Evidence of multi-decadal behavior and ecosystem-level changes revealed by reconstructed lifetime stable isotope profiles of baleen whale earplugs

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Introduction

Time-series datasets from biological tissues can provide invaluable opportunities to reconstruct past ecosystems and assess how individuals and populations respond to changing environments through time (Fleming *et al.* 2016; 2018). Carbon (δ^{13}C) and nitrogen (δ^{15}N) stable isotope analysis can be used to infer historical foraging locations and trophic status of organisms, due to the predictable change in isotope ratios through the trophic level relative to the prey (McMahon *et al.* 2013). In addition, in marine ecosystems, δ^{13}C and δ^{15}N values at the base of the food web (i.e., baseline) vary both latitudinally and along inshore/offshore gradients. This creates spatially distinct isotopic values, known as an isoscape, that can be used to track movement patterns and trophic interactions of organisms (Magozzi *et al.* 2017, MacKenzie *et al.* 2011, Graham *et al.* 2010, McMahon et al. 2013).

Increasing human terrestrial and ocean-based activities, accompanied by anthropogenic climate change, have impacted key marine hydrological and physiochemical processes, such as sea surface temperature, turbidity, wind, stratification, and nutrient concentration (Borrell *et al.* 2018, Hou *et al.* 2018, Keeling *et al.* 2017, Durant *et al.* 2004, Ullah *et al.* 2018, O'Connor *et al.* 2009, Poloczanska *et al.* 2016). Variability in oceanographic parameters could alter primary productivity and force individuals' foraging at higher trophic levels to temporarily move beyond their predictable foraging habitat or niche, subsequently changing population spatial dynamics and trophic interactions (Briscoe *et al.* 2017). These environmental and behavioral alterations may be reflected in biological time series datasets through changing δ^{13}C and δ^{15}N values. Additionally, the emission of CO_2 from fossil fuel combustion increases ^{13}C values in marine ecosystems resulting in reduced baseline isotopic values through time due to preferential uptake of ^{12}C by phytoplankton (Borrell et al. 2018, Hou et al. 2018, Keeling et al. 2017). This process,

called the Suess effect, alters $\delta^{13}C$ throughout the food web and has been reflected in time series datasets from the marine organisms (Borrell et al. 2018, Hou et al. 2018, Keeling et al. 2017). Previous studies have shown decadal trends in $\delta^{13}C$ profiles of coral skeleton from the North Pacific Ocean (0.015‰ year^{-1}; 1955-2003) (Williams *et al.* 2007) and northern fur seal teeth from the Gulf of Alaska (0.021‰ year^{-1}; 1948-2000) (Newsome *et al.* 2007).

Baleen whales are long-lived marine mammals that that are known to undertake annual long-distance migrations between high-latitude summer grounds and low-latitude winter grounds (Aguilar 2009, Sears & Perine 2009, Clapham 2009). Baleen whales are often referred to as marine sentinels because of their sensitivity to changing environmental and ecological factors; thus, variation in whale feeding, foraging, and migration could be indicative of change in the marine ecosystem (Bengtson Nash *et al.* 2018, Moore 2008, Bossart 2011, Fleming et al. 2016). Baleen whale earplugs are formed from the lifetime secretion and accumulation of cerumen. Earplugs, historically used as an aging proxy in baleen whales, consist of semiannual bands of alternating dark and light laminae (i.e., growth layer groups). Recently, it was determined that labile (*e.g.,* hormones) (Crain *et al.* 2020, Trumble *et al.* 2018) and inert compounds (*e.g.,* persistent organic contaminants) (Trumble *et al.* 2013, Winfield *et al.* 2020) can be archived within the cerumen, providing an opportunity to retrospectively construct lifetime chemical profiles spanning birth to death with six-months resolution (Trumble et al. 2018; 2013, Crain et al. 2020, Winfield et al. 2020). The combination of the chemical archival capacity with an age estimation provides an unprecedented opportunity to retrospectively examine cause-and-effect relationships involving aspects of behavior and ecosystem-level changes on regional and global scales (Glibert *et al.* 2019, McMahon & McCarthy 2016). Due to their long life-spans, baleen whale earplugs can serve as biological recorders of changing environmental conditions, and

reconstruction of time-series δ^{13}C and δ^{15}N datasets from baleen whales can serve to examine cause-and-effect relationships involving aspects of behavior and ecosystem-level changes on regional and global scales (Glibert et al. 2019, McMahon & McCarthy 2016). Therefore, reconstruction of lifetime δ^{13}C and δ^{15}N profiles (i.e., birth to death) using whale earplugs could provide an opportunity with which to investigate yearly and decadal changes in both ocean ecosystem and individual foraging ecology.

The goal of this study was to use baleen whale earplugs to reconstruct the first lifetime δ^{13}C and δ^{15}N profiles. These profiles were used to 1) assess life history behavior changes in foraging (*e.g.,* shift in foraging location or trophic position), 2) assess life history evidence of long-term environmental change (i.e., increase or decrease in the stable isotope profiles), 3) correct for the global known sources of long-term change in δ^{13}C values (i.e., the Suess effect), and 4) assess for possible occurrence of multiple regional drivers of long-term changes in δ^{13}C values.

Method

Sample collection, preparation, and age determination

Earplugs from three species of baleen whales; fin (*Balaenoptera physalus, N* = 2), blue (*Balaenoptera musculus, N* = 2), and humpback (*Megaptera novaeangliae, N* = 2) were sampled to reconstruct lifetime δ^{13}C and δ^{15}N profiles (*N* = 6; *n* = 337 laminae; Table 1). Baleen whale earplugs, collected between 1955 and 2001, were donated by the Natural History Museum of London, the National Museum of Natural History, and the Glacier Bay National Park and Preserve in Southeast Alaska. Earplugs were aged and delaminated according to the methods described in Trumble et al. (2018). Briefly, baleen whale earplugs were weighed and measured before storing at -30 °C until processing. After removal from the freezer, all whole earplugs were

bisected using medical grade zirconia ceramic scalpel blades or ceramic knives. A frozen bisected earplug was polished using progressively finer grain sandpaper (80-600 grit), rinsed using deionized water, and photographed using a Canon DSLR camera with a macro lens (Canon 6D Mark II). The SLR camera was mounted to a copy stand with adjustable fluorescent lighting (Bencher Copymate). Digital photographs were taken and used to age the whale by counting the number of dark and light laminae, assuming the combination of one dark and one light lamina (growth layers) constitutes one year of life. Prior to delamination, two independent readers used digital photographs to age each earplug included in this study. One additional reader was used if there was greater than a ± 5% discrepancy in the total laminae counts.

Stable Isotope Analysis

$\delta^{13}C$ and $\delta^{15}N$ analysis of earwax were conducted at the Stable Isotope Laboratory, Baylor University. A Costech ECS 4010 Elemental Combustion System (ECS), connected to a Thermo Delta V Advantage continuous flow Isotope Ratio Mass Spectrometer (EA-IRMS) through a Thermo Conflo IV interface, was used to determine nitrogen and carbon stable isotope composition of earplug laminae. Approximately 1 mg of homogenized laminae were wrapped in tin capsules and loaded together with references into a Zero-Blank auto-sampler of the Costech ECS. Samples were then dropped into a combustion tube that is packed with oxide catalyst and heated up to 1000 °C and converted to nitrous oxides and carbon dioxide by dynamic flash combustion. The mixed gases, carried by a constant helium flow, first pass through a reduction tube to convert all nitrous oxides into nitrogen; then through a water trap filled with magnesium perchlorate to remove water; and eventually through a gas chromatography column to separate nitrogen and carbon dioxide. The separated gases were then introduced into the Thermo EA-

IRMS to acquire isotope data. Nitrogen and carbon weight percentages of the samples were determined by Costech EAS Clarity software (Version 2.6.6.574) using a three-point calibration curve and had an analytical error of ±0.07 for C and ±0.01 for N based on 34 replicate analyses of High Organic Content Standard (Elemental Microanalysis, UK). $\delta^{13}C$ and $\delta^{15}N$ values of the samples were acquired by Thermo Isodat 3.0 software and expressed in parts per thousand (‰) as defined by the following equation:

$$\delta X = \left(\left(\frac{R_{Sample}}{R_{Standard}} \right) - 1 \right) * 1000 \tag{1}$$

Where X is ^{13}C or ^{15}N, and R corresponds to the $^{13}C/^{12}C$ or $^{15}N/^{14}N$ ratio of the samples and standards.

Raw isotope data were then converted to VPDB scale using a two-point normalization method involving USGS40 and USGS41 international references. To check the precision of the isotopic measurements, an internal lab standard (Acetanilide#1, from Indiana University, USA) was placed at the beginning, middle, and end of each batch of analysis; and the standard deviation for 102 duplicate analyses was ± 0.08 for $\delta^{13}C$ and ± 0.09 for $\delta^{15}N$.

$\delta^{13}C$ values were corrected for earwax lipid composition using the modified McConnaughey and McRoy (1979) model as described in Mansouri et al. (2020). Subsequently, lifetime $\delta^{13}C$ and $\delta^{15}N$ profiles (six-month resolution) were reconstructed by normalizing $\delta^{13}C$ and $\delta^{15}N$ values to the year (or age) estimates of each laminae.

Assessing behavior changes in stable isotope profiles

Baleen whales can follow annual migration patterns between higher latitude foraging grounds and lower latitude breeding grounds. However, these whales have been reported to switch foraging locations or prey, which may result in an increase or decrease in tissue $\delta^{13}C$ and

$\delta^{15}N$ composition (Magozzi et al. 2017, MacKenzie et al. 2011, Graham et al. 2010, McMahon et al. 2013). For example, if an individual baleen whale consistently migrates between two isoscapes and feeds at the same trophic level, the long-term isotopic profile should be relatively consistent with a relatively low variability. However, moving to a different isoscape or prey may result in either acute change or high variability in $\delta^{13}C$ and $\delta^{15}N$ values. For this study, short-term abrupt behavior changes in $\delta^{13}C$ and/or $\delta^{15}N$ values were identified as behavioral events using the standard signal-to-noise ratio (S/N) of 3:1 (Fleming 2011). Here, the signal (S) represents the magnitude of change in stable isotope values, while the noise (N) represents the background stable isotope values. Additionally, long-term behavior changes were identified using ± standard deviation (SD) in $\delta^{13}C$ and $\delta^{15}N$ profiles, which provides insight into the variability in the stable isotope over the lifetime of the individual.

Suess Effect Correction

To correct for increases in depleted $^{13}CO_2$ input from burning fossil fuels into the atmosphere and subsequent marine system and provide comparable $\delta^{13}C$ values between recent and historical samples, $\delta^{13}C$ time-dependent values of earplugs were corrected for the Suess effect using Hilton et al. (2006) equation:

$$\text{Suess effect correction factor} = a * exp^{(b*0.027)} \tag{2}$$

Where *a* is the annual rate of $\delta^{13}C$ decrease for the water body and *b* is the assigned year for laminae minus 1850 (i.e. onset of the industrial revolution and mass fossil fuel burning). Since rate of $\delta^{13}C$ depletion of dissolved inorganic carbon (DIC) varies globally due to the physiochemical properties of water, -0.014‰ and -0.018‰ were used for the annual rate of $\delta^{13}C$ depletion in the North Pacific and the North Atlantic Ocean, respectively (Quay *et al.* 2007,

Quay *et al.* 1992, Clark *et al.* 2019, Misarti *et al.* 2009). Since the contribution of atmospheric CO_2 associated with burning fossil fuels varies as a function of time, the Suess effect correction factor was calculated for each year and subsequently corrected $\delta^{13}C$ values of corresponding laminae. For instance, $\delta^{13}C$ values of laminae from 2010 were adjusted by +1.05 and those from 1950 were adjusted by +0.27.

Statistical Analysis

To identify significant long-term behavior changes, two-tailed tests to compare the ratio of variances of both $\delta^{13}C$ and $\delta^{15}N$ between two different periods of an individual's life were conducted. First, the stable isotope series were checked for significant autocorrelation, and if present, an autoregressive model of order p (AR(p)) was fit, according to model diagnostics. Then, bootstrap samples were constructed, retaining the time series structure but assuming under the null hypothesis that the variances in each period of the individual's life were the same. Then, for each of 999 bootstrap samples, the ratio of the variances was computed, and the sampling distribution under the null hypothesis was created. The observed ratio of variances was compared to this distribution, and an empirical *p*-value was calculated.

Secondly, the significance of the linear trends in both lipid and the Suess corrected $\delta^{13}C$ profiles was explored. First, a simple linear regression (SLR) of the stable isotope value at time *t* was regressed on the year of the observation. As before, the autocorrelation function (ACF) and partial autocorrelation function (PACF) of the residuals of this model were estimated to determine whether the residuals exhibit significant autocorrelation. For two of the whales, no autocorrelation in the residuals was detected, indicating that the SLR model is sufficient. In the remainder of the whales, the shape and strength of the ACF and PACF plots indicated that

autocorrelation in the residuals does exist, and each one followed the pattern of an autoregressive model of order 1 (AR(1)). Thus, the slope and its standard error in the SLR were adjusted for this dependence. All statistical analyses were performed using the R-4.0.3 software (R Development Core Team, 2020), and the astsa package was used for analysis related to time series (Stoffer, 2020).

Results

δ^{13}C and δ^{15}N values of all laminae ($N = 6$, $n = 337$ laminae) were successfully measured, and δ^{13}C values were corrected for lipid and the Suess effect (Fig. 1). Lifetime δ^{13}C and δ^{15}N isotopic means ± SD were evaluated for all individual whale earplugs. Within all six individuals, mean ± SD for δ^{13}C values ranged from -25.81 ± 0.14‰ to -16.80 ± 0.38‰ (Table 1). Among the Northeast Atlantic (NEA) whales, earplugs from fin whales EP006 and EP016 yielded δ^{13}C values of -20.06 ± 0.16‰ and -20.54 ± 0.26, while relatively lower δ^{13}C values were determined for earplugs from two blue whales; EP041 and EP040 (-25.81 ± 0.14‰ and -25.69 ± 0.18‰, respectively). Among the Northeast Pacific (NEP) whales, earplugs from humpback EP027 demonstrated δ^{13}C values of -16.80 ± 0.38‰ and -19.55 ± 0.83‰ for EP022.

The mean ± SD for δ^{15}N values from earplugs ranged from 6.02 ± 0.25‰ to 13.69 ± 0.73‰ among six individuals. Within the NEA whales, mean values of δ^{15}N ranged from 6.02 ± 0.25‰ (EP040) to 10.74 ± 0.34‰ (EP016) (Table 2). Among the NEP whales, mean values of δ^{15}N earplugs ranged from 10.91 ± 0.27‰ (EP027) to 15.72 ± 0.73‰ (EP022) (Table 2).

Short-term behavior events

Short-term behavior events (i.e., identified using S/N 3:1 over 1-2 yrs) were identified in δ^{13}C and δ^{15}N signatures of blue whales EP040 and EP041 (Fig. 1a and b). Specifically, δ^{13}C values of blue whale EP040 decreased from -25.80‰ to -26.28‰ from 1950 to 1951 (S/N = 5.3) followed by an increase to -25.86‰ the following year. In addition, δ^{15}N value of blue whale EP041 increased from 5.87‰ to 7.14‰ from 1937 to 1938 (S/N = 7.9) and decreased to 5.82‰ in the following year (Fig. 1a and b).

Long-term behavior changes

Long-term behavior changes were identified using variation in isotopic composition of earplugs (± SD), which were used as a proxy of consistency in foraging location and diet of individual baleen whales. Comparison of standard deviation on humpback whale EP022 δ^{13}C values illustrated that the SD is significantly greater during 1980 to 2001 (SD = ± 1.19) compared to 1944 to 1980 (SD = ± 0.50) ($p < 0.01$). (Fig. 1.c). More specifically, for this particular humpback whale, there was a 4.56‰ shift in δ^{13}C values (-17.73‰ to -22.29‰; ± 1.45) from 1986 to 1992 as compared to a 2.29‰ shift in δ^{13}C values (-18.43‰ to -20.72‰; ± 0.50) from 1945 to 1980 era. Comparison of the standard deviations on humpback whale EP022 δ^{15}N values also showed a significantly greater SD during 1989 to 2001 (SD = ± 0.81) in comparison to 1971 to 1988 (SD = ± 0.31) ($p < 0.01$). Specifically, humpback EP022 δ^{15}N values decreased from 14.84‰ to 12.48‰ during 1993 to 1996 and increased from 12.56‰ to 15.72‰ between 1998 and 2000 (Fig. 1.d), with changes in δ^{15}N values during 1964 to 1968 ranging between 13.19‰ to 14.63‰. Additionally, humpback earplug δ^{15}N values (EP027) increased from 12.77‰ to 14.12‰ during 1958 to 1963 and from 14.14‰ to 12.68‰ during 1965 to 1969.

Long-term ecosystem-level changes

To assess the long-term ecology change, each life history profile (lipid and the Suess corrected) was assessed for autocorrelation using plots of the estimated ACF and PACF. Dependence was identified in EP016, EP041, EP022, and EP027, while no dependence was identified in EP006 and EP040. Life history $\delta^{13}C$ profiles for EP016, EP041, EP022, and EP027 were corrected using an AR(1) model. No trend was identified within the life history profiles of EP022 in either $\delta^{13}C$ ($p > 0.75$) or $\delta^{15}N$ ($p > 0.25$). Estimated slopes, each one's associated 95% CI, model R^2 are presented in Table 2 and S1. Slopes for the lipid corrected $\delta^{13}C$ ranged from -0.031 ± 0.006‰ yr^{-1} to -0.015 ± 0.003‰ yr^{-1} with R^2 ranging from 0.48 to 0.75 ($p < 0.05$) (Fig. 2, Table 2). While slopes for the Suess corrected $\delta^{13}C$ ranged from -0.009 ± 0.004‰ yr^{-1} to -0.023 ± 0.006‰ yr^{-1} with R^2 ranging from 0.32 to 0.66 ($p < 0.05$) (Fig. 2, Table S.1). Moreover, the 95% confidence intervals of the slopes of the regression lines for the Suess corrected and non-corrected profiles overlapped, indicating no significant difference in the slopes for each of the five individuals.

Discussion

Reconstructed $\delta^{13}C$ and $\delta^{15}N$ profiles from baleen whale earplugs ($N = 6$, $n = 337$ laminae) in this study provide the first recorded birth to death stable isotope values for baleen whales. These longitudinal profiles reveal changes in both individual whale behavior such as possible shifts in foraging location and/or trophic level as well as ecosystem-level changes that could be associated with the Suess effect and/or long-term changes in biogeochemical cycling.

Reconstructed life history δ^{13}C and δ^{15}N profiles from earplugs also revealed inter- and intra-species differences. Specifically, within NEA earplugs, mean lifetime δ^{13}C values of blue whales (EP040, -25.69 ± 0.18‰ and EP041, -25.81 ± 0.14‰) were more depleted than fin whales (EP006, -20.06 ± 0.16‰ and EP016, -20.54 ± 0.26‰) (Table 2) and lower than previously published δ^{13}C values sampled from blue whale tissues from the NEA (Silva et al. 2019). It has been determined that bulk δ^{13}C values at the base of the food web (i.e., baseline) get more depleted poleward or in pelagic regions (Newsome *et al.* 2010). Thus, the more depleted δ^{13}C values of blue whales (EP040 and EP041) from earwax in this study may be indicative of increased foraging in more pelagic or higher latitudinal sub-polar feeding grounds of the NEA. Another possibility for depleted δ^{13}C values of blue whales between tissues could be associated with diet-tissue discrimination factors (Borrell *et al.* 2012). It has been reported that δ^{13}C discrimination varies across consumer tissues due to difference in isotope assimilation routes and tissue composition (Borrell et al. 2012). Thus, depleted δ^{13}C values of two blue whale earplugs could be associated with different stable isotope discrimination factors between earplug and epidermis (Silva et al. 2019). Intra-species differences were also observed in δ^{13}C composition of humpback whale earplugs from the NEP; mean lifetime δ^{13}C value of humpback whale EP022 (-19.55 ± 0.83‰) had relatively more depleted values than EP027 (-16.80 ± 0.38‰) during the same period of time (1945-1975). Previous stable isotope analysis of humpback whales revealed multiple isotopically distinct feeding grounds in the NEP (Witteveen *et al.* 2009, Witteveen *et al.* 2011). Thus, the difference in mean lifetime δ^{13}C values of two humpback whales may be indicative of residing in two geographically distinct feeding ground of the NEP.

Inter-species differences were also observed in δ^{15}N values of individual earplugs from the NEA; mean δ^{15}N values of blue whales EP040 (6.02 ± 0.25‰) and EP041 (6.10 ± 0.31‰) were

depleted relative to fin whales EP006 (10.84 ± 0.25‰) and EP016 (10.74 ± 0.34‰) (Table 2).

Previous studies showed that blue whales are dietary specialists, foraging specifically on krill

(Gavrilchuk *et al.* 2014); however, fin whales are considered generalists and are known to forage

on both krill and small schooling fish (Ryan *et al.* 2013, Gavrilchuk et al. (2014), Gauffier *et al.*

2020). Therefore, the differences in mean lifetime δ^{15}N values of blue and fin whales observed in

this study are possibly a result of prey differences. However, in the NEP humpback whales,

mean lifetime δ^{15}N values of EP022 (13.69 ± 0.73‰) and EP027 (13.23 ± 0.59‰) showed

similar values in earplugs. Humpback whales in the NEP are known for foraging on

geographically distinct feeding aggregations, which is maternally derived fidelity to a feeding

ground (Witteveen et al. 2009, Witteveen et al. 2011), and they feed on a variety of prey ranging

from zooplankton to schooling fish (Wright *et al.* 2015, Straley *et al.* 2018). Thus, similarity in

mean δ^{15}N values of two humpback whales with different δ^{13}C values could be indicative of

foraging on comparable trophic level preys such as Pacific herring (*Clupea pallasii*) or capelin

(*Mallotus villosus*) (Witteveen et al. 2009, Witteveen et al. 2011), while inhabiting distinct NEP

feeding grounds.

Short-term behavior events

Reconstructed lifetime δ^{13}C and δ^{15}N profiles from earplugs also displayed short-term behavioral

changes corresponding to a shift in foraging location and/or trophic level. A depletion in δ^{13}C

values observed in blue whale EP040 (S/N = 5.3; 1950-1951, age estimates 18-19), with

consistent age-related δ^{15}N values (Fig. 1a and b), could represent an abrupt change in foraging

location while little or no change in trophic level. Additionally, an increase in δ^{15}N value of blue

whale EP041 (S/N = 7.9; 1937-1938, age estimates 5-6), with no corresponding age-related

change in δ^{13}C value (Fig. 1a and b), may indicate residing in the same isoscape, while abruptly

shifting trophic level prey. Baleen whales have been reported to target prey important to other

marine consumers (*e.g.,* krill) (Tulloch *et al.* 2019, Gavrilchuk et al. 2014); thus, competition for

available prey could lead to variation in feeding behavior of individuals and reduced foraging

specialization. Moreover, impact of regional anthropogenic climate change on sea surface

temperature and the stratification layer change nutrient cycle and primary production leading to

ecological changes such as shift in temporal and spatial distribution of marine species (Findlay *et

al.* 2017, Fleming et al. 2016). Ecological changes combined with impact of commercial fishing

(Weinstein *et al.* 2017) could affect foraging behavior of baleen whales and (Briscoe et al. 2017)

result in a change in δ^{15}N and/or δ^{13}C values of earwax. In addition, previous studies have

indicated that exposure to anthropogenic noises may impact baleen whale foraging efficiency as

well as prey patch displacement (Goldbogen *et al.* 2013, Blair *et al.* 2016, Trumble et al. 2018,

Melcon *et al.* 2012). Thus, a high degree of variability observed in δ^{13}C and δ^{15}N values in the

shorter term may be reflective of a behavior change in response to environmental stimuli

(Goldbogen et al. 2013, Blair et al. 2016, Trumble et al. 2018, Melcon et al. 2012). It is worth

noting that a more comprehensive assessment on the frequency of potential behavioral changes

in baleen whales from lifetime δ^{13}C and δ^{15}N profiles will provide details regarding transient

changes associated with increased anthropogenic changes.

Long-term behavior changes

Long-term behavior changes were also observed within reconstructed lifetime δ^{13}C and δ^{15}N

profiles. These temporal variabilities could be indicative of variation in an individual's diet

and/or foraging behavior. Within this dataset, δ^{13}C values of fin (EP006 and EP016) and blue

(EP040 and EP041) whales demonstrated SD that range between 0.14 and 0.26, while humpback whales EP022 and EP027 demonstrated SD of 0.83 and 0.38, respectively. Humpback whale EP022 showed the highest overall variability in isotopic values (SD) when compared among whale earplugs. While the overall variability provides an opportunity to assess lifetime shifts, the scale of changes may be better highlighted by assessing specific periods of life. For example, humpback whale EP022 demonstrated relatively lower $\delta^{13}C$ variability early in life (SD = ± 0.50, n = 69 laminae; 1944-1980) compared to later in life (SD = ± 1.19, n = 44 laminae; 1980-2001) (p < 0.05). More specifically, the $\delta^{13}C$ composition of humpback whale EP022 earplug changed from -20.64 to -18.45‰ during 1951 to 1955; however, $\delta^{13}C$ values showed relatively larger changes from -21.46 to -17.64‰ during 1982 to 1987 and from -17.73 to -22.29‰ during 1989 to 1992 (Fig. 1c). Previous studies report a high degree of site fidelity in humpback whales who frequent the same breeding and feeding grounds during their annual migration (Baracho *et al.* 2012, Witteveen & Wynne 2017). However, 4-5‰ changes in $\delta^{13}C$ values of EP022 earplug (1982 to 1987 and 1989 to 1992), could indicate a broad-scale movement between multiple isotopically distinct regions in the north Pacific Ocean for this particular humpback whale. Interestingly, interpretations associated with $\delta^{13}C$ values for humpback whale EP022 are supported by the variability of $\delta^{15}N$ values recorded within the earplug. Humpback whale EP022 showed relatively lower $\delta^{15}N$ variability during 1971 to 1988 (SD = ± 0.31) compared to 1989 to 2001 (SD = ± 0.81) (p < 0.05). Specifically, the $\delta^{15}N$ values of EP022 earplug changed from 13.19‰ to 14.63‰ during 1964 to 1968; however, it demonstrated relatively larger variation from 14.84‰ to 12.48‰ during 1993 to 1996 and from 12.56‰ to 15.72‰ during 1998 to 2000 (Fig. 1d). The magnitude of changes in $\delta^{15}N$ composition in humpback whale EP022 was similar to the average difference observed between trophic levels (i.e., 3.4‰), indicating possible

trophic level prey switching (Magozzi et al. 2017, MacKenzie et al. 2011, Graham et al. 2010, McMahon et al. 2013). It is important to note that the North Pacific Ocean experienced multiple climate regime shifts in 1977, 1989, and 1998 that may have influenced physiochemical characteristics of water as well as nutrient cycles in this region (Williams et al. 2007, Greene *et al.* 2013, Alheit 2009). These changes may alter community structure, prey abundance, and habitat quality that impact foraging behaviors of marine mammals within this region (Williams et al. 2007, Greene et al. 2013, Alheit 2009). Furthermore, humpback EP027 demonstrated an increase in $\delta^{15}N$ values from 12.77‰ to 14.12‰ during 1958 to 1963 and subsequently a decrease from 14.14‰ to 12.68‰ during 1965 to 1969. This magnitude of change in $\delta^{15}N$ values with a relatively constant $\delta^{13}C$ values during aforementioned period of time could be indicative of shifting to a different trophic level prey while foraging in the same isoscape. Recent studies have provided evidence of redistribution and/or a shift in diet composition of the North Pacific (Fleming et al. 2016), as observed in Southern humpback whales (Findlay et al. 2017) that were assumed to be a temporal response to a shift in prey availability and distribution due to climatic changes. Therefore, temporal variability observed in lifetime stable isotope profiles of the humpback whales EP022 and EP027 may provide evidence of large-scale decadal changes in habitat suitability and/or favorable prey abundance (Silva et al. 2019, Gauffier et al. 2018) and the resultant behavior of migratory marine mammals. It is also worthwhile to note that the isotopic variability measured across the individual whales' lifespan provides an added layer of interpretation otherwise lost from other sampling techniques. Although opportunistic sampling has provided a wealth of information regarding trophic position and food web dynamics (Newsome et al. 2010), there are limitations due to the difficulty in collecting repeat samples from free ranging marine mammals (*e.g.,* sampling significant numbers across age classes).

Additionally, single point measurements typically represent relatively short time periods and may not provide insight into an individual's past behaviors (Busquets-Vass *et al.* 2017). Therefore, reconstruction of earplug stable isotope profiles can not only can be used to determine past behavior but can also be used to predict future behavior changes of baleen whales with concomitant shifts in the environment.

Long-term ecosystem-level changes

More interestingly, longitudinal δ^{13}C profiles provide evidence of long-term declines in δ^{13}C values in five of six individual baleen whales. Decadal decreases in δ^{13}C values recorded in baleen whale earplugs could be attributed to the Suess effect (i.e., anthropogenic source of depleted δ^{13}C) (Williams et al. 2007, Newsome et al. 2007), which is consistent with reconstructed δ^{13}C profiles from Beluga whales (*Delphinapterus leucas*) teeth dating back to the 1960s (Nelson *et al.* 2018). Additionally, while the Suess effect impact on marine baseline δ^{13}C values is considered a global phenomenon, the rate of isotopic depletions varies by region (*e.g.,* NEP and NEA) (Quay et al. 2007, Quay et al. 1992, Clark et al. 2019, Misarti et al. 2009). The rate of depletion in δ^{13}C values of earplugs varies from -0.031 ± 0.006‰ yr^{-1} to -0.015 ± 0.003‰ yr^{-1} within five individuals sampled from different isoscapes and ocean basins. This may provide evidence of spatial differences in the Suess effect across ocean basins (Quay et al. 2007, Quay et al. 1992, Clark et al. 2019, Misarti et al. 2009). The absence of a significant trend in the δ^{13}C profile from humpback whale EP022 could be attributable to the high variability in δ^{13}C values associated with behavior changes and foraging between different regions in the NEP, thereby concealing long-term decline in oceanic δ^{13}C values.

Life history δ^{13}C profiles were corrected for the Suess effect using the Suess correction model to provide a comparable measurement between historical and modern data. The Suess corrected δ^{13}C profiles were re-evaluated for the temporal decline using simple linear regression with possibly autocorrelated errors, and this revealed significant long-term depletion in δ^{13}C profiles of the five individuals ($p < 0.05$). However, the comparison of the estimated slope between the Suess corrected profile from its corresponding non-corrected profile demonstrated no significant difference within all five individuals ($p > 0.05$). Significant decline in δ^{13}C Suess corrected values ranging from -0.009 ± 0.004‰ yr^{-1} to -0.023 ± 0.006‰ yr^{-1}, suggest that contributions from other sources could also impact δ^{13}C values of baseline on regional and global scales. Terrestrial discharge of depleted ^{13}C, as well as changes in primary productivity and community composition due to climate regime shift or changes in upwelling system and nutrients concentration, could alter δ^{13}C values of the baseline over time and change δ^{13}C values of earwax (Hood & Scott 2008, Dyurgerov & Meier 2000, Williams et al. 2007, Borrell et al. 2018, Silva et al. 2019, Greene et al. 2013, Alheit 2009).

Conclusion

Results of this study illuminate the ability of baleen whale earplugs to archive years to decades of δ^{13}C and δ^{15}N values. Additionally, this longitudinal dataset provides life history behavioral changes (e.g., shift in foraging location or trophic position) as well as long-term ecosystem-level changes associated with the Suess effect. After correcting for the Suess effect, re-evaluated δ^{13}C profiles provide the opportunity to assess additional potential sources of change in δ^{13}C values such as terrestrial run-off and changes in primary composition and productivity using a more top-down approach (Trumble et al. 2018, Crain et al. 2020, Trumble et

al. 2013, Winfield et al. 2020). Additionally, comparison of time series stable isotope profiles from baleen whale earplugs, as marine sentinels, with regional and global external datasets such as sea surface temperature and chlorophyll concentration, could provide a proxy for change in marine productivity in association with climate change and oceanographic events.

Authors Contributions

FM: lab work, analysis, writing, ZW: lab work, DC: delaminating and aging earplugs, BM and PC: lab work, CWP and RS: provided archived earplugs as well as insight, ASH: statistical analysis, writing, JF: provided insights into the Suess effect correction, SU & SJT: concept, funding, writing.

Conflict of interest statement

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest

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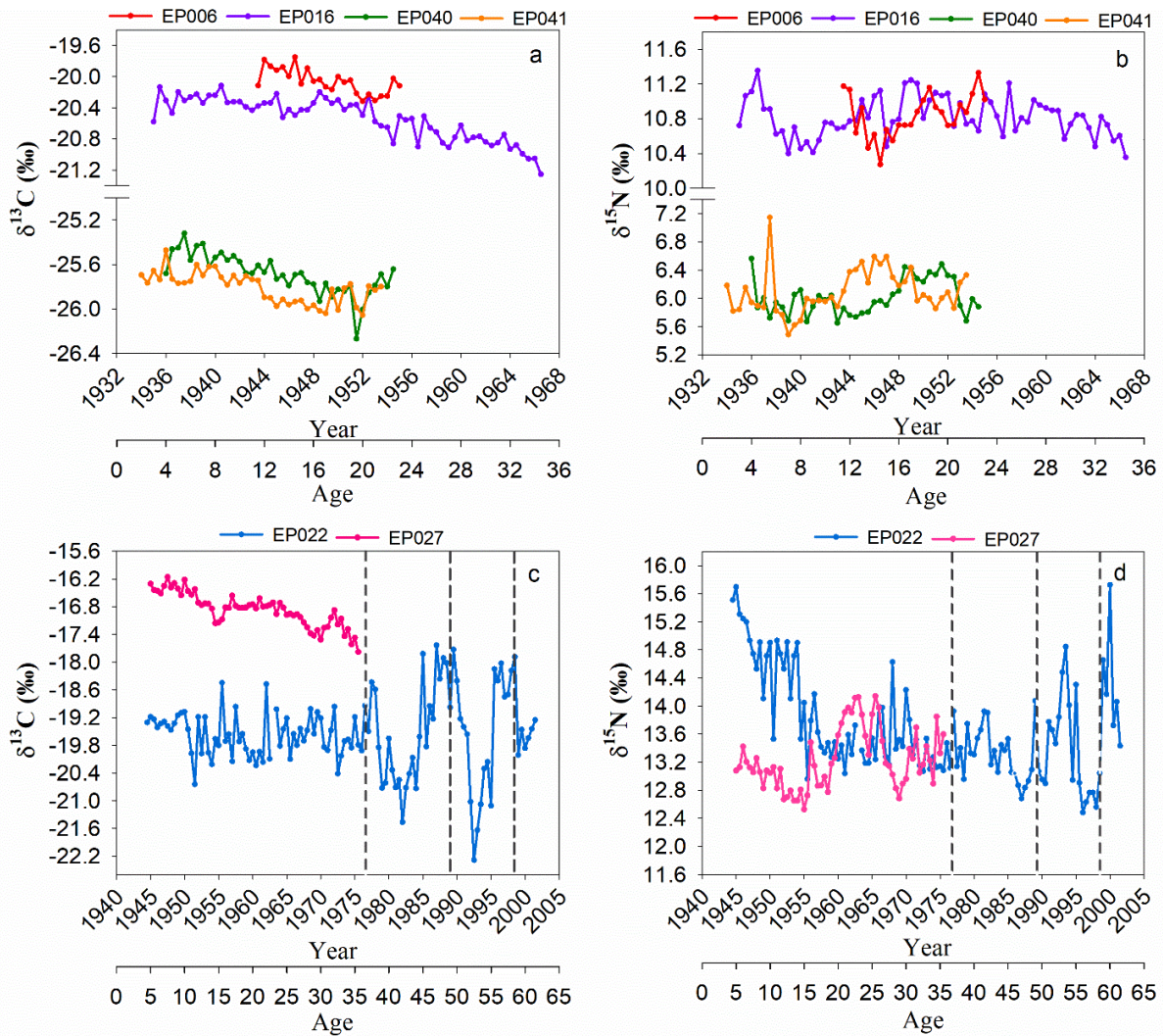
Figure 1. Time-series $\delta^{13}C$ and $\delta^{15}N$ profiles for baleen whale earplugs. Figures (a) and (b) illustrate lifetime stable isotope profiles of two fin whales (EP1006 and EP1016) and two blue whales (EP1040 and EP1041) from the NEA Ocean. Figures (c) and (d) illustrate life history stable isotope profiles of two humpback whales (EP1022 and EP1027) from the NEP Ocean. The vertical black dashed lines represent regime shifts in 1977, 1989, and 1998.
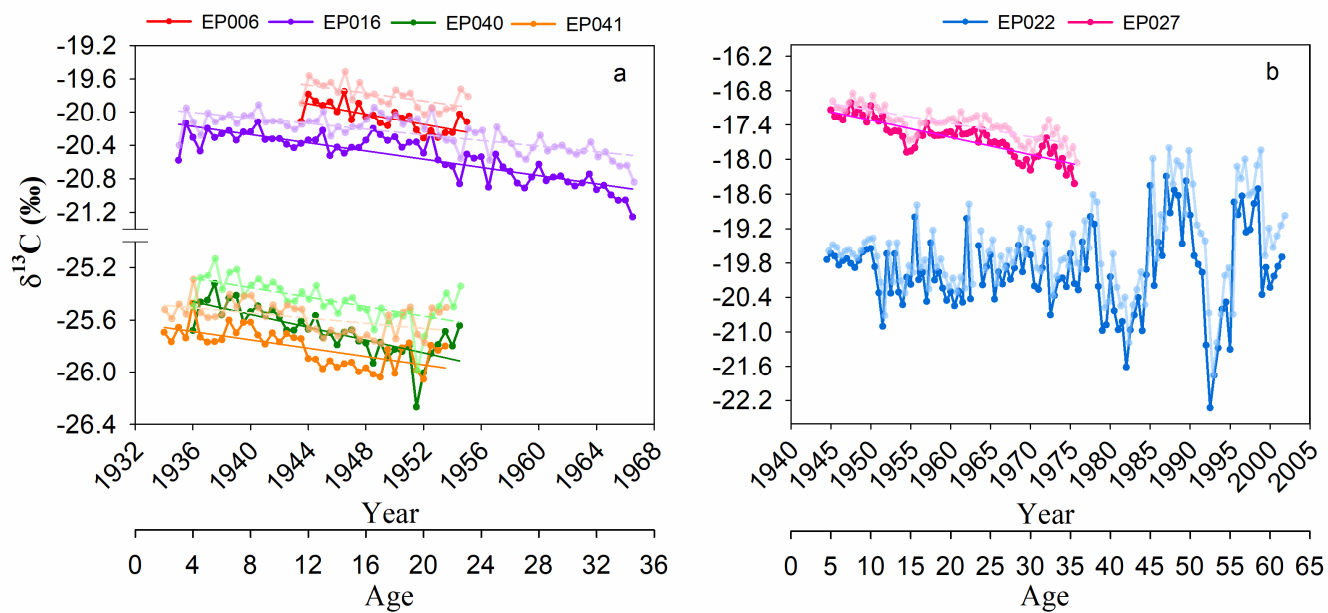
Figure 2. The decadal trend in $\delta^{13}C$ values of earplugs from the NEA (a) and the NEP (b). The Suess corrected $\delta^{13}C$ profiles for individuals are denoted by lighter shades.

Table 1. Sex, ocean of origin, approximate lifespan, and age estimates obtained from six whale earplugs used for stable isotope analysis.
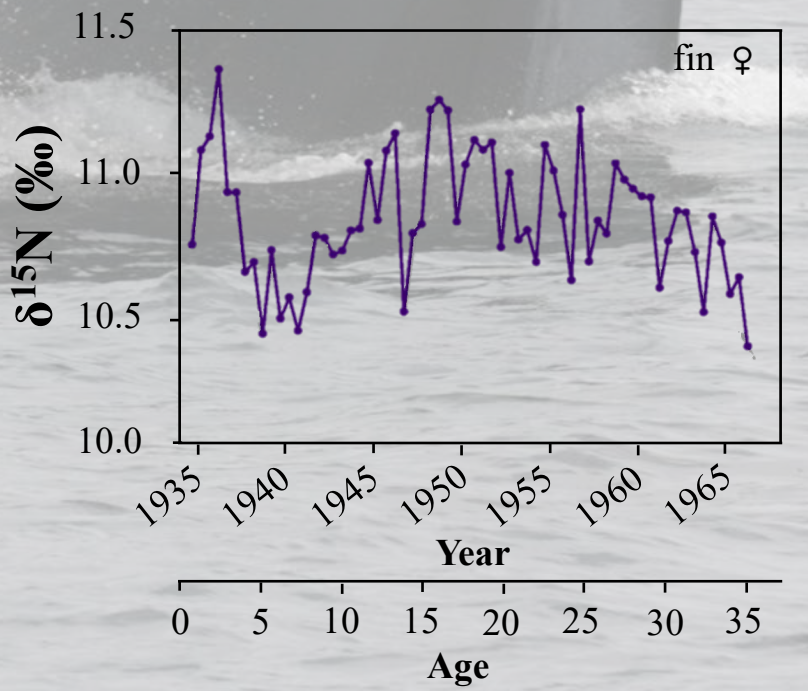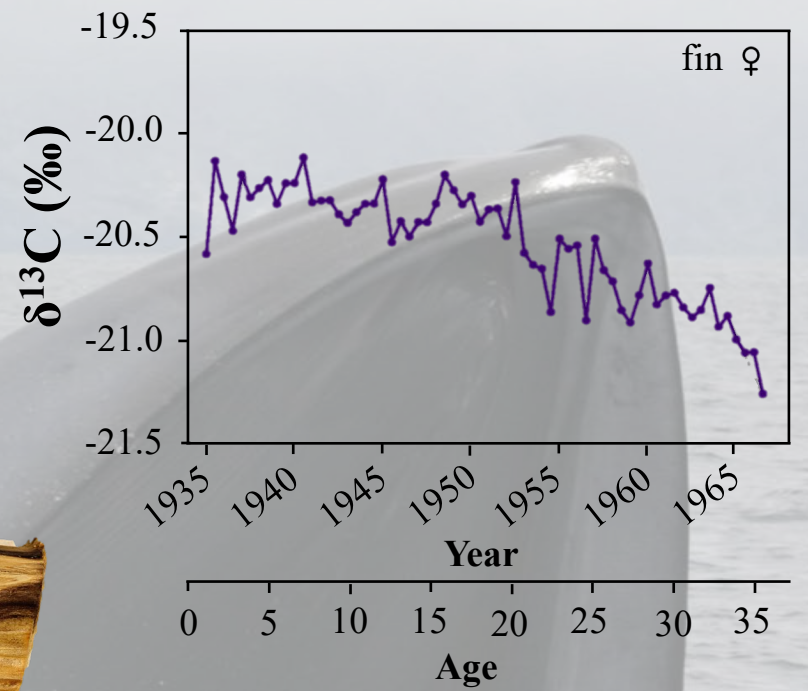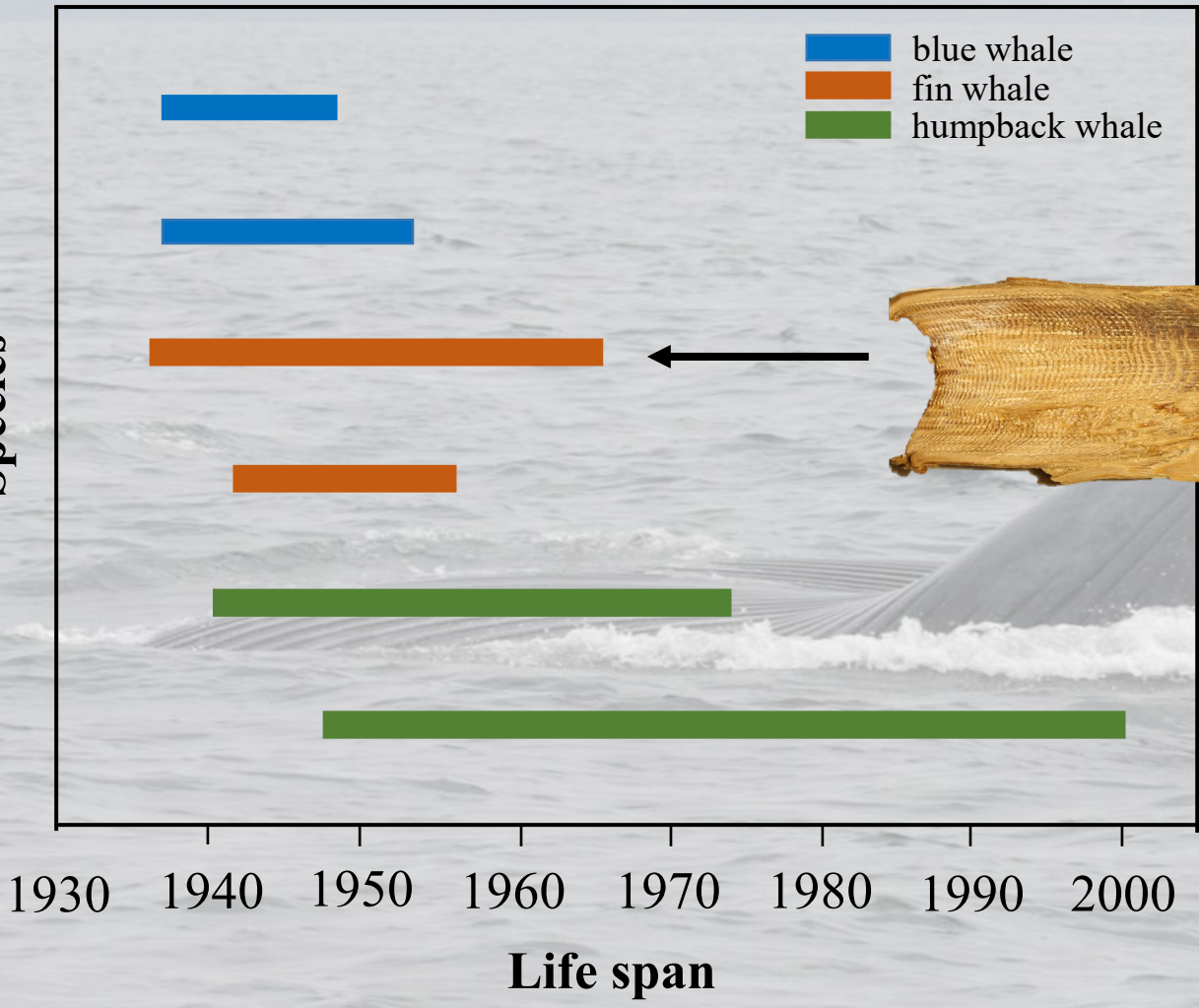
	Sample ID	Species	Sex	Ocean of origin	Estimated Lifespan	Estimated Age
	EP006	*Balaenoptera physalus* (fin)	♀	Northeast Atlantic	1943-1955	12
	EP016	*Balaenoptera physalus* (fin)	♀	Northeast Atlantic	1935-1966	31
	EP040	*Balaenoptera musculus* (blue)	♀	Northeast Atlantic	1936-1955	19
	EP041	*Balaenoptera musculus* (blue)	♀	Northeast Atlantic	1935-1955	19
	EP022	*Megaptera novaeangliae* (humpback)	♀	Northeast Pacific	1944-2001	57
	EP027	*Megaptera novaeangliae* (humpback)	♀	Northeast Pacific	1945-1975	30

Table 2. Species, ID number, number of laminae (n), mean ±SD of δ^{13}C and δ^{15}N values, slope ±SE of δ^{13}C profiles, R^2, and the slope's 95% confidence interval (CI) from each of the six baleen whale earplugs. All δ^{13}C values were corrected using a lipid normalization model.

| Species | Sample ID | n | δ^{13}C (‰) | | | | δ^{15}N (‰) |
			Mean ±SD	Slope ±SE	R^2	CI (lower, upper)	Mean ±SD
Fin	EP006	24	-20.06 ± 0.16	-0.031 ± 0.006	0.48	-0.044, -0.018	10.84 ± 0.25
Fin	EP016*	62	-20.54 ± 0.26	-0.017 ± 0.004	0.66	-0.083, -0.026	10.74 ± 0.34
Blue	EP040	38	-25.69 ± 0.18	-0.025 ± 0.004	0.57	-0.030, -0.017	6.02 ± 0.25
Blue	EP041*	39	-25.81 ± 0.14	-0.015 ± 0.003	0.51	-0.007, -0.022	6.10 ± 0.31
Humpback	EP022	113	-19.55 ± 0.83	NA	NA	NA	13.69 ± 0.73
Humpback	EP027*	61	-16.80 ± 0.38	-0.022 ± 0.007	0.75	-0.008, -0.035	13.23 ± 0.59

*AR(1) correction model was applied on δ^{13}C (‰).