



Global oxygen isoscapes for barnacle shells: Application for tracing movement in oceans



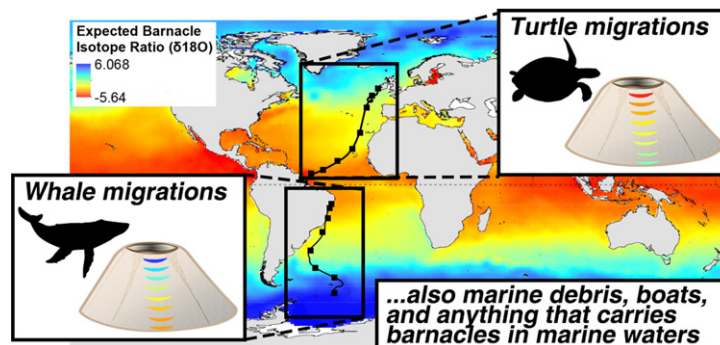
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HIGHLIGHTS

- Barnacle shell isotopes can inform the past movement of host animals or objects.
- We assess tracking resolution and temporal shifts using first global isoscapes.
- Barnacle isotopes could identify host origin to <100 km in many areas.
- Mid-latitudes have highest temperature-driven isotope shifts each year.
- Case studies demonstrate applicability for future investigations.

GRAPHICAL ABSTRACT



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ABSTRACT

It is helpful to understand the movement of animals and objects to inform species conservation and broader environmental management (e.g. by identifying the origin of marine debris). Tagging techniques are limited to investigations of future movement (e.g. after a tag has been applied), with no ability to understand where an animal or object has come from prior to encounter. However, studies that apply chemical techniques are able to address questions about historical movement prior to encounter, particularly through the analysis of stable isotopes from the tissues of migrating animals, or from barnacle shells that attach to migrating hosts. Barnacle shell isotope analysis is a promising technique that could provide a new understanding of the ecology of migrating marine fauna, or additionally the origin of marine debris. Here we use global datasets to assess the applicability of barnacle shell isotope techniques for identifying the origin and travel pathways of animals and objects that carry hitchhiking barnacles. We present the first global isoscapes for barnacle shell calcite, using these to identify areas that are likely to offer the finest spatial resolution for this application. We further demonstrate how isoscapes can be applied to back-trace animal migrations using real-world migration case studies of sea turtles and whales. We demonstrate that coastal areas and mid-latitude oceanic regions are likely to offer the best spatial resolution, and that migration pathways are able to be identified from successive barnacle shell samples. We

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expect that this work will allow for more efficient and precise future applications of barnacle shell isotope analyses to trace the movement and origin of barnacle hosts through marine waters.

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1. Introduction

Understanding the origin and movement pathways of marine animals and objects can inform conservation efforts for threatened species, management of environmental impacts (e.g. identification of pollutant sources) or inform search efforts for marine wrecks (e.g. the missing flight MH370). Various techniques have been used to understand movement in marine systems, each with their own strengths and weaknesses. For example, ocean current and/or wind modelling (Brushett et al., 2016) and written language analysis (Slip and Burton, 1989) have been used successfully to investigate aspects of the origin or movement of marine debris, while mark-recapture, satellite and radio tracking (Eckert and Stewart, 2001; Hays et al., 2016) have been used to understand the ecology of marine megafauna. However, most tracking techniques typically require the animal or object to be encountered prior to a journey to attach a tag (or label), and sometimes additionally during (e.g. radio tracking) or after (e.g. mark-recapture) the migration, in order to understand movement patterns (e.g. Campbell et al., 2015; Balmori, 2016). Thus, physical tagging techniques can rarely delineate where an animal has come from, only where it goes post-encounter, and often involve low replication due to high costs (but not always; e.g. Scott et al., 2012).

Chemical analyses of animal tissues have been growing in popularity for use in understanding movement that occurred prior to capture (e.g. O'Toole et al., 2012; Trueman et al., 2012), particularly through stable isotope analysis (SIA) (e.g. Hobson and Wassenaar, 1999; Pearson et al., 2017; Cruz-Flores et al., 2018). Generally, these analyses involve sampling of soft-tissues from marine animals (e.g. skin or blood), and associating differences in chemical signals (e.g. isotope values) to differential habitat use, geographic location, or placement within the food web. Spatial origins and movement is often inferred by comparing measured isotope values from animal tissues with isoscapes (maps showing the geographic distribution of isotope values; e.g. Graham et al., 2010; McMahon et al., 2013; Trueman et al., 2016; Tornaiainen et al., 2017; Hobson et al., 2019). However, soft-tissue analyses are affected by the dietary-choices of the individual, which could confound geographic placements if individuals are highly mobile and/or consuming different prey items in the same area. For example, variation in isotope ratios in sea turtles has been shown to increase in areas with higher prey diversity (Pajuelo et al., 2016). Compound-specific isotope analysis of amino acids can disentangle some diet-related effects, including trophic levels, and aid in identifying where an animal has been feeding where bulk-tissue analyses may not (e.g. Brault et al., 2019; Close, 2019). However, while analysis of multiple tissues, with different assimilation rates (e.g. plasma versus skin; Reich et al., 2008) enables some broad inferences of recent versus long-term feeding behaviour (e.g. Prior et al., 2016), analyses of soft-tissues are unable to provide time-sequenced values that allow re-creation of migration pathways for individuals across several locations. Isotope analysis of bones provide relationships to water chemistry as well as diet choices, and can provide sequential records to re-create movement over multiple locations (e.g. Rooker et al., 2008; Turner Tomaszewicz et al., 2017). Indeed, the analyses of isotopes in fish otoliths has been widely applied to recreate fish movement and migration patterns (e.g. Kennedy et al., 2002; Huxham et al., 2007; Rooker et al., 2008; Trueman et al., 2012), but require the animal to be killed in order to sample. Further animal tissues that offer a sequential record of isotopic history are whale baleen (e.g. Best and Schell, 1996) and seal vibrissae (e.g. Hall-Aspland et al., 2005), and can be used to re-create movement and/or feeding history through different water

bodies if growth and incorporation rates, and the drivers behind isotopic changes are known. Both soft-tissue and bone techniques are also restricted to assessments of animal movement and cannot recreate the historical movement of inanimate objects such as floating debris.

One underutilised, but potentially useful, technique for recreating host animal or object movement is via SIA of the calcite from barnacle shells. Barnacles readily attach to marine megafauna and other floating items, and the oxygen isotope content in barnacle calcite is affected by water temperature and salinity (Killingley and Newman, 1982), rather than diet. Higher salinity results in higher oxygen isotope ratios in barnacle shells, while higher temperatures will have the opposite effect, making values more negative (Killingley and Lutcavage, 1983). Killingley and Newman (1982) described this strong relationship between oxygen isotopes from barnacle shells ($\delta^{18}\text{O}_{\text{calcite}}$) and the physico-chemical conditions under which they were formed (specifically, the oxygen isotope ratio of seawater ($\delta^{18}\text{O}_{\text{water}}$) and water temperature) in the form of the balanomorph barnacle paleotemperature equation (BBPE). A similar equation has long existed for mollusc shell (Epstein et al., 1953). With knowledge of any two of the three variables ($\delta^{18}\text{O}_{\text{calcite}}$, $\delta^{18}\text{O}_{\text{water}}$, water temperature) it is possible to estimate the third using the BBPE.

Barnacle shells are laid down sequentially, within which SIA ratios remain stable over time, reflecting the time (and hence location) that they were formed. Indeed, isotope ratios in calcium carbonate are so stable that similar techniques have been used to re-create past climatic conditions from fossil carbonates (e.g. Gagan et al., 1998) and recent sea conditions (temperature and salinity) using isotopes from marine animal shell carbonates (e.g. mussels; Zhao et al., 2019). Thus, it is possible to analyse isotope ratios across multiple layers in order to build an understanding of how water physico-chemistry (temperature/salinity) has changed over time (e.g. Killingley and Lutcavage, 1983; Zhao et al., 2019). In turn, it might be possible to identify a suite of plausible origins or movement pathways by analysing the stable isotope content of barnacle shells, and comparing values to known sea surface temperatures (SSTs), and measured (or predicted) $\delta^{18}\text{O}_{\text{water}}$. With many species of migratory marine fauna carrying barnacles, as well as many items of marine debris carrying barnacles, this technique could allow for broad scale understanding of the historic movement of any animal or object that hosts barnacles on its journey through marine waters.

SIA of barnacle shells has been used to infer the movement of hosts in only a handful of studies to date. Examples include an investigation into the oceanic migration of California gray whales (*Eschrichtius robustus*) (Killingley, 1980), the movement of loggerhead turtles (*Caretta caretta*) between high and low salinity areas (Killingley and Lutcavage, 1983), and regional-scale oceanic movements of green turtles (*Chelonia mydas*) (Detjen et al., 2015). Oxygen isotopes in barnacle shells have also been recently used to recreate modern and ancient movement patterns for whales (Collareta et al., 2018; Taylor et al., 2019). Additionally, a technique was recently described that enables age determination of samples from barnacle shells (Doell et al., 2017), which, in combination with isotope analyses, was able to distinguish between discrete sea turtle foraging areas with high accuracy and at management-relevant spatial resolutions (Pearson et al., 2019).

To our knowledge, the development of isoscapes for barnacle shell $\delta^{18}\text{O}_{\text{calcite}}$ has been attempted only once to date, in the tropical Pacific (Detjen et al., 2015). This study used isoscapes, estimated using the BBPE and incorporating remote temperature data along with published $\delta^{18}\text{O}_{\text{water}}$ values (LeGrande and Schmidt, 2006). Detjen et al. (2015) then compared the $\delta^{18}\text{O}_{\text{calcite}}$ isoscape to measured values from

Platylepas sp. barnacles in an effort to identify regional movement patterns for host sea turtles (Detjen et al., 2015). Results suggested that for this species of barnacle (for which there is limited information about growth rate or age) in this part of the tropical Pacific, $\delta^{18}\text{O}_{\text{calcite}}$ was able to delineate the origin of shell formation to within a broad spatial resolution, many 1000s km^2 (Detjen et al., 2015). However, we expect that resolution could improve with additional variables in analyses and improved understanding of regional variations and growth rates to age samples. For example, incorporation of regional variations in salinity (as in Schmidt et al., 2007) is likely to improve the accuracy of isotope estimates (thus, improving spatial resolution), and using barnacle growth rates to age samples (e.g. Doell et al., 2017) will allow for more precision in estimates by accounting for temporal variation.

It must be noted here that all previous studies that infer host movement from barnacle shell isotopes have focused on balanomorph barnacles, and that none yet have attempted similar techniques using pedunculate (stalked) barnacles. This distinction is important for several reasons, particularly because growth rates and isotopic incorporation are likely to vary between these disparate barnacle groups, and also because different ocean regions are likely to promote differential attachment and growth rates between barnacle types. Indeed, Killingley and Newman (1982) postulated that oxygen isotopes in the pedunculate barnacles were likely intermediate between balanomorph barnacles and mollusc shell, which are offset from one another at the same temperature. Additionally, knowledge of barnacle growth rates and how these vary with environmental factors (e.g. water temperature, food availability) is critical for linking isotopic ratios with those expected in specific times and locations. Uncertainty in barnacle growth rate estimates, or estimates of spatio-temporal variation in isotopes, will reduce the applicability of the techniques we present here. The most complete understanding of both growth rates and isotopic incorporation into shell material exists for balanomorph barnacles, specifically the turtle barnacle (*Chelonibia testudinaria*), that has been the subject of three growth rate studies to date (Sloan et al., 2014; Ewers-Saucedo et al., 2015; Doell et al., 2017) and three studies analysing shell isotopes (Killingley and Newman, 1982; Killingley and Lutcavage, 1983; Pearson et al., 2019). The three growth rate studies returned comparable growth rate estimates, despite being assessed in geographically distant regions (Gulf of Mexico, eastern USA and eastern Australia), suggesting that samples from this barnacle species are able to be reliably dated. Given the current lack of understanding on pedunculate barnacle shell isotopes and growth rates, we focused analyses in this study on established paleotemperature equations and growth dynamics for balanomorph barnacles, assuming *C. testudinaria* is a model species. This assumption is on the basis that similar techniques can be applied to other barnacle taxa as future research improves understanding around specific growth dynamics and isotopic incorporation for additional species. It would be of great benefit for future studies of oceanic movement in particular to gain a better understanding of pedunculate barnacle growth rates and isotopic incorporation.

The aims of this study were to use global gridded sea surface temperature and $\delta^{18}\text{O}_{\text{water}}$ data to create isoscapes for barnacle shell carbonates, and assess the utility of applying similar isoscapes for the purpose of understanding the movement of barnacle hosts. Specifically, we investigate the effect of spatial and temporal variation in isotope values by addressing four aims:

1. to understand spatial variation in predicted barnacle shell isotope values by creating global isoscapes for barnacle shell;
2. to understand the spatial resolution at which areas could be separated in oceanic (non-coastal) waters using barnacle shell isotopes, identifying regions with high/low resolution. We do this by quantifying the rate of change in barnacle isotope values between adjacent areas and also by assessing the effect that heterogeneity within a barnacle may have on resolution;

3. to understand the effect of seasonal temperature changes on isotope values, by comparing isotope estimates within the same area at different times; and,
4. to demonstrate potential applications of these techniques to animal tracking studies, using case study examples. Specifically we aim to demonstrate how barnacle shell isotope values are likely to vary over space and time along typical animal migration routes, and the importance of accurately dating shell samples in these types of analyses.

2. Methods

2.1. Modelled prediction of global barnacle calcite $\delta^{18}\text{O}$ isoscapes

We developed global isoscapes from modelled isotope values that estimate oxygen isotope values for barnacle shell in all oceans, for four time periods (one week in each of January, April, July, and October 2015, approximating seasonal differences) using techniques similar to those applied in predicting otolith isoscapes by Trueman et al. (2012). We note that the techniques applied here can be used to investigate any time period for which suitable data are available, but we targeted 2015 as a model period because it is relevant to several recent investigations of marine movement involving barnacles and/or isotopes. For example, this period was when samples were collected for the most recently published analysis of barnacle shell isotopes to infer the movement of host animals (Pearson et al., 2019) and also the period during which barnacle covered plane parts began to wash ashore from the missing Malaysian Airlines flight MH370 triggering a new wave of investigations into its whereabouts (e.g. Nesterov, 2018), including the potential application of barnacle shell isotopes. To do this we collated existing global data for SST (Reynolds et al., 2002) and $\delta^{18}\text{O}_{\text{water}}$ (LeGrande and Schmidt, 2006) and fit values to a $1^\circ \times 1^\circ$ grid in ArcMAP (ESRI, 2010). The SST (as weekly mean) and $\delta^{18}\text{O}_{\text{water}}$ were extracted from these data sets for each time and grid cell. We chose to use a weekly mean because a single barnacle shell sample may incorporate periods ranging a few days to weeks, depending on the rate at which barnacles were growing at the time of deposition (Doell et al., 2017; Pearson et al., 2019). Thus, on average, a weekly temperature mean is likely to be more indicative of observed isotope values than daily or monthly time resolutions. These values were then used to predict the expected $\delta^{18}\text{O}_{\text{calcite}}$ for barnacle shell layers formed under those conditions (using the BBPE Killingley and Newman, 1982) at each time period, with values then projected spatially to create time specific isoscapes displaying estimates of barnacle shell $\delta^{18}\text{O}_{\text{calcite}}$ globally. We note here that the BBPE equation, as well as the existing studies of growth rates that we base these assumptions on, is specific to balanomorph (acorn) barnacles and as yet these assumptions cannot be extended to peduncle (stalked) barnacles. Thus, while applying these techniques to stalked barnacles is a feasible future application, further work is needed to develop a better understanding around the growth rates and isotope incorporation dynamics for these barnacle taxa.

2.2. Estimating spatial resolution in applications of barnacle calcite $\delta^{18}\text{O}$ isoscapes

We estimated the spatial resolution at which barnacle shell isotopes may be able to distinguish between specific areas in different parts of the world. Pearson et al. (2019) demonstrated that the technique was highly accurate when areas were at least 400 km apart in eastern Australia, and we hypothesised that this resolution may be finer in other areas where there are steeper salinity and/or temperature gradients spatially. To assess this, we conducted a slope analysis in ArcMAP to determine the maximum rate of change in isotope values between adjacent $1^\circ \times 1^\circ$ cells (slope). Areas of ocean with higher rates-of-change of $\delta^{18}\text{O}_{\text{calcite}}$ between adjacent cells will presumably provide

finer spatial resolution when attempting to use barnacle calcite oxygen stable isotopes to track the location and/or movement of their host. Thus, by visually representing the change in slope at a global scale (over different times of the year), it is possible to identify oceanic areas that are likely to offer high (or low) spatial resolutions for tracking barnacle host movements.

We then applied several thresholds to estimate the ability to separate areas spatially, accounting for inherent variation within measurements of barnacle shells. If differences in isotope values between adjacent areas are less than the error in the measurement of isotopes from barnacle shell then we will be unable to distinguish between them. Pearson et al. (2019) showed that variation within adjacent shell samples of the same age from the sea turtle barnacle (*Chelonibia testudinaria*) were approximately 0.2‰. We applied four potential levels of variation around this example (0.1‰, 0.2‰, 0.3‰ and 0.4‰) in our analyses in order to assess the effect that changes in the magnitude of this error may have on achievable resolution. These levels were selected for two reasons: firstly, to apply a realistic level of uncertainty based on previous barnacle analyses (the 0.2‰ level; Pearson et al., 2019); and second, to assess the possible effect that uncertainty of different magnitudes may have on the ability to identify origins from barnacle shell isotopes. This larger variation could feasibly be apparent from variation at all levels of the analyses including (but not limited to) uncertainty in $\delta^{18}\text{O}_{\text{water}}$ measurements, estimates of incorporation into barnacle shell, and variation between barnacle species. Unfortunately, there are not yet estimates of uncertainty available in the BBPE, nor the global $\delta^{18}\text{O}_{\text{water}}$ dataset, so we have applied these proxy levels as representative estimates. We applied these levels to the slope analyses, mapping areas where the slope was greater than the respective level of variation. This enabled visual assessment of areas where the ability to distinguish between adjacent areas is achievable at a resolution of $<100\text{ km}^2$ (the approximate size of our grid cells) for each of these levels of error, highlighting areas that are likely to offer the finest spatial resolution in these types of analyses. These analyses should be interpreted as potential relative differences between regions, and an indication of how

uncertainties of different magnitudes may affect the spatial separation that is achievable in identifying origin (because there were no measures of uncertainty provided in the data and equations used in the development of these isoscapes). Uncertainty at all levels should be quantified, where possible, in future applications.

2.3. Estimating how temperature changes affect isotope values within the same area

We also aimed to assess how isotope values are likely to vary alongside seasonal changes in temperature (i.e. how much temperature-driven variation there may be at the same place within a year). To date, no data are available showing the temporal variation in $\delta^{18}\text{O}_{\text{water}}$; the only available global dataset is an amalgamation of measurements across many years. Sea water isotope values are driven primarily by salinity, which varies through time, as a result of isotope values in precipitation, which varies regionally but remains comparatively stable and predictable spatially (e.g. Cerar et al., 2018; Hollins et al., 2018). Despite a known linear relationship between salinity and $\delta^{18}\text{O}_{\text{water}}$, the nature of this relationship (particularly the gradient) varies regionally and we are not aware of any published equations for converting salinity values into $\delta^{18}\text{O}_{\text{water}}$ beyond those for the tropics globally, and the north Atlantic extra-tropics (Schmidt et al., 2007). Thus, the data we use for $\delta^{18}\text{O}_{\text{water}}$ are an approximation that is representative of regional differences in salinity and precipitation isotopes, but do not account for temporal changes within the same area, so not necessarily exact values in areas at the times investigated. Thus, we were unable to assess the effect of salinity changes over time globally, but have incorporated regional equations (where available) into our case study calculations to assess this at a finer scale.

Given the $\delta^{18}\text{O}_{\text{water}}$ static variable, we were able to examine the magnitude of the effect that temperature alone is likely to exert on barnacle $\delta^{18}\text{O}_{\text{calcite}}$ throughout the world's oceans. With static $\delta^{18}\text{O}_{\text{water}}$ values, the algebraic calculations are relatively simple, with approximately 1‰ change for every 4 °C. Regardless, temperature analysis

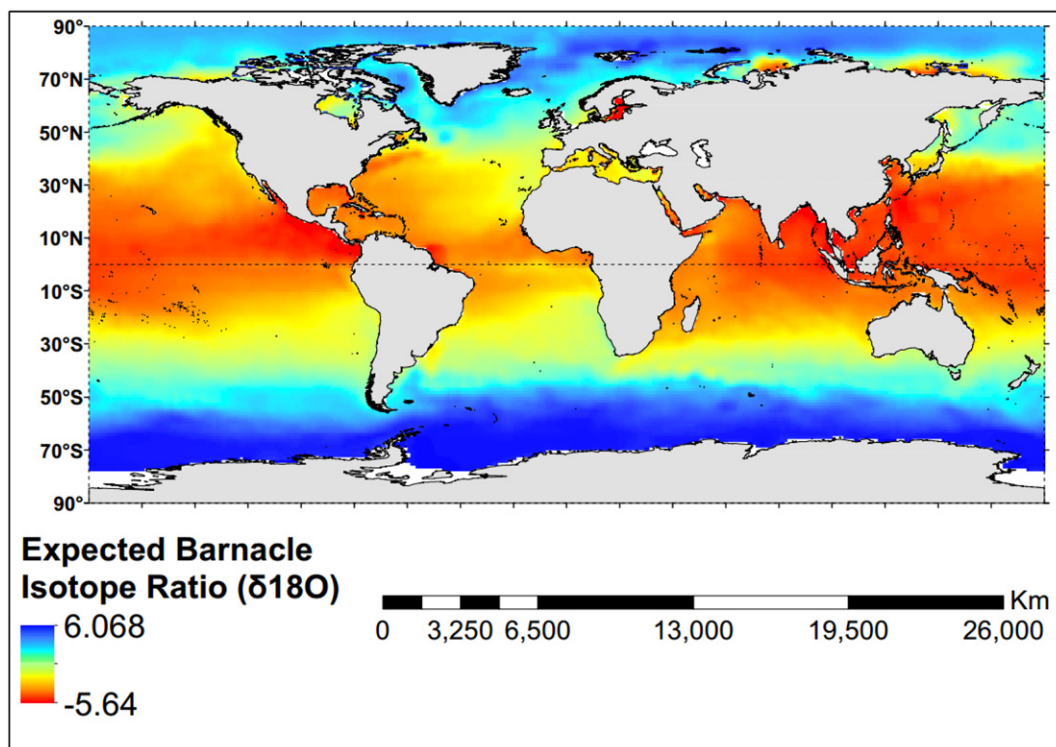


Fig. 1. Global barnacle isotope ratios ($\delta^{18}\text{O}_{\text{calcite}}$) calculated from the BBPE using SST and $\delta^{18}\text{O}_{\text{water}}$ values from 2 to 8 July 2015. Isoscapes were also created for several other time periods (including Jan, Apr, and Oct, 2015) for use in subsequent analyses, but are not presented visually here.

independent of varying $\delta^{18}\text{O}_{\text{water}}$ provides useful insight into which oceanic areas could be expected to see large shifts in $\delta^{18}\text{O}_{\text{calcite}}$ throughout the year. To test this, global barnacle $\delta^{18}\text{O}_{\text{calcite}}$ maps (isoscapes) were created for four time periods in 2015: January; April; July; and October. We present only one visually (for July; Fig. 1), but use all four in subsequent analyses. We investigated the magnitude effects on $\delta^{18}\text{O}_{\text{calcite}}$ from seasonally driven temperature changes by grouping predicted values into latitudinal bands (10°) and comparing the mean values for each time period. We also estimated the maximum difference between time periods to understand which latitudes are expected to see the largest shifts within a year.

2.4. Case studies

We further aimed to demonstrate theoretically, the way that these techniques could be employed to back-trace the movement of migrating animals. We did this by replicating the known migrations of two previously tracked animals along their Atlantic Ocean migrations, a leatherback turtle that crossed the north Atlantic (from Doyle et al., 2008) and a humpback whale on its southern migration through the south Atlantic (from Zerbini et al., 2011). We created sample profiles for barnacles that could have hypothetically been collected from these animals at the end of their migrations, and estimated barnacle isotope values for samples that match the time and location that each animal was recorded at for specific time periods throughout their migrations.

We selected these two animals because they undertook long migrations through two characteristically different regions, where we expect one, the southern Atlantic, to offer large differences spatially (thus high-resolution) and the other, the north Atlantic, to offer comparatively smaller differences spatially (thus lower resolution; from slope analyses). We compared these long migrations as an example of how the technique could be used in practice, and to show differences in the ability to identify origin and movement between water bodies with inherently different environmental gradients.

In the leatherback case study, we were further able to assess the effect of salinity in the predictions because there are existing equations

that allow conversion from salinity to $\delta^{18}\text{O}_{\text{water}}$ for the global tropics and North Atlantic extra-tropics (Schmidt et al., 2007), both regions that the leatherback turtle migrated through. Thus, we investigated the effect that including salinity observations into predictions may have on $\delta^{18}\text{O}_{\text{water}}$ and $\delta^{18}\text{O}_{\text{calcite}}$ estimates by comparing values throughout the north Atlantic leatherback turtle migration (Doyle et al., 2008) using $\delta^{18}\text{O}_{\text{water}}$ values obtained or estimated using two methods; a) those directly from the LeGrande and Schmidt (2006) data as in our previous analyses; b) new values converted from observed salinity using the equations that describe regional relationships between salinity and $\delta^{18}\text{O}_{\text{water}}$ from Schmidt et al. (2007). Salinity values for these calculations came from GODAS data provided by the NOAA/OAR/ESRL PSD from <http://www.esrl.noaa.gov/psd/> (Behringer et al., 1998). We extracted the values for each time/location, and converted to $\delta^{18}\text{O}_{\text{water}}$ using the north Atlantic extratropical equation for turtle locations 1–4, and the global tropical equation for locations 5–8.

3. Results and discussion

3.1. Global barnacle calcite $\delta^{18}\text{O}$ isoscapes

Oxygen isotope ratios in barnacle shell layers, estimated here using the BBPE, varied spatio-temporally due to the regional and temporal differences in seawater physico-chemical properties in which they were formed. Generally, the predicted oxygen isotope ratios in barnacle shells from the truly oceanic waters (i.e. not coastal or estuarine) were highest near the poles (max: 6.07‰) and lowest in the tropics (min: -5.64‰ ; Fig. 1), agreeing with trends found in previous work (e.g. in otoliths by Trueman et al., 2012). Notable areas with considerably lower isotope ratios than neighbouring areas exist in the proximity of large freshwater inputs, suggesting that salinity is playing a larger role than temperature in these locations. For example, the Baltic Sea, and an area in the west Atlantic (near the equator) where effects of freshwater outflows from the Amazon River, are notable as far as 1000 km from the mouth (Fig. 1).

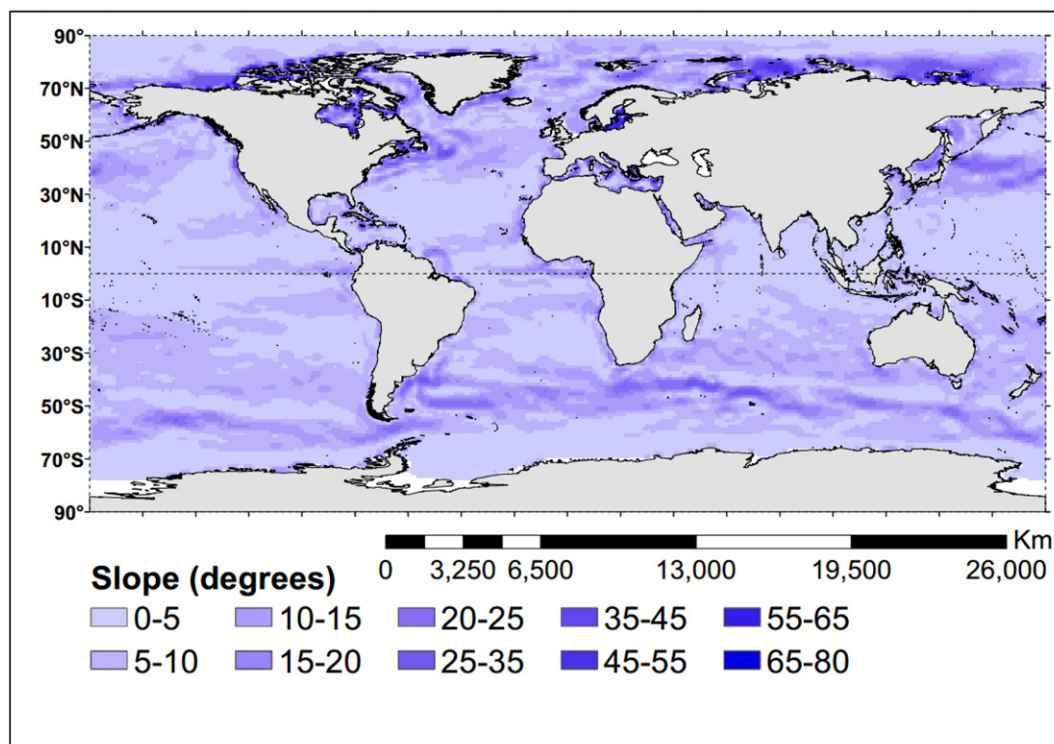


Fig. 2. Analysis of the rate of change (slope (degrees)) in calculated barnacle isotope ratios ($\delta^{18}\text{O}_{\text{calcite}}$) between adjacent cells ($1^\circ \text{ lat} \times 1^\circ \text{ lon}$) for 2–8 July 2015.

3.2. Spatial resolution in assigning origin using barnacle calcite $\delta^{18}\text{O}$ isoscapes

By assessing the rate of change in $\delta^{18}\text{O}_{\text{calcite}}$ between adjacent $1^\circ \times 1^\circ$ cells, we were able to identify areas where these techniques may offer the highest spatial resolution in distinguishing between areas. In general, mid to high latitude areas are likely to offer the best resolution for identifying the origin of calcareous shell formation, and hence tracking location and movement of barnacle hosts (Fig. 2). These slope analyses show that minimal change in $\delta^{18}\text{O}_{\text{calcite}}$ ratios occurs over vast areas of tropical open ocean globally (with slopes generally $<10^\circ$), indicating that resolution would be poorest if applying the barnacle isotope techniques to infer locations in these regions (Fig. 2). This is consistent with the findings of Detjen et al. (2015), which showed only low resolution ability in identifying the origin of barnacle shells formed in the tropical Pacific using $\delta^{18}\text{O}_{\text{calcite}}$. Areas between approximately 30° and 70° in both hemispheres show considerably steeper slopes (most areas $>10^\circ$) than the tropics, indicating that these regions could offer high resolution when attempting to identify a point of origin from $\delta^{18}\text{O}_{\text{calcite}}$ (Fig. 2). Other potential high resolution areas occur in the Arctic ocean and Baltic sea (Fig. 2), where changes may have been driven by lower salinity compared with nearby regions further from freshwater sources.

Another key component affecting the resolution that is achievable in using these techniques to identify origins lies in the variability of $\delta^{18}\text{O}_{\text{calcite}}$ within barnacle shells formed under the same conditions (i.e. replicates of the same sample). Unsurprisingly, our analyses show that lower variation within $\delta^{18}\text{O}_{\text{calcite}}$ formed under the same spatio-temporal conditions will result in higher resolution for geographic analyses. If variation between barnacle shell sample replicates remains under 0.1‰, we expect this method to be able to provide information on host movement and location at a resolution of $1^\circ \text{ lat} \times 1^\circ \text{ lon}$ or better

in many regions of the world's oceans (Fig. 3A). With increasing sample replicate variation, the regions in which this resolution is possible reduce dramatically (Fig. 3B, C, D). Variation above 0.4‰ is likely to render the method unable to resolve origin at this resolution in any areas except those with the most rapid spatial changes (e.g. regions in the Arctic and south Atlantic oceans; Fig. 3D). The only study to date that reports an error value of this nature is Pearson et al. (2019). The error recorded in that study (0.18‰) is closest to our 0.20‰ level (Fig. 3B), suggesting that these techniques are unlikely to separate regions that are $<100 \text{ km}$ apart in most areas, with notable exceptions at mid-latitudes or near many coastlines that are likely to offer the highest resolutions (Fig. 3B).

3.3. Influence of temperature on $\delta^{18}\text{O}_{\text{calcite}}$

Analysis of the effect of temperature changes through the year on $\delta^{18}\text{O}_{\text{calcite}}$ shows that ratios in January and April are similar. July and October also return similar values to one another, but different from January/April (Fig. 4). Large shifts occur in the mid-latitudes between April and July, and then in the reverse direction between October and January (Fig. 4). Little change occurs year round in the tropics and southern polar regions due to temperature alone (Figure 4).

Analyses of the magnitude of temperature-driven change within each latitude band reveals that mid-latitude areas (30° to 60°) are likely to experience the largest temperature driven shifts in isotope ratios (Fig. 4), which is consistent with expectations given these temperate latitudes tend to experience the largest temperature ranges. Latitudes between 40° and 50° in the northern hemisphere return the highest differences between periods ($1.90 \pm 0.72\text{‰}$) suggesting that these areas are likely to experience the largest temperature driven changes. This is considerably larger than at similar latitudes in the southern hemisphere, where the largest shift occurs between 30° and 40° ($1.15 \pm 0.25\text{‰}$) (Fig. 4). Very high latitudes (-70° to -80°) in the southern

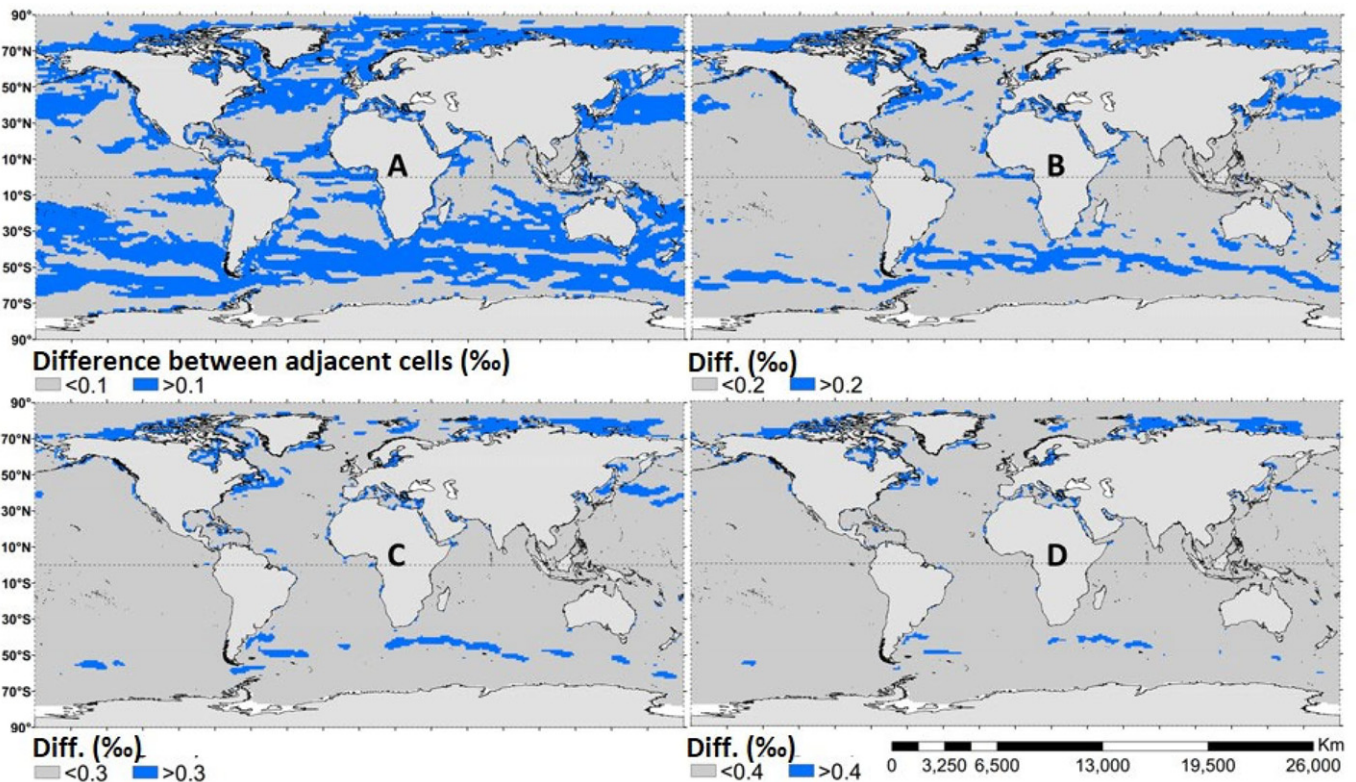


Fig. 3. High-resolution areas (blue) at four potential within-area error levels, represented as maximum difference between adjacent cells (‰). These areas will be able to identify $\delta^{18}\text{O}_{\text{calcite}}$ origin to $\leq 1^\circ \times 1^\circ$ if within-area variation is less than the indicated value. I.e. if difference in barnacle isotopes between adjacent cells is greater than the variation within a cell, then geographic resolution will be $\leq 1^\circ \times 1^\circ$. A - 0.1‰; B - 0.2‰; C - 0.3‰; D - 0.4‰.

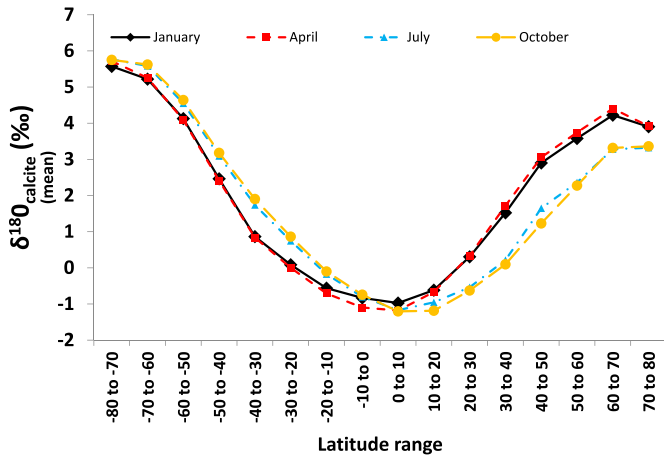


Fig. 4. Calculated $\delta^{18}\text{O}_{\text{calcite}}$ values within 10° latitude bands for four periods throughout 2015.

hemisphere are the most stable year-round, with temperature-driven shifts in $\delta^{18}\text{O}_{\text{calcite}}$ only accounting for a maximum difference between periods of $0.20 \pm 0.14\text{‰}$ (Fig. 4). These shifts in isotope values over time (but in the same place) suggest a strong need to incorporate, as precisely as possible, accurate isotope sample ages into analyses that infer origin or movement of hosts from barnacle shell isotopes. For barnacles, this relies on accurate estimation of growth rates, and acknowledgement of uncertainties in growth rates in the calculation of sample ages. Failure to account for sample age is likely to lead to incorrect assignments of origin, especially where seasonal differences are large (e.g. temperate regions).

3.4. Case studies: host migrations through high versus low resolution areas

Our case studies demonstrated hypothetical application of barnacle isotope technique to real animal migration pathways. Both the leatherback turtle (approx. 6300 km, 8 months) and humpback whale (approx. 4700 km, 7 months) undertook extensive oceanic migrations in a roughly north-south direction (Fig. 5). The leatherback traveled through an area of minimal change in $\delta^{18}\text{O}_{\text{calcite}}$ in the north Atlantic, while the humpback traveled through an area of rapid change in the south Atlantic (see Figs. 2, 5). These water body characteristics were reflected in the $\delta^{18}\text{O}_{\text{calcite}}$ profiles of each theoretical commensal barnacle, where the leatherback (3.4‰) exhibited a considerably lower range in $\delta^{18}\text{O}_{\text{calcite}}$ than the humpback (5.5‰), despite the leatherback traveling further (Fig. 5).

Notable features are evident within the $\delta^{18}\text{O}_{\text{calcite}}$ profile of each theoretical commensal barnacle where $\delta^{18}\text{O}_{\text{calcite}}$ ratios remain stable each time the host remained within the same region for a length of time. For example, the leatherback turtle remained in the same region between points 2 and 3 for approx. 2.5 months (see loop at this time in Fig. 5A). Our estimation predicts a change in $\delta^{18}\text{O}_{\text{calcite}}$ of only 0.01‰ between these points. Similarly, the humpback whale remained in the breeding area (along the coast of Brazil, points 1 and 2) for just over two months, resulting in a change in $\delta^{18}\text{O}_{\text{calcite}}$ of only 0.04‰ over this time.

It is possible to identify the migration period of both animals from their $\delta^{18}\text{O}_{\text{calcite}}$ ratios; however, the humpback whale's migration period is considerably more obvious (Fig. 5B, C). Between points 2 and 7, the humpback traveled approx. 3800 km in 44 days, with $\delta^{18}\text{O}_{\text{calcite}}$ ratios shifting 4.15‰ over this period (Fig. 5). The rate-of-change in the humpback whale's profile reduces dramatically as it slows migration upon arriving at the feeding ground with change between points 7 to 11 being

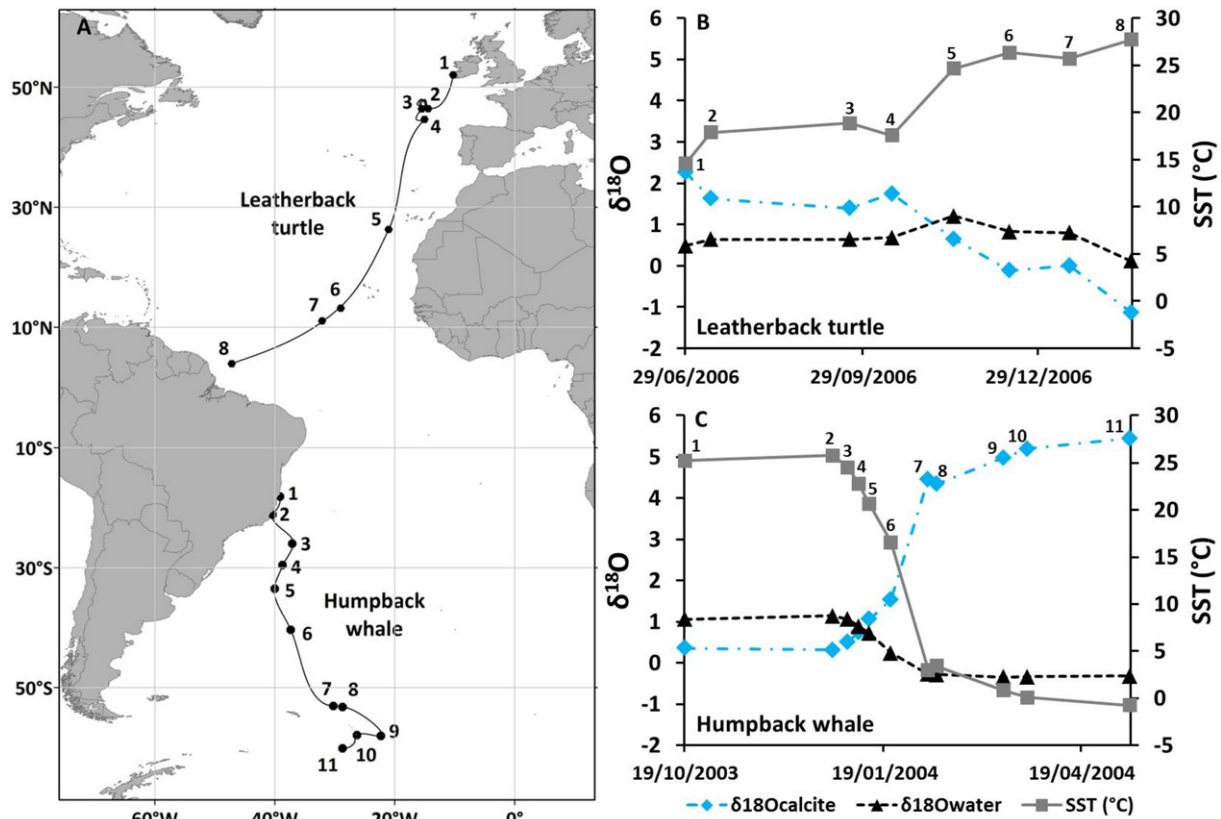


Fig. 5. (A) Migration pathways for a male leatherback turtle (ID T2) in the north Atlantic satellite tagged in 2006 (from Doyle et al., 2008) and a female humpback whale (ID 24642) in the south Atlantic, satellite tagged in 2003 (from Zerbini et al., 2011). Profiles of sea surface temperature (SST), seawater oxygen isotope ratio ($\delta^{18}\text{O}_{\text{water}}$), and the theoretical oxygen isotope ratio expected in barnacle shell layers ($\delta^{18}\text{O}_{\text{calcite}}$) for the leatherback turtle (B) and humpback whale (C). Numbers in each graph on right represent the corresponding numbered locations (and times) for each animal in A.

0.99‰ over 93 days. In this simulation, the leatherback did not remain in the breeding area (Ireland) for any length of time, thus we do not see this reflected in the profile. It spent the entire time traveling, apart from the period between points 2 & 3 that has already been discussed. All other points (especially between 4 and 8) display a shift in $\delta^{18}\text{O}_{\text{calcite}}$ consistent with the expectation that the animal is continuously moving (Fig. 5B).

We further assessed the sensitivity of these technique to temporal shifts in salinity by assessing differences in predicted isotope values using the long-term static $\delta^{18}\text{O}_{\text{calcite}}$ values (LeGrande and Schmidt, 2006) with values predicted from observed salinity across the full migration of the leatherback turtle (Doyle et al., 2008) in our case study. In these assessments the total variation in sea surface salinity (SSS) was 1.5‰ (range: 35.49 to 36.98‰), with a mean of 35.93‰ ($\pm 0.46\%$ S.D.) (Fig. 6). Incorporating these observed SSS values into the leatherback turtle migration profile shows that temporal variation in SSS in the north Atlantic drives some (although minimal) difference in expected barnacle isotope ratios for the north Atlantic through during the 2006/07 migration of this turtle (Fig. 6). In the extra-tropical region (leatherback points 1–4; Fig. 5A) incorporating salinity returned almost identical predictions to the model using LeGrande and Schmidt (2006) $\delta^{18}\text{O}_{\text{water}}$ values. However, once the animal moved into the tropics (early November 2006) the $\delta^{18}\text{O}_{\text{water}}$ values began to deviate from the LeGrande and Schmidt (2006) values, resulting in empirical differences in the $\delta^{18}\text{O}_{\text{calcite}}$ predictions from the two methods (leatherback points 5–8 in Fig. 5A), but likely not significantly given the error in measurement accuracy in previous work (e.g. Pearson et al., 2019). For example, expected differences in $\delta^{18}\text{O}_{\text{calcite}}$ across all eight sample points were $0.17 \pm 0.06\%$ (mean ± 1 S.E.), which within the 0.18‰ margin of error reported by Pearson et al. (2019).

This example illustrates that temporal shifts in ocean salinity can induce an effect on both $\delta^{18}\text{O}_{\text{water}}$ and $\delta^{18}\text{O}_{\text{calcite}}$ but that the effect is likely negligible in affecting location assignments. That said, the effect was more prominent in the tropics during the period examined in our leatherback turtle case study, which aligns with expectations given the variability of tropical rainfall regimes that cause sea surface salinity changes (Trenberth, 2011), suggesting that similar sensitivity analyses should be undertaken if applying these techniques in areas with larger salinity ranges than investigated here.

4. Conclusions, limitations and future research

We show here that oxygen isotopes from barnacle shells could be used to understand the origin or movement of host animals or objects through oceanic waters. Future applications will require assessment of

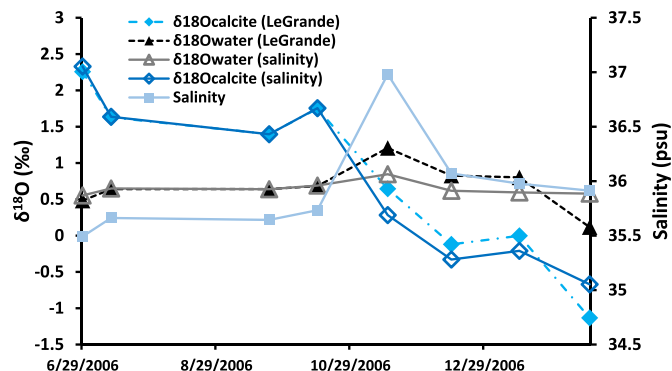


Fig. 6. Predicted $\delta^{18}\text{O}$ profiles (from SST and salinity/ $\delta^{18}\text{O}_{\text{water}}$) throughout leatherback turtle migration (Doyle et al., 2008) showing expected effect of salinity on $\delta^{18}\text{O}_{\text{water}}$ and $\delta^{18}\text{O}_{\text{calcite}}$. LeGrande profiles as in Fig. 5, using $\delta^{18}\text{O}_{\text{water}}$ values directly from the LeGrande and Schmidt (2006) dataset, with no temporal variation in salinity. Salinity profiles using $\delta^{18}\text{O}_{\text{water}}$ values calculated using global tropical and north Atlantic extra-tropical equations from Schmidt et al. (2007), using observed sea surface salinity (SSS) values (NCEP GODAS; Behringer et al., 1998).

the growth rates of their target barnacle species prior to attempting to identify an origin of the material. This will enable a time-of-formation to be applied to each sample, greatly improving the ability to place hosts in time and space. Further understanding of the spatio-temporal variation in temperature and $\delta^{18}\text{O}_{\text{water}}$ in the focus region is also vital for this application. In many cases, this will require development of a regional model that describes the relationship between salinity and $\delta^{18}\text{O}_{\text{water}}$, allowing for conversion to $\delta^{18}\text{O}_{\text{water}}$ from the more readily available salinity data.

Further, in our case studies, we used surface temperature and $\delta^{18}\text{O}_{\text{water}}$ values only when estimating barnacle isotope values. Both of our case study species are known to perform relatively deep dives, which is likely to expose barnacles to lower temperatures than at the surface and, thus, alter observed barnacle isotope values. Incorporating the effect of these dives requires further research that is beyond the scope of this study. However, the purpose of these case studies was to demonstrate how barnacle shell isotopes can be estimated for specific times and locations and allow inferences of migration pathways by matching estimated values to those measured from shell samples. We demonstrate that this is possible for animals and objects at the surface, but suggest that future work aiming to apply these techniques to deep-diving animals will need to factor these behaviours into calculations. Additionally, there is an inherent level of complexity in re-creating movement pathways from barnacle samples that we have not attempted here. Each barnacle sample is likely to provide a coarse spatial area of potential origin, making it difficult to align consecutive samples to recreate a high-resolution movement pathway in some cases. Sakamoto et al. (2019), however, recently demonstrated an effective method of recreating pathways of fish movement from similar data (otolith isotopes) using simulation modelling. We suggest that this could be an effective approach for barnacle isotopes as well.

Despite these limitations, we show that the resolution to which a barnacle host can be placed in time and space will vary globally, with mid-high latitudes offering consistently higher resolution than in the tropics. There is likely to be more temperature-driven variation in mid-high latitudes throughout the year. However, it appears that greater variability in salinity may have a larger effect on $\delta^{18}\text{O}_{\text{calcite}}$ in the tropics than at mid-high latitudes. We note that coastal regions are not included in these data and, due to more rapid changes in salinity over shorter distances (thus also $\delta^{18}\text{O}_{\text{water}}$) in coastal systems, achievable resolution may be considerably better in these areas if robust salinity data are available along with regional conversion equations to $\delta^{18}\text{O}_{\text{water}}$.

With thoughtful application, we expect that SIA of the shells of hitchhiking barnacles could be used to identify the migration pathway or attachment point (i.e. origin) of any manner of marine based host. This method can be applied to ecological studies of migratory marine fauna or anthropocentric studies to understand the origin of human debris (e.g. plastic pollution or transport wreckage). A vital next step in validating these techniques would be to test these methods by recreating the migration pathways of a barnacle host alongside actual records of spatio-temporal dispersal, perhaps with concurrent satellite telemetry.

Declaration of competing interest

The authors declare no conflict of interest.

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