



Alkenone $U_{37}^{k'}$ index differs between thermally separated populations of fin whales and krill

Diego Rita^{1,*}, Asuncion Borrell¹, Gísli Víkingsson^{2,†}, Alex Aguilar^{1,3}

¹Department of Evolutionary Biology, Ecology and Environmental Sciences, and Institute of Biodiversity Research (IRBio), University of Barcelona, Barcelona 08028, Spain

²Marine and Freshwater Research Institute, 220 Hafnarjörður, Iceland

³Reial Acadèmia de Ciències i Arts de Barcelona, Barcelona 08002, Spain

ABSTRACT: Although habitat temperature is an important determinant of species distributions, its measurement is difficult in mobile marine organisms. Chemical tracers such as alkenones constitute an alternative tool for gauging marine habitat temperature, something particularly relevant in the current scenario of global warming. The unsaturation index of alkenones, the $U_{37}^{k'}$ index, can be used to estimate sea surface temperature (SST) in living organisms. Here, we analyse alkenone concentrations in a predator species, the fin whale, and its prey, the northern krill, both sampled in 2 areas with different SSTs: SW Iceland and NW Spain. In NW Spain (but not in SW Iceland), alkenone concentrations were higher in krill than in fin whale blubber, suggesting that they may biodilute along the trophic transfer. Consistently with local SST, the $U_{37}^{k'}$ index was lower in the Icelandic samples of both fin whales and krill than in those from NW Spain, confirming the ability of this index to distinguish populations that are thermally separated. Whales are migratory animals; thus, the alkenones present in their blubber are a mix of those ingested locally and in recently visited regions. Consistently, the $U_{37}^{k'}$ index showed a higher correlation with the local SST in krill than in fin whales. Alkenone turnover rates should be considered when using this proxy to assess the thermal range of the feeding habitat of a species. We conclude that the $U_{37}^{k'}$ index is a potentially efficient tool to study the behaviour of whales, thus providing an alternative perspective to other chemical tracers.

KEY WORDS: Alkenones · $U_{37}^{k'}$ index · *Meganyctiphanes norvegica* · *Balaenoptera physalus* · Sea surface temperature · North Atlantic Ocean

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1. INTRODUCTION

Temperature is a critical factor in the distribution of any living being (Hamazaki 2002). It directly impacts a species' fitness, i.e. its capacity to reproduce, feed, grow and survive (Bronson 1985, Russell et al. 2002), and it also affects the community in which the species resides (Richardson 2004). Both factors limit the habitats used by a species and, ultimately, constrain its distribution range. Therefore, ambient temperature requirements are a basic component for a species that needs to be evaluated to establish its ecological niche. In the current scenario of global

warming, these requirements are central to determine a species' potential response to temperature shifts. This is particularly true in homeothermic organisms that live in marine waters, such as cetaceans, because their temperature constraints are particularly stringent and the determination of their thermal niche is essential to construct bioclimatic envelope models that allow predictions about resilience and potential response to warming (Lambert et al. 2011, Albouy et al. 2020). A further reason for focusing on the determination of thermal niches of cetaceans is that many species have experienced substantial demographic declines as a result of human impacts,

*Corresponding author: diegorita@ub.edu

†Deceased

and changing temperatures may pose an added pressure that compromises their recovery (MacLeod 2009). Among the species that have received more attention in this respect are mysticete whales, not only because their populations have been severely reduced by whaling (Clapham & Baker 2018) but also because these species undergo long-range latitudinal migrations, and their life cycle may therefore become compromised if any of the locations visited becomes environmentally ill-suited.

However, ambient temperature cannot always be straightforwardly measured, especially in the highly stratified marine environment. For example, in species that have separate feeding and reproductive grounds or that live within a wide temperature range, some of the occupied areas may remain unknown and thus the temperature is impossible to determine. In these cases, a chemical tracer may be a useful tool to obtain information from those habitats.

Alkenones are a group of molecules often used by palaeoceanographers to estimate water temperature. These molecules are exclusively produced by a group of haptophyte organisms, mainly *Emiliana huxleyi* (Marlowe et al. 1984), which are ubiquitous in most oceans (Volkman 2000). Although the term alkenone includes many molecules of different lengths (de Leeuw et al. 1980, Volkman et al. 1980a), the two used most to infer temperature are $C_{37:2}$ and $C_{37:3}$. The proportion of $C_{37:2}$ over the combined $C_{37:2}$ and $C_{37:3}$ is known as the U_{37}^k index (Brassell et al. 1986), which is strongly correlated with the temperature of the water where the synthesising organisms grow (Prahl & Wakeham 1987, Conte et al. 2006). Alkenones are extremely stable and accumulate in marine sediments, which permits their use to study the surface water temperature of the past (McCaffrey et al. 1990, e.g. Brassell et al. 2004, Sánchez-Montes et al. 2020). Although some organisms do not absorb alkenones (Volkman et al. 1980b, Rowland & Volkman 1982, Grice et al. 1998), these molecules can enter the trophic web and be found in krill (Rita et al. 2020) as well as in the tissues of predators, such as in the blubber of some cetaceans (Rita et al. 2020, 2021). Thus, the analysis of alkenones in marine animals can provide information on the water temperature where a species feeds. This information may be valuable to assist in the identification of the feeding grounds of some species, to gauge the effect of global warming on them, or to differentiate populations that feed in thermally separated areas.

The goal of this study was to compare the alkenone concentration and the U_{37}^k index at 2 trophic levels in 2 widely separated geographical zones with contrast-

ing sea surface water temperatures (SST). To do so, we analysed alkenones in whole body of krill *Meganyctiphanes norvegica* and in the blubber tissue from one of its predators, the fin whale *Balaenoptera physalus*, a cetacean mysticete that undergoes long-range latitudinal migrations. Samples from both species were collected off NW Spain and SW Iceland. It should be noted that the fin whales from these locations belong to 2 independent populations (or stocks) that do not intermingle (International Whaling Commission 2009, Vighi et al. 2016). The objective of the research was to assess the ability of alkenones in these organisms to gauge the thermal difference existing between the 2 sampling locations. Our hypothesis was that the alkenones detected in the krill would mirror those of the local water since the transition time from the synthesisers to the krill is expected to be relatively short compared to the fin whales, which are massive organisms that undertake seasonal, long-range migrations.

2. MATERIALS AND METHODS

From 31 fin whales caught in NW Spain in 1984–1985 and from 15 fin whales caught in SW Iceland in 1986, we collected samples of the internal blubber layer (adjacent to the muscle) and stomach content (which, visually, was only composed of krill). The whales had been taken during commercial whaling operations (Table 1). All samples were immediately frozen and stored at -20°C until analysis. From these samples, 5 krill and 5 fin whale samples from NW Spain had been analysed previously and the results published by Rita et al. (2020).

Samples were analysed following Rita et al. (2020). Briefly, approximately 5 g of internal blubber or stomach content (multiple individuals of krill) were freeze-dried for 48 h. Once dried, 1 g of sample was homogenized and introduced into test tubes; 50 μl of internal standard (2-pentatriacontanone; 20 $\text{ng } \mu\text{l}^{-1}$ in n-hexane) was then added to the test tubes. Later, samples were saponified in methanolic KOH solution (4 ml $\text{H}_2\text{O}:\text{MeOH}$, 1:9; 3 M KOH) for 60 min at 80°C . The

Table 1. Number of samples analysed for each location, year and species

Location	Year	Fin whale	Krill
NW Spain	1984	16	0
	1985	15	12
SW Iceland	1986	15	12

non-saponifiable lipids were extracted 3 times using n-hexane (4 ml). Because some amphipathic molecules were also extracted with the n-hexane, the extracted material was combined with KOH water solution (12 ml H₂O; 3 M KOH) and the mix was vortexed and centrifuged; the n-hexane phase was separated and passed through Na₂SO₄ to eliminate any possible remaining water. The n-hexane was reduced to 1–2 ml under the N₂ stream and then purified using solid-phase extraction (Supelclean LC-NH2 SPE tubes; 3 ml). Two fractions of increasing polarity (hydrocarbons and ketones) were obtained by elution with n-hexane (4 ml) and n-hexane:DCM 3:1 (v/v; 6 ml), respectively. The second fraction was evaporated under an N₂ stream and dissolved in 50 µl of n-hexane before performing gas chromatography (GC).

Chromatographic analysis was carried out on a Shimadzu GCMS-QP2010 equipped with a 30 m Sapiens-X5MS silica capillary column (0.25 mm i.d., 0.25 µm film thickness) and a mass spectrometer detector. Helium was the carrier gas with a flow of 1 ml min⁻¹. The GC temperature program was as follows: injection at 60°C; 1 min isothermal 60°C to 310°C at 40°C min⁻¹; 20 min isothermal with a total run time of 36 min. Peak identification of C₃₇ alkenones was based on the retention time of the peak and the comparison of the ion spectrum with those of pure alkenone standards. The concentration of each alkenone was quantified using the area of the ion with *m/z* 81.

U_{37}^k was calculated as:

$$U_{37}^k = \frac{[C_{37:2}]}{[C_{37:2}] + [C_{37:3}]} \quad (1)$$

where $[C_{37:2}]$ and $[C_{37:3}]$ are the concentrations of each alkenone in the sample (Prahl & Wakeham 1987). U_{37}^k was later transformed to temperature (U_{37}^k -temperature) using the Conte et al. (2006) equation for the Atlantic region:

$$U_{37}^k\text{-temperature} = 48.673(U_{37}^k)^3 - 94.569(U_{37}^k)^2 + 80.176(U_{37}^k) - 5.977 \quad (2)$$

For each sample, the U_{37}^k -temperature was compared to the actual measured temperature, which was obtained from the AVHRR_OI_NCEI-L4.GLOB.v2.0 data set. This measured temperature was calculated as the average SST present in each area. The coordinates of the feeding ground in NW Spain and SW Iceland were extracted from Sanpera & Aguilar (1992) and Víkingsson (1997), respectively.

The variability of the U_{37}^k index was higher when the concentration of the alkenones was low. This was probably due to the analytical error being more

important when the concentration was low (Grimalt et al. 2001). For this reason, those samples with a total alkenone concentration lower than 70 ng g⁻¹ were resampled and reanalysed. The average between the 2 analyses is presented in the results. If the average concentration of any alkenone was still under 30 ng g⁻¹, the U_{37}^k index of that sample was deemed unreliable and not used in further analysis.

Data analysis was performed in the statistical program R version 4.0.3 (R Core Team 2020) with RStudio interface version 1.1.447 (RStudio Team 2016). Homoscedasticity and normality of the data were tested using Bartlett's test and the Shapiro test, respectively. Alkenone concentration and U_{37}^k index data were not homoscedastic; thus, non-parametric tests (Kruskal-Wallis [KW] test) were used to detect significant differences between groups. Pairwise Wilcoxon rank sum tests were used as a post hoc analysis to detect differences between group pairs. The Kendall correlation coefficient was used to calculate the correlation between the U_{37}^k -temperature and the SST in each species and location. Linear models were used to examine the bioaccumulation of the alkenones in the blubber using the age of the individual as an explanatory variable. The age of the whales was determined by counting the growth layers in the earplugs, following Lockyer (1984b) and Aguilar & Lockyer (1987). The residuals of the model were used to check the homoscedasticity of the data, and the QQ-plot was used to detect departures from normality. Finally, the variation of the alkenone concentration over time was analysed with a general additive model (GAM) using the date of capture as a smooth variable and the location and species as fixed variables.

3. RESULTS

Alkenone concentration was significantly different among the interaction of area and species (KW test: $\chi^2 = 20.09$, *df* = 3, *p* < 0.001; Fig. 1). Specifically, in NW Spain, the alkenone concentration (mean ± SD) was significantly higher in the krill than in the fin whales (krill, 2485 ± 2363 ng g⁻¹; fin whale, 286 ± 417 ng g⁻¹; pairwise Wilcoxon rank sum tests, *W* = 343, *p* < 0.001), while in SW Iceland there was no significant difference between the 2 species (krill, 348 ± 331 ng g⁻¹; fin whale, 243 ± 211 ng g⁻¹; *W* = 87, *p* = 1). In addition, the alkenone concentration in krill samples was higher in NW Spain than in SW Iceland (*W* = 18, *p* = 0.004), although that was not the case for the blubber samples (*W* = 248, *p* = 1) (Fig. 1).

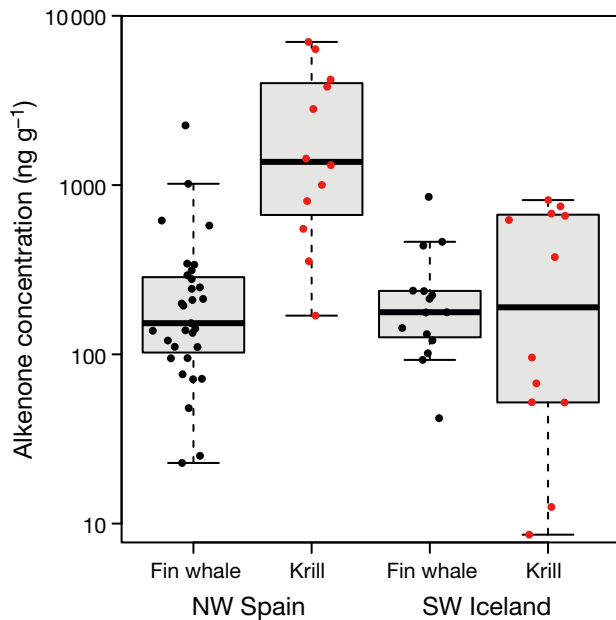


Fig. 1. Alkenone concentration measured in fin whale blubber (black) and krill (red) in the 2 locations. Horizontal lines: medians; boxes: interquartile ranges; whiskers: values within 1.5 times the interquartile range from the boxes. Note the log-transformed scale of the vertical axis

A weak positive linear relationship was detected between the alkenone concentration and the age of the whale in the NW Spain population (linear model, $t = 2.8$, $p = 0.013$; Fig. 2), but that was not the case in the Icelandic population ($t = 0.097$, $p = 0.92$; Fig. 2).

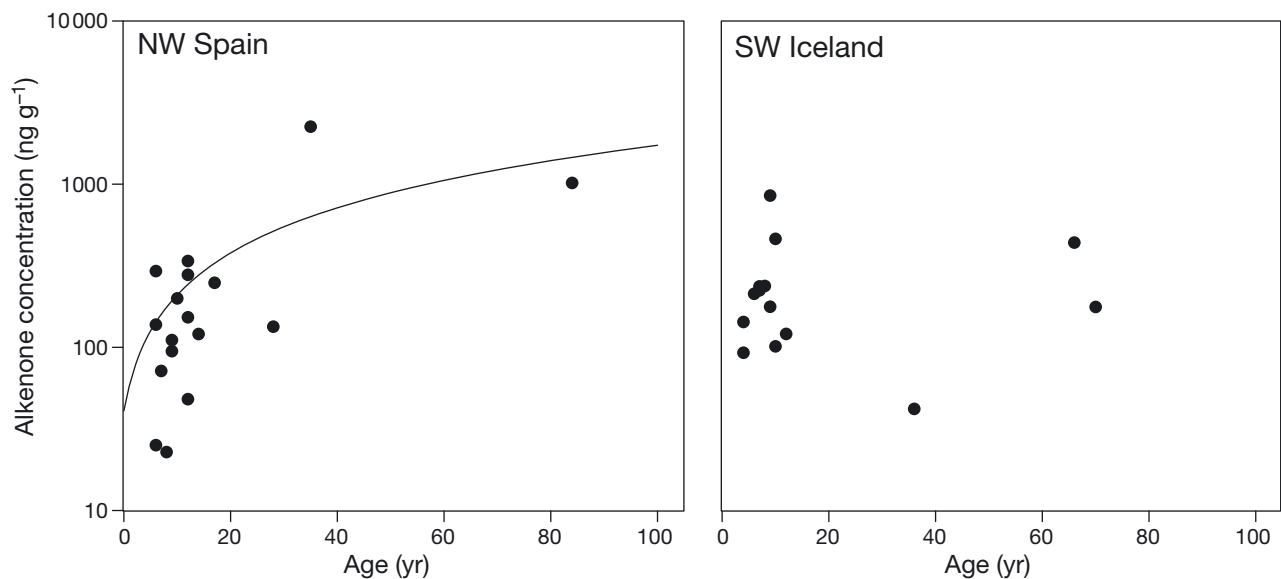


Fig. 2. Relationship between the alkenone concentration in blubber and the age of the fin whales from the NW Spain population (left) and SW Iceland population (right). The positive regression in the NW Spain population is shown as a black line. Note the \log_{10} -transformed scale of the vertical axis, which also transforms the straight linear regression into the shown logarithmic function

The GAM analysis showed no effect between the date of sampling and the concentration of alkenones in either the krill or the whales from NW Spain (GAM: krill, $F = 0.34$, $p = 0.574$; fin whale, $F = 1.07$, $p = 0.38$) or in the fin whales from SW Iceland ($F = 1.55$, $p = 0.23$) but there was an effect in the Icelandic krill ($F = 5.255$, $p = 0.03$).

The U_{37}^k index was significantly different among the interaction of species and location (KW test: $\chi^2 = 33.488$, $df = 3$, $p < 0.001$). Specifically, the U_{37}^k index was higher in NW Spain than in SW Iceland for both tissues (pairwise Wilcoxon rank sum tests: fin whales, $W = 26.5$, $p < 0.001$; krill, $W = 0$, $p = 0.002$) but they were not statistically different between the fin whales and the krill within each area (Iceland, $W = 32$, $p = 1$; NW Spain, $W = 176$, $p = 1$). The variability of the U_{37}^k index was not statistically different between the 2 tissues in either location, although it was close to significance. However, in both cases, the standard deviation was higher in fin whale than in krill (NW Spain: fin whale, $SD = 0.10$, krill, $SD = 0.076$; SW Iceland: fin whale, $SD = 0.12$, krill, $SD = 0.018$).

The U_{37}^k -temperature varied during the season (Fig. 3) and was strongly correlated with the SST in the krill samples (Kendall correlation: SW Iceland, $\tau = 0.39$; NW Spain, $\tau = 0.52$), but showed little correlation in the blubber samples of either location (SW Iceland, $\tau = -0.14$, NW Spain, $\tau = 0.19$) (Fig. 4)

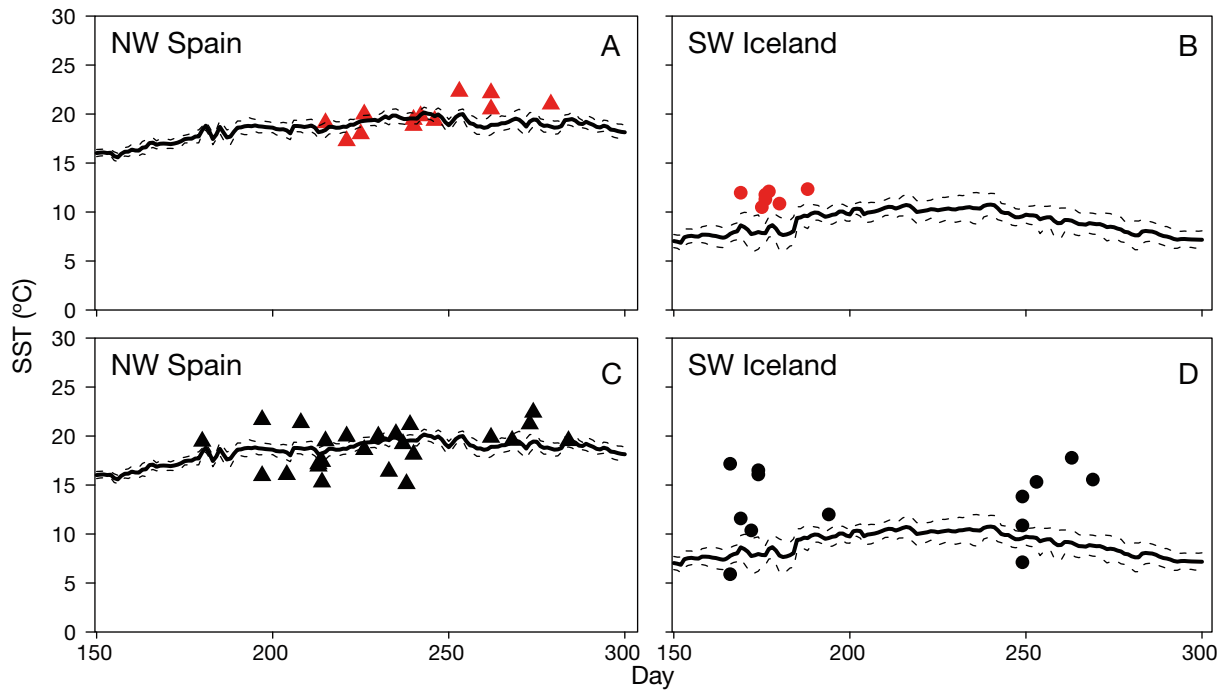


Fig. 3. Variation in U_{37}^k -temperature during the summer season in (A,B) krill and (C,D) fin whale samples. Solid line: average sea surface temperature (SST) in the corresponding feeding grounds in 1985 (NW Spain) and 1986 (SW Iceland); dashed lines: standard deviation of the measured SST across the feeding grounds on any particular day

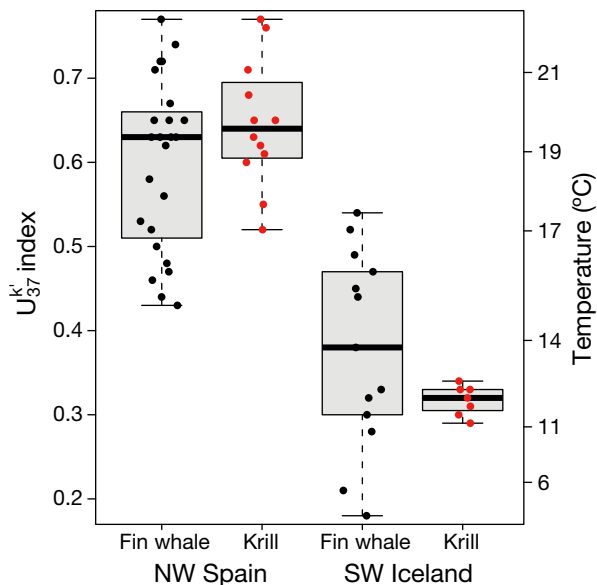


Fig. 4. U_{37}^k index measured in fin whale blubber (black) and krill (red) in the 2 locations. Horizontal lines: medians; boxes: interquartile ranges (IQR); whiskers: values within $1.5 \times$ IQR from the boxes. When each sample type and location is examined separately, the U_{37}^k -temperature was close to the measured sea surface temperature (SST) in the samples from NW Spain but higher than expected in those of SW Iceland (Fig. 3). When data from the 2 locations were pooled for each species, U_{37}^k -temperature and the measured SST were positively correlated in both, with the correlation higher in the krill ($\tau_b = 0.67$) than in the fin whale ($\tau_b = 0.35$) samples. For further details on the results, see Table S1 in the Supplement at www.int-res.com/articles/suppl/m725p157_supp.pdf

4. DISCUSSION

The results of this study show that alkenones can be detected in 2 different trophic levels, thus confirming previous research that indicated that they are transferred through the trophic web (Rita et al. 2020, 2021). It should be noted that alkenones may not necessarily be transmitted from the krill to the fin whale, but they

may be absorbed directly from the krill gut contents into whale tissues without necessarily having penetrated the krill tissues. In addition, we cannot discard that some haptophyte cells are accidentally mixed with the krill consumed by the whales, as the baleen of fin whales is built to capture relatively large prey such as krill or small fish, and are thus too coarse to selectively filter and concentrate minute organisms such as haptophytes (Nemoto 1959). As a result, the haptophyte cells thus ingested would represent only a negligible part of the stomach contents. However, it is possible that the whales ingested the haptophyte cells that had been previously ingested by the krill, which certainly have the filtering ability to capture and concentrate haptophytes.

In SW Iceland, the concentration of the alkenones was similar in krill and in fin whales, but in NW Spain it was higher in the krill than in fin whales. The apparent inconsistency in the results between the 2 areas does not allow us to discern whether alkenones maintain similar concentrations through trophic transfer or become biodiluted.

In addition, we found a slight indication of alkenone bioaccumulation in the population of fin whales from NW Spain, although the results were strongly influenced by 2 old individuals with extremely high alkenone concentrations. If these 2 individuals are removed from the statistical set, the remaining 29 would not present a correlation between age and alkenone concentration. This, combined with the lack of indication of bioaccumulation found in the Icelandic population, prevents us from reaching a final conclusion on whether bioaccumulation of alkenones occurs or does not occur in baleen whales. The accumulation of alkenones in other tissues is unlikely because the lipophilic nature of alkenones would favour the preferential accumulation in adipose tissue over other less lipid-rich tissues (Rita et al. 2020). It is worth noting that the transport of alkenones from the blood to the whale tissues is probably mediated by passive diffusion. Therefore, their concentration in the tissues would be determined by the rate of the alkenone diffusion from the blood to the tissue and from the tissues to the blood. Bioaccumulation may occur only if the latter is equal to or close to zero.

Alkenone concentration in suspended material strongly correlates with the abundance of haptophytes. In the 2 studied regions, alkenone-producing haptophytes live in surface waters all year round (Conte & Eglinton 1993, Ausín et al. 2018), although their abundance may change seasonally and short but intense haptophyte blooms may increase alkenone production for short periods of time (Conte & Eglinton 1993). Consequently, seasonality is expected to have a stronger effect on alkenone concentration than would variation between geographical locations (Conte & Eglinton 1993, Conte et al. 2001, Prahel et al. 2005).

In our study, the alkenone concentration in krill, which is expected to reflect the local alkenone production, showed both geographical and temporal variations. Alkenone concentration in krill from NW Spain was an order of magnitude higher than in SW Iceland. In addition, in Iceland, the concentration was affected by sampling date, while there was no consistent temporal trend in the samples from NW Spain. As in Iceland, alkenone production in Spain

should change seasonally, following changes in haptophyte abundance, but the low sample resolution in the area does not allow detection of such trends. In fin whales, the lack of short- or long-term seasonal variation may be explained by the low turnover rate of alkenones in blubber.

Although it is not yet clear whether alkenones bioaccumulate or not, their turnover in tissues is certainly not instantaneous. Thus, alkenones would remain in the tissue for some period of time and their overall composition would be a weighted average of those ingested during that period. This effect would tend to smooth any short-term variation in both the alkenone production and their ingestion by the whale, although alkenone composition in whale tissues may be skewed towards the alkenones produced during haptophyte blooms.

The mean value of the U_{37}^k index was higher in NW Spain than in SW Iceland for both species, probably in response to the higher SST in NW Spain compared to that in SW Iceland. These results are consistent with those obtained with another proxy for temperature previously investigated in the same fin whale populations, the oxygen stable isotope ratio or $\delta^{18}O$ value (Vighi et al. 2016), and confirm the ability of the U_{37}^k index to discriminate populations that are thermally separated. In addition, because whales are highly mobile organisms and integrate the heterogeneity of local environmental signals into their tissues, the determination of this index in their blubber may be used, alone or in conjunction with other chemical proxies of temperature, to assess temperature shifts in large water masses similarly to studies carried out with other types of tracers (e.g. Borrell et al. 2018).

Fin whales presented a higher variability in the U_{37}^k index than krill, probably due to a combination of the physiology of fin whales and their migratory behaviour. Thus, the alkenone turnover rate is expectedly higher in krill than in the fin whale tissues due to the larger body size and lower metabolism of the latter species (White & Seymour 2003). As a result, the alkenones detected in the fin whale blubber would indeed be a compendium of the local food ingested during the stay of the individuals at the feeding grounds and of that consumed during the winter or during the autumn or spring migrations, which likely encompass water masses separated by thousands of kilometres (Aguilar & García-Vernet 2018). Moreover, variability in fin whales is likely to be enhanced by the fact that some individuals may overwinter in the feeding grounds (Sanpera & Aguilar 1992, Gunnlaugsson & Víkingsson 2014),

and also because those that migrate may visit different locations with dissimilar alkenone profiles (Geijer et al. 2016).

A further complication is that fin whales are capital breeders that accumulate large reserves of energy in the form of lipids to cope with the demands of reproduction and migration in a scenario where food availability is subject to strong seasonality (Lockyer 1984a). But blubber, the main body depot of lipids, is not a homogeneous tissue; rather, it is structured into layers and its composition varies between body regions, reflecting heterogeneities in the dynamics of lipid deposition and mobilization both inside the tissue and between body locations (Lockyer et al. 1984, Aguilar & Borrell 1990). Consequently, not all blubber depots are mobilized at the same rate, and this would also contribute to introducing some variation within the tissue samples collected. This, combined with the variation in winter locations, likely explains the higher variability in the U_{37}^k index of fin whales than that of krill.

Consistent with the above results, we found that the correlation between U_{37}^k -temperature and the average measured SST was stronger in krill than in fin whales. The correlation between the 2 variables would probably increase if the half-life of alkenones in krill and fin whale tissues had been known and considered in the calculations. Unfortunately, all samples were taken during summer, when water temperature peaked and temperature variation was low. This prevented us from obtaining an accurate cross-correlation between the U_{37}^k -temperature time series and the SST time series. In SW Iceland, for example, the sampling period of the stomach content samples encompassed 21 d, which corresponded to a local change in SST of 1.16°C, while the sampling period in NW Spain encompassed 64 d, during which period the SST experienced a change of 1.55°C. These values are very low compared with the analytical error of alkenone quantification (between $\pm 0.78^\circ$ and $\pm 2.5^\circ$ depending on the temperature; Rita et al. 2020). A larger number of samples, especially if collected over a longer period of time, would allow a further exploration of the lag between the SST and the U_{37}^k -temperature measured in krill and whale tissues.

Surprisingly, the estimated temperature in Icelandic krill was 4.9°C higher than the average SST during that period. The reason for this discrepancy is unclear, although it does not appear to be related to the transport of alkenones through the trophic web, as previous studies in the region found similarly high U_{37}^k indices in suspended organic matter (Conte &

Eglinton 1993, Rodrigo-Gámiz et al. 2015). A possible explanation for this difference may be that the alkenones present in the Icelandic krill had indeed been produced in warmer waters and transported horizontally (Benthien & Müller 2000, Häggi et al. 2015). This hypothesis would be substantiated by the fact that SW Iceland is located at the northern end of the Gulf Stream extension region and is thus under the influence of a strong mid-latitude western current that brings abundant water from warmer latitudes (Wu et al. 2020). Another possible explanation is that the alkenones $C_{37:3}$ and $C_{37:2}$ are transmitted differently through the trophic web. Alkenones can be biodegraded or modified differently in certain situations, thus modifying the U_{37}^k index (Rontani et al. 2005). However, this latter possibility seems unlikely because the same process would probably affect the alkenones from the NW Spain samples in the same manner, and they did not show such alteration. Nonetheless, we cannot discard that some characteristic of the Icelandic ecosystem, which may not occur in the ecosystem of NW Spain, may have caused an uneven modification of the alkenone ratios.

The use of the U_{37}^k has some limitations that future studies should aim to solve in order to improve the efficiency of this tool. Firstly, the high variability observed in the U_{37}^k index, especially in the blubber samples, may hinder the finding of statistical differences in water temperature, especially when the sample size is small. Secondly, alkenones $C_{37:3}$ and $C_{37:2}$ may be affected differently by the transport through the trophic web. If one of them is transmitted more efficiently than the other, the resulting U_{37}^k index would be biased. Finally, haptophytes are not uniformly distributed seasonally or geographically. This may not affect krill samples as much due to the high turnover rate in these samples but it may bias the measured U_{37}^k index of fin whales, as they integrate alkenones over a relatively longer period of time. The resulting U_{37}^k index will be a weighted average over that period, and it will likely be biased towards those locations and seasons with higher concentrations of alkenone-producing haptophytes.

While the second limitation could be solved with a controlled diet study, the first and third are likely to hinder interpretation of results when analysing species with low alkenone turnover rates. In particular, these limitations will not allow the measurement of SST where the whale population had fed. However, this technique still provides information on the behaviour of these populations. For example, this study shows that alkenones are a successful chemical proxy to distinguish thermally separated cetacean

populations. The U_{37}^k index also captures the diversity of winter grounds that individuals of the same stock may visit. This may be particularly interesting in the case of the population of fin whales feeding off SW Iceland, the structure of which is still unclear and could actually be composed of several subpopulations that winter in different geographical areas (International Whaling Commission 2009). Under a global warming scenario, alkenones may be useful to detect a change in migratory behaviour through the comparison of historical and modern samples.

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