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A carbon and nitrogen isotope perspective on ancient human diet in the British Isles

SHORT TITLE: Stable isotopes and ancient diet in the British Isles

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ABSTRACT

The stable carbon (δ^{13}C) and nitrogen (δ^{15}N) isotope composition of human bone collagen is increasingly used to investigate past mobility and subsistence strategies. This study presents a compilation of 1298 carbon and nitrogen isotope analyses of archaeological human bone collagen from the British Isles spanning much of the Holocene, along with a compilation of 4148 analyses of modern and ancient isotope analyses from the major marine and terrestrial dietary resources from the same region. We convert ancient human stable isotope data to modern diet equivalent (MDE) values for humans, and convert the isotope composition of ancient dietary items to modern equivalent tissue (MTE) isotope values. These conversions enable a direct comparison of ancient and modern datasets. Results for food groups (plants, grain, herbivores, omnivores, shellfish, freshwater fish and marine fish) show a remarkably broad range of $\delta^{13}C_{MTE}$ values from ~-36 to -7‰ and $\delta^{15}N_{MTE}$ values from ~-2 to +21 ‰ and we provide estimates for each food type that can be used in dietary reconstruction in the absence of site-specific data. We further show that there is no significant change in terrestrial stable isotope baseline values over the Holocene, with observed variability in baseline values due to local eco-physiological, edaphic and microclimatic factors. The range of values expressed in the human sample set from the beginning of the Iron Age is relatively tightly clustered with 50% of all human modern diet equivalent results falling within a ~2 ‰ range in $\delta^{13}C_{MDE}$ values (-25.5 to -27.5 ‰) and a ~3.5 ‰ range in $\delta^{15}N_{MDE}$ values from (+4 ‰ to +8 ‰). From the Iron Age to post-medieval times there is a consistent progressive shift to higher $\delta^{13}C_{MDE}$ and $\delta^{15}N_{MDE}$ values at the population level. This shift likely reflects a combination of successive innovations associated with food production, preservation and transport that enabled a broader cross-section of the population of the British Isles to incorporate a higher proportion of animal, and particularly marine protein, into their diets.

1. Introduction

Over the past several decades, the stable carbon and nitrogen isotope composition of ancient human organic material has been investigated as a proxy for differentiating human dietary components (Schoeninger et al., 1983; DeNiro, 1985, Ambrose, 1986). Carbon isotope composition (δ^{13}C value) provides an indication of relative contributions of aquatic and/or different terrestrial sources of carbon in the diet. Nitrogen isotope composition (δ^{15}N value) is used to draw inferences regarding protein source and/or trophic level of an individual in the months or years before their death (Hedges and Reynard, 2007). Stable isotope techniques have been employed on ancient human remains and the contemporaneous remains of food items preserved from Holocene to historical times to identify changes in subsistence strategies and technologies (e.g. agriculture and pastoralism; Lightfoot and Stevens, 2012; Treasure et al., 2019; Blanz et al., 2020), as well as to infer changes in social status and structures (e.g. Lamb et al., 2014).

Interpretation can be relatively straightforward when measured differences in isotope composition are relatively large (e.g. Bonsall et al., 1997), however the interpretation of smaller differences are complicated by the complexities associated with different collagen turnover times and disentangling the impact of human agency from the ecosystem processes driving C and N isotope fractionation within the food webs supporting human diet (e.g. Guiry, 2019; Barrientos et al., 2020).

Interpretation of dietary protein source is also complicated by the better preservation of the remains of some food items, such as bones, over more degradable items such as derived from primary biomass (grain, fruit, vegetables), such that the archaeological record is incomplete and biased by issues of taphonomy and preservation (Lightfoot and Stevens, 2012, Hendy et al., 2018). Individual studies often rely on relatively few direct measurements of the stable isotope composition of food items to represent the range of stable isotope compositions of local food items available to eat, augmented by other results from published studies, or else make assumptions about the range of likely isotope values for food items not represented in an archaeological assemblage. The paucity of food remains derived from vegetation (grains, tubers, nuts, vegetables, fruit) in many deposits in the temperate zone means that the stable isotope compositions of primary production in particular tend to be assumed to lie within the relatively narrow range reported for C_3 biomass (trees, shrubs and temperate grasses). Similar assumptions can be required for some marine resources such as shellfish, which are an important component of some archaeological assemblages (e.g. Noble et al., 2018), but leave no organic component from which to directly infer stable isotope composition.

It has also been demonstrated that the range, or potential range, of stable isotope compositions for protein in different food items can overlap to a significant degree. As a result of these overlaps, for example, it becomes problematic in some instances to identify freshwater fish in human diet (Dufour et al., 1999; Hedges and Reynard, 2007; Guiry, 2019) and there is the potential for the stable isotope composition of grain to be not distinguishable from that of herbivore tissues (e.g. Lightfoot and Stevens, 2012). In addition, humans have exerted some influence on the stable isotope composition of their diet through time, directly, through the selection and cultivation/husbandry of particular plant and animal species, and indirectly, through the implementation of strategies such as organic amendment to improve crop productivity (Bogaard et al., 2007; Lodwick et al., 2020; Gron et al., 2020; Gröcke et al., 2021), and forest clearance to enable more extensive crop and pasture production (Hofman-Kamińska et al., 2018).

The number of potential controls on the $\delta^{13}C$ and $\delta^{15}N$ values even at the base of a local food web is large, and become more complex with increasing trophic level. In this context, the British Isles represents a comparatively geographically constrained, well-studied, and relatively uniform humid temperate region. Given that the climate is humid and temperate and terrestrial biomass is exclusively C_3 vegetation, the range of $\delta^{13}C$ values for primary production is likely to be comparatively smaller than in regions where vegetation experiences significant water stress and/or in regions where C_4 vegetation can occur. While climate has changed over the course of the Holocene, climate across the British Isles has remained cool and humid; therefore changes in carbon isotope discrimination in C_3 plants are likely to have been small (Kohn, 2010). The UK is also surrounded by shallow shelf seas where the range of both $\delta^{13}C$ and $\delta^{15}N$ values for primary production has also been shown to be generally <3 ‰ (St John Glew et al., 2019) and stable over at least the last millennium (MacKenzie et al., 2014).

The British Isles, is a relatively small, data-dense region (Bird et al., 2021). As such it provides an opportunity to examine, at the spatial scale of a large humid temperate island surrounded by relatively uniform shallow shelf seas, the range of stable isotope compositions recorded in human skeletal material, in the context of the range of stable isotope compositions of the potential dietary items available to them, over the course of the Holocene.

2. Methods

We undertook and exhaustive search of the literature using Google Scholar and a range of keywords designed to identify papers based on material from the British Isles relating to the carbon and nitrogen isotope composition of Mesolithic to 19th century archaeological human, animal and fish bone collagen and vegetable material. We augmented these with data available for the modern composition of plants, animals and marine resources from the same region, where both carbon and nitrogen isotope composition was available. We included a large dataset of fish bone collagen from Belgium (Fuller et al., 2012), and another shellfish tissue dataset from Northern Ireland (Reddin et al., 2018), along with an ancient human dataset from 'Doggerland' (Van der Plicht et al., 2016), all less than 100 km from the British mainland, once connected to the British Isles in the case of Doggerland, and representative of conditions on the British mainland.

We compared the UK data with 917 western European and 395 Scandinavian results from human bone collagen to provide a regional context for the range observed in the British human material. From the total human dataset, we removed analyses of infant bone material, where identified as 'infant' or less than 2 years old, due to apparent trophic enrichment associated with breastfeeding (Reynard and Tuross, 2015) and removed analyses outside the recommended range of C:N ratios for collagen, where reported (2.9-3.6; DeNiro, 1985). We did not further interrogate the techniques or instrumentation used to perform the specific analyses reported in the literature. While not incorporating all published analyses as we excluded studies not available on line (mostly theses) and studies where primary individual data points were not reported, this survey yielded a total of 1298 analyses of human material and 4148 analyses of potential dietary samples of all types and ages, from terrestrial and marine environments on and around the British Isles.

We do not undertake an explicit spatial analysis of the data for several reasons (though locations are provided in Supplementary Table 1). The area of the British Isles is small – more than three quarters of the land is within 50 km, and none more than 116 km, from the coast. In this context, Hamilton et al. (2019) has shown that by as early as the Iron Age (400–200 BCE) livestock, and by implication humans, were moving up to 150-200 km and substantially more mobility is likely in more recent times. Further, Thornton et al. (2015) has demonstrated that baseline variability of an amplitude of significance to the range of human collagen isotope values occurs over tens of kilometres in Scotland (>5‰ for δ^{13}C and δ^{15}N), and the same is likely to be true of the rest of the British Isles. These considerations mean that it is unlikely that isotope composition of individual specimens can be simply and unequivocally linked to the place where they were found.

We divide the ancient human population into four broad time periods to ensure sufficient data is available for interpretation in each: (i) later Mesolithic and Neolithic (beginning of the Holocene to ~2,200 BCE; n = 177; note the transition from Mesolithic to Neolithic in the British Isles has been considered in detail elsewhere e.g. Bownes, 2018) (ii) Bronze and Iron ages (~2200 BCE to 43 AD; n = 119) and (iii) Roman to the Norman conquest (43 AD to 1066 AD; n = 448) and (iv) post Norman conquest to post-Medieval (1066 AD – 1900 AD n = 654) to investigate the possibility of broad temporal variation in diet, due to natural and/or human mediated factors (Supplementary Table 1). In order to ensure sufficient analyses of individual terrestrial species we divide the herbivore (cattle, sheep/goat, horse and deer) and omnivore (pig) data into only two populations, representing analyses from specimens older and younger than 43 AD to assess temporal variation in terrestrial stable isotope baseline values.

It is conventional to present archaeological stable isotope data directly, as the measured values, usually on bone collagen. Trophic level, for example, is then evident in an offset between the data for humans and the data for potential food items. Here we use an alternative approach whereby we approximate the fractionation factors associated with conversion of nitrogen and carbon isotope composition from primary production at the base of a food web, into the tissues of consumer organisms at higher trophic levels within a food web. This approach enables comparisons of archaeological data with more complete modern data sets.

For humans we present all human data as Modern Diet Equivalent ($\delta^{13}C_{MDE}$ value and $\delta^{15}N_{MDE}$ value). We do this using a consensus human collagen-diet (c-d) fractionation where $\varepsilon_{c\text{-}d}$ is +4.8 ‰ for $\delta^{13}C$ value and +5.5 ‰ for $\delta^{15}N$ value (Fernandes et al., 2015). To convert to modern (2010) CO_2 equivalent values, due to changes in the $\delta^{13}C$ value of atmospheric CO_2 over the last century we subtract a further 1.9 ‰ from each ancient $\delta^{13}C$ value when calculating MDE (Schmitt et al., 2012; Graven et al., 2017).

For potential dietary items we present all data as Modern (muscle) Tissue Equivalent ($\delta^{13}C_{MTE}$ value and $\delta^{15}N_{MTE}$ value). No adjustment is required for analyses of modern plants, soil, animals, fish or shellfish tissues. For ancient samples, the atmospheric CO_2 $\delta^{13}C$ value correction of -1.9 ‰ is applied to all ancient terrestrial and freshwater aquatic organisms. This correction is not applied to ancient marine samples as the modern coastal ocean still largely reflects pre-industrial CO_2 $\delta^{13}C$ value. The fractionations between collagen and tissues differ in detail between species and tissues (e.g. Fischer et al., 2007). Here we adopt the calculated fractionation factors between muscle and collagen ($\varepsilon_{m\text{-}c}$) for terrestrial animals to calculate muscle equivalent value isotope values assuming $\varepsilon_{m\text{-}c}$ is -1.9 ‰ for $\delta^{13}C$ value and +0.3 ‰ for $\delta^{15}N$ value (Bownes, 2017; 2018). For all fish we use -2.7 ‰ for $\delta^{13}C$ value and +0.4 ‰ for $\delta^{15}N$ value, based on the results of Fernandes et al. (2014). By presenting the data in this way we enable a direct comparison between the stable isotope composition of human diet and the candidate tissues of the plants, animals or fish that could have been consumed. We also enable direct comparison with modern results, including for food items not preserved in the archaeological record (Hendy et al., 2018), such as shellfish tissues and plant biomass other than grain.

The magnitude of isotope fractionations between different tissue types for different organisms are known with a varying degree of certainty, however, the conversions applied are simple arithmetic additions/subtractions that apply to all data in a population. It is also the case that fractionation factors vary between species and between different tissues of the same organism (Webb et al., 2016l Fischer et al., 2007). In addition, in some instances, an original isotope composition can be modified by human activities such as cooking (e.g. Fernandes et al., 2014; Fraser et al., 2013; Disspain et al., 2016). The assumption is made that these considerations might lead to variations of up to around 1 ‰ for either isotope, a small change in the context of the range observed across all data.

Given the large size of the dataset, bag plots or modified bivariate boxplots were constructed to visualise the data distribution by way of its half-space depth or Tukey depth (see Rousseeuw et al. 1999). The 'bag' encloses the central 50% of the data points while the modified 'loop' encloses 95% or 100% of the points (as indicated in the Figure legends), allowing for the simple identification of the location and spread of the data cloud.

3. Results

All data for humans and potential dietary items used in this study, including location and time period where appropriate, are available in Supplementary Table 1, including raw data and data transformed to the modern equivalent values discussed here. The vast majority of human data from the British Isles, across the entire Holocene, occupies a range defined by $\delta^{13}C_{MDE}$ values from ~-31 to -19 ‰ (μ = -26.2 ± 1.5 ‰ 1σ; n = 1298) and $\delta^{15}N_{MDE}$ values from ~+1.7

to +11.5 ‰ (μ = +5.8 ± 1.7 ‰). The data are clustered in a similar range to the majority of both the Western European and Scandinavian data, but the Western European data tend to extend to higher $\delta^{13}C_{MDE}$ values and the Scandinavian data to higher $\delta^{15}N_{MDE}$ values (see Figure 1).

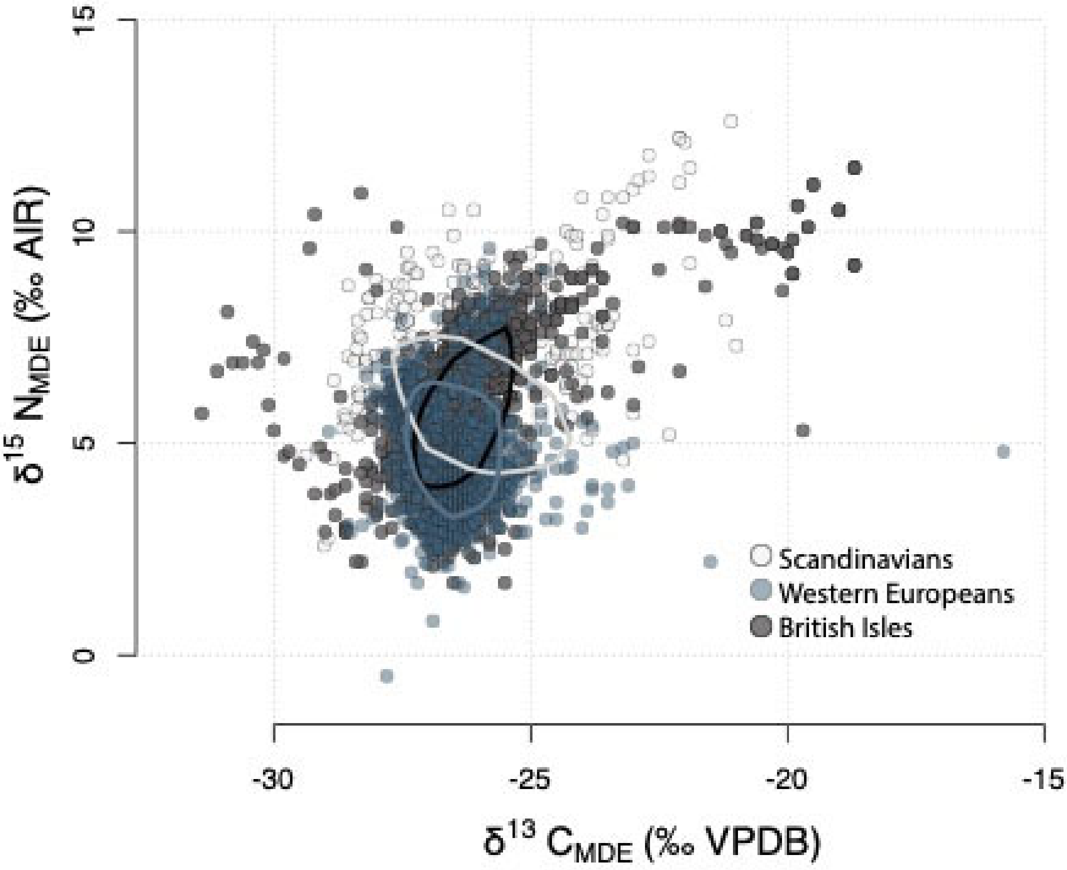

Figure 1. $\delta^{15}N_{MDE}$ and $\delta^{13}C_{MDE}$ bagplots of Scandinavians (light grey), British Isles (dark grey/black) and Western Europeans (blue grey). Solid contours (loops) of same colour enclose the central 50% of points in each group.

In contrast to the range for human samples, potential diet groups cover a much broader range with $\delta^{13}C_{MTE}$ values from ~-36 to -7‰ and $\delta^{15}N_{MTE}$ values from ~-2to +21 ‰ (Figure 2). Within this very broad range, individual diet types variously cluster in distinct ranges $\delta^{13}C_{MTE}$ - $\delta^{15}N_{MTE}$ space. The general overlap among modern and ancient values for different diet types, where both are available, suggests that the conversion of measured ancient values to modern equivalent tissue values is robust (Figure 2).

Terrestrial biomass (plant and soil) exhibits a broad range in $\delta^{13}C_{MTE}$ values (-35.9 to -24.5 ‰) and $\delta^{15}N_{MTE}$ values (-2.3 to +15.4 ‰), overlapping with the grain population to some degree, but with little overlap to other sample types. Terrestrial herbivore, omnivore and grain samples substantially overlap with each other, grain data extending to lower $\delta^{15}N_{MTE}$ values, and both omnivores and herbivores extending to higher $\delta^{15}N_{MTE}$ values. The fish samples have generally higher $\delta^{15}N_{MTE}$ values (+6 to +20 ‰) than all other sample types, with marine fish, having $\delta^{13}C_{MTE}$ values between -22.7 and -14 ‰ and freshwater fish extending to much lower $\delta^{13}C_{MTE}$ values (as low as -33 ‰). Shellfish and marine plant biomass share a similar range of $\delta^{13}C_{MTE}$ values to marine fish but tend to lower $\delta^{15}N_{MTE}$ values in the range of +3.9 to +17.1‰.

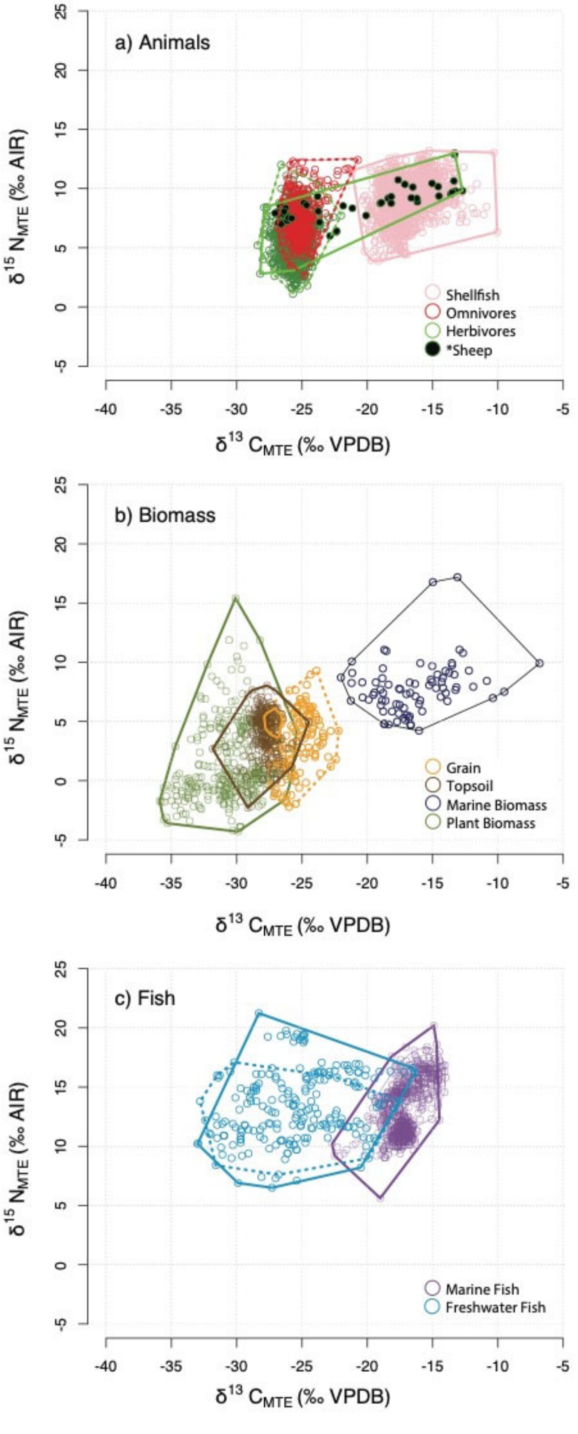

Figure 2. $\delta^{15}N_{MTE}$ and $\delta^{13}C_{MTE}$ bagplots of common food groups and isotope sources a) animals, b) biomass and c) fish. Solid contours (loops) enclose 100% of modern data points, dashed loops enclose 100% of ancient data points of the same category - 50% bags are not shown. *Sheep refers to modern sheep in the herbivore population experimentally fed a diet of seaweed Blanz et al. (2020).

4. Discussion

4.1 δ^{13}C values in potential diet

The carbon isotope composition of primary production controls the δ^{13}C value of the base of every food web. For the British Isles, the range of potential carbon isotope discrimination for terrestrial primary production is small in a global context as a result of the presence only of C_3 species (Kohn, 2010). Changes in the magnitude of isotope discrimination against ^{13}C during photosynthesis as a result of changes in temperature and/or precipitation in the Holocene in the UK may be present, but also relatively muted. For example, Cooper et al. (2013) estimated decadal excursions of ± 15% around the long-term mean in rainfall in Southern England over the last millennium. Rydval et al. (2017) report multidecadal increases in relative summer temperature of ~1 ˚C and decreases of up to ~2˚C over the long-term mean in Scotland over the last 800 years, consistent with earlier studies in the UK. Longer-term records of sea surface temperature through the Holocene likewise suggest small temperature variations of less than 2˚C from western Scottish waters (Wang et al., 2012) and the northern North Sea more generally (Hald et al., 2007). Variations in climate of this order are unlikely to induce more than very minor water use efficiency driven changes in discrimination by terrestrial C_3 biomass.

Figure 3 shows that the range of $\delta^{13}C_{MTE}$ values for terrestrial primary production is larger than the ~1-3 ‰ range generally assumed for C_3 biomass in palaeodietary studies (e.g. Pickard and Bonsall, 2020). Modern data include both plants and soil, with the 50% 'bags' encompassing a range from between -27 and -33.5 ‰. The wide range observed, particularly toward relatively lower $\delta^{13}C_{MTE}$ values, implies other processes apart from changes to discrimination during photosynthesis are important in the $\delta^{13}C_{MTE}$ value at the base of food webs in the British Isles. The first of these is the re-assimilation of low δ^{13}C value CO_2 from plant respiration as canopy cover increases (e.g. Hofman-Kamińska et al., 2018; Bonafini et al., 2013). This 'canopy effect' applies in closed forest and woodland settings and is stronger in sub-canopy species than canopy species. The second is the incorporation of low-^{13}C CO_2 derived from methane oxidation in soils into biomass (e.g. Le Mer and Roger, 2001; Brewer et al., 2018; Angel et al., 2012). This effect is likely in grasses and herbs close to the soil interface where the soils are at least seasonally anoxic, enabling the production of methane that is then oxidized to CO_2 and assimilated by photosynthesis.

The $\delta^{13}C_{MTE}$ values of modern and ancient grain scatter over a similar range to other plant biomass reflecting the same set of environmental drivers as biomass, but offset to higher values with the 50% bags covering -23.9 to -27.3 ‰. This offset is due to the higher proportion of protein and starch in grain, with $\delta^{13}C$ values 1-5 ‰ higher than other plant compounds (Kodina, 2010), meaning that grains have $\delta^{13}C_{MTE}$ values that are ~2-3 ‰ higher than other plant tissues (e.g. Farquhar and Richards, 1984; Merah et al., 2001; Badeck et al., 2005). It is also known that the $\delta^{13}C$ value of grain decreases as grain yield increases, and thus grain $\delta^{13}C_{MTE}$ values are likely to have been higher during the initial period of domestication, and decrease through time as improvements to yield were enabled (e.g. Araus et al., 2001; Monneveux et al., 2004).

Information on the isotope composition of terrestrial animal tissues comes from both modern tissue analyses and also from tissue equivalent values calculated from ancient bone collagen. Ancient and modern animal tissues overlap to a large degree suggesting the conversion to tissue for ancient samples is appropriate. There is a relatively narrow, and similar, range in $\delta^{13}C_{MTE}$ values for both herbivores (sheep, cattle, horses, deer and sheep/goats) and omnivores (pigs) with the 50% bags in the range -24.4 to -26.2 ‰ indicating, not surprisingly, a diet of terrestrial biomass for the majority of samples (allowing for a trophic offset from the biomass values). A scatter of $\delta^{13}C_{MTE}$ values to as low as -28 ‰ reflects the consumption of biomass with lower $\delta^{13}C$ value (discussed above; Figure 2), but this is for a minority of samples. A scatter of $\delta^{13}C_{MTE}$ values to as high as -21 ‰ (Figure 2) reflects consumption of seaweed and other marine resources in some coastal locations (e.g. Blanz et al., 2020).

Terrestrial freshwater $\delta^{13}C_{MTE}$ values for the 50% bags cover a range of values from -30.2 to -20.5 ‰ (Figure 3). The scatter of $\delta^{13}C_{MTE}$ values to as high as -16 ‰ (Figure 2) derive from organisms, such as salmon and eels, that spend a part of their life cycle in the ocean and therefore have a marine-influenced stable isotope composition (Guiry, 2019). All other freshwater aquatic resources ultimately derive from C_3 terrestrial primary production, but with significant heterogeneity in $\delta^{13}C_{MTE}$ values introduced by the assimilation of a variable proportion of CO_2 derived from the oxidation of low-^{13}C methane into all levels of the aquatic food web, as has been clearly demonstrated in the modern environment (Sanseverino et al., 2012).

The range of $\delta^{13}C$ values for marine primary productivity in the coastal seas around the UK is small in a global context (>15‰; Magozzi et al., 2017), with values lying within a narrow range from -15.2 to -18.5 ‰ (St John Glew et al., 2019), and likely stable over the last millennium at least (MacKenzie et al., 2014). The range observed in modern marine plants and the $\delta^{13}C_{MTE}$ values of ancient and/or modern shellfish, crustaceans, fish and sea mammals are centred on these modern values for primary productivity. However, some values extend up to -12 ‰ (Figure 2), reflecting trophic enrichment in part, but also the relative importance of seaweed over phytoplankton in the diet of some species (von Biela et al., 2016). Some $\delta^{13}C_{MTE}$ values also extend to values to lower values around -20 ‰ (Figure 2), likely reflecting the incorporation of low ^{13}C terrestrial biomass into some coastal, and particularly estuarine/saltmarsh, food webs including into potential human dietary items (e.g. Graham et al., 2001; Wilson et al., 2005).

4.2 $\delta^{15}N$ values in potential diet

Application of the global relationship between climate parameters and soil δ^{15}N values presented by Amundson et al., (2003) suggests a small range of values should apply for the UK, from ~0 to +3 ‰. This is at odds with the considerably larger range of $\delta^{15}N_{MTE}$ values observed even for the 50% bags for soil, terrestrial plants and grain which show a range from -1.6 to +6.3 ‰. This range includes considerable relatively local scale variability. For example, measured values in Scottish soils cover much the same total range of values over spatial scales of tens of kilometres (Thornton et al., 2015). Part of this variability is likely due isotope fractionation effects associated with soil nutrient status, mycorrhizal associations and edaphic factors influencing soil nitrogen cycling processes, particularly ammonia volatilization and denitrification, (Spzak, 2014) that vary on comparatively small spatial, and short temporal scales (Casey and Post, 2011). Additional variability is likely due to 'legacy' high-^{15}N nitrogen in soils developed on marine sediments in areas that were inundated by post-glacial sea level rise up to ~30m above modern sea level (Shennan et al., 2018), given modern estuarine sediments have δ^{15}N values of ~5-12 ‰ (e.g Graham et al., 2001; Bristow et al., 2013). Part of the observed range in values is also potentially due to sustained land use change involving forest clearance and the intensification of agriculture and animal husbandry, involving manuring (Treasure et al., 2019; Gröcke et al., 2021), further considered below.

The $\delta^{15}N_{MTE}$ values for modern and ancient herbivores reflect some of this range in δ^{15}N baseline values in biomass, but with an increase in trophic level, so values for the 50% bag range from +4.5 to +8 ‰. The range in $\delta^{15}N_{MTE}$ values for omnivores (pigs) is similar but higher again (+5.5 to +9.3 ‰), likely reflecting a consistent 'human trophic subsidy' (*sensu* Jessop et al., 2012) in the form of food scraps, excrement and other waste (Halley and Rosvold, 2014). The large number of trophic levels in terrestrial aquatic food webs, along with the broad range in terrestrial baseline δ^{15}N values is reflected in the high and variable δ^{15}N$_{\mathrm{MTE}}$ values for freshwater fish. These range from +8 to +10 ‰ (Figure 2) for fish that feed dominantly on invertebrates such as brown trout (*Salmo Trutta*) to almost +20 ‰ for carnivorous predatory fish such as pike (*Exos Lucius*).

As is the case for carbon isotopes, the range of δ^{15}N values for marine primary productivity in the coastal seas around the UK is small in a global context (>10‰; Brandes and Devol, 2002), being generally < 3 ‰ (St John Glew et al., 2019). MacKenzie et al. (2014) have observed that δ^{15}N values in the marine environment in the North Sea have been relatively constant for at least the last millennia. As a result, baseline δ^{15}N values can reasonably be inferred for any coastal location, with variation in local δ^{15}N values of food items related mainly to the trophic level of organisms consumed as food by humans. The trophic level effect is apparent in the progression from detritus-feeding shellfish through to fish to marine mammals. Shellfish have a 50% bag range in δ^{15}N$_{\mathrm{MTE}}$ values from +7 to +11 ‰. These values overlap with fish species, such as herring (*Culpea Harengus*) that feed on phytoplankton and small crustaceans that have δ^{15}N$_{\mathrm{MTE}}$ values from +9 to +12 ‰. Predatory fish such as cod (*Gadus Morhua*) have higher δ^{15}N$_{\mathrm{MTE}}$ values which range from +12 to +18 ‰ (Figure 2), with marine mammals at the highest end of this range. The 50% bag range for marine fish is from +10 to +17 ‰ (Figure 4).

4.3 Temporal variation in terrestrial stable isotope baseline values

Discussion in the previous section suggests that 'natural' changes in stable isotope baseline values over time that could impact the range of values observed in humans are likely to be small. It is possible to test this assertion for the terrestrial environment at least by segmenting the data available for herbivores and omnivores. Figure 3 demonstrates the median range of $\delta^{13}C_{MTE}$ values for both herbivores and omnivores representing animals living before 43 AD is essentially identical to the results animals living after 43 AD. The median $\delta^{15}N_{MTE}$ values for both herbivores and omnivores after 43 AD is 1-1.5 ‰ higher than for those living before 43 AD. This difference is not statistically significant but may be an indication of, for example, an increase in manuring in the post 43 AD population (Bogaard et al., 2007; Lodwick et al., 2020; Gron et al., 2020). Within the species represented by the herbivore population on Figure 3 there are small ~1-2 ‰ differences in median $\delta^{13}C_{MTE}$ and $\delta^{15}N_{MTE}$ values both between individual species and within species before compared to after 43 AD that may, in the case of deer for example, relate to preference for forested habitats (Supplementary Figure 1; Supplementary Table 1).

In combination, the data indicate that there is little evidence for any significant shift in terrestrial isotope baseline values over time, and the dispersion in the data therefore likely due to the range of edaphic processes identified in Sections 4.1 and 4.2 that operate on relatively local scales (Casey and Post, 2011).

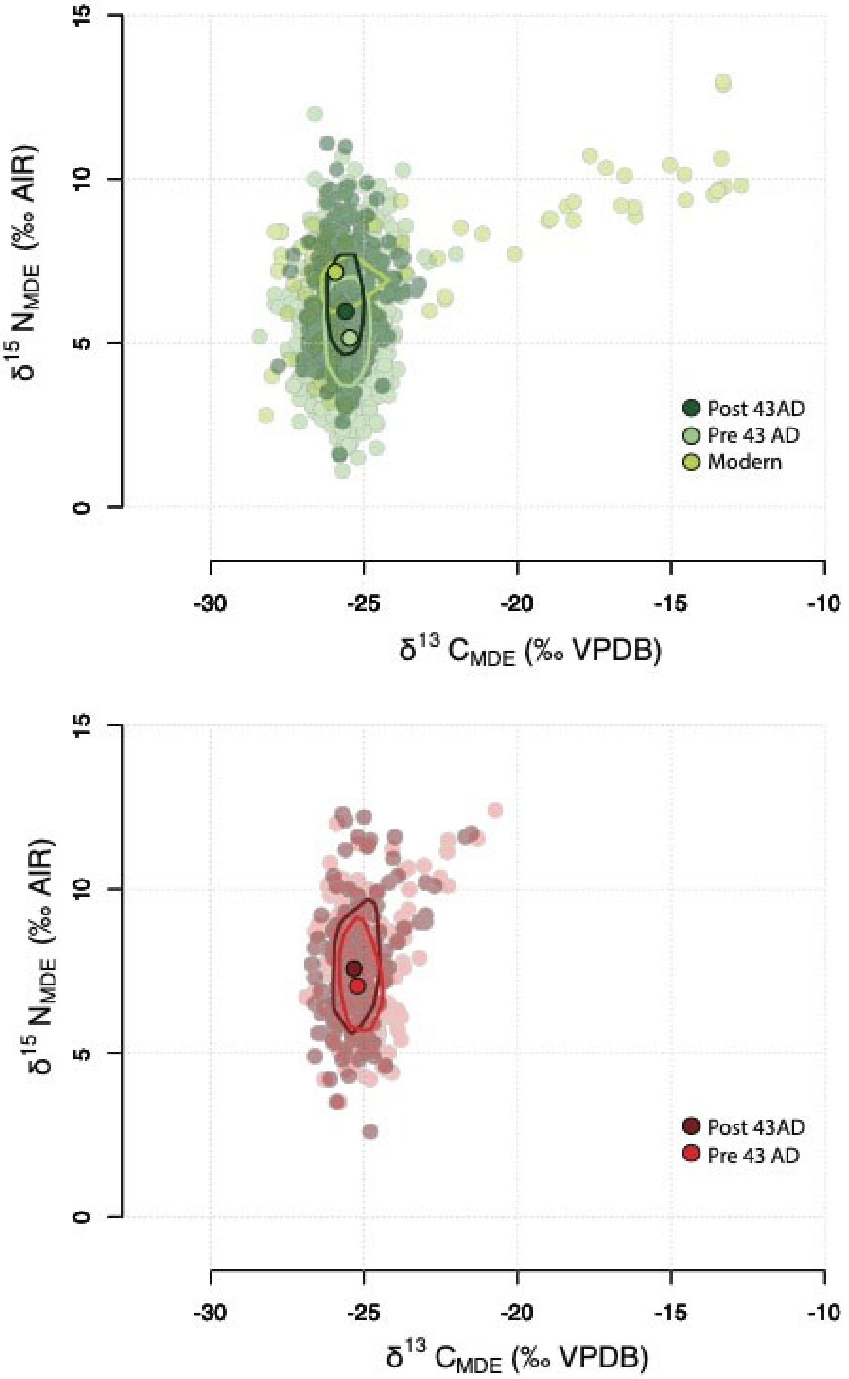

Figure 3. $\delta^{15}N_{MTE}$ and $\delta^{13}C_{MTE}$ values of the herbivores (green, top panel) and omnivores (brown, bottom panel) shown in Figure 2 categorised by time (pre- or post-43 AD). Bags enclose central 50% of the data points with the bag centre (median) indicated. Note that one herbivore (-34.9 ‰, +3.3 ‰) and one omnivore (-31.5‰, +9.6 ‰) are not plotted. Note also that the modern herbivore data set includes a scatter to very high $\delta^{15}N_{MTE}$ (up to +13 ‰) and $\delta^{13}C_{MTE}$ (up to -12.8 ‰) values. These represent a population of modern sheep experimentally fed a diet of seaweed (Blanz et al., 2020) that are included for completeness, but do not represent 'natural variability' (see Figure 2).

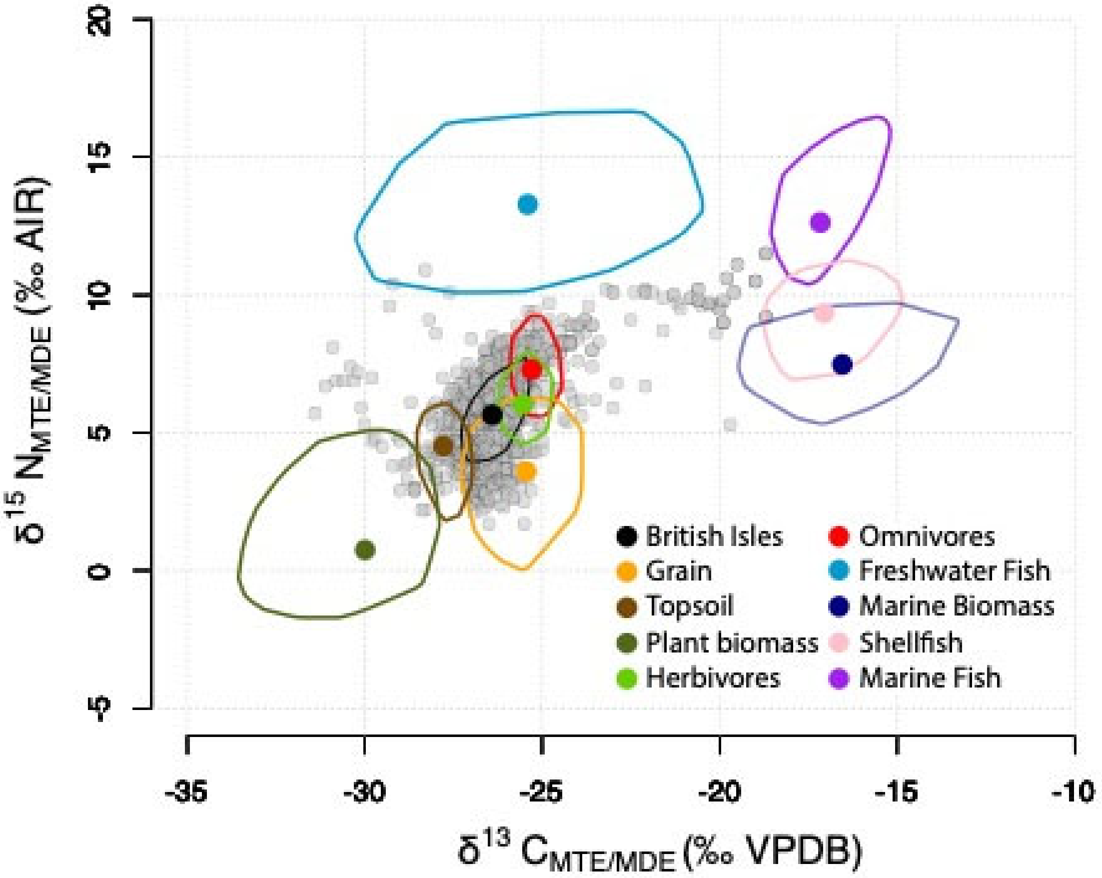

Figure 4. $\delta^{15}N_{MDE}$ and $\delta^{13}C_{MDE}$ of the British Isles individuals (grey dots/black bag) relative to common food groups and isotope sources ($\delta^{15}N_{MTE}$ and $\delta^{13}C_{MTE}$) shown in Figure 2; grain (orange), topsoil (brown), plant biomass (dark green), herbivores (light green), omnivores (red), freshwater fish (light blue), marine biomass (dark blue), shellfish (pink) and marine fish (purple). Isotope dietary items are presented as bagplots, bags enclose central 50% of the data points.

4.4 Human diet in the British Isles in the past

The 50% bag for all human isotope values for all locations and times can be described as an ellipse with a ~1.65 ‰ range in $\delta^{13}C_{MDE}$ values from -25.6 to -27.3 ‰ and a ~3.9 ‰ range in $\delta^{15}N_{MDE}$ values from +4.0 ‰ to +7.9 ‰ (Figure 4). This range overlaps significantly with the range of several common terrestrial food items available for consumption simply because the range of stable isotope values expressed at the base of the food chain - even across a relatively small humid temperate landmass – is relatively large. While the range of freshwater aquatic and marine stable isotope values is even larger than that expressed in the terrestrial environment, these foods are clearly distinguishable from terrestrial foods in the stable isotope space they occupy.

The observation that the relatively wide range of isotope values for each food type is due to relatively local processes operating at the base of the food web (See section 4.3) means that dietary inferences from the stable isotope composition of human remains must be based on local comparisons of material available in a local archaeological context if the intent is to define the proportion of particular food stuffs contributing to the diet of a local population, or change in the proportion of different foodstuffs over time (Bonsall et al., 2002; Müldner and Richards, 2007; Müldner, 2013). It is also possible, for example, to draw inferences with regard to the relative trophic position of individuals within a local population relative to other individuals in that same population (Lamb et al., 2014; Walter et al., 2020). This is not a new observation (e.g. Fischer et al., 2007; Cheung and Spzak, 2020) but the large compilation of data from a relatively small geographic region presented here does enable an assessment of the errors that should be assumed to be associated potential food isotope values for the British Isles, in the absence of detailed local isotope information on potential food items, and these are provided in Supplementary Table 2.

With the knowledge that stable isotope baselines for carbon and nitrogen have been stable over time (section 4.3), it is possible assess the entire human dataset in the context temporal change in diet at the population level (Figure 5).

The most ancient population in Figure 5 span the Mesolithic and Neolithic, including the time during which farming was established in the British Isles (Bownes, 2018; Brace, et al., 2019). This population occupies a very wide range of dietary space reflecting local, specialist subsistence strategies (Bownes, 2018). While many analyses can be characterized as having a terrestrially dominated diet, particularly in the samples of Neolithic age, two 'extreme' populations stand out.

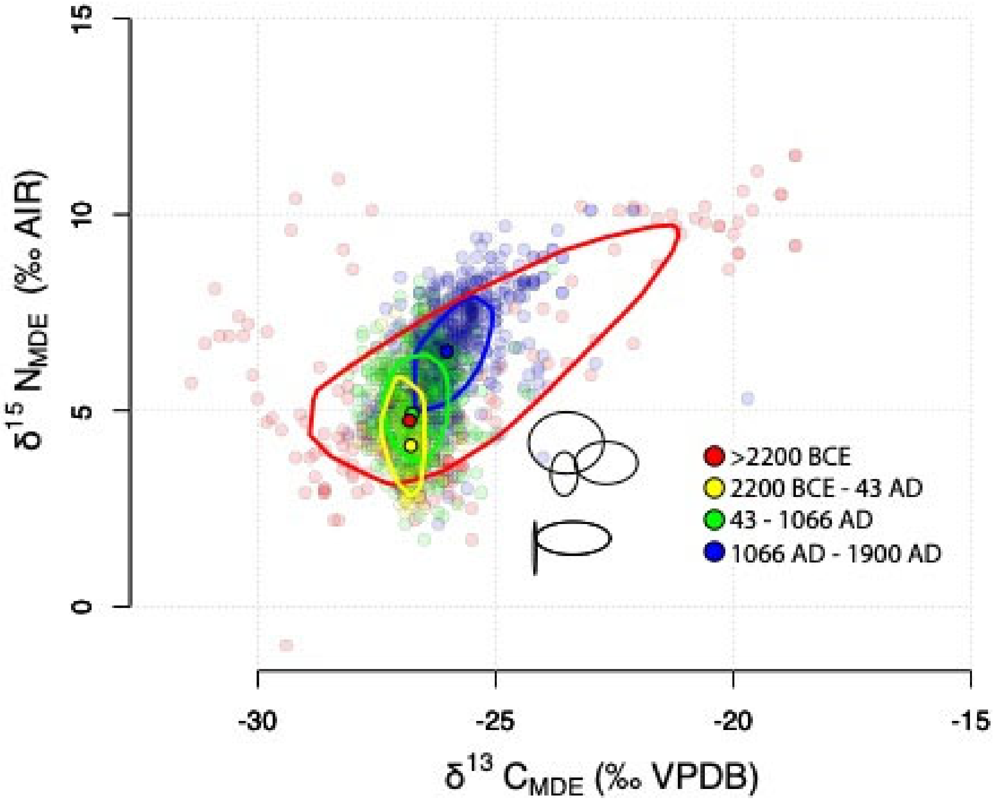

Figure 5. $\delta^{15}N_{MDE}$ and $\delta^{13}C_{MDE}$ of humans categorised by time. Bags enclose central 50% of the data points with the bag centre (median) indicated. Black ellipses represent the mean and two standard deviations for published studies of modern human diet in the British Isles from Bol and Pflieger, (2002) and O'Connell and Hedges, (1999), with lower $\delta^{15}N_{MDE}$ derived from vegetarian and vegan populations.

The first is a group dominated by coastal midden sites in Scotland (e.g. Bownes, 2018) and also represented in the Doggerland material (Van der Plicht et al., 2016). The more common preservation of middens in Scotland than in England (Gutiérrez-Zugasti et al., 2011) is a direct result of the differential history of post-glacial sea level change between the two regions. In the southern UK, midden evidence was largely flooded by sea level rise, whereas in Scotland, middens were preserved by sea level fall (Shennan et al., 2018). Material from these sites is characterized by low $\delta^{13}C_{MDE}$ (-27.5 to -33 ‰) and a wide range of $\delta^{15}N_{MDE}$ values from +2 to +11 ‰. Comparison with the data for food items in Figures 2 clearly indicate a diet dominated by freshwater wetland fish and plant resources, most results being biased to particularly low $\delta^{13}C_{MDE}$ values by the incorporation of carbon from extensive methane oxidation to CO_2, ultimately assimilated into local food webs through photosynthesis. The results are similar to results from the Ukrainian Neolithic, for sites on the similarly low-lying, wetlands of the Dnieper River floodplain (Budd et al., 2020). The second population is also dominated by material from coastal Scottish sites and Doggerland. This population is characterized by very high $\delta^{13}C_{MDE}$ (-18 to -22 ‰) and high $\delta^{15}N_{MDE}$ values of +8.0 to +12 ‰. This population, which subsisted on a similar diet from western Scotland to Doggerland is clearly identified as heavily reliant on marine resources.

From Mesolithic to Neolithic times evidence for these discrete subsistence strategies declines rapidly (Charlton et al., 2016), consistent with replacement by a farming population (Brace et al., 2019). Diet breadth from the beginning of the Iron Age to the Roman conquest (AD 43) exhibits a relatively small range (noting this is the smallest sample population; n = 117) with the 50% bags indicating a very narrow range in $\delta^{13}C_{MDE}$ (-26.5 to -27.5 ‰) and low $\delta^{15}N_{MDE}$ values in the range of +2.5 to +6 ‰. The values are indicative of a substantial intake of plant-based protein with some contribution from animal and/or grain high protein sources.

It is important to note that from the Roman Conquest on, there is broad geographic spread in the larger datasets available across the British Isles from north to south and coast to inland, and that therefore the trends observed are not due to sample bias in location from one period to the next. The period from the beginning of the Roman Conquest to the Norman Conquest is characterized by an increase in dispersion of $\delta^{13}C_{MDE}$ values (between ~-26 and -28 ‰), coupled with a shift to higher median $\delta^{15}N_{MDE}$ values by ~1 ‰, compared to the preceding period. Some of the dispersion may be due to the increase in sample size, but the absence of a change in median $\delta^{13}C_{MDE}$ values and increase in $\delta^{15}N_{MDE}$ values, in some cases to as high as +8 ‰ is suggestive of a rise in the consumption of freshwater fish (Figure 4) contributing to the observed changes in comparison to pre-Roman times along with an increase consumption of animal protein (Figure 2). Barrett et al., (2004), for example, noted that freshwater fish bones were a common component of archaeological assemblages from Roman to early medieval times, and depletion of freshwater fish stock may have partly catalysed a shift to marine species in later times.

Post-Medieval time is characterized by an increase of ~2 ‰ in median $\delta^{15}N_{MDE}$ values coupled with a ~1 ‰ increase in of median $\delta^{13}C_{MDE}$ values, relative to the previous period. The highest isotope values in this period ($\delta^{15}N_{MDE}$ values >+8 ‰; $\delta^{13}C_{MDE}$ values > -25 ‰ n = 40 or 6% of the total in this age class) include 26 individuals from Orkney and 4 from Plymouth, representing clearly coastal locations, however the remainder represent non-coastal Medieval and post-Medieval individuals from York, London, Hereford and Oxford. The observed change in the isotope composition of this population relative to earlier periods is not driven by these individuals but a broad shift in the median of the entire population. While the dispersion in the data for $\delta^{15}N_{MDE}$ values below ~+6 ‰ mirrors that of the earlier period, the range extends to higher values for both carbon and nitrogen isotopes.

Previous work on temporal change in fish bone assemblages in England has suggested a rapid rise in the harvest, trade and consumption of marine species (e.g. cod and herring) occurred shortly after the Norman conquest (Barret et al., 2004). An increase in the $\delta^{13}C$ and $\delta^{15}N$ values of human bone collagen from the Roman Period to the early 19th century has also been demonstrated at the scale of a city (Müldner and Richards, 2007), linked to an increase in the consumption of marine resources. The data presented here indicates that this 'fish event horizon' (Barrett et al., 2004) is evident in the stable isotope data in the increase in median carbon and nitrogen isotope values in this period relative to earlier times at the population scale.

Considering the data over time in terms of trophic level it is clear that, since the Mesolithic at least and into post-Medieval times, there have been individuals or populations of individuals that subsisted largely on a diet derived from terrestrial plant sources. These individuals are identified (approximately) by low $\delta^{15}N_{MDE}$ values (+2 to +4 ‰) and $\delta^{13}C_{MDE}$ values mostly in a small range from -25.5 ‰ to -27.5 ‰. From the Roman Conquest the over-arching trend has been one of progressive 'uplift' in trophic level for a progressively larger proportion of the total population represented in each time interval.

4.4 Identifying outliers

As noted above, the approach adopted here obscures local detail, but the compilation of data from all places segmented into broad time intervals, does enable the identification of outlier individuals who had a diet statistically dissimilar to the broader population of the British Isles, potentially because they spent time outside the UK in the months to years prior to their death. Figure 6 compares the 95% confidence interval for the entire British Isles populations in two of the time periods considered here.

The first time period is 43-1066 AD, covering the time period during which individuals suspected of being Vikings were massacred near the Dorset coast at Ridgeway Hill (Chenery et al., 2014). Comparison with a limited amount of data from the British Isles in that study suggested that some of the individuals had a diet more consistent with a Scandinavian origin.

Comparison with the much larger dataset presented here, indicates 6 out of 10 individuals lie at or beyond the 95% confidence interval for the British Isles, in a region that is occupied by the broader Scandinavian dataset (Figure 1). In this case complementary strontium and oxygen isotope analysis also supported a potential Viking origin for most individuals (Chenery et al., 2014). The data also suggests a further 15 individuals with 'anomalous' isotope compositions, some of whom occupy the space of the Dorset Vikings and may also be of Scandinavian origin. Clear outliers with $\delta^{13}C_{MDE}$ values of >-25 ‰ represent individuals from studies in Dorset (Redfern et al., 2010), Winchester (Bonsall et al., 2015) and York (Müldner and Richard, 2007), who had potentially arrived from at least as far afield as Western Europe (Figure 1) prior to their deaths.

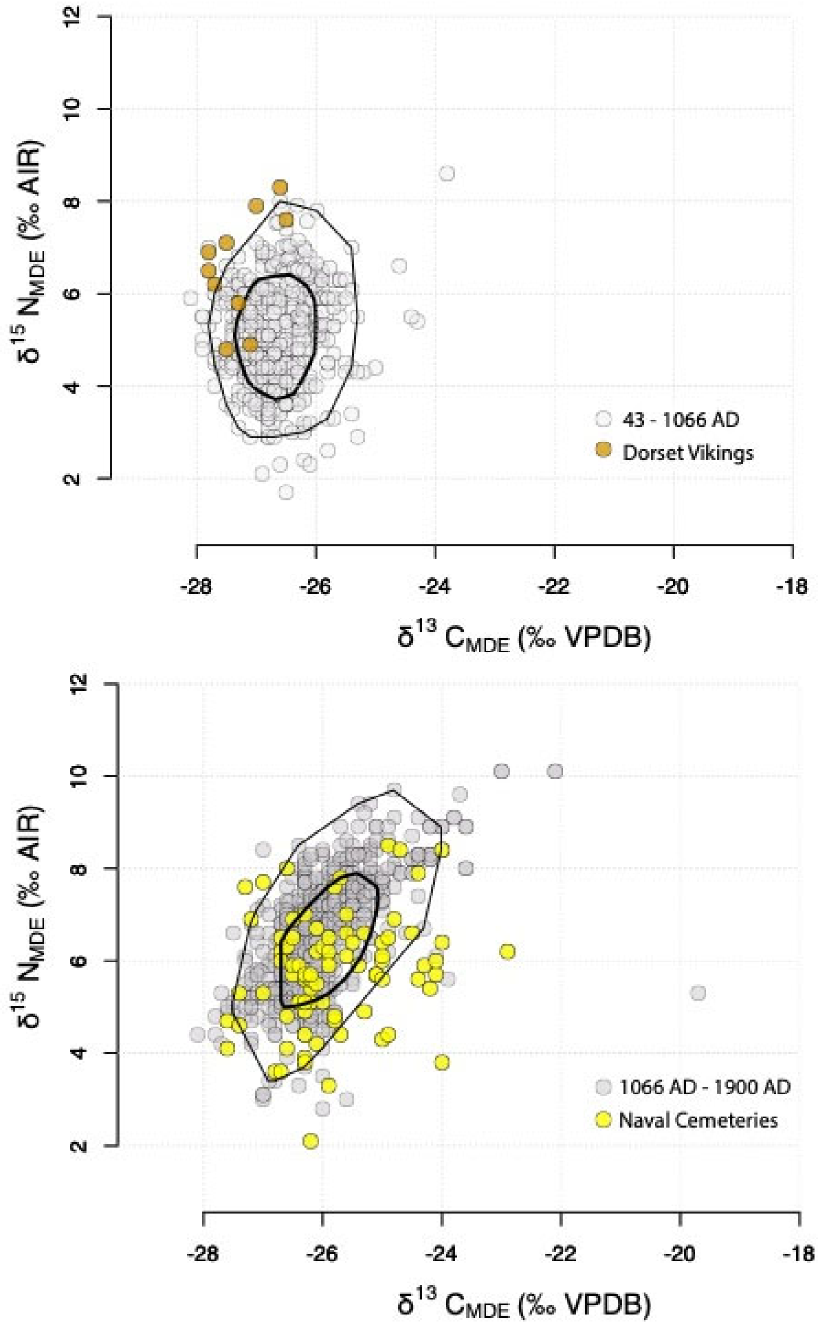

Figure 6. $\delta^{15}N_{MDE}$ and $\delta^{13}C_{MDE}$ of human remains from (top) the Dorset Viking massacre (orange) against the remains of other individuals from the British Isles from the time period (grey; 43-1066AD) and (bottom) British Naval Cemeteries (yellow) against the remains of other individuals from the British Isles from the time period (grey; 1066-1900AD). Bagplots of the data are shown as a baseline enclosing central 95% of values (thin black contour) and central 50% of values (thick black contour).

The second time period is 1066-1900 AD, and Figure 6 (right) identifies the individuals that lie at or beyond the 95% confidence intervals for the period. The most conspicuous population of outliers derives from 26 individuals out of 84 buried in the Plymouth and Gosport Naval Cemeteries (Roberts et al., 2012) who may potentially have returned from foreign service prior to their deaths, with other similarly anomalous outliers reported in multiple studies of sites across the British Isles.

5. Conclusions

We present the largest compilation to-date of stable isotope analyses of human bone collagen and potential dietary items, from a large humid temperate island, spanning much of the Holocene. By recasting the data as contemporary equivalent values we have thereby been able to include estimates for dietary items not usually available from the archaeological record, including biomass and shellfish. The conversion from original ancient bone collagen isotope compositions to modern diet or tissue equivalent values seems robust in that the data for ancient samples, after conversion, and modern equivalent values overlap to a large degree. We provide realistic estimates of the mean and standard deviations for dietary items in Supplementary Table 2. By examining modern ecological isotope data, and by comparing the ancient data from herbivores over time, we establish that there is little, if any, systematic temporal change in stable isotope baselines over the Holocene. Therefore, the range of values observed in the terrestrial biosphere at any time relates to eco-physiological, edaphic and microclimatological variations that can occur over relatively small spatial scales (Casey and Post 2011).

As temporal change in isotope baselines are small, the observed changes in human isotope composition over time can be reliably interpreted at the population level in term of dietary change. Initially a very large range in isotope values before 2,200 BCE, implies niche subsistence strategies focused closely on particular marine, freshwater wetland, or upland terrestrial environments (Bownes, 2018). From the Iron Age, the range of isotope compositions decreases dramatically and is initially represented by the exploitation of terrestrial resources to a large degree. Coherent changes in isotope composition at the population level, generally characterized by an overall increase in trophic level over time, are apparent from the Iron age, through the period from the Roman Conquest to the Norman Conquest, and from the Norman Conquest into post-Medieval times, as has been noted in many studies of individual locations over specific time intervals (e.g. Redfern et al., 2010; Müldner and Richards, 2007).

There is unlikely to be a single cause for the progressive increase in trophic level of the population of the British Isles over time since the Iron Age. It is likely that the episodic and/or semi-continuous introduction of innovations in agriculture, fisheries, animal husbandry, food preservation and transport, accelerating from the Roman Conquest on, enabled the distribution of food that was surplus to immediate requirements to locations remote from the site of production (Müldner and Richards, 2007). This food was then available for purchase and consumption by individuals with the means to do so (Lamb et al., 2014; Walter et al., 2020). It is also clear, that over the entire period encompassed here, a proportion of the population did not have the means to acquire these foodstuffs and remained dependent on a plant-based diet, with a remarkably consistent isotope signature over entire period. The isotope data is consistent with the development of marine fisheries around the time of the Norman conquest representing a significant event in this broader process (Barrett et al., 2004), but is likely that some of the same, or other, innovations led to the wider availability of meat protein sources in parallel with the rise in the importance of marine fisheries.

Of course, dietary changes do not cease at the end of the 20th century. Figure 5 shows that late the stable isotope composition of late 20th century diet in the British Isles has shifted dramatically to lower $\delta^{15}N_{MDE}$ values (<+5 ‰, similar to the Iron Age) and higher $\delta^{13}C_{MDE}$ values (>-24 ‰). To a large extent the lower nitrogen isotope values are due to the pervasive incorporation of industrial fertilizers into the food chain (average -0.2 ± 2 ‰, Bateman and Kelly, 2007; Bird et al., 2021). The higher carbon isotope values are due to the incorporation $\delta^{13}C$ value C_4 biomass into modern diets in the British Isles and globally, in the form of animal feed and sugar (e.g. Valenzuela et al., 2011; Bird et al., 2021).

There is increasing general recognition of the need to develop isoscapes for carbon, nitrogen and other elements across many disciplines, including archaeology (e.g. West et al., 2010). This contribution lays the foundation for developing carbon and nitrogen isoscapes for the British Isles, as has already been achieved for strontium isotopes (Evans et al., 2010).

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Author contributions

M.I.B and C.R.W conceived the research. M.I.B. led the research and all authors contributed to data collation, analysis and writing of the paper.

Competing Interests

The authors declare no competing interests.

Additional Information

Supplementary information is available for this paper at, ???

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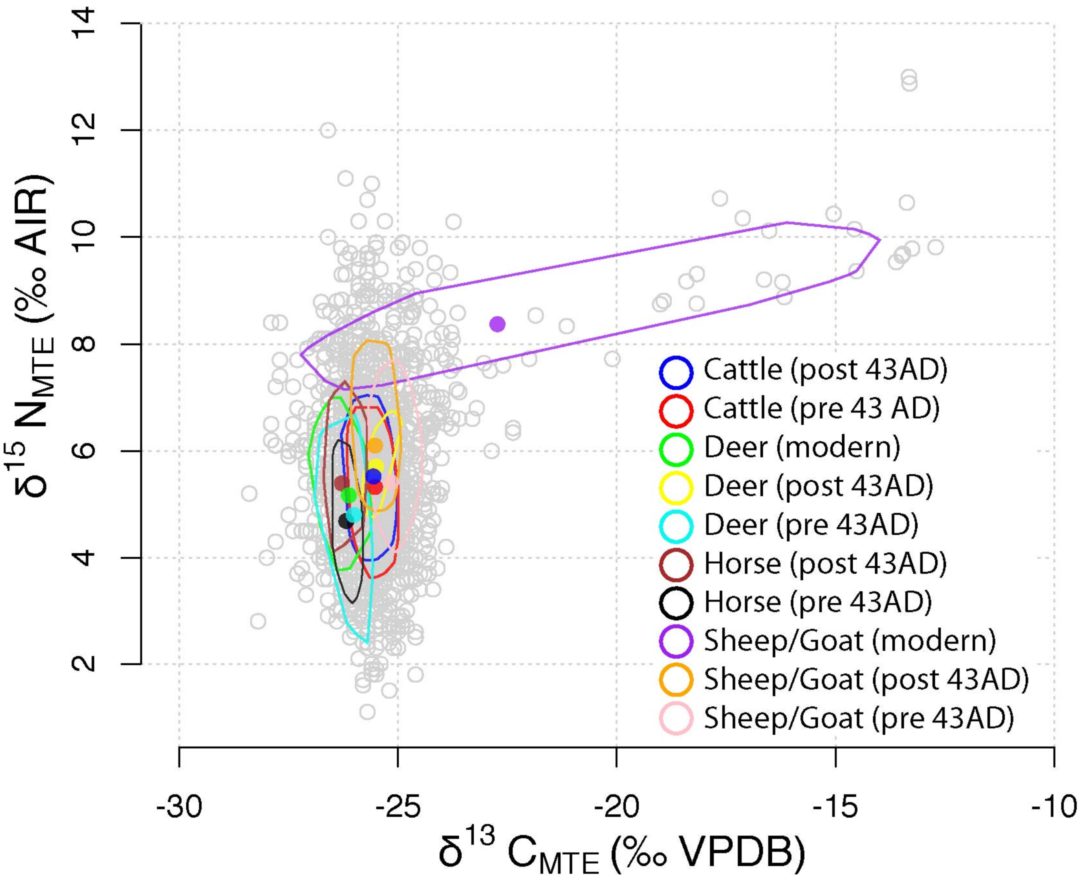
Supplementary Figure 1



Supplementary Figure 1. δ^{15}N$_{MTE}$ and δ^{13}C$_{MTE}$ values of the herbivores in Figure 3 (grey circles) separately categorized by species and time (pre- or post-43 AD and modern). Bags enclose central 50% of the data points with the bag centre (median) indicated. Note that one herbivore (-34.9 ‰, +3.3 ‰) is not plotted. Note also that the modern herbivore data set includes a scatter to very high δ^{15}N$_{MTE}$ and δ^{13}C$_{MTE}$ values. These represent a population of modern sheep experimentally fed a diet of seaweed (Blanz et al., 2020) that are included for completeness, but do not represent 'natural variability' (see Figure 2).