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# Sensitivity of $\delta^{13}C$ values of seabird tissues to combined spatial, temporal and ecological drivers: A simulation approach

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ABSTRACT

Biologging technologies have revolutionised our understanding of the foraging ecology and life history traits of marine predators, allowing for high resolution information about location, and in some cases, foraging behaviour of wild animals. At the same time, stable isotope ecologists have independently developed methods to infer location and foraging ecology (trophic geography). To date, relatively few studies have combined these two approaches, despite the potential wealth of complementary information.

In marine systems, spatial and trophic information are coded in the isotopic composition of carbon and nitrogen in animal tissues, but interpretation of isotope values is limited by both the lack of reference maps (isoscapes) needed to relate the isotopic composition of an animal's tissues to a location, and the relatively large number of variables that could influence tissue isotope compositions. Simulation modelling can help to interpret measured tissue isotope compositions of migratory animals in the context of spatio-temporally dynamic isotopic baselines.

Here, we couple individual-based movement models with global marine isotope models to explore the sensitivity of tissue $\delta^{13}C$ values to a range of extrinsic (environmental) and intrinsic (behavioural, physiological) drivers. We use *in-silico* experiments to simulate isotopic compositions expected for birds exhibiting different movement and foraging behaviours and compare these simulated data to isotopic data recovered from biologger-equipped female northern giant petrels *Macronectes halli* incubating eggs on sub-Antarctic Marion Island.

Our simulations suggest that in the studied system, time is a strong driver of isotopic variance. Accordingly, this implies that caution should be used when comparing $\delta^{13}C$ values of marine predators' tissues between seasons and years.

We show how an *in-silico* experimental approach can be used to explore the sensitivity of animal tissue isotopic compositions to complex and often interacting drivers. Appreciation of the principle drivers behind isotopic variance specific to a given animal and geographic context can enhance inferences of geolocation as well as foraging behaviour, and can be applied to any mobile predator. Models can be relativey simple or complex and multi-layered depending on the level of ecological realism required. Future investigations can use other isoscapes, including terrestrial isoscapes and more complex or different movement models.

## 1. Introduction

Stable isotope ecology has become a common and powerful tool for retrospective geolocation of animals in both marine (e.g. Graham et al., 2010) and terrestrial systems (e.g. West et al., 2014). Approximate foraging locations of consumers can be reconstructed by linking the stable isotope compositions of their tissues to spatial models of the isotopic composition of organisms at the base of food webs. In marine

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systems, animal movement is commonly inferred by linking the ratios of the stable isotopes of carbon ($^{13}C/^{12}C$; $\delta^{13}C$) of predator tissues to latitudinal gradients in $\delta^{13}C$ values of phytoplankton ($\delta^{13}C_{plk}$; Jaeger et al., 2010; MacKenzie et al., 2011; Trueman et al., 2012; Bird et al., 2018; Trueman and St John Glew, 2018).

The accuracy and precision associated with isotope-based reconstruction of animal movements depends on the quality of the reference spatial models of the underlying isotopic gradients, commonly termed isoscapes. Isoscape models of $\delta^{13}C_{plk}$ are typically constructed by spatial interpolation between empirical reference data sampled from known locations (Francois et al., 1993; Quillfeldt and Masello, 2013; MacKenzie et al., 2014; Trueman et al., 2016). Interpolation models may also include predictive statistical relationships between widely measured environmental variables and reference isotope data (Wunder, 2010; MacKenzie et al., 2014; West et al., 2014) or isotopic values of predator tissue for which movements were known (Cherel and Hobson, 2007; Jaeger et al., 2010). The uncertainty associated with isoscape models clearly increases with decreasing spatial coverage of reference samples. In marine systems, phytoplankton are at the base of food webs. They are small-celled organisms with rapid growth which means that their isotopic compositions reflect local and short-term variations in oceanic conditions (Graham et al., 2010; Magozzi et al., 2017). Therefore, static maps of $\delta^{13}C_{plk}$ across the global oceans capture large scale latitudinal patterns of isotopic variability but may be relatively poor predictors of isotopic compositions at any particular place and time. This reduces the confidence that can be placed in isotope-based inferences about animal movements. In the open ocean, gathering reference samples from regularly spaced and spatially extensive locations is particularly challenging; consequently, relatively few ocean basin-scale isoscape models have been created, and no temporally-explicit sample-based isoscapes have been created for oceanic ecosystems (Trueman and St John Glew, 2018).

As isotope-based geolocation is primarily concerned with carbon and nitrogen in marine systems, interpretation of the spatial signal is inherently intertwined with variation in diet and physiological isotopic transformations through the food web between primary production and consumer tissues. Consequently, the isotopic composition of a mobile consumer's tissue depends on a number of intrinsic (behavioural and physiological) and extrinsic (environmental) variables:

(1) spatio-temporal variations of stable isotope compositions of phytoplankton at the base of the food web,
(2) location(s) of consumers over the timescale of isotopic incorporation,
(3) isotopic averaging and physiological fractionation through intermediate trophic levels, and
(4) isotopic turnover rates and physiological transformations in the consumer.

The isotopic expression associated with the variables expressed above is usually incompletely known, and interpreting stable isotope compositions of mobile marine consumers is challenging. Simulation modelling provides a framework to identify those variables likely to impact the isotopic compositions of consumer tissues, given a context-specific interaction between the scale and nature of baseline isotopic variability, foraging range, phsyiology, and food web interactions.

Magozzi et al. (2017) developed a process-based carbon isotope model to predict the spatio-temporal distribution of $\delta^{13}C$ values in phytoplanton ($\delta^{13}C_{plk}$) across the global ocean at one degree spatial and monthly temporal resolution (Fig. 1). The model uses an ocean general circulation model of intermediate complexity, averaged over 10 years (2001 − 2010) to minimize the effect of interannual variability, combined with general assumptions related to carbon isotope fractionation to produce monthly isoscapes. It provides a spatio-temporal framework for *in-silico* modelling and experimentation to better understand the movement of marine predators using intrinsic stable isotope markers (Bird et al., 2018; St John Glew et al., 2018; Trueman and St John Glew, 2018).

Here, we explore the likely sensitivity of $\delta^{13}C$ values of marine predator tissues to a suite of environmental and ecological variables using *in-silico* experiments. We simulate the at-sea movement and distribution of a land-breeding marine predator, by building a simple agent-based movement model. The agent based model outputs time and location, which are then integrated with the temporally-specific isoscapes produced by Magozzi et al. (2017) to simulate expected $\delta^{13}C$ values in the predator's tissues. We then explore the senstitity of simulated tissue $\delta^{13}C$ values to intrinsic and extrinsic drivers by systematically varing terms in the agent based model or in the isoscape model.

Simulation results are compared to isotopic data measured from individual consumers equipped with global positioning system (GPS) devices. We investigate 1) the effect of the choice of reference isoscape used on inference of predator $\delta^{13}C$ values, and 2) the effect of predator behavioural changes on their $\delta^{13}C$ compositions. We use female northern giant petrels *Macronectes halli* (NGP) incubating eggs at sub-Antarctic Marion Island as a model species, but note that the approach outlined here could be adapted to explore the potential drivers behind isotopic variability for any mobile marine consumer principally by modifying the agent based model rules to approximate foraging behaviour and isotopic integration rates for the study species and tissue type.

## 2. Materials and methods

### 2.1. Study site and species

The Prince Edward Archipelago is made up of the larger Marion Island (240 $km^2$) and Prince Edward Island (45 $km^2$) and provides critical breeding and moulting habitat for approximately 5 million seabirds and seals (Ryan and Bester, 2008). It is located in the Indian sector of the Southern Ocean within the Polar Frontal Zone, between the sub-Antarctic front (SAF) in the north and Antarctic polar front (APF) in the south (Ansorge and Lutjeharms, 2002).

On Marion Island there are approximately 400 northern giant petrel (NGP) breeding pairs (Ryan et al., 2009). Eggs are laid in mid-August and are incubated for approximately 60 days (Cooper et al., 2001). Parental duties are evenly distributed between parents (Cooper et al., 2001). Male NGPs are primarily scavengers, feeding on penguin and seal carrion, whereas females tend to rely on marine prey resources – fish, crustaceans and cephalopods (Hunter and Brooke, 1992; Forero et al., 2005).

### 2.2. Data collection

#### 2.2.1. Field work

Field work was conducted along the south-east coast of Marion Island (46°54′S; 37°45′E) during September and October 2015 and 2016. Global positioning system loggers (CatLog-S GPS loggers, Perthold Engineering LLC USA, 50 × 22 × 8 mm, 8 g) covered in heat shrink tubing for water-proofing were deployed on 20 female NGPs (2015: $n$ = 6 and 2016: $n$ = 14). Loggers were programmed to record locations hourly. To facilitate retrieval of devices, loggers were deployed during late incubation.

At retrieval of GPS data loggers after one foraging trip, ~1 ml of blood was collected from the tarsal vein using a heparinised 25 gauge needle. Approximately half of the blood sample was stored directly in 70% ethanol and frozen until preparation for further analysis. The remainder of the blood was centrifuged within 3–4 h after collection, separated into red blood cells and plasma, stored in 70% ethanol and frozen until preparation for stable isotope analysis. Seventy percent ethanol has been shown to be an effective method of preserving blood without affecting its isotopic composition (Hobson et al., 1997).

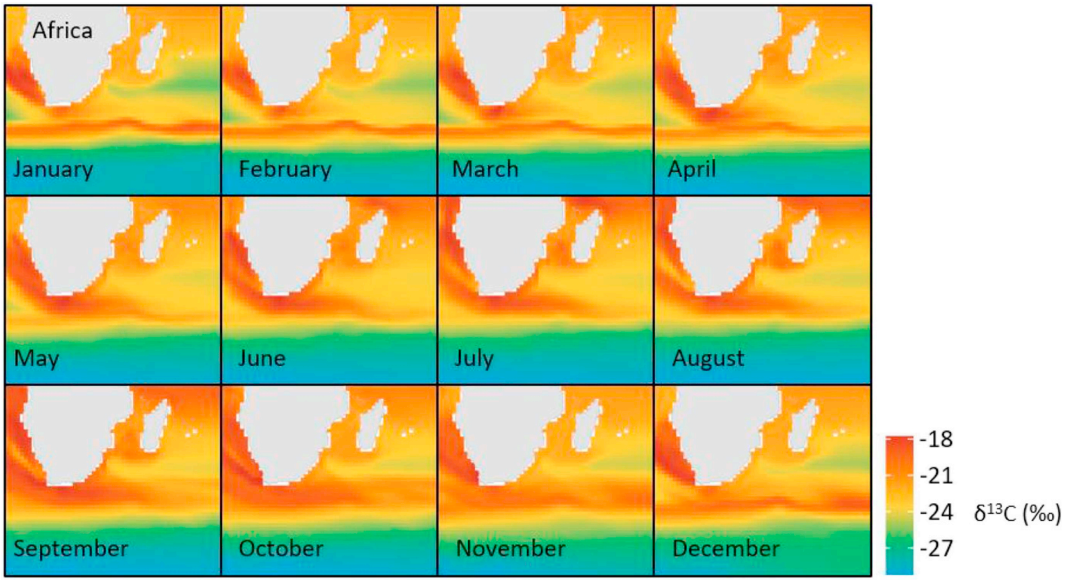


**Fig. 1.** Monthly maps of the distribution of $\delta^{13}C$ of phytoplankton resulting from a processed-based carbon model produced by Magozzi et al. (2017).

*2.2.2. GPS analyses*

GPS locations indicating unrealistic movement speeds were identified by plotting the speed between consecutive GPS locations and removing those identified as outliers (2 of the total 966 locations). From the filtered data, new positions were linearly interpolated at one hour intervals (R package: adehabitatLT; Calenge, 2006) and the average duration, distance travelled and maximum distance from breeding ground were calculated for each trip.

*2.2.3. Stable isotope analyses*

Plasma was dried at 50 °C for 24–48 h before being powdered. Lipids are depleted in $^{13}C$ (DeNiro and Epstein, 1977); therefore, lipids were removed from plasma samples by immersing powdered plasma in a 2:1 chloroform:methanol solution with a solvent volume three to five times greater than sample volume. Samples were then vortexed for 10 s every 10 min for one hour before being centrifuged for five minutes. The supernatant containing lipids was discarded, and samples dried at 50 °C overnight.

The isotopic compositions of carbon and nitrogen in aliquots (~0.4 mg) of homogenized delipidated plasma samples were determined by combusting samples in a Flash 2000 organic elemental analyser and passing gasses through a Delta V Plus isotope ratio mass spectrometer via a Conflo IV gas control unit (Thermo Scientific, Germany). All samples were processed at the Stable Light Isotope Unit at the University of Cape Town, South Africa. Replicate measurements of internal laboratory standards indicated minimal standard deviations within and among runs (Merck gel: $\delta^{13}C = 0.2‰$, $\delta^{15}N < 0.1‰$; valine: $\delta^{13}C < 0.2‰$, $\delta^{15}N = 0.1‰$; seal bone: $\delta^{13}C < 0.2‰$, $\delta^{15}N < 0.1‰$). All in-house standards were calibrated against International Atomic Energy Agency standards. Carbon is expressed in terms of its value relative to Vienna PeeDee Belemnite.

*2.3. Model framework*

*2.3.1. Stable isotope baseline model*

We used the monthly isotopic prediction surfaces for $\delta^{13}C_{plk}$ produced by Magozzi et al. (2017) as primary inputs for simulation modelling. To account for trophic attenuation of $\delta^{13}C$ values through trophic levels, we produced a new suite of monthly prediction surfaces estimating isotopic compositions of four successive trophic levels by calculating a moving average of each cell of the $\delta^{13}C$ isotopic maps. The initial model predicts $\delta^{13}C$ values in phytoplankton (trophic level 1) at monthly resolution. We developed surfaces for additional time-integration steps by creating a moving average over 2 months (trophic level 2), 4 months (trophic level 3) and 6 months (trophic level 4) successively.

*2.3.2. Environmental baseline*

Sea-surface temperature (°C, 1° resolution) and phytoplankton abundance (mmol $N.m^{-3}$, for combined diatom and non-diatom communities) were extracted at monthly intervals from the same NEMO–MEDUSA simulations used to estimate $\delta^{13}C_{plk}$ values (Yool et al., 2013; Magozzi et al., 2017). Water depth (m, 1° resolution) was extracted from the General Bathymetric Chart of the Oceans (GEBCO) global bathymetry dataset (http://www.gebco.net/data_and_products/gridded_bathymetry_data/).

*2.3.3. Agent-based northern giant petrel movement model*

We draw on an agent-based model (ABM) to provide time-specific location data for integration with isoscape models. It is important to note that the ABM is not developed as a tool to infer movement behaviour. In principle, an ABM could be developed with relatively few movement rules and large numbers of repeat simulations. Alternatively a highly constrained ABM could be developed ideally yielding few unrealistic movement or position estimates. For this example we develop a relatively basic ABM informed from data logging GPS data to reduce computational time associated with running very large combinations of unlikely parameter fields.

The movements of incubating female NGPs were simulated using a simple agent-based model (Fig. 2). In the model, daily direction and extent of movement are drawn from probability distributions influenced by foraging trip duration, daily step distance, sea surface temperature, water depth and phytoplankton concentration (as a proxy for zooplankton food availability). Although the model is limited to using these variables to simulate the movement of NGPs, we feel they are adequate as Reisinger et al. (unpubl. data) showed that sea surface temperature, chlorophyll-a concentration and depth are important drivers of these birds' movement. It is important to note that the aim of the model is simply to provide movement tracks that broadly replicate known movements and not as an exploration of potential ecological drivers of movement. Movement rules were established based on known movement parameters:

(i) Daily step distance. The GPS tracks ($n = 20$) of incubating female

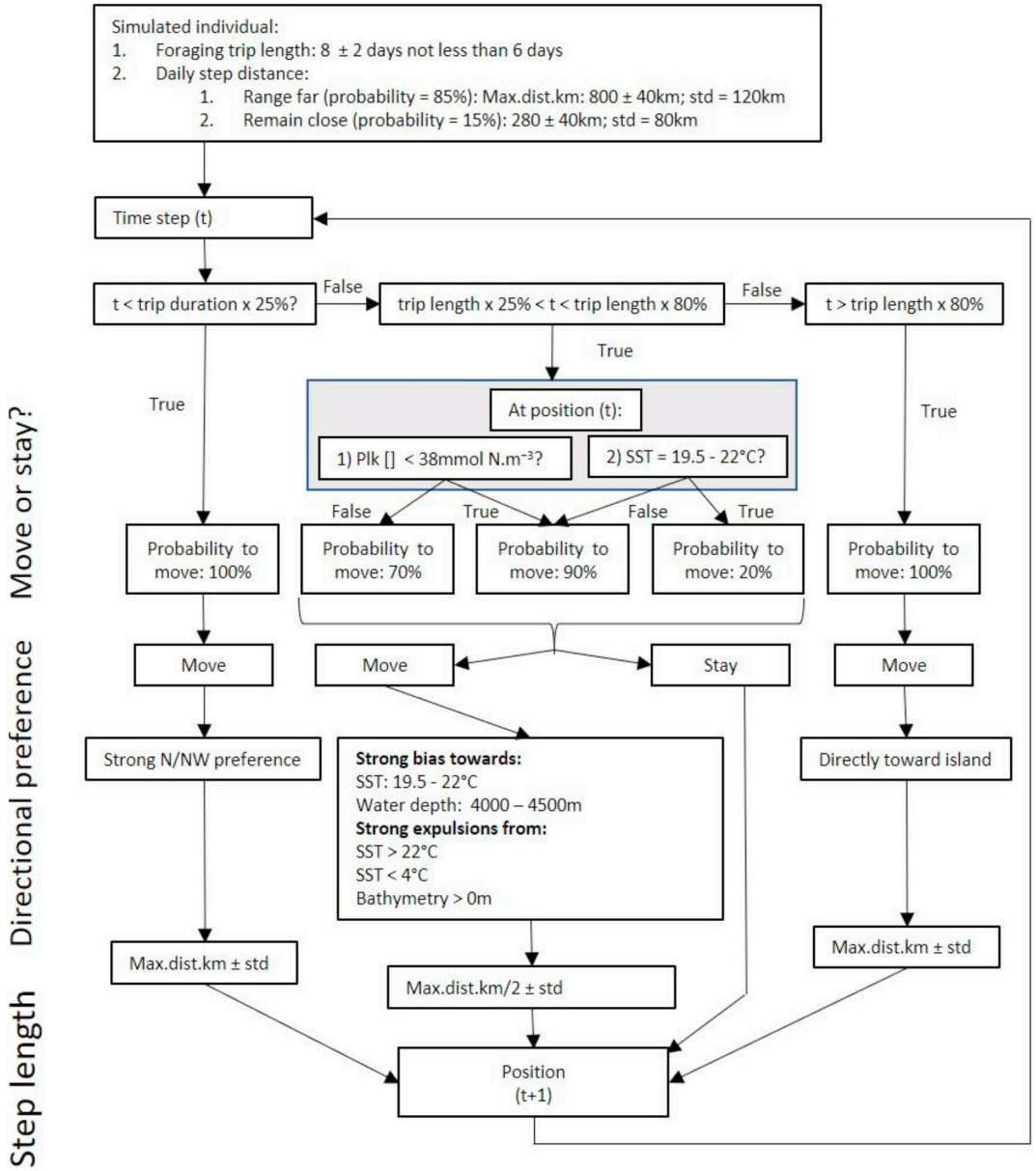


**Fig. 2.** The computational process used to simulate the movement of female incubating northern giant petrels (NGP) using an agent-based movement model. In the model, daily likelihoods, directions and extents of movement are drawn from probability distributions influenced by foraging trip duration, daily step distance, sea surface temperature (SST), water depth and phytoplankton concentration Plk[]. At the initiation of the model the simulated NGP is assigned a foraging trip duration, a decision to perform long or short trips and maximum daily step distance (Max.dist.km). During each time step, each simulated NGP may move to a new location or decide to stay where is it depending on how far it is into its foraging trip and its surroundings. The model was run for 60 days (approximate length of NGP incubation) starting on 15 August (approximate laying initiation date for giant petrels).

NGPs revealed the birds performed two types of trips: (1) a smaller maximum daily step distance ($n = 4$; 331.01 ± 115.02 km per day) remaining close to the island or (2) a greater daily step distance ($n = 16$; 965.01 ± 112.17 km per day) travelling further afield from the island. Therefore, within the movement model, the modelled NGPs could choose to perform either type of trip, with the probability of choosing to remain close to the island set as 20%.

(ii) Foraging trip length. Mean foraging trip duration, based on GPS tracks, was 8 ± 2 days and this was then used as foraging trip duration of the modelled NGPs. Furthermore, when either leaving for or returning from a foraging trip, NGPs displayed more directed movement either towards favoured environmental conditions or towards the island, respectively, compared to during the middle of the foraging trip.

(iii) Food availability. Phytoplankton concentration was included as a proxy for food availability. If phytoplankton concentrations were above 38 mmol $N.m^{-3}$, the mean probability of remaining in that cell was increased by 30%.

(iv) Sea surface temperature. Simulated NGPs were more likely to move towards warmer temperatures up to a maximum of 22.0 °C. If sea surface temperatures were < 19.5 or > 22.0 °C (temperatures which are typically associated with the Agulhas Current, Lutjeharms and Valentine, 1984), the mean probability of moving away from the current cell was increased to 80%.

(v) Water depth. Female NGPs preferred open water to shelf regions and were coded to prefer foraging in water depths between 4000 and 4500 m and were less likely to move towards waters outside this range.

Modelled birds left for their first foraging trip on 15 August, the

mean egg laying date (Cooper et al., 2001), and simulations lasted for approximately 60 days, the approximate incubation time of an NGP (Cooper et al., 2001). Birds alternated between incubation shifts (i.e. remaining on the nest to incubate their egg while their partner departed on a foraging trip) and foraging trips.

R code for the agent-based movement model together with underlying isoscape and environment raster files will be available on GitHub on acceptance.

Values within this section (2.3.3) are given as mean ± standard deviation.

#### 2.3.4. Simulating blood $\delta^{13}C$ tissue values

For each location produced during a movement simulation model, the $\delta^{13}C$ value reflecting $\delta^{13}C_{plk}$ values integrated as a moving average across the previous 6 months was sampled, simulating potential temporal averaging across four trophic levels. The blood plasma $\delta^{13}C$ values of modelled birds returning from a foraging trip were calculated by firstly weighting $\delta^{13}C$ values by the relative abundance of food at that location (inferred from model phytoplankton concentrations). While fasting, the $\delta^{13}C$ values of animal tissue may decrease as the animal may incorporate $^{13}C$ depleted lipids into proteins to meet energy demands (Cherel et al., 2005). To simulate the impact of fasting during incubation on blood $\delta^{13}C$ values, $\delta^{13}C$ values assimilated during days associated with fasting were down-weighted by multiplying by 0.1. Attenuation of prey $\delta^{13}C$ values into bird tissues was simulated using a moving average of 7 days, the approximate turnover rate of plasma (Hobson and Clark, 1992). The $\delta^{13}C$ blood value on the day the bird returned to the island was taken to represent that foraging trip.

### 2.4. Testing sensitivity of blood $\delta^{13}C$ values with in-silico experiments

#### 2.4.1. The effect of temporal variation in the reference isoscape on predator $\delta^{13}C$ tissue values

Previously, retrospective geolocations of marine predators have been made from temporally-static isoscapes which represent single trophic levels (e.g. Francois et al., 1993; Cherel and Hobson, 2007). Here, we investigated the potential influence of three components of temporal variability in baseline isotopes on consumer tissue carbon isotope values. We tested:

i) Temporal attenuation in stable isotope compositions with increasing trophic level: For each position of a simulated NGP resulting from the original movement model $\delta^{13}C$ values were extracted from the suite of maps using moving averages of 1 month, 2 months and 4 months (approximating trophic attenuation over 1, 2 and 3 trophic levels *See Stable isotope baseline model*).
ii) Temporal resolution in baseline isoscapes: To identify the difference expected when estimating isotopic compositions based on a single static isoscape compared to temporally varying reference isoscapes, a single biomass-weighted annual average isoscape was calculated by averaging all the monthly isoscapes and weighting relative monthly values by the total biomass in each month.
iii) Seasonal mis-matching: To investigate whether using a single temporal isoscape, but from a different season, would have an influence on the $\delta^{13}C$ plasma values of NGPs, the original movement model was initiated 4 months before and after the original starting date (i.e. 15 April and 15 December).

#### 2.4.2. The effect of predator behavioural changes on their isotope composition

During years of variable prey availability, some species of seabirds have shown plasticity in the date they initiate breeding (e.g. Dobson et al., 2017) and foraging effort (e.g. Green et al., 2015; Whitehead et al., 2017). By making the following modifications to the agent-based movement model, we investigated whether behavioural changes such as these would influence the $\delta^{13}C$ composition of NGPs' plasma:

i) Laying initiation date: The date the female NGPs initiated breeding was changed by 15 days before and after mean date of laying (15 August; Cooper et al., 2001) at increments of 5 days.
ii) Foraging trip duration: The mean foraging trip duration of NGPs (8 ± 2 days) was increased to 14 days at 2 day increments.
iii) Daily step length: The daily step length was increased and decreased by 150 km at increments of 50 km.

### 2.5. Statistical analysis

Kernel density distributions (Worton, 1989) were used to visualize the distribution of time spent at sea of real and modelled NGPs using the *adehabitatHR* package in R (Calenge, 2006). The most appropriate smoothing factor was chosen using the ad hoc method (Worton, 1989) and grid size was set at 1°, matching the resolution of the underlying environmental maps. The 50% and 95% kernel contours were calculated and plotted as they are thought to represent the home range and core areas of use by an animal (Fieberg and Kochanny, 2005).

Distributions of most of the $\delta^{13}C$ plasma values of simulated birds returned by the agent-based movement models, and their modifications were negatively skewed, reflecting the variable use of sub-polar and polar regions with relatively low model-predicted $\delta^{13}C$ values. To compare the distributions of $\delta^{13}C$ plasma values between model runs we used Bayesian estimation for two groups with a skewed-normal distribution family (R package: brms: Bürkner, 2017) to estimate the mean, standard deviation and skewness of $\delta^{13}C$ plasma values.

## 3. Results

The agent-based movement model successfully reproduced broad foraging distribution and movement path characteristics of female NGP's (Fig. 3 a, b). Simulations correctly identified the two core areas where the NGPs spent time while at sea, one closer to Marion Island and the other along the coast of southern Africa. The movement model based on 100 simulated individuals resulted in 356 simulated blood plasma $\delta^{13}C$ values.

Measured $\delta^{13}C$ values of NGP plasma (−20.0 ± 1.1‰ (mean ± SD), $n = 15$, Fig. 4a) were higher than simulated $\delta^{13}C$ plasma values (−22.4 ± 1.4‰ (mean ± SD); Fig. 4b) resulting from the original movement model. As simulated NGPs accumulated plankton $\delta^{13}C$ values, our model did not incorporate the process of $\delta^{13}C$ discrimination through the food web (bioaccumulation of carbon's heavier isotope ($^{13}C$) opposed to its lighter isotope ($^{12}C$); Newsome et al., 2010). Our model outputs therefore simulate the senstitivy of NGP plasma proteins to expected temporal and spatial variations in the isotopic baseline in the absence of additional isotopic variation related to diet composition.

### 3.1. The effect of temporal variation in the reference isoscape on predator $\delta^{13}C$ tissue values

The degree of temporal averaging between plankton and predator tissues influenced simulated blood plasma $\delta^{13}C$ compositions. Compared to our control simulation using temporal averaging of 6 months (simulated for trophic level 4), $\delta^{13}C$ plasma values in NGPs assimilating $\delta^{13}C$ values from isoscapes with 1, 2 and 4 month moving averages were lower (Table 1, Fig. 4). The resulting plasma $\delta^{13}C$ plasma values using temporal averaging windows of two, four and six all were more negatively skewed and had a greater range (Table 1, Fig. 4). However, a moving average of 2 months (theoretical trophic level of 2) resulted in $\delta^{13}C$ plasma values with a similar mean value.

The original model simulated isoscape conditions for August, changing the reference isoscape for a simluated isoscape reflecting conditions either 4 months before (April) or after (December) had a large effect on the estimated $\delta^{13}C$ plasma values (Table 1; Fig. 4). Birds initiating their trips in April had higher mean $\delta^{13}C$ plasma values and

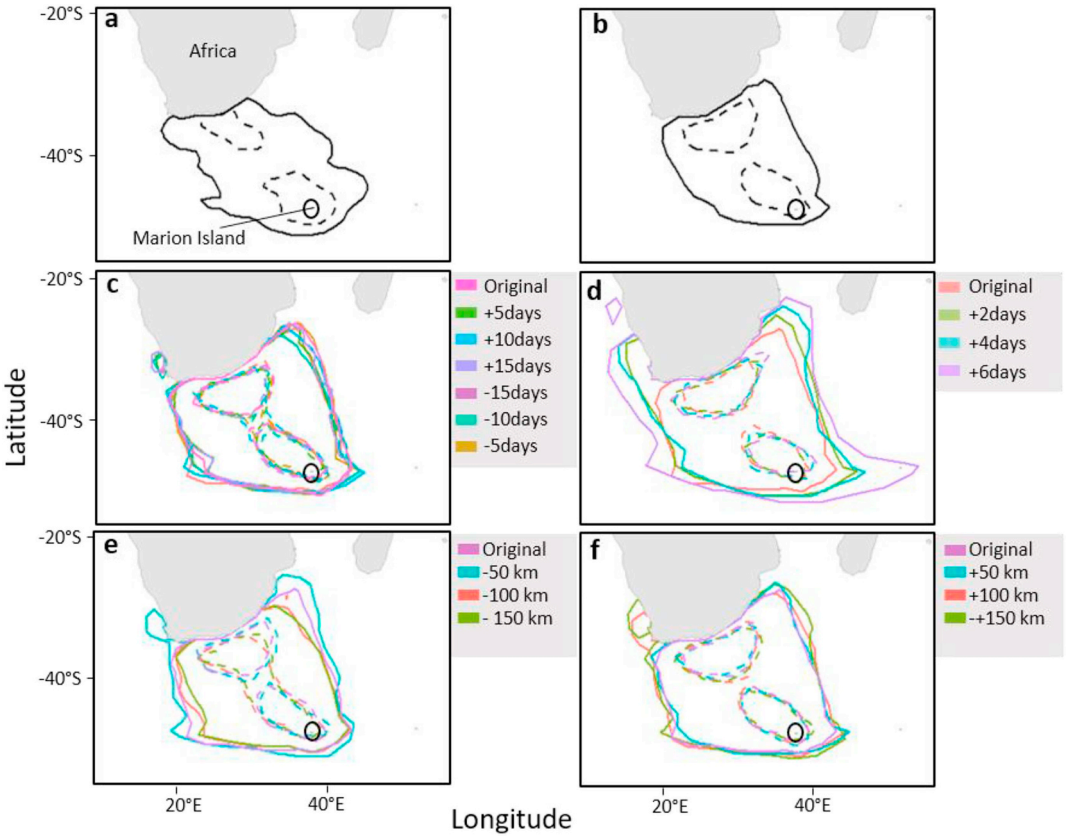


**Fig. 3.** 50% and 90% kernel density based on a) GPS tracks of incubating female northern giant petrels at Marion Island 2015 and 2016; b) tracks resulting from an agent-based movement model based on movement parameters from GPS tracks in a); c) – f) modifications of the original agent-based movement to test for the sensitivity of $\delta^{13}C$ values of NGP plasma to different stimuli. Modifications are: c) the date the simulated birds initiated breeding was changed to 15, 10, 5 days before and 5, 10, 15 days after the average laying day d) foraging trip length was increased by 2, 4 and 6 days e) the daily step length of simulated birds was decreased by 50 km, 100 km and 150 km and f) the daily step length of simulated birds was increased by 50 km, 100 km and 150 km.

birds initiating their simulations in December had lower $\delta^{13}C$ plasma values. Changing the resolution of the reference isoscape from monthly to yearly did not lead to a significant change in $\delta^{13}C$ plasma values (Table 1, Fig. 4).

### 3.2. The effect of predator behavioural changes on their isotope composition

Some of the modifications in behaviour of the birds within the agent-based movement model led to noticeable changes in resulting $\delta^{13}C$ plasma values (Fig. 4). When modelled birds initiated laying 15 days before and after the average laying date of NGPs, resulting $\delta^{13}C$ plasma values were higher and lower, respectively (Table 1, Fig. 4), even though all simulations lead to almost identical at-sea distributions (Fig. 3c). Increasing the length of a foraging trip by 4 and 6 days led to lower and more negatively skewed plasma $\delta^{13}C$ values (Table1, Fig. 4) which correlated to expansions in the simulated birds at-sea distribution (Fig. 3). Decreasing and increasing the step length of the simulated birds did not result in greatly different $\delta^{13}C$ plasma values (Table 1; Fig. 4) even though there was minor contraction and expansion respectively of at-sea distribution (Fig. 3e; f).

## 4. Discussion

This study introduces a method to perform controlled experiments on the sensitivity of $\delta^{13}C$ tissue values of free ranging marine predators by using *in-silico* models.

Our intention was to generate a platform allowing us to explore the sensitivity of tissue isotope values to separate drivers of isotopic variance which in nature act simultaneously and potentially interactively. We build agent based movement models to generate experimental datapoints reflecting the time and space occupied by our consumer, and isoscape models to simulate the isotopic composition of diet expected at that time and place. The nature of the coupled model system chosen reflects a balance of transparency (i.e. relatively simple models) with realism and computational demands. We argue that for sensitivity testing as described here, generating simple models conditioned on general movement rules is preferable as the trade-off is weighted towards ease of comprehensioon of results. More complex, but realistic model systems may be more appropriate for drawing inference from measured data.

Daily plasma $\delta^{13}C$ values of female NGPs incubating at Marion Island were simulated by mimicking the daily at-sea movement and distribution of these birds using a relatively simple agent-based movement model. Mutations of this movement model allowed us to investigate how the $\delta^{13}C$ value of a marine predator's tissue might respond to variations in foraging behaviour and temporal dynamics of the isotopic baseline and food web. Mutations to the movement model lead to significant variability in the simulated NGP $\delta^{13}C$ plasma values providing evidence to the importance of using temporally accurate isoscapes for retrospective geolocation of marine predators.

### 4.1. The effect of temporal variation in the reference isoscape on predator $\delta^{13}C$ tissue values

While the diet of specific seabird species are generally confined to a relatively narrow range of trophic levels, the proportion of dietary constituents can show substantial temporal and spatial as well as interspecific variability (Quillfeldt and Masello, 2013). Partitioning sources

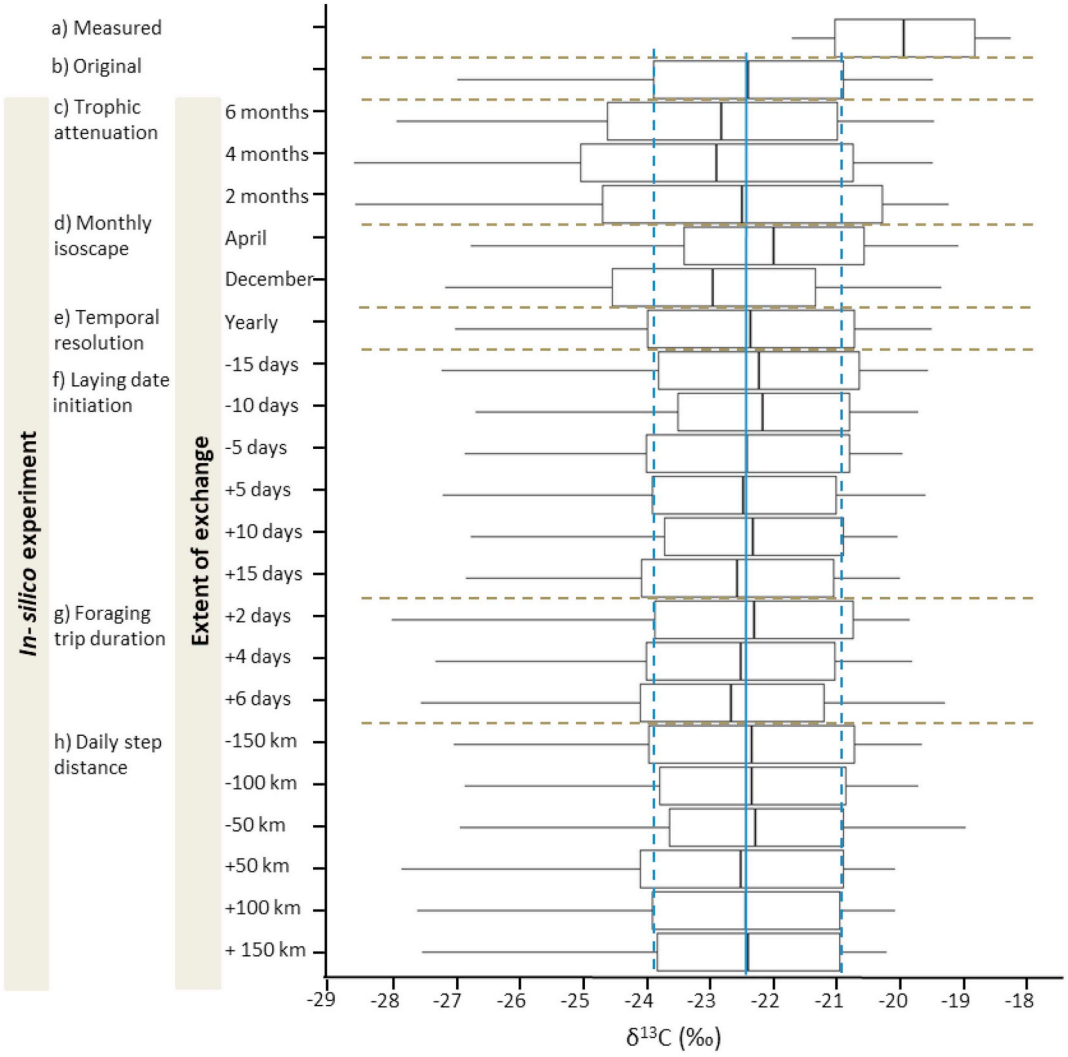


**Fig. 4.** Box plots (range, standard deviation and mean) showing the a) measured $\delta^{13}C$ values of plasma collected from incubating female northern giant petrels at Marion Island in 2015 and 2016 ($n = 15$); b) Simulated $\delta^{13}C$ values of blood plasma resulting from an agent-based movement model based on incubating NGPs which accumulated daily $\delta^{13}C$ values from modified monthly isoscapes produced by Magozzi et al. (2017) which incorporated trophic attenuation over 4 trophic levels (i.e. 6 months). c) – g) are modifications of the original agent-based movement to test for the sensitivity of $\delta^{13}C$ values of NGP plasma to different stimuli. Modifications are: c) simulated birds assimilated $\delta^{13}C$ values from modified isoscapes produced by Magozzi et al. (2017) over trophic levels 1, 2 and 3 (i.e 1, 2, and 4 months), all further *in-silico* experiment assimilated $\delta^{13}C$ values from maps account for attenuation over 4 trophic levels d) the original simulation was initiated in April and December; e) simulated birds assimilated $\delta^{13}C$ values from an isoscape with a temporal resolution of yearly; f) the date the simulated birds initiated breeding was changed to 15, 10, 5 days before and 5, 10, 15 days after the original start date of the movement model; g) foraging trip duration was increased by 1, 4 and 6 days; h) the daily step length of simulated birds was decreased by 150 km, 100 km and 50 km and increased by 50 km 100 km and 150 km. Blue solid and the two dashed lines represent the mean and standard deviations of the $\delta^{13}C$ values which resulted from the original simulation. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

of variance within stable isotope measurements is difficult, simulation modelling allows us to exclude or explicitly define sources of variance and quantify their likely contribution to variance in consumer tissue isotopic compositions. The *in-silico* experiments we performed within this study showed that in the absence of any isotopic variance associated with diet composition, changes in temporal averaging of $\delta^{13}C$ values across trophic levels (i.e. trophic attenuation) can strongly influence the distribution of $\delta^{13}C$ plasma values of seabirds. This is a noteworthy finding, as the temporal relationship between the creation of an isoscape, and temporal attenuation of short term variation through the food web are important considerations for (or limitations to) finer scale retrospective geolocation of marine predators.

By allowing the simulated NGPs in this study to incorporate $\delta^{13}C$ values from isoscapes within a different period of the year (i.e. April and December) and from a different temporal resolution (i.e. yearly), we tested the effect of environmentally realistic levels of temporal variability in baseline isoscapes on the plasma $\delta^{13}C$ value of marine predators. As simulations initiated at different times of the year resulted in differences in both skewness and mean simulated plasma $\delta^{13}C$ values of the birds, we have provided evidence supporting the use of temporally resolved isoscapes for refined retrospective geolocation of marine predators. However, biomass-weighted annual average $\delta^{13}C$ isoscape models provided a reasonable representation of more temporally explicit simulations. This is in agreement with previous studies that successfully used temporally static isoscapes to limit retrospective geolocation of seabirds' foraging areas from $\delta^{13}C$ tissue values within the Southern Ocean to water masses or fronts (e.g. Cherel et al., 2014; Whitehead et al., 2017; Connan et al., 2018).

Many of the alterations made to either the agent-based model or the reference isoscape resulted in changes to the distribution of simulated $\delta^{13}C$ plasma values, but not necessarily to the average value. We suggest that distributions of isotopic compositions of measured animals

**Table 1**

a) Simulated $\delta^{13}C$ plasma values resulting from an agent-based movement model for female northern giant petrels incubating eggs on Marion Island and accumulating daily $\delta^{13}C$ values estimated from an isotope enabled biogeocheimcal model Magozzi et al. (2017) n = number of plasma $\delta^{13}C$ values resulting from 100 simulations of the model. b) – f) are modifications of the original model conditions to test for the sensitivity of $\delta^{13}C$ values of NGP plasma to different stimuli or assumptions. Modifications are: b) simulated birds assimilated $\delta^{13}C$ values from isoscapes with a temporal attenuation reflecting isotopic incorporation over trophic levels 1, 2 and 3 (i.e. 1, 2 and 4 months) c) the original simulation was initiated in either April or December d) simulated birds assimilating $\delta^{13}C$ values from a single biomass-weighted yearly average rather than separate month-specific isoscapes e) the date the simulated birds initiated breeding was changed to 15, 10, 5 days before and 5, 10, 15 days after the original start date of the movement model; f) foraging trip duration was increased by 2, 4 and 6 days; g) the daily step length of simulated birds was decreased by 150 km, 100 km and 50 km and increased by 50 km, 100 km and 150 km. The effect of model conditions on the distribution of simulated $\delta^{13}C$ plasma values was investigated using Bayesian estimation for two groups and a skewed-normal model distribution. Resulting posterior estimates of the population mean, standard deviation (SD) and skewness are given with their resulting upper and lower 95% credible intervals (CI).

| *In-silico* experiment | Extent of Change | Temporal resolution of isoscape: | Isoscape representing attenuation over: | n | Mean (CI) | SD (CI) | Skewness (CI) |
|---|---|---|---|---|---|---|---|
| a) Original model | | Monthly | 4 trophic levels | 356 | −22.5 (−22.6: −22.3) | 0.3 (0.3: 0.4) | −4.9 (−6.6: −3.6) |
| b) Trophic attenuation | 4 months | Monthly | 3 trophic levels | 356 | −22.9 (−23.3: −22.5) | 0.5 (0.3: 1.0) | −5.5 (−9.5: −5.2) |
| | 2 months | Monthly | 2 trophic levels | 356 | −23.0 (−23.4: −22.6) | 0.7 (0.5: 1.1) | −6.9 (−11.1: −3.4) |
| | 1 months | Monthly | 1 trophic level | 356 | −22.6 (−23.0: −22.3) | 0.7 (0.5: 1.1) | −5.7 (−9.3: −2.4) |
| c) Monthly isoscape | April | Monthly | 4 trophic levels | 325 | −22.1 (−22.4: −21.8) | 0.3 (0.1: 0.7) | −4.6 (−8.2: −1.4) |
| | December | Monthly | 4 trophic levels | 348 | −23.0 (−23.4: −22.6) | 0.4 (0.2: 0.8) | −3.7 (−7.0: −0.7) |
| d) Temporal resolution | | Yearly | 4 trophic levels | 357 | −22.5 (−22.8: −22.1) | 0.4 (0.2: 0.8) | −4.9 (−8.5: −1.8) |
| e) Laying initiation date | −15 days | Monthly | 4 trophic levels | 354 | −22.4 (−22.7: −22.0) | 0.4 (0.2: 0.8) | −6.6 (−11.0: −3.0) |
| | −10 days | Monthly | 4 trophic levels | 349 | −22.2 (−22.6: −21.9) | 0.2 (0.1: 0.7) | −5.1 (−9.3: −1.6) |
| | −5 days | Monthly | 4 trophic levels | 366 | −22.5 (−22.8: −22.1) | 0.4 (0.2: 0.8) | −6.7 (−11.5: −3.0) |
| | +5 days | Monthly | 4 trophic levels | 357 | −22.5 (−22.9: −22.2) | 0.3 (0.1: 0.7) | −4.4 (−7.9: −1.2) |
| | +10 days | Monthly | 4 trophic levels | 354 | −22.4 (−22.8: −22.1) | 0.3 (0.1: 0.7) | −4.9 (−9.4: −2.2) |
| | +15 days | Monthly | 4 trophic levels | 368 | −22.6 (−23,0: −22.3) | 0.4 (0.2: 0.8) | −4.5 (−8.2: −1.4) |
| f) Foraging trip duration | +2 days | Monthly | 4 trophic levels | 299 | −22.4 (−22.8: −22.0) | 0.4 (0.2: 0.8) | −5.5 (−10.1: −1.8) |
| | +4 days | Monthly | 4 trophic levels | 244 | −22.6 (−23.0: −22.2) | 0.4 (0.2: 0.8) | −3.7 (−7.4: −0.6) |
| | +6 days | Monthly | 4 trophic levels | 198 | −22.7 (−23.1: −22.3) | 0.4 (0.1: 0.8) | −2.7 (−6.1: 0.4) |
| g) Daily step length | −150 km | Monthly | 4 trophic levels | 343 | −22.4 (−22.8: −22.1) | 0.4 (0.2: 0.8) | −5.7 (−10.0: −2.2) |
| | −100 km | Monthly | 4 trophic levels | 364 | −22.4 (−22.8: −22.1) | 0.3 (0.1: 0.8) | −4.6 (−8.1: −1.4) |
| | −50 km | Monthly | 4 trophic levels | 335 | −22.4 (−22.7: −22.0) | 0.2 (0.1: 0.7) | −3.4 (−7.1: −0.8) |
| | +50 km | Monthly | 4 trophic levels | 344 | −22.6 (−22.9: −22.2) | 0.4 (0.2: 0.8) | −7.6 (−13.4: −3.4) |
| | +100 km | Monthly | 4 trophic levels | 350 | −22.5 (−22.9: −22.2) | 0.3 (0.1: 0.7) | −5.6 (−9.8: −2.0) |
| | +150 km | Monthly | 4 trophic levels | 342 | −22.5 (−22.8: −22.2) | 0.3 (0.1: 0.7) | −6.4 (−11.3: −2.6) |

may similarly provide more ecological information than estimates of population average isotopic compositions.

### 4.2. The effect of predator behavioural changes on their isotope composition

Changes in breeding phenology (e.g. Dobson et al., 2017) or foraging effort (e.g. Green et al., 2015; Whitehead et al., 2017) of seabirds are often interpreted in terms of inter-annual variability in prey availability. Here, we used our female NGP agent-based movement model to investigate whether these behavioural changes would also lead to changes in predator $\delta^{13}C$ tissue values. We found that only the extreme changes in laying initiation date lead to significantly different plasma $\delta^{13}C$ values (i.e. 15 days before and after average laying date).

Increased foraging trip duration of simulated NGPs led to an extension of at-sea distribution and significantly different $\delta^{13}C$ values. This supports the common interpretation that foraging location is the most important driver of marine predator $\delta^{13}C$ tissue values (e.g. Graham et al., 2010; Newsome et al., 2010), and is unsurprising in a region with large, directional (latitudinal) gradients in the isotopic compositions of primary producers. However, increasing the daily step length of the simulate NGPs did not result in significant changes in their $\delta^{13}C$ values, even though there were some range contraction or expansion. This is likely an artefact of the birds' preference for sea surface temperatures between 19.5 and 22.0 °C, which lead to similar core foraging areas despite changing step lengths.

### 4.3. Caveats

The simulation results presented here are context-dependent. The Southern Ocean is characterised by large, persistent latittudinal gradients in $\delta^{13}C$ values which likley dominate the response of predicted tissue $\delta^{13}C$ values to changes in temporal or spatial variables. We recommend taking a simulation sensitivity approach specific to a study region as a desk-based initial step within the design of field sampling protocols, and prior to interpretation of stable isotope data from consumer tissues.

It is important to note that the monthly isoscapes used within this study are simulations and are not expected to accurately represent $\delta^{13}C$ values at local and short timescales. Simulations were produced from a 10 year average of climatic variables, reducing potential inter-annual variation (Magozzi et al., 2017). We stress that the current study uses models to explore potential isotopic sensitivity to environmental and ecological variables, rather than attempting to infer location or behaviour based on measured data. In addition, we did not simulate intrinsic physiological factors that may influence the carbon isotopic value of marine predators' tissues, such as reproduction (Hobson and Clark, 1992; Connan et al., 2017), nutritional stress (Hobson et al., 1993) or differential routing of carbon-containing metabolic compounds (Newsome et al., 2010).

## 5. Conclusion

In summary, we show that *in-silico* simulations provide a method of testing the sensitivity of consumer tissue isotope compositions to multiple simultaneous sources of variance.

In our case study we show that caution should be used when comparing $\delta^{13}C$ values of marine predators' tissues between seasons and years as temporal variation in baseline compositions has potential to confound isotopic variances that are commonly inferred to represent differences in either foraging location and/or diet composition.

The method presented here is applicable to any consumer that moves around its environment to forage. It is not restricted to the use of Magozzi et al. (2017)'s monthly isoscapes or the rules of our agent-based movement model: future investigations can use other isoscapes, including terrestrial isoscapes (e.g. West et al., 2014), more complex or different movement models, and or isotopically variable diets.

## Author's contribution

TCK, PAP and CT conceived the study; TCK carried out the fieldwork; TCK and MC analysed the samples; SM constructed and provided underlying isoscape maps; TCK, CT, RRR and MC analysed the data; TCK and CT led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

## Data accessibility

R code of agent-based movement model presented here is depopsited at Carpenter-Kling et al. (2019): https://doi.org/10.6084/m9.figshare.7531445.v1

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