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Seaweed-eating sheep and the adaptation of husbandry in Neolithic Orkney: new insights from Skara Brae

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Abstract: *The Neolithisation of Europe involved socio-economic and biological adaptations to new environments. The use of seaweed as livestock fodder, for example, was key to the introduction of animal husbandry to the Orkney archipelago, c. 3500 cal BC. Using stable isotope analysis of faunal remains from Skara Brae, this study provides new evidence for, and clarifies the chronology of, the adoption of seaweed consumption by sheep. The results show that sheep consumed moderate amounts of seaweed from the moment of their introduction to Orkney—a practice that facilitated the successful spread of the farming lifeways to the most remote areas of Europe.*

Keywords: Orkney, Neolithic, seaweed, stable isotopes, sheep, husbandry

Introduction

Cattle and sheep, along with farming, were introduced to southern England c. 4000 cal BC, reaching Orkney off the north coast of Scotland c. 3500 cal BC during the final stage of the spread of Neolithic lifeways across Europe (Tresset & Vigne 2011; Whittle *et al.* 2011; Bayliss *et al.* 2017). The success of this expansion across the continent, starting in the seventh/sixth millennia BC, involved socio-economic, cultural and biological reconfigurations (Tresset & Vigne 2011), including innovations in husbandry practices and physiological changes in animals. Adaptation to new environmental settings and pasture resources, and the consequences of these changes on animal feeding practices, were of particular importance.

In contrast with continental Europe, where Holocene deciduous forests provided tree-leaf fodder in times of a scarcity of grass, on Orkney, farming was introduced into a predominantly treeless landscape (Farell *et al.* 2014; Bunting *et al.* 2018). Traditionally, marine seaweed has been used as an alternative fodder in coastal North-western Europe (Amorosi *et al.* 1998). This practice still persists in the present day on Orkney, where it has reached an extreme level in the sheep farming on North Ronaldsay, the northernmost island of the archipelago. Confined to the shore by a dike (or drystone wall) constructed in 1832 around the entire island, these sheep now feed exclusively on seaweed

(MacLachlan 1988)—a diet that has produced a series of metabolic adaptations (MacLachlan & Johnston 1982; Orpin *et al.* 1985; Feldmann *et al.* 2000). This practice is attested by ethnographic and historical sources from medieval times onwards (Amorosi *et al.* 1998; Balasse *et al.* 2006), although stable isotope analyses have revealed that sheep in Orkney switched to marine resources as early as the third millennium cal BC (Balasse *et al.* 2006, 2009; Balasse & Tresset 2009; Schulting & Richards 2009; Schulting *et al.* 2017).

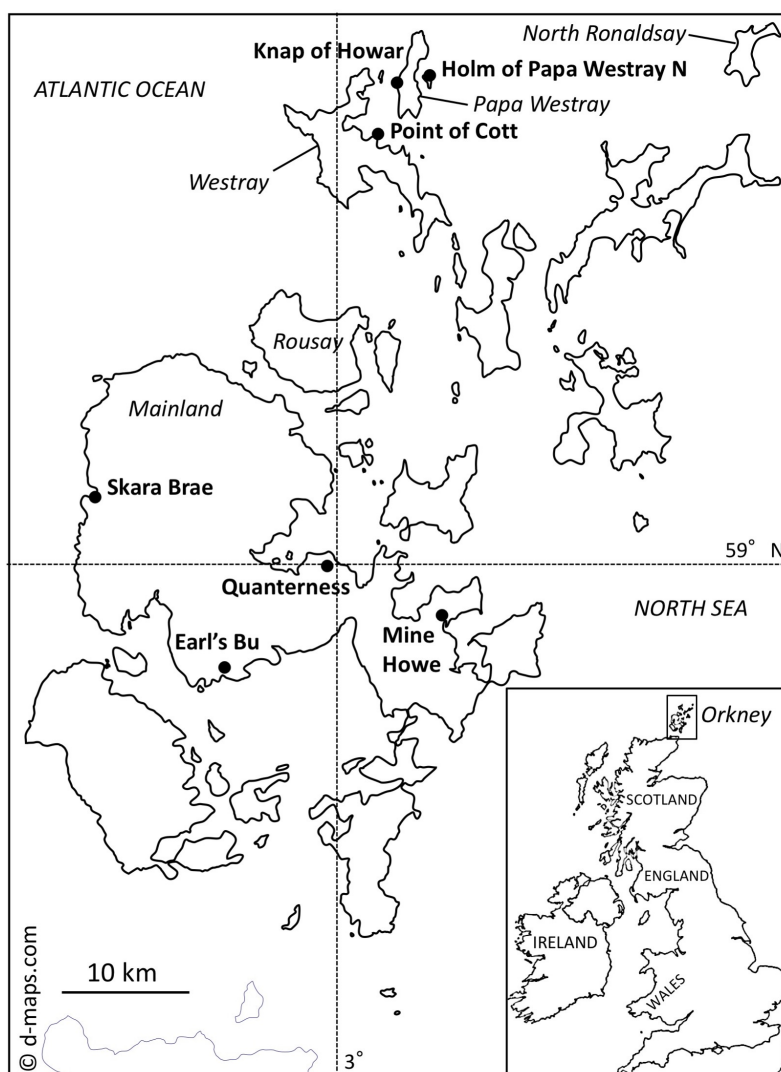


Figure 1. Location of the archaeological sites.

To date, seaweed consumption has not been identified at the Knap of Howar on Papa Westray, the site of the earliest introduction of sheep farming to Orkney in the fourth millennium cal BC (Figure 1). This contrasts sharply with the systematic contribution of seaweed to the winter sheep diet in the first half of the third millennium attested at the chambered cairn at Holm of Papa Westray (Figure 1) (Balasse *et al.* 2006; Balasse & Tresset 2009). The 500 years separating these two sheep populations may partly explain this difference in feeding practices. This chronological argument implies that there may have been a time lag between the introduction of the sheep to Orkney and the development of

a physiological adaptation for the significant ingestion of seaweed. Alternatively—or additionally—the isolated location of Holm of Papa Westray on a small islet (Figure 1), may have involved additional environmental constraints, introducing a remoteness argument to explain seaweed consumption by sheep at this site. A few other indisputable examples of seaweed-eating sheep have been reported in Neolithic Orkney that are potentially contemporaneous with the sheep from Holm of Papa Westray: one specimen from the Point of Cott burial cairn from the third millennium cal BC (Balasse *et al.* 2009), and two specimens from Quanterness, which date to the early third and early to third millennium cal BC (Schulting *et al.* 2017). The location of these sites on the Westray and Mainland islands (Figure 1) demonstrates that the remoteness argument alone cannot account for the introduction of seaweed into the sheep diet.

In the present study, we investigate the role of seaweed in Neolithic husbandry at Skara Brae, in the Bay of Skail on Mainland Orkney (Figure 1). Excavations at the settlement have yielded a large assemblage of cattle and sheep remains (Clarke 1976). Skara Brae was occupied from c. 3400–2500 cal BC (Bayliss *et al.* 2017), contemporaneous with Knap of Howar and Holm of Papa Westray. The first aim of this study is to confirm the chronology of the appearance of seaweed consumption practices and behaviours during the fourth and third millennia BC. The second aim is to test for seaweed consumption amongst Neolithic Orkney cattle. At Knap of Howar, seaweed did not contribute significantly to the diet of cattle (Balasse *et al.* 2006); this hypothesis could not be tested at Holm of Papa Westray, due to the scarcity of cattle remains. At Skara Brae, it is possible to analyse both sheep and cattle populations, thereby providing a more holistic view of Neolithic husbandry. We investigate seaweed eating at Skara Brae using a new methodological approach, in which co-variations in carbon and oxygen isotope sequences in teeth are modelled as a means of highlighting deviation from the expected seasonal cycle in terrestrial grass $\delta^{13}\text{C}$ values. The objective is to detect minor contributions of seaweed to animal diet.

Material and methods

Occupation of the small village of Skara Brae can be divided into three phases. The earliest human occupation, Phase 0, began c. 3400 cal BC and ended c. 3200 cal BC. This was followed by a 300-year hiatus until the establishment of nucleated settlement (phase 1) c. 2900 cal BC. This first village was abandoned after a short period of use and the settlement re-occupied (phase 2) between c. 2750 and 2500 cal BC (Bayliss *et al.* 2017). Sheep and cattle teeth were selected for analysis from all of these occupation phases (see the online supplementary material (OSM) Table S1).

Seaweed consumption can be investigated through the analysis of stable carbon isotope ratios. In Orkney, $\delta^{13}\text{C}$ values varying between -32.8‰ and -29‰ have been measured in modern terrestrial grasses, while marine seaweed collected on the shore have yielded $\delta^{13}\text{C}$ values fluctuating between -19.9‰ and -16.5‰ (Balasse *et al.* 2009). These $\delta^{13}\text{C}$ values are inherited along the food chain. In archaeological animal remains, this signal may be retrieved from the skeleton mineral fraction (bioapatite), whose carbon isotope composition is influenced by diet (Krueger & Sullivan 1984). As enamel retains a record of the animal's dietary history over the duration of tooth formation, the changing contribution of seaweed to the diet can be investigated using sequential analysis of tooth enamel. The parallel analysis of oxygen isotope composition ($\delta^{18}\text{O}$) allows for the investigation of seaweed consumption on a seasonal scale (Balasse *et al.* 2005, 2009).

Seasonal changes in $\delta^{13}\text{C}$ values are expected in diets based on both terrestrial plants and seaweed. Variations of 1‰–2‰ have been reported in the $\delta^{13}\text{C}$ values of C_3 terrestrial plants—the prevalent type in this area of Europe—with the highest values occurring during the summer and the lowest during the winter (Smedley *et al.* 1991). Seasonal variation in the relative proportion of seaweed species available for sheep grazing on the Orkney shores are also reported. *Laminaria digitata* and *L. hyperborea*, which account for over 75 per cent of the modern North Ronaldsay sheep diet in the summer, have higher $\delta^{13}\text{C}$ values than *Palmaria palmata*, which contributes around half of their winter diet (Raven *et al.* 2002; Hansen *et al.* 2003; Balasse *et al.* 2009). This leads to higher values in the enamel for a summer seaweed diet compared to winter. Finally, changes in the relative contributions of seaweed and grass to the diet are expected on a seasonal scale, with reduced availability of terrestrial grass in winter coinciding with greater access to seaweed driven ashore by winter storms. This would lead to higher $\delta^{13}\text{C}$ values for animal diet in the winter, compared with the summer. In all cases, seasonal change in diet is expected to lead to co-variations in enamel $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values. This co-variation would, however, follow different patterns:

- 1) A diet composed exclusively of terrestrial plants throughout the year would lead to lower overall $\delta^{13}\text{C}$ values and seasonal variations in the $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ sequences (pattern 1).
- 2) A diet composed exclusively of seaweed throughout the year would lead to higher $\delta^{13}\text{C}$ values and seasonal variations in the $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ sequences (pattern 2).
- 3) A diet with a higher proportion of seaweed during the winter would lead to variations in the $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ sequences; the higher the relative proportion of seaweed, the higher the $\delta^{13}\text{C}$ values (pattern 3).

These hypotheses can be tested using $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ sequences from modern sheep with known diets as reference populations (Table S2). Pattern 1 is tested using the grazing sheep from Rousay Island (ROU, Figure 1; Balasse *et al.* 2009). Additionally, the sample for grazing sheep is enlarged with samples (KMZ) from Kemenez Island (Molène, Finistère, France). To check for consistency in $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ sequences between modern and preindustrial times, we also include one sheep from the Bronze Age '22 bis' site on Kemenez Island (Gandois 2017). The references for pattern 2 are sequences measured in modern North Ronaldsay sheep (NR, Figure 1) feeding on seaweed year-round (Balasse *et al.* 2005). Recently, parts of the dike encircling North Ronaldsay have fallen into disrepair, allowing sheep increased access to terrestrial grazing. Some of these animals, which feed partly on terrestrial grass during summer (Balasse *et al.* 2005, 2009), are used as references for pattern 3.

Enamel from the anterior lobe of the second molar (M2) or the middle lobe of the third molar (M3) was sequentially sampled, following Balasse *et al.* (2005). Powdered archaeological enamel samples were pre-treated to eliminate diagenetically introduced carbonates (0.1M acetic acid for 4 h, 0.1ml/mg). Bioapatite samples weighing 580–620 μg were reacted with 100% phosphoric acid at 70°C in individual vessels, in an automated cryogenic distillation system (Kiel IV device), interfaced with a DeltaV Advantage isotope ratio mass spectrometer. The analytical precision within each run—estimated from repeated analyses of our laboratory carbonate standard (Marbre LM, normalised to NBS19)—was lower than 0.06‰ for $\delta^{18}\text{O}$ values and lower than 0.03‰ for $\delta^{13}\text{C}$ values.

The phase shift between the $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ sequences was determined through a sinusoidal model (Table S3). When both signals are in phase (i.e. the highest and lowest $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ values are

acquired respectively at the same time of the annual cycle), the phase shift would be 0° or 360°. Opposed phased signals (the highest $\delta^{18}\text{O}$ value is measured when the $\delta^{13}\text{C}$ value is the lowest, and vice versa) would lead to a 180° shift.

Results

Reference grazing and seaweed-eating sheep

Results from the sequential analysis of the Kemenez sheep are shown in Figure S1. Results from the modelling of the $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ sequences for the Kemenez, Rousay and North Ronaldsay sheep are reported in Table S3, and the phase shift for each specimen is presented in Table S2. Figure 2A shows intra-tooth variations in enamel $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values in three chosen specimens, illustrative of patterns 1, 2 and 3, respectively. Figure 2B is a plot of the phase shift between the $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ sequences against the highest value measured in the $\delta^{13}\text{C}$ sequence ($\delta^{13}\text{C}_{\text{max}}$) for all 21 reference specimens. All $\delta^{13}\text{C}$ values measured in modern sheep were corrected (+1.5‰) for the fossil fuel effect (Francey *et al.* 1999). The $\delta^{13}\text{C}_{\text{max}}$ value clearly discriminates between a purely grass diet in pattern 1 (-15.0‰ to -12.9‰) and a purely/predominantly seaweed diet in patterns 2 and 3 (-4.9‰ to -0.4‰).

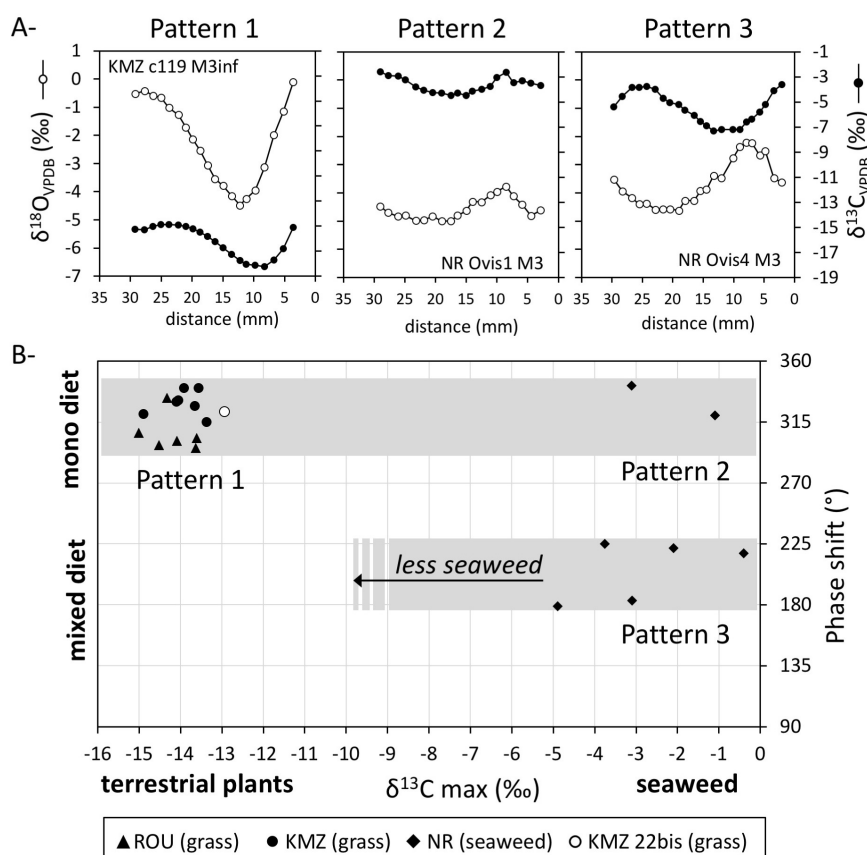


Figure 2. A) Sequential analysis of stable carbon ($\delta^{13}\text{C}$) and oxygen ($\delta^{18}\text{O}$) isotope ratios in sheep tooth enamel, illustrating patterns 1, 2 and 3. The samples are located in the tooth crown using their distance from the enamel-root junction; B) phase shift between the $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ sequences plotted vs the highest value measured in the $\delta^{13}\text{C}$ sequence ($\delta^{13}\text{C}_{\text{max}}$). Pattern 1 = grazing sheep; pattern 2 = seaweed-eating sheep; pattern 3 = mixed diet with higher contribution of seaweed in winter. All $\delta^{13}\text{C}$ values measured in modern sheep corrected (+1.5‰) for the fossil fuel effect.

The phase shift between the $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ sequences clearly discriminates between a monotype diet (terrestrial only/marine only: patterns 1 and 2) and a mixed diet with changing proportions of terrestrial/marine plants (pattern 3). In patterns 1 and 2, the $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ sequences vary in phase, although with a slight shift (296° to 342° , instead of the 360° expected in-phase signals). By contrast, in pattern 3, the $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ sequences show opposed variations (phase shift from 179° to 225°). The phase shift between $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ sequences in the Bronze Age sheep from Kemenez (KMZ, '22 bis') is similar to those observed in modern sheep from the same island, suggesting that pre-industrial-age sheep can be compared to these modern references.

Neolithic sheep and cattle

Results from the sequential analysis of the sheep and cattle from Skara Brae are shown in Figures S2–5. The range of intra-tooth variation in $\delta^{13}\text{C}$ values is presented in Figure 3B, where it is compared to other Neolithic datasets. At Skara Brae, there is a gradient towards higher $\delta^{13}\text{C}$ values in sheep from phases 0–2. All of the sheep from phase 0 and most from phase 1 demonstrate consistently low $\delta^{13}\text{C}$ values ($\leq -11\text{‰}$), comparable to those measured at Knap of Howar. One sheep from Skara Brae phase 1 and most from phase 2 (6 of 10) show higher $\delta^{13}\text{C}$ values ($> -10\text{‰}$), compared with some of those measured at Holm of Papa Westray. Overall, the sequences measured at Holm of Papa Westray show higher $\delta^{13}\text{C}$ values compared with Skara Brae phase 2 (Figure 3B). All cattle teeth from Skara Brae (phases 0–2) show consistently low $\delta^{13}\text{C}$ values ($\leq -11\text{‰}$), compared with those measured in the cattle from Knap of Howar (Figure 3B).

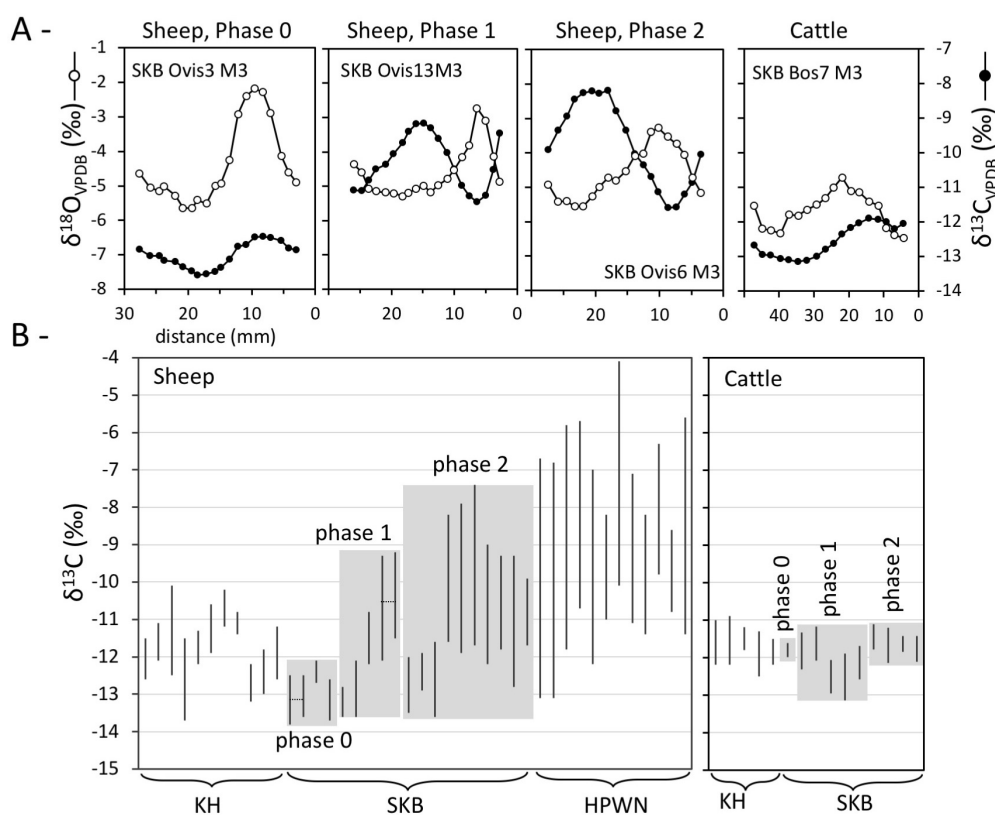


Figure 3. A) Typical patterns of co-variation of $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ sequences in the sheep, cattle and red deer teeth from Skara Brae; B) range of intra-tooth variation of the $\delta^{13}\text{C}$ values measured in Skara Brae (SKB) sheep, cattle and red deer molars, compared to values at Knap of Howar (KH) and Holm of Papa Westray (HPWN). Specimens

linked by hyphens belong to the same individual (SKB Ovis3 M2–M3; SKB Ovis13 M2–M3). The red deer from Links of Noltland (LN) are also included for comparison. Data from KH and HPWN from Balasse *et al.* (2006) and Balasse and Tresset (2009) (figure by M. Balasse).

Figure 3A shows typical patterns of co-variation in the $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ sequences in sheep from phases 0–2 and in cattle. Results from the modelling of the Skara Brae, Knap of Howar and Holm of Papa Westray $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ sequences are presented in Table S4. The model cannot be applied to a number of $\delta^{13}\text{C}$ sequences, either due to the very low amplitude of intra-tooth variation (<1‰), or because of the absence of a suitable sinusoidal pattern. For all the remaining specimens, the phase shift between the $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ sequences is plotted against the $\delta^{13}\text{C}_{\text{max}}$ value in Figure 4. At Skara Brae, all the phase 0 sheep are very close in values to the reference grazing sheep (pattern 1). In phase 1, one animal follows pattern 1 and a second falls within the area defined for the winter seaweed contribution (pattern 3). In phase 2, the vast majority of sheep follow pattern 3. The cattle from Skara Brae show very limited amplitude in intra-tooth variation ($\leq 1.3\text{‰}$, Figure 3B). The phase shift between the $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ sequences places the cattle in pattern 1.

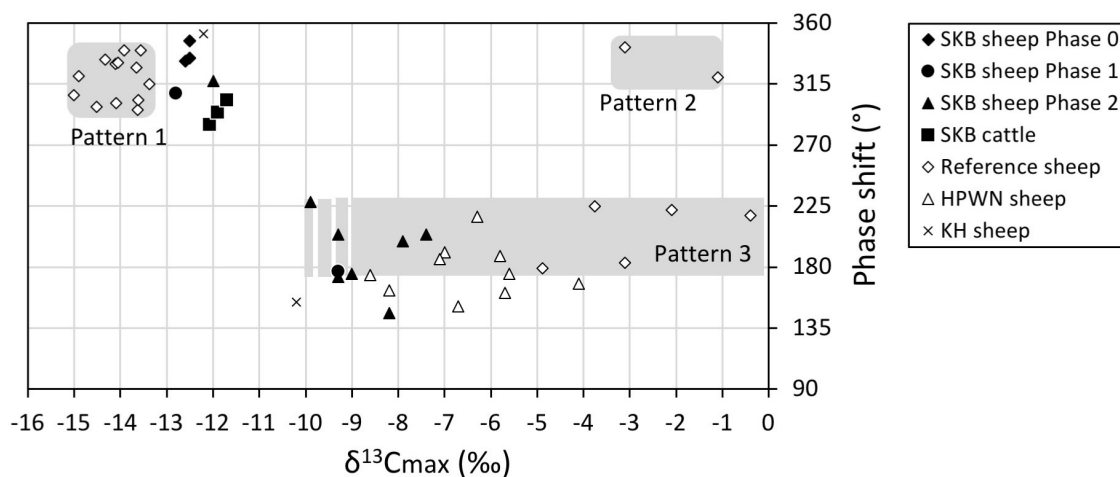


Figure 4. Phase shift between the $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ sequences plotted vs the highest value measured in the $\delta^{13}\text{C}$ sequence: comparison of the Neolithic sheep from Skara Brae (SKB), Knap of Howar (KH) and Holm of Papa Westray (HPWN) with the reference sheep. Pattern 1 = grazing sheep; pattern 2 = seaweed-eating sheep; pattern 3 = mixed diet with higher contribution of seaweed in winter.

The modelling of previously published sequences from Holm of Papa Westray (Balasse *et al.* 2006; Balasse & Tresset 2009) confirms that all of the sheep from this assemblage follow pattern 3. During phase 2, the winter seaweed contribution to the sheep diet is higher at Holm of Papa Westray than at Skara Brae. None of the archaeological sheep samples following pattern 3 reach the level of seaweed contribution observed in the modern North Ronaldsay sheep.

The results for the sheep from Knap of Howar demonstrate a variety of patterns for seasonal variations in $\delta^{13}\text{C}$ values, most of which do not follow a sinusoidal trend (Balasse *et al.* 2006; Balasse & Tresset 2009). Two $\delta^{13}\text{C}$ sequences can be modelled. KH Ovis9M3, which shows the lowest $\delta^{13}\text{C}_{\text{max}}$ value (-12.2‰) for this assemblage, falls within pattern 1, with a phase shift of 352°. KH Ovis7M3 has a relatively low $\delta^{13}\text{C}_{\text{max}}$ value (-10.2‰—also the highest for this assemblage), but is very close to pattern 3 with a phase shift of 154° (Figure 4)—suggesting seaweed consumption during winter.

Taking note of this result, three other sheep from Knap of Howar deserve special attention: KH Ovis3, KH Ovis4 and KH Ovis6 all show clear trends towards higher $\delta^{13}\text{C}$ values in winter (Figure 5). In KH Ovis4 and KH Ovis6, the contribution of seaweed was insufficient to induce a complete reversal of $\delta^{13}\text{C}$ values in the annual variation cycle, although the trend is clearly initiated.

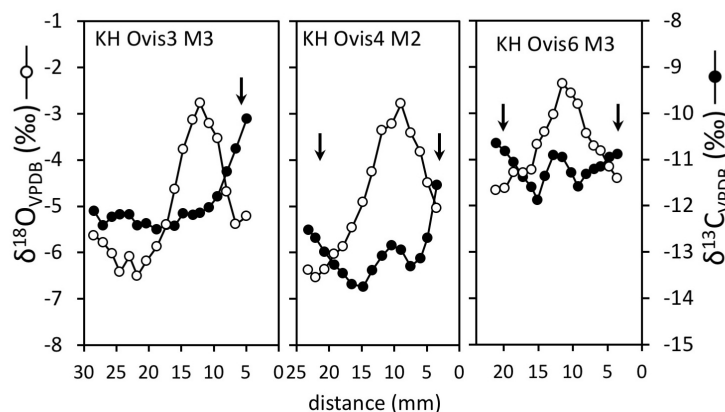


Figure 5. Variation patterns of $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ sequences in some of the sheep from Knap of Howar (data from Balasse *et al.* (2006) and Balasse and Tresset (2009)). Contrasting variation of $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values in some portions of the annual sequence (arrows).

Discussion

Reevaluation of the previous results from Knap of Howar (Balasse *et al.* 2006; Balasse & Tresset 2009) highlights a reversal of the expected pattern of co-variation in $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values in four specimens. This emphasises the contribution of seaweed to the diet of sheep right from the start of the introduction of animal husbandry to Orkney. While seaweed has not been detected in Skara Brae phase 0, which is contemporaneous with Knap of Howar (Bayliss *et al.* 2017), the small sample size from this period must be acknowledged; the contribution of seaweed to sheep diet evidenced in phase 0 at Knap of Howar is much lower than in later phases. The significant consumption of seaweed during winter is visible in the majority of the sheep from Skara Brae phase 2, which are contemporaneous with the sheep from Holm of Papa Westray (Bayliss *et al.* 2017). Thus, the chronology of a well-established behaviour evidenced at Holm of Papa Westray is confirmed (Balasse *et al.* 2006; Balasse & Tresset 2009). At Skara Brae, this clear pattern is observed even earlier in one specimen from phase 1, dating to the beginning of the third millennium BC. These results confirm the progressive introduction of seaweed to the Neolithic sheep diet, reaffirming the chronological argument, which possibly reflects a progressive adaptation of the digestive physiology of sheep to seaweed.

A higher contribution of seaweed at Holm of Papa Westray

Although the pattern of seasonal seaweed contribution to the sheep winter diet observed at Skara Brae is similar to that evidenced at Holm of Papa Westray, the relative proportion of seaweed in the diet is almost always higher at the latter site. The same is true for the seaweed-eating sheep from Point of Cott (Westray Island), the remains of which were found in the infilling of the monument's passage. This event corresponds with a separate period of activity to the primary use of

the cairn for burial, and dates to between the mid third millennium and the mid second millennium BC (Bayliss *et al.* 2017). Although this is later than the sheep from Holm of Papa Westray, the Point of Cott sample has yielded a $\delta^{13}\text{C}_{\text{max}}$ value of -7.9‰ (Balasse *et al.* 2009), reflecting a lower contribution of seaweed than at the former site.

These results tend to support the remoteness argument. This is particularly relevant to the small Holm of Papa Westray islet, which may have served as a natural penning area. Here, free-ranging sheep may have had no alternative but to turn to marine resources in times of the severe scarcity of grass during winter (Balasse & Tresset 2009). Nevertheless, the significant contribution of seaweed to the diet of the sheep found at Skara Brae—a Mainland village context—suggests that the remoteness argument alone cannot explain why sheep turned to seaweed. Furthermore, by this time, seaweed may have developed into a fully established element of the husbandry system, rather than an unintentional consequence of unpenning sheep.

Differences between sheep and cattle

At Skara Brae, sheep and cattle were taken to different pasture grounds during the winter: sheep were brought to the shore, whereas cattle were kept on terrestrial pastures. Previous studies have also demonstrated the terrestrial grazing of Neolithic cattle in Orkney, as well as the Outer Hebrides (Jones & Mulville 2016; Schulting *et al.* 2017). Cattle feeding on seaweed is attested on the islands of Brittany (Arzel 1987) and in Iceland, where it is used as a substitute for hay due to a lack or inaccessibility of grasslands (Hallson 1964). In Iceland, seaweed is observed to have been used to a lesser extent for cattle than for sheep, although the reasons for this are unclear (Hallson 1964). Schulting *et al.* (2017) suggest that during the Neolithic in Orkney, the greater value of cattle in relation to sheep may explain why they were given priority access to grassland resources and hay supplies.

Conclusion

Re-evaluation of the results from stable isotope analysis of faunal remains from the mid to late fourth-millennium cal BC Knap of Howar site indicates that sheep may have included moderate amounts of seaweed in their winter diet from the time of their first arrival in Orkney. Seaweed consumption is clearly detected in one sheep from phase 1 (early third millennium cal BC) at Skara Brae and found in the majority of specimens from phase 2 (c. 2750–2500 cal BC), and therefore appears to be an established practice by this time. It is not possible to establish whether Neolithic sheep turned to seaweed of their own accord, or were brought to the shore by herders. In any case, these results confirm the chronology of the gradual introduction of seaweed into the Neolithic sheep diet in Orkney, which may have been the result of changes in sheep behaviour or physiology. When compared with Skara Brae, the considerably higher relative contribution of seaweed to the winter sheep diet at Holm of Papa Westray also confirms the validity of the remoteness argument, at least as far as the quantity of seaweed consumption is concerned.

The introduction of seaweed to the diet of Orkney's Neolithic sheep, however, was not the start of an unbroken tradition that endures to the present. Winter seaweed consumption by sheep has been detected through isotope analysis for a single animal from the Iron Age site of Mine Howe (Figure 1; Balasse *et al.* 2009), although microwear analysis on the same assemblage does not confirm seaweed-eating as a common pattern in sheep at the site (Mainland *et al.* 2016). Further, the colonisation of Orkney by Viking settlers from Norway brought new animal husbandry practices, and

the settlers may have imported their own livestock (Mainland *et al.* 2016). Currently, both stable isotope (Balasse *et al.* 2009) and tooth microwear analyses (Mainland *et al.* 2016) suggest a year-round terrestrial diet for sheep at the Viking/Norse settlement at Earl's Bu (late 800s to mid 1100s AD). There is, therefore, little evidence for unbroken continuity in the history of Orkney husbandry between the Neolithic and the present.

Finally, none of the evidence for seaweed-eating sheep on Orkney from the Neolithic to the Viking period shows any significant contribution of seaweed to diet outside the winter period. Moreover, none of them reached the level of seaweed contribution found in modern sheep on North Ronaldsay. Here, the exclusive reliance on seaweed is a consequence of sheep being confined to the shore to prevent grazing on cultivated grounds. The associated physiological adaptations, therefore, may have arisen only following human intervention in the nineteenth century. In terms of husbandry practices and animal behaviour, however, the practice certainly has ancient roots, dating to the first arrival of farmers and sheep in Orkney.

Assessing whether this pattern was unique to Orkney or more widespread across prehistoric North-western Europe requires additional research. Today, seaweed-eating sheep are known in Shetland (latitude 60° north) and the Faroe Islands (62° north), but the archaeology of this practice has not yet been investigated in these places. At a number of sites of Neolithic to Iron Age date in the Scottish Western isles (57.5° north), bone collagen (as opposed to enamel bioapatite) stable isotope analysis has failed to demonstrate seaweed consumption by sheep (Jones & Mulville 2016). But, as sheep bone metabolism varies with the season—showing a peak in bone formation in summer and increased bone resorption in autumn and winter (Arens *et al.* 2007)—winter seaweed consumption could be more difficult to identify in bone collagen. Future investigations using seasonal resolution (i.e. sequential analysis in teeth) may reveal a different picture in these locations. Exploitation of marine resources reflects not only a zotechnical innovation by Neolithic farmers to cope with local environmental constraints, but also a revolution in thinking, by exploiting the littoral margins to sustain terrestrial domestic livestock. This innovation is emblematic of a series of other changes, adopted over the course of the European Neolithic, in terms of farming practices and animal and plant physiology (Marinova & Valamoti 2014; Orton *et al.* 2016; Ivanova *et al.* 2018). These changes illustrate how Neolithic farmers faced the challenges of introducing domesticates and establishing sustainable agropastoral systems in the most remote areas of Europe.

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[Supplementary material]**Seaweed-eating sheep and the adaptation of husbandry in Neolithic Orkney: new insights from Skara Brae**

Marie Balasse, Anne Tresset, Gaël Obein, Denis Fiorillo & Henri Gandois

Table S1. Provenience and dates of the selected sheep (*Ovis*) and cattle (*Bos*) second (M2) and third molars (M3). Dates after Bayliss *et al.* (2017). Highest $\delta^{13}\text{C}$ values within the tooth, and phase shift between $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ sequences as determined from the modelling.

Specimen ID	Context	Phase	Date cal BC	$\delta^{13}\text{C}_{\text{max}}$ (‰)	Phase shift (°)
SKB Ovis 3 M2	157	Phase 0	~ 3400-3100	-12,5	347
SKB Ovis 3 M3	157			-12,5	334
SKB Ovis 4 M3	168			-12,1	nd
SKB Ovis 17 M3	157			-12,6	332
SKB Ovis 2 M3	213	Phase 1	~ 2900-2825	-10,8	nd
SKB Ovis 12 M3	213			-12,8	308
SKB Ovis 13 M2	213			-9,3	177
SKB Ovis 13 M3	213			-9,2	nd
SKB Ovis 14 M3	213			-12,1	nd
SKB Ovis 1 M3	102	Phase 2	~ 2750-2500	-11,9	nd
SKB Ovis 5 M3	102			-12,0	317
SKB Ovis 6 M3	102			-8,2	146
SKB Ovis 7 M3	102			-7,9	199
SKB Ovis 8 M3	102			-7,4	204
SKB Ovis 9 M3	102			-9,0	175
SKB Ovis 10 M3	102			-11,6	nd
SKB Ovis 11 M3	102			-9,3	173
SKB Ovis 15 M3	102			-9,3	204
SKB Ovis 16 M3	102			-9,9	228
SKB Bos 6 M3	168	Phase 0	~ 3400-3100	-11,6	nd
SKB Bos 3 M3	213	Phase 1	~ 2900-2825	-11,3	nd
SKB Bos 4 M3	213			-11,2	nd
SKB Bos 5 M3	162			-12,1	285
SKB Bos 7 M3	213			-11,9	294
SKB Bos 10 M3	162			-11,7	303
SKB Bos 1 M3	102	Phase 2	~ 2750-2500	-10,1	nd
SKB Bos 2 M3	102			-11,2	nd
SKB Bos 8 M3	102			-11,4	nd
SKB Bos 9 M3	102			-11,4	nd

Table S2. Provenience and diet of the sheep used as references for pure grass, pure seaweed and mixed seaweed/grass diet. Highest $\delta^{13}\text{C}$ value measured in the annual cycle; phase shift between the $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ sequences. References: 1) this study; 2) Balasse *et al.* (2009); 3) Balasse *et al.* (2005).

Specimen ID	Location	Time		Ref.	$\delta^{13}\text{C}_{\text{max}}$ (‰)	Phase shift (°)
		period	Diet			
ROU01 M2	Rousay (Orkney)	Modern	Grass	2	-15.8	333
ROU04 M2	Rousay (Orkney)	Modern	Grass	2	-16.0	298
ROU09 M2	Rousay (Orkney)	Modern	Grass	2	-15.1	296
ROU17 M2	Rousay (Orkney)	Modern	Grass	2	-16.5	307
ROU16 M2	Rousay (Orkney)	Modern	Grass	2	-15.6	301
ROU6 M2	Rousay (Orkney)	Modern	Grass	2	-15.1	303
KMZc128 M3	Kemenez (Brittany)	Modern	Grass	1	-15.4	340
KMZc119 M3	Kemenez (Brittany)	Modern	Grass	1	-14.9	315
KMZc123 M3	Kemenez (Brittany)	Modern	Grass	1	-15.1	340
KMZ00004 M3	Kemenez (Brittany)	Modern	Grass	1	-16.4	321
KMZ00018 M3	Kemenez (Brittany)	Modern	Grass	1	-15.6	330
KMZ10033 M3	Kemenez (Brittany)	Modern	Grass	1	-15.6	331
KMZ10026 M3	Kemenez (Brittany)	Modern	Grass	1	-15.2	327
KMZ22bisOvis1 M3	Kemenez (Brittany)	Bronze Age	Grass	1	-12.9	323
NROvis1 M3	North Ronaldsay (Orkney)	Modern	Seaweed	3	-2.6	320
SWN02 M2	North Ronaldsay (Orkney)	Modern	Seaweed	2	-4.6	342
NROvis3 M3	North Ronaldsay (Orkney)	Modern	Seaweed/grass	3	-1.9	218
NROvis4 M3	North Ronaldsay (Orkney)	Modern	Seaweed/grass	3	-3.6	222
NROvis5 M3	North Ronaldsay (Orkney)	Modern	Seaweed/grass	3	-4.6	183
NBN01 M2	North Ronaldsay (Orkney)	Modern	Seaweed/grass	2	-6.4	179
TWN05M2	North Ronaldsay (Orkney)	Modern	Seaweed/grass	2	-5.3	225

Table S3. Results from the modelling of the phase shift between the $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ sequences in sheep teeth (Rousay = ROU, Kemenez = KMZ and North Ronaldsay = NR, NBN, SWN and TWN).

Specimen	$\delta^{18}\text{O}$ (‰)				$\delta^{13}\text{C}$ (‰)			
	A (‰)	D (mm)	φ (°)	M (‰)	A (‰)	D (mm)	φ (°)	M (‰)
ROU01 M2	1.89	29.26	241.77	-4.27	0.69	29.26	268.45	-16.58
ROU04 M2	2.04	32.26	284.04	-4.41	0.71	32.26	345.70	-16.78
ROU09 M2	1.76	33.69	250.20	-4.39	0.68	33.69	314.13	-16.15
ROU17 M2	1.75	35.88	253.90	-4.14	0.61	35.88	306.45	-16.90
ROU16 M2	1.75	36.39	241.76	-4.53	0.73	36.39	300.84	-16.12
ROU6 M2	1.57	38.35	277.89	-4.05	0.74	38.35	334.53	-16.04
KMZc128 M3inf	1.19	17.70	282.31	-3.15	0.50	17.70	302.24	-15.84
KMZc119 M3inf	1.90	26.46	361.13	-2.28	1.67	26.46	406.27	-16.35
KMZc123 M3inf	1.71	23.41	350.19	-2.26	1.37	23.41	369.78	-16.72
KMZ00004 M3inf	1.27	23.06	378.22	-3.52	1.18	23.06	417.24	-17.76
KMZ00018 M3inf	1.55	22.96	309.88	-3.20	1.58	22.96	340.11	-17.10
KMZ10033 M3inf	0.87	24.58	307.10	-3.73	0.87	24.58	336.08	-16.71
KMZ10026 M3inf	1.11	23.80	276.15	-3.26	0.95	23.80	309.06	-16.57
KMZ22bisOvis1 M3	1.37	19.95	226.15	-3.26	1.04	19.95	-96.42	-14.16
NROvis1 M3	0.53	20.32	187.38	-4.53	0.69	20.32	227.21	-3.83
NROvis3 M3	0.81	25.22	278.68	-3.67	2.60	25.22	60.56	-4.60
NROvis4 M3	1.14	26.77	246.91	-3.62	1.67	26.77	384.44	-5.60
NROvis5 M3	0.93	32.50	281.84	-3.80	1.49	32.50	459.16	-6.25
NBN01 M2	0.52	25.21	215.15	-3.23	2.98	25.21	396.06	-9.48
SWN02 M2	0.51	26.91	266.88	-3.33	0.90	26.91	285.32	-5.66
TWN05 M2	0.65	25.55	221.97	-3.69	1.41	25.55	356.21	-6.56

The $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ sequences have been processed using a sinusoidal model approach. Although the anticipated pattern is not strictly sinusoidal, it is assumed to be periodic with the same period for both signals, corresponding to a full year. Moreover, the signal resulting mainly from an opposition between winter and summer, only two inflections per period are expected, with a smooth transition between the high and low signal. In this context, a sinusoidal model is the most adapted. Nevertheless, this assumption can be wrong in the particular case of a very brief period of seaweed consumption during winter, which could create two additional inflections not be taken into account with this model.

Data were fitted by the following model:

$$\begin{cases} \hat{\delta}^{18}\text{O}(d) = A_{\delta^{18}\text{O}} \sin\left(\frac{2\pi}{D}d + \varphi_{\delta^{18}\text{O}}\right) + M_{\delta^{18}\text{O}} \\ \hat{\delta}^{13}\text{C}(d) = A_{\delta^{13}\text{C}} \sin\left(\frac{2\pi}{D}d + \varphi_{\delta^{13}\text{C}}\right) + M_{\delta^{13}\text{C}} \end{cases} \quad [1]$$

Where:

d is the distance in mm.

D is period of the signal in mm

$\varphi_{\delta^{13}\text{C}}$ and $\varphi_{\delta^{18}\text{O}}$ are respectively the phase for $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ in degree ($^\circ$)

$M_{\delta^{13}\text{C}}$ and $M_{\delta^{18}\text{O}}$ are respectively the signal averages for $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ in ‰

$A_{\delta^{13}\text{C}}$ and $A_{\delta^{18}\text{O}}$ are respectively the signals magnitude for $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ in ‰

$A_{\delta^{13}\text{C}}$, $A_{\delta^{18}\text{O}}$, $M_{\delta^{13}\text{C}}$, $M_{\delta^{18}\text{O}}$, $\varphi_{\delta^{13}\text{C}}$, $\varphi_{\delta^{18}\text{O}}$ and D are adjusted simultaneously using a least square method.

From the fitted parameters, the phase shift between $\hat{\delta}^{18}\text{O}(d)$ and $\hat{\delta}^{13}\text{C}(d)$ is computed as

$$\Delta\varphi = \varphi_{\delta^{18}\text{O}} - \varphi_{\delta^{13}\text{C}} \quad [2]$$

Table S4. Results from the modelling of the phase shift between the $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ sequences in sheep and cattle teeth from Skara Brae (SKB), Holm of Papa Westray (HPWN) and Knap of Howar (KH). Highest $\delta^{13}\text{C}$ value measured in the sequence and phase shift between the $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ sequences.

Specimen	$\delta^{18}\text{O}$ (‰)				$\delta^{13}\text{C}$ (‰)				$\delta^{13}\text{C}_{\text{max}}$ (‰)	Phase shift (°)
	A (‰)	D (mm)	φ (°)	M (‰)	A (‰)	D (mm)	φ (°)	M (‰)		
SKB Ovis3 M2	1.81	28.30	247.44	-5.27	0.61	28.30	260.92	-13.10	-12.5	347
SKB Ovis3 M3	1.70	20.63	196.91	-4.24	0.56	20.63	222.60	-13.02	-12.5	334
SKB Ovis 17 M3	1.99	25.34	232.43	-5.71	0.57	25.34	260.76	-13.14	-12.6	332
SKB Ovis 12 M3	1.85	21.26	157.96	-5.70	0.42	21.26	209.92	-13.23	-12.8	308
SKB Ovis 13 M2	0.84	19.14	215.34	-4.30	1.34	19.14	38.78	-10.82	-9.3	177
SKB Ovis 5 M3	1.31	17.84	89.13	-2.96	0.70	17.84	131.67	-12.71	-12.0	317
SKB Ovis 6 M3	1.00	24.35	203.58	-4.58	1.66	24.35	57.46	-9.72	-8.2	146
SKB Ovis 7 M3	0.59	22.18	113.84	-3.58	1.31	22.18	-85.03	-10.72	-7.9	199
SKB Ovis 8 M3	1.13	20.70	134.75	-2.73	1.94	20.70	-69.40	-9.85	-7.4	204
SKB Ovis 9 M3	1.13	24.89	169.09	-4.13	1.61	24.89	-5.80	-10.72	-9.0	175
SKB Ovis 11 M3	0.89	20.87	75.74	-4.27	1.11	20.87	-96.95	-10.96	-9.3	173
SKB Ovis 15 M3	0.73	26.43	263.78	-5.08	1.79	26.43	59.53	-11.22	-9.3	204
SKB Ovis 16 M3	0.97	18.99	155.91	-4.86	0.78	18.99	-72.10	-10.98	-9.9	228
SKB Bos5 M3	0.88	43.56	199.98	-5.47	0.44	43.56	-85.42	-12.55	-12.1	285
SKB Bos 7 M3	0.60	43.18	176.75	-5.64	0.64	43.18	-117.29	-12.59	-11.9	294
SKB Bos 10 M3	0.74	41.44	238.96	-5.76	0.37	41.44	-63.66	-12.23	-11.7	303
HPWN Ovis1 M3	0.85	24.21	177.48	-3.85	3.15	24.21	386.70	-9.73	-6.7	151
HPWN Ovis3 M3	1.15	22.38	301.61	-3.67	3.03	22.38	113.92	-9.13	-5.8	188
HPWN Ovis4 M3	0.90	29.98	350.44	-3.92	2.82	29.98	189.04	-8.91	-5.7	161
HPWN Ovis5 M2	0.71	35.78	309.94	-3.67	2.67	35.78	118.70	-9.79	-7.0	191
HPWN Ovis7 M3	0.85	22.61	218.50	-2.79	2.80	22.61	50.99	-6.48	-4.1	168
HPWN Ovis8 M3	1.26	25.29	340.01	-3.03	1.79	25.29	153.58	-9.19	-7.1	186
HPWN Ovis9 M3	0.76	16.40	199.81	-3.58	1.55	16.40	36.89	-9.61	-8.2	163
HPWN Ovis10 M3	0.82	24.40	251.40	-2.59	1.62	24.40	34.19	-7.87	-6.3	217
HPWN Ovis11 M3	1.06	19.92	224.05	-3.54	0.91	19.92	49.69	-9.44	-8.6	174
HPWN Ovis12 M3	0.61	18.03	228.80	-3.12	2.63	18.03	53.55	-8.18	-5.6	175
KH Ovis7 M3	0.99	25.44	249.94	-4.23	0.36	25.44	95.72	-10.76	-10.2	154
KH Ovis9 M3	1.81	20.01	14.02	-3.94	0.36	20.01	21.92	-12.72	-12.2	352

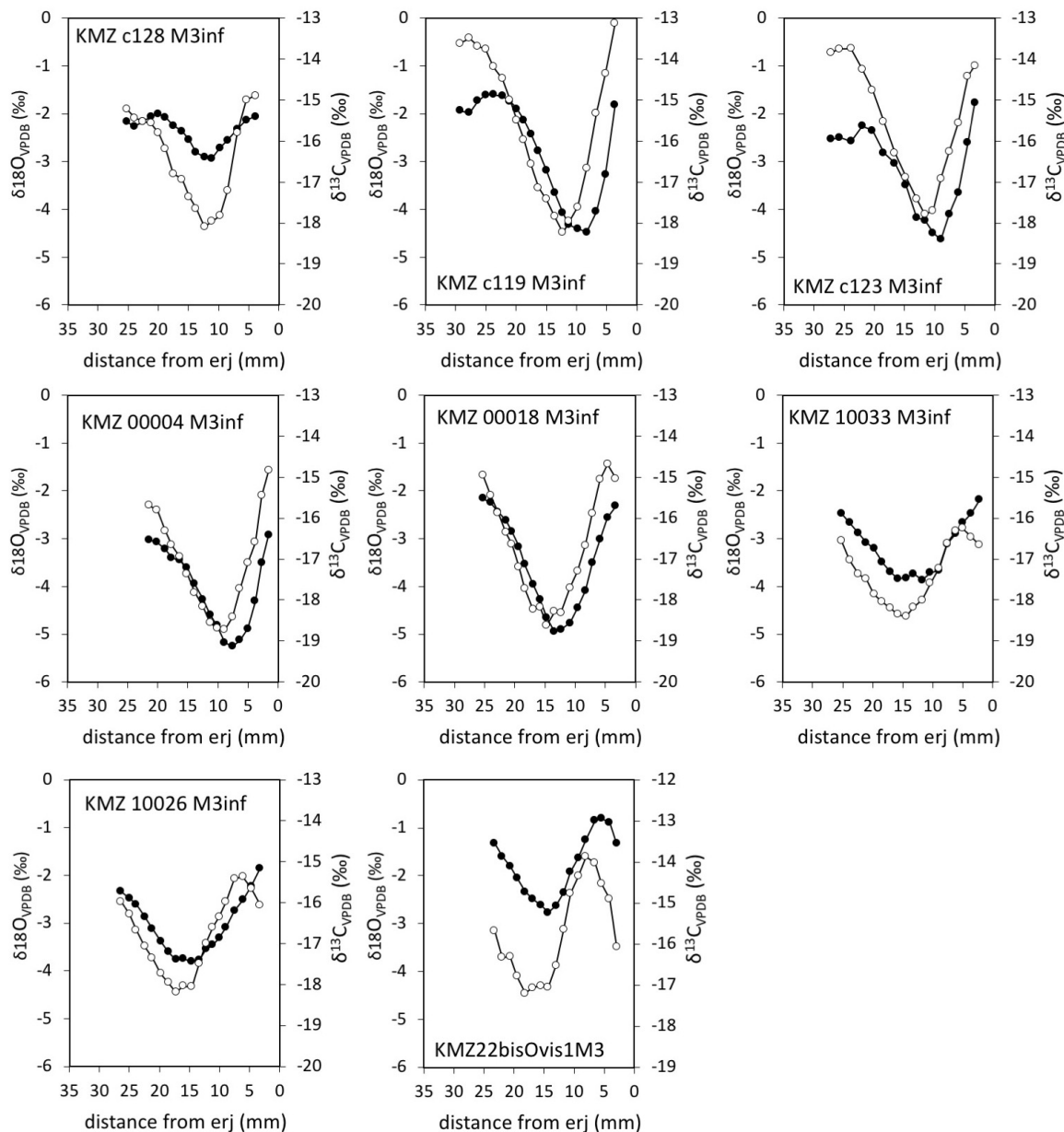


Figure S1. Results from sequential analysis of stable carbon ($\delta^{13}\text{C}$ in black) and oxygen isotope ratios ($\delta^{18}\text{O}$ in white) in the modern and Bronze Age ('22 bis') sheep from Kemenez.

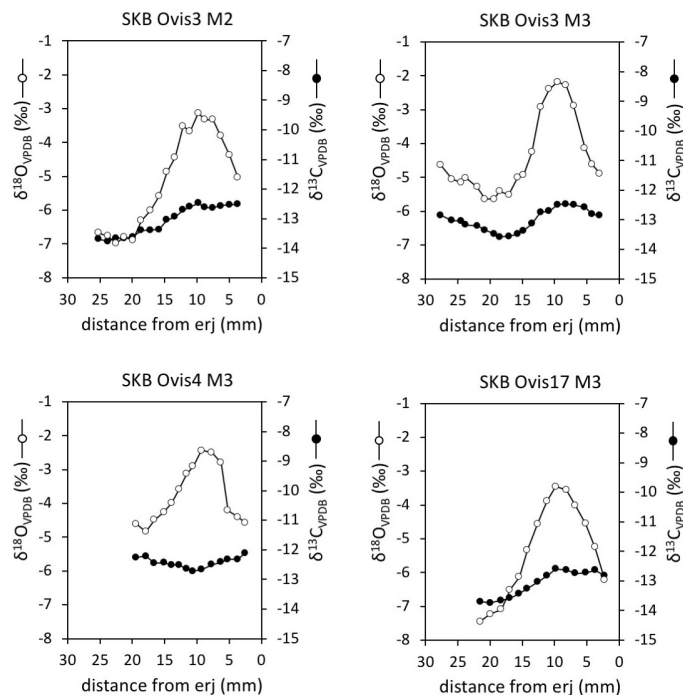


Figure S2. Results from sequential analysis of stable carbon ($\delta^{13}\text{C}$ in black) and oxygen isotope ratios ($\delta^{18}\text{O}$ in white) in sheep teeth from Skara Brae phase 0 (contexts 157 & 168).

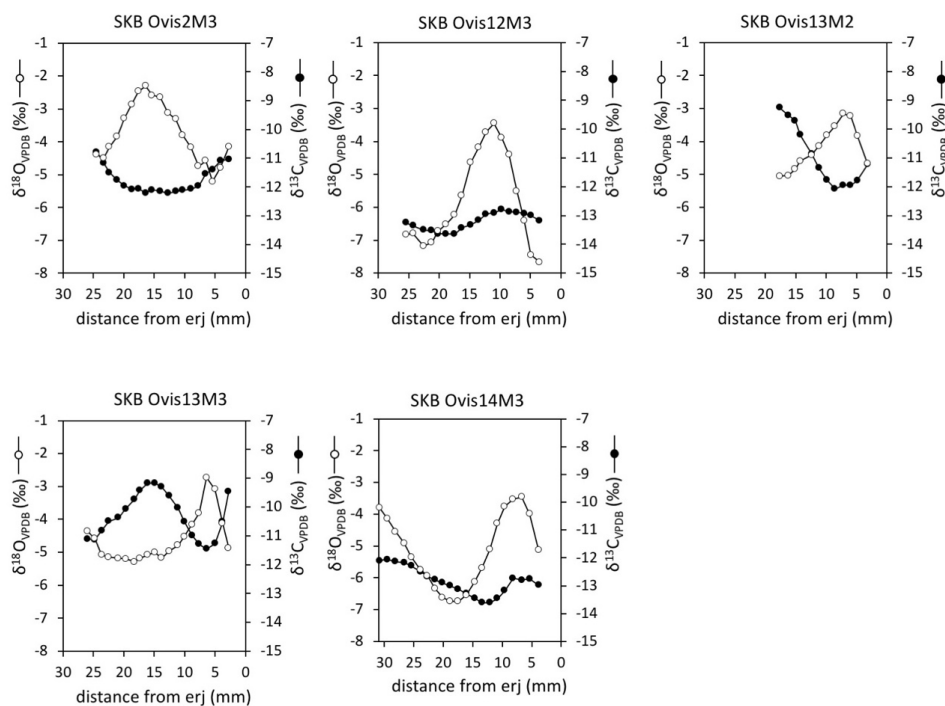


Figure S3. Results from sequential analysis of stable carbon ($\delta^{13}\text{C}$ in black) and oxygen isotope ratios ($\delta^{18}\text{O}$ in white) in sheep teeth from Skara Brae phase 1 (context 213).

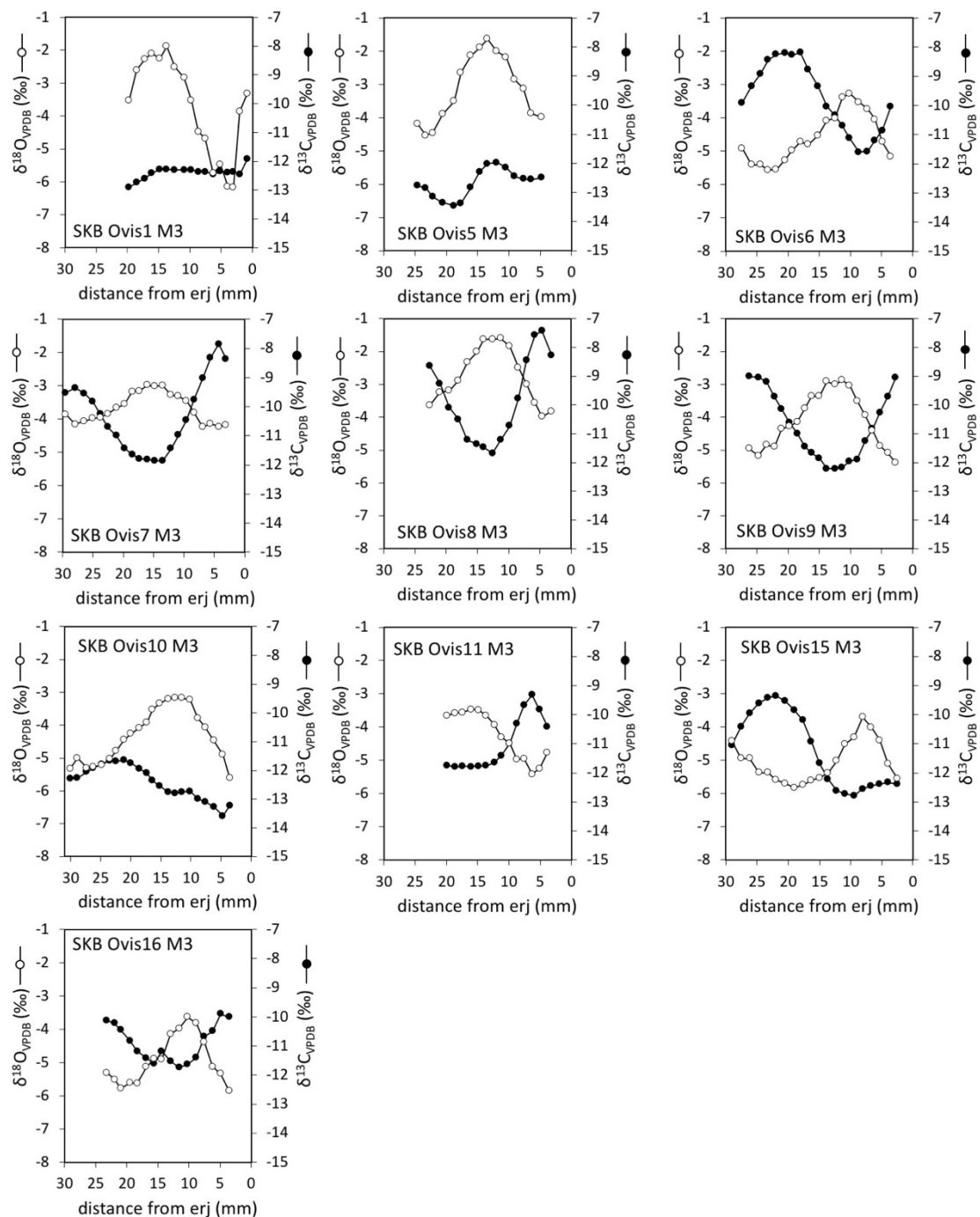


Figure S4. Results from sequential analysis of stable carbon ($\delta^{13}\text{C}$ in black) and oxygen isotope ratios ($\delta^{18}\text{O}$ in white) in sheep teeth from Skara Brae phase 2 (context 102).

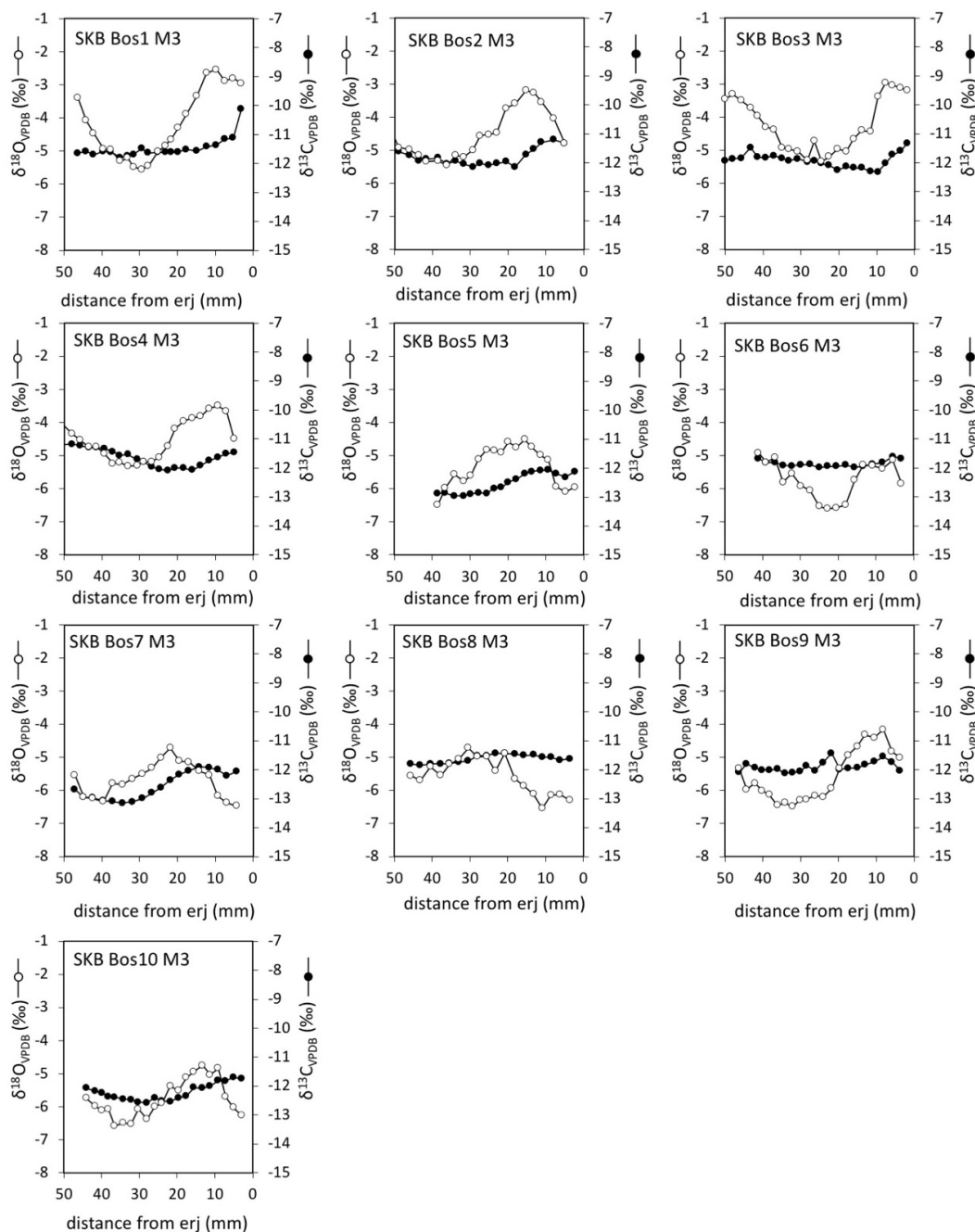


Figure S5. Results from sequential analysis of stable carbon ($\delta^{13}\text{C}$ in black) and oxygen isotope ratios ($\delta^{18}\text{O}$ in white) in cattle teeth from Skara Brae.

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