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Bone deep: Variation in stable isotope ratios and histomorphometric measurements of bone remodelling within adult humans

G.E. Fahy [a, *], C. Deter [a], R. Pitfield [a], J.J. Miszkiewicz [b], P. Mahoney [a]

[a] Human Osteology Lab, Skeletal Biological Research Centre, School of Anthropology and Conservation, University of Kent, Canterbury, UK
[b] School of Archaeology and Anthropology, College of Arts and Social Sciences, A.D. Hope Building, The Australian National University, 14 Ellery Crescent, Acton ACT 2601 Australia

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ABSTRACT

Stable carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotope studies of ancient human diet increasingly sample several skeletal elements within an individual. Such studies draw upon differences in bone turnover rates to reconstruct diet during different periods of time within an individual's lifetime. Rib and femoral bone, with their respectively fast and slow remodelling rates, are the bones most often sampled to reconstruct shorter and longer term signals of diet prior to death. It is poorly understood if $\delta^{13}C$ and $\delta^{15}N$ vary between bone types within a single individual, or if this variation corresponds with bone turnover rate (BTR). Here, we determined $\delta^{13}C$ and $\delta^{15}N$ for ten different bones from ten adult human skeletons ($n = 5$ males; $n = 5$ females). Isotope values were compared to the rate that each bone remodeled, calculated from osteon population (OPD) density. Results reveal that isotope ratios varied within each skeleton ($\delta^{13}C$: max = −1.58‰; $\delta^{15}N$: max = 3.05‰). Humeri, metacarpals, and ribs had the highest rate of bone remodelling; the occipital bone had the lowest. A regression analyses revealed that higher rates of bone remodelling are significantly and negatively correlated with lower $\delta^{15}N$. Our results suggest that the occipital bone, with its slow rate of bone renewal, may prove useful for isotopic studies that reconstruct diet over longer periods of time within an individual's lifetime. Isotope studies that compare individual skeletal elements between populations should standardize their methodology to bones with either a slow or fast turnover rate.

1. Introduction

Stable isotope analyses of biological tissues can provide a long-term record of diet (Deniro and Epstein, 1978; Rundel et al., 2016). Because of this, stable carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotope analyses of bone and dentin collagen have become a standard approach in archaeological science for reconstructing dietary ecology of past modern human populations (Ambrose and DeNiro, 1989; Deniro and Epstein, 1978; DeNiro and Epstein, 1981; Hedges and Law, 1989; Reynard and Hedges, 2008), with applications extending to non-human primates and fossilized remains (Bocherens et al., 1999; Fahy et al., 2013, 2014, 2015; Sponheimer et al., 2013). Increasingly, such studies incorporate isotopic signals from several skeletal elements to reconstruct ancient diet during different periods of time within an individual's lifetime (Sealy et al., 1995; Cox and Sealy, 1997; Schroeder et al., 2009; Pollard et al., 2012; Chenery et al., 2012; Lamb et al., 2014). The adult human rib and femur are the skeletal elements most commonly sampled because of apparent differences in bone turnover rates (see Section 1.3). However, little is known about relationships between $\delta^{13}C$ and $\delta^{15}N$ and remodelling in other skeletal elements. Here we 1) explore variation in $\delta^{13}C$ and $\delta^{15}N$ in ten different bones from ten archaeological human skeletons and 2) identify associations between these ratios and histomorphometric measurements of bone remodelling.

1.1. Stable carbon and nitrogen isotopes

Ratios of heavy to light stable isotopes of carbon ($^{13}C/^{12}C$) and nitrogen ($^{15}N/^{14}N$) display distinctive patterns of distribution that enable them to be employed in the interpretation of various aspects of life history. Body tissue isotopic composition is highly influenced by food and drink consumed in life (Sealy et al., 1995), variation in

* Corresponding author. School of Anthropology and Conservation, Marlowe Building, University of Kent, Canterbury CT2 7NR, UK.
E-mail address: g.fahy@kent.ac.uk (G.E. Fahy).

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food sources (Hopkins and Ferguson, 2012) and water availability (Stewart et al., 1995; Amundson, 2003; Swap and Aranibar, 2004); consequently isotopic analyses of body tissues can offer clues to aspects of diet and lifestyle. The main source of terrestrial carbon is atmospheric CO_2 whereas the main source of marine carbon is dissolved CO_2 and biocarbonate ions (HCO_{3-}). These sources of carbon express $\delta^{13}C$ of −7.5 and + 1.5‰, respectively (Lee-Thorp et al., 1989; Van Klinken, 1991). The differences then continue up the food chain from primary producers to apex predators (Lee-Thorp et al., 1989; Van Klinken, 1991). This expression is dependent on the biochemical mode of photosynthesis with most plants utilizing the C_3 cycle (expressing $\delta^{13}C$ around −26‰) compared to those few utilizing the C_4 pathway (expressing $\delta^{13}C$ around −12‰) (Smith and Epstein, 1971). Nitrogen incorporation into plant biomolecules can occur in three different ways: direct nitrogen fixation from air, ammonium or nitrate in soil water, recycled organic nitrogen from soil (Lee-Thorp, 2008). Similar to $\delta^{13}C$, there is a stepwise increase in $\delta^{15}N$ with trophic level (DeNiro and Epstein, 1981). Isotope data from bone collagen have long been shown to largely reflect the protein component of an individual's diet (Ambrose and Norr, 1993; Lee-Thorp et al., 1989; Schoeninger et al., 1997, 1998; Schroeder et al., 2009).

1.2. Bone remodelling rates

Human bones form through intramembranous and endochondral ossification. Bone modeling commences *in utero* and continues until the early teenage years, depending upon the bone type (Pitfield et al., 2017). Bone remodelling occurs throughout the whole human lifespan (Burr and Allen, 2014; Katsimbri, 2017; Robling et al., 2006; Peacock, 2010) as osteoclasts resorb old tissue and osteoblasts produce new tissue (Robling et al., 2008; Miszkiewicz and Mahoney, 2016). Metabolic activity, including the exchange of nutrients, calcium, oxygen and mechanical signaling (Miszkiewicz and Mahoney, 2016), along with targeted remodelling, maintains and repairs bone (Burr, 2002; Robling et al., 2001). As new bone forms, it incorporates the isotopic composition of an individual's diet (Fry and Arnold, 1982). However, the rate that different bone within a skeleton remodel is not consistent. Age, health, biological sex, mechanical loading, and genetic predisposition can all regulate the rate at which Bone Multicellular Units (BMUs) add or remove bone (Burr, 2002; Sealy et al., 1995; Pfeiffer et al., 2006; Hedges et al., 2007; Pollard et al., 2012; Robling et al., 2001; Wolff, 1899).

Evidence of remodelling is retained in bone as basic structural and somewhat independent functional units, as secondary osteons. Osteon population density (OPD) is a measure of complete and fragmentary secondary osteons per section area, which together represent past remodelling events (Frost, 1994; Gocha and Agnew, 2016). As such, OPD can represent a measure of bone remodelling dynamics, or accrued bone density (Miszkiewicz, 2015). Increasing OPD is closely associated with advancing age, and eventually an asymptote is reached where new secondary osteon formations begin to remove traces of earlier osteons (Stout and Lueck, 1995). When age-at-death is controlled for, OPD variation may indicate differences in bone structure and response to mechanical stress (Britz et al., 2009; Schlecht et al., 2012), dietary changes (e.g, Pfeiffer and Lazenby 1994; Paine and Brenton, 2006), or health status (e.g., Martin and Armelagos, 1979; Storm et al., 1993), or general human lifestyle (Miszkiewicz and Mahoney, 2016).

An estimated rate of remodelling varies across bone types, because of surface to volume ratio differences in bone shape and size (Parfitt, 2002). For example, a cancellous bone sample (~135 μm thick) from a modern adult human ilium remodels at an average rate of 17.7% per year, whereas a turnover rate for a cortical sample (~1225 μm thick) from the same individual would remodel at approximately 7.7% per year (Parfitt, 2002). When considering cortical bone only, its renewal varies quite substantially throughout the skeleton (Hobson & Clark 1992; Katsimbri, 2017). For example, ribs are bones are never at rest due to the load arising from respiration (Skedros et al., 2013); with a greater surface area to volume ratio ribs have a relatively fast cortical turnover rate, which is approximately 4% a year after age 50 (Frost, 1969; Hill & Orth 1998). The dense cortical bone of the femoral shaft is thought to have a slow turnover rate relative to rib bone (Hill & Orth 1998; Hedges et al., 2007; Skedros et al., 2013).

1.3. Human bone remodelling and isotope variation

Dietary reconstruction using standard isotope methodology tries to account for variation in bone remodelling. Studies compare various skeletal elements between individuals; usually only one bone type is sampled, though sometimes one bone is substituted for another (e.g. Fahy et al., 2015). Multiple sampling of bone (and teeth) is increasingly utilised to reconstruct diet during different periods of time from an individual's lifetime (e.g. Lamb et al., 2014). For example, it is thought that the slower turnover of femoral bone collagen, isotopically, reflects a longer-term and average dietary signal, which may be more than ten years prior to death (Hedges et al., 2007). In contrast, ribs, with faster turnover rates, may represent diet from a more recent period prior to death (e.g. Cox and Sealy, 1997).

Olsen et al. (2014) directly compared $\delta^{13}C$ and $\delta^{15}N$ to an inferred rate of remodelling for different bones within 59 adult human skeletons. While they suggest that paleodiet researchers should avoid sampling collagen close to pathological lesion sites due to differing isotope values, they state that normal, non-pathological bone show limited intraskeletal variation in $\delta^{13}C$ and $\delta^{15}N$. Similarly, Deniro and Schoeniger (1983) examined the mean isotopic composition of collagen extracted from mink humeri and femora and found that it did not differ significantly for either $\delta^{13}C$ or $\delta^{15}N$, leading them to suggest that differences in the isotopic composition of collagen extracted from different bones of an individual are small. Research by Larson and Longstaffe (2007) on deer, Brady et al. (2008) on sheep and Luz and Kolodny (1985) on rat bone, looked at the relationship between $\delta^{13}C$ and $\delta^{18}O$ and osteon lacunar density, and research by Balasse et al. (1999) examined the intra-individual variability in $\delta^{13}C$ and $\delta^{15}N$ of mineralized tissues in modern steers. All of these studies reported significant variation in isotopic ratios for different bones from the same individual.

2. Materials and methods

2.1. Samples

Ten human skeletons, dating to the early medieval period, from St Gregory's cemetery in Canterbury, England, were selected (Hicks and Hicks, 2001). Historical texts state that burials were from a single socio-economic group that lived and worked in Canterbury, and represent non-catastrophic mortality (Brent, 1879; Duncombe, 1785; Somner, 1703). We selected complete individuals without skeletal signs of pathology. This collection is curated in the Skeletal Biology Research Centre, University of Kent, UK. All sectioning adhered to the British Association of Biological Anthropology and Osteoarchaeology code of practice (2014), and guidelines for invasive sampling (Mays et al., 2013). No permits were required as these are archaeological samples from before the 19th Century AD.