when values depart from the expected value for a given latitude (Fig. 1b).

Oxygen isotope markers in the calcium carbonate tissues of ectothermic marine animals are a prime candidate to apply the universal marker concept and would be most useful for geolocating individuals over larger latitudinal gradients (100 s to 1000 s km) where there are known regional differences in water temperature and salinity. Furthermore, markers analysed in biominerals or hard tissues have several advantages over markers analysed in soft tissues, such as muscle and liver. For example, biominerals are metabolically inert, and as such, chemical data remains permanently "locked" within the structure, they do not degrade and are easy to store and archive. In fact, extensive archives of biomineralised structures already exist in many research agencies worldwide, whereby data can be generated retrospectively at relatively little cost (Doubleday et al., 2018). Also, while seasonal temporal variations are expected in $\delta^{18}O_{biomin}$ values, especially in temperate seas, most marine biominerals are incrementally grown, allowing specific time windows to be targeted in analyses and further increasing the precision of geolocation at higher special resolutions. An obvious limitation of $\delta^{18}O_{biomin}$ values is that they are roughly mirrored in the northern and southern hemispheres and animals collected along the same latitudes (in either hemisphere) will likely have similar values (Fig. 1). Further, oxygen isoscapes are relevant to surface waters, with further sampling required to assess how $\delta^{18}O$ varies in intermediate waters (LeGrande and Schmidt, 2006). However, by merging $\delta^{18}O_{biomin}$ with other potential universal markers, the spatial resolution and precision of geolocation could be refined.

## 3. Other candidate markers with universal potential

Neodymium isotopes, specifically $^{143}Nd/^{144}Nd$ ratios expressed as $\varepsilon_{Nd}$ values, exhibit similar properties to Sr isotopes. But, in contrast $\varepsilon_{Nd}$ exhibits distinct, temporally-stable geographic profiles in the ocean, which are driven by the underlying geology and relatively short residence times of Nd ions in seawater. The application of $\varepsilon_{Nd}$ to trace the origins of marine animals remains virtually unexplored. Yet, pioneering research suggests that the $\varepsilon_{Nd}$ values of seawater are reflected in both shell material and soft tissues of shellfish (Saitoh et al., 2018; Zhao et al., 2019) and remains an untapped resource for tracing the provenance of coastal marine animals on a universal scale. However, concentrations of Nd in biominerals are low, and currently $\varepsilon_{Nd}$ analysis is only routinely possible in the soft tissues of some taxa (e.g. fish), which limits the temporal precision of the analysis, and also requires relatively expensive technology that is not widely available.

Hydrogen isotopes ($^{1}H/^{2}H$ ratios expressed as $\delta D$ values) reflect variation in ocean latitude, as well as changes in riverine and subsurface groundwater inputs (McMahon et al., 2013). While $\delta D$ markers have received little attention as a provenance or tracing tool in marine species; one study has shown that $\delta D$ values in the muscle tissue and the organic matrix of otoliths of multiple freshwater fish species closely track $\delta D$ values of the water and could be a powerful tool to trace provenance (Whitledge et al., 2006). Sulfur isotopes ($^{34}S/^{32}S$ ratios expressed as $\delta^{34}S$ values) are an underexplored tool in marine systems, as they undergo relatively limited biochemical fractionation and increasing evidence suggests that there is some spatial variance in marine systems (St. John Glew et al., 2019). Sulfur isotope values from the macromolecular matrix of biomineralized tissues also track environmental variation in $\delta^{34}S$ values, but diet is an influencing factor which may limit the marker's universal applicability (Doubleday et al., 2018).

Stable isotope compositions of essential nutrient biomolecules (that can only be synthesised by microbes at the base of the food chain) potentially offer a range of candidate markers that are both variable in the oceans and minimally influenced by biological processes. For instance, the carbon framework of phenylalanine, an essential amino acid, cannot be synthesised de novo by eukaryotes and thus are transferred unaltered through food webs. The isotopic composition of carbon in phenylalanine, therefore, is retained and could be potentially used to link a sample to a reference population or to construct reference isoscapes (e.g. McMahon and Newsome, 2019; Vokhshoori et al., 2014). Similarly, the compound-specific analysis of nitrogen isotopes in phenylalanine has shown to be useful in studying the movement history of fish, without the effects of trophic transfer associated with bulk nitrogen isotope analyses (Harada et al., 2022; Matsubayashi et al., 2020). At the time of writing, however, the cost and labour-intensive nature of amino acid-specific stable isotope analyses generally precludes their use in routine monitoring, but future developments in analytical techniques may allow compound-specific isotope analyses as a promising tool in universal provenance analysis.

Anthropogenic pollutants, including radioactive isotopes, could also provide opportunities to develop powerful universal markers, as they can drive spatial variation to seawater chemistry that would otherwise be homogeneous (although temporal variation would be an obvious issue). For instance, lead isotopes ($^{207}Pb/^{206}Pb$ and $^{208}Pb/^{206}Pb$ ratios), which are not subject to biochemical fractionation but are naturally homogenous in the oceans, are being increasingly influenced by mining and industrial processes (e.g.Li et al., 2020).

Individual elemental markers, as opposed to isotopic markers, are typically too variable for universal marker applications as they are influenced by a suite of interacting biological and environmental factors to a less predictable degree. However, elemental concentrations of barium holds promise, with a large number of studies now showing that barium in fish otoliths predominantly reflects concentrations of barium in the seawater, which, in turn, is influenced by nutrient levels and salinity (Hüssy et al., 2020). Furthermore, a major advantage of trace element markers is that they can be analysed using cost-effective, readily available, and high-throughput techniques.

By combining the geolocation properties of $\delta^{18}O_{biomin}$ with other complementary universal markers, we can begin to test the spatial accuracy and precision of a universal chemical "fingerprint". For example, $\delta^{18}O_{biomin}$ could provide latitudinal data in offshore waters, while $\varepsilon_{Nd}$ could provide finer resolution longitudinal data in inshore waters. However, first we need to validate the universal properties of chemical markers, like $\varepsilon_{Nd}$, more thoroughly, particularly testing whether homogeneity across taxa holds true over time and space.

## 4. Using isoscapes to build a unified global framework

Traditional comparative approaches have long been used in the fields of both marine ecology and food forensics to estimate the relative likelihood of origin of an unknown biological sample based on chemical markers compared to those determined in candidate reference populations (Camin et al., 2016; Campana et al., 1999; Carter and Chesson, 2017). This comparative approach could equally be applied to universal chemical markers, however, to use discrete assignment approaches, reference datasets must be established (Li et al., 2016). The cost of building reference datasets can be prohibitive unless they are commercialised, limiting the accessibility to provenance technology to more wealthy states or commercial organisations. A more unified and efficient approach to geolocating marine animals could be achieved by

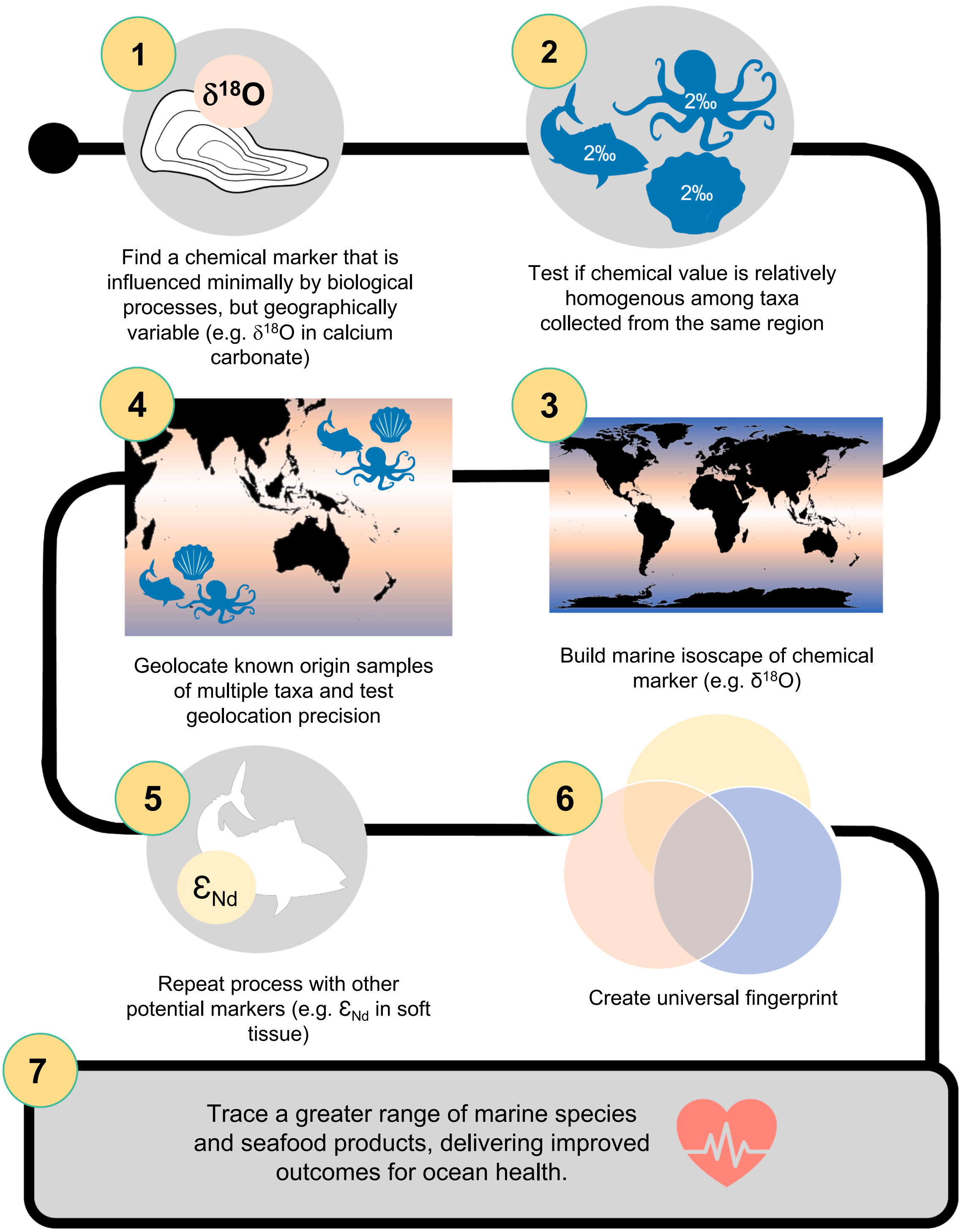


**Fig. 2.** Conceptual workflow to harness universal chemical markers and develop a globally relevant framework to trace the provenance of marine animals and seafood products.

developing spatial models (maps) of the distributions of universal markers across oceans, otherwise known as "isoscapes" (Fig. 2). Isoscapes reflect the spatial variation of select isotopic ratios and have been used to track Earth's processes, as well as the movement and migration of animals, humans, and materials on regional and global scales.

While most isoscapes have been developed for terrestrial systems (e.g. Holt et al., 2021), emerging studies are showing that marine isoscapes can be used as a tool to retrospectively geolocate marine animals back to their region of origin (Trueman and St John Glew, 2019). By merging the existing marine isoscape methodology with the concept of universal chemical markers, we could effectively develop a global approach to chemically geolocating individuals across oceans regardless of jurisdictional boundaries. For instance, Bayesian statistical assignment methods have been developed to probabilistically link samples to likely regions of origin based on isoscape models, accounting for uncertainty in both isoscapes and the mapping of universal markers to species or products of interest (e.g. Ma et al., 2020). The conceptual theory, analytical capability and statistical algorithms needed to apply universal marker approaches to provenance problems are therefore in place. Global efforts to compile data on the spatial distribution of elements and isotopes across the oceans are continuing and hold great promise for improving our ability to develop and detect new universal markers to assist in the development of a global framework (e.g. https://www.geotraces.org). We anticipate an increase in our ability to establish provenance and movement of marine animals or seafood products retrospectively.

## 5. Applying universal markers to a real-world problem: Seafood provenancing

Universal markers, alongside spatial models of their oceanic distributions (i.e. isoscapes), could underpin a global framework to trace the provenance of seafood species, whereby multiple species could be geolocated simultaneously back to their harvest location (see Fig. 2 for conceptual workflow). Seafood is the most traded food commodity in the world and supply chains are particularly vulnerable to fraud, including provenance fraud (Asche et al., 2015; FAO, 2020; Leal et al., 2015). Provenance fraud occurs when people are intentionally deceived about the provenance of seafood for criminal profit, and continues to threaten sustainable fisheries, livelihoods, consumer health and food security (Lindley, 2021). Genetic, digital, and chemical marker methods are the main tools being developed to identify the provenance of marine food products (Gopi et al., 2019; Leal et al., 2015), but they are focussed at the species-level, or on specific taxonomic groups or seafood industries (Camin et al., 2016; Galimberti et al., 2013; Hardt et al., 2017). A key challenge with seafood is that it constitutes a large and diverse range of animals, from fish to molluscs to crustaceans to echinoderms, with new or poorly studied species continually added to the market. In fact, the FAO global marine fisheries database, includes catch data for more than 1,700 species (FAO, 2020). Furthermore, many nations are likely to not have the resources or government support to develop species-specific provenance technology, particularly for species that have low commercial, cultural or social value.

Thus, the application of universal markers could be particularly useful for the many species which lack a species-specific provenance method. Furthermore, our approach would negate the need for the compilation of costly reference databases, which are required for more traditional chemical profiling methods (Li et al., 2016), and may, therefore, make provenance validation more accessible to smaller producers and lower-income countries. While oxygen isotopes are only applicable to biomineralized tissues and thus seafood that has undergone minimal processing, for seafood that is processed, biomineralised tissues could be retained and cheaply stored at the processing stage, and then analysed on as-needs basis. Furthermore, biomineral-based markers are also permanently fixed within the tissue structure and are not affected by biological processes throughout the life of an individual or post-mortem. And, with additional research, potential universal markers like $\mathcal{E}_{Nd,}$ could also be developed to target processed, soft tissue products.

## 6. Concluding remarks

By harnessing the properties of select isotopic and elemental markers we could increase our capacity to trace the provenance of marine animals, particularly species that are commercially harvested and face increasing pressure from provenance fraud. Underpinning research on oxygen isotopes within calcite and aragonite biominerals is already advanced, we can apply this knowledge now to test universal markers in a real-world context. We can then determine whether other potential markers yield a common pattern among species. While some isotopic and elemental markers are more cost-effective to analyse than others (i.e. elemental barium versus neodymium isotopes), analytical technology is advancing and becoming cheaper, alongside the accessibility and spatial coverage of biogeochemical datasets. The goal of this study is to promote universal markers to the marine community so that we can build research momentum and collectively create a universal fingerprint of marine provenance.

## CRediT authorship contribution statement

**Zoe Doubleday:** Conceptualization, Visualization, Writing – original draft, Writing – review & editing, Funding. **Jasmin Martino:** Resources, Data curation, Formal analysis, Visualization, Writing – review & editing. **Clive Trueman:** Conceptualization, Writing – review & editing.

## Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

## Data availability

Data are provided as Supplementary Material.

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*Data availability statement*

The database of published $\delta^{18}O$ values ($n = 325$) and associated metadata are provided as Supplementary Material. The unpublished $\delta^{18}O$ values ($n = 11$) presented in the database are available upon private request, with the associated metadata provided in the database.

## Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecolind.2022.109481.

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